

THE CRANIAL ANATOMY OF POLYPTERUS, WITH SPECIAL REFERENCE TO *POLYPTERUS BICHIR*

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INTRODUCTION

THE present work was begun in 1899, on two large specimens of *Polypterus bichir* purchased in Germany, but it was soon found that they would not suffice for the work contemplated. Several large specimens from the material collected by N. R. Harrison in Abyssinia, and said to also be of *Polypterus bichir*, were later sent me by Professor Bashford Dean, of Columbia University, and still later Professor Dean sent me three heads of *Polypterus ornatipinnis* from the collections at the American Museum of Natural History, New York

City. In addition to this adult material I have had four specimens from 29 cm. to 32 cm. in length, which, as they had only 8–12 finlets, were probably of *Polypterus Lapradei* though said to be of *Polypterus bichir*; and three larvae of *Polypterus senegalus*, 73 mm. to 83 mm. in length, kindly sent me by Professor J. Graham Kerr from the material collected by J. S. Budgett in the Gambia. The dissection of the adult specimens was confided to my assistant, Mr Jugiro Nomura, and the drawings used for the accompanying illustrations are all by him. The three larvae were sectioned, and the one series that proved of any value was given to my assistant, Mr John Henry, with instructions to carefully trace the nerves and blood vessels. While waiting, at different times, for additional material the work was necessarily interrupted, other work undertaken in the meantime still further delayed it, and before it was fully completed and controlled both Mr Nomura and Mr Henry died.

The work has thus not been limited to a single species, which is unfortunate, and it has not been carried through to the extent that was intended, this applying particularly to the nervous system. While it has been in progress I have published several works in which certain of the features of the cranial anatomy have been more or less fully described and discussed, and just as the work is ready for publication I have received a copy of the *Zeitschrift für angewandte Anatomie und Konstitutionslehre* in which there is an important article by Dr Charlotte Lehn, published in Berlin in 1918 and describing the neurocranium of a larva of *Polypterus senegalus*, 76 mm. in length. As my descriptions relate largely to the adult, and include the visceral arches, muscles, nerves and blood vessels as well as the neurocranium, the manuscript is sent to press with but little alteration beyond frequent reference to Lehn's work. Many features referred to, and more or less fully described, in my earlier works are here again described, in order to make the work complete.

NEUROCRANIUM

The neurocranium of one of the large specimens from Abyssinia, shown in figs. 7–14, has approximately the proportions of that of the 30 cm. specimen of *Polypterus Lapradei* described by Bridge (1888), but is relatively longer, and less tall and wide than that of the small specimen of *Polypterus* (presumably *senegalus*) described by Traquair (1871) and of the 21 cm. specimen (species not given) described by Pollard (1892). Its dorsal surface is formed by the paired parieto-dermopterotics, frontals, nasals, accessory nasals, ossa terminalia, and premaxillaries, by a single median ethmoid, and by a small portion of the postfronto-sphenotic of either side which is exposed along the lateral edge of the posterior portion of the frontal. Its ventral surface is formed by the premaxillaries, the large median parasphenoid, a small portion of the basi-exoccipital that is exposed between the diverging hind ends of the parasphenoid, and by three small portions of the ethmoid cartilage which appear anterior and lateral to the anterior end of the latter bone.

The orbital fossa is long and low, and occupies about two-fifths of the total length of the neurocranium. Its anterior half, only, is occupied by the eyeball, the posterior half lying internal to the postorbital and prespiracular bones and being completely filled by what Pollard calls the pterygoid and temporal divisions of the musculus adductor mandibulae. The external opening of the fossa leads into the part occupied by the eyeball, and is bounded dorsally by the frontal, posteriorly by the postorbital, ventrally by the lachrymal and the latero-sensory component of the maxillary, and anteriorly by the lachrymal and the antorbital process of the premaxillary. The postorbital process lies at a considerable distance posterior to the hind edge of the external opening of the fossa, and the mesial wall of the posterior half of the fossa corresponds, morphologically, to the hind wall of the orbits of *Amia* and most of the Teleostei; the flattening out and consequent lengthening of this part of the orbit of *Polypterus* being an important factor in giving to the entire neurocranium its unusual length.

The nasals, accessory nasals, and ossa terminalia can all be readily removed in alcoholic specimens, but the frontals and parieto-dermopterotics could not be removed, intact, in any of my specimens, without injury to the underlying cartilage. The latter bones could, however, when filed very thin, be stripped off the underlying cartilage without injury to it. The ascending processes of the parasphenoid apparently include the proötics, as will be later explained, and this part of each process could not be removed without breakage of the cartilage.

The primordial cranium, or so-called chondrocranium of the adult is almost entirely of cartilage in the otic and ethmoidal regions, but almost entirely of bone in the orbitotemporal and occipital regions. There is, in the orbitotemporal region, a large perforation of the basis cranii, and directly dorsal to it a still larger perforation of the tegmen cranii. The perforation of the basis cranii may be called the basicranial fontanelle, a name already given to it by other authors, but it is apparently the strict homologue of the fontanelle that I have recently (Allis, 1919*b*, p. 228) called, in *Amia* and the Teleostei, the fenestra ventralis myodomus. It is closed ventrally by the parasphenoid, and will be further considered when describing the sphenoid bone. The perforation of the tegmen cranii is the supracranial fontanelle. It is roofed by the frontals and parieto-dermopterotics, and is closed, in the natural state, by membrane; and in this membrane, at the posterior third or quarter of the length of the fontanelle, and between the hind ends of the vertical plates of the sphenoid, there was, in the one specimen examined in this respect, the small thin round plate of cartilage described by Pollard, perforated by a small hole. In my 75 mm. specimen of *Polypterus senegalus* there is here a complete bridge of cartilage, as there also was in the larvae described by Budgett (1902) and Lehn (1918). On either side of the supracranial fontanelle there is, in the adult, a large supraorbital fontanelle, which perforates the roof of the posterior portion of the orbital fossa. It is closed dorsally by the frontal, and the tem-

poral division of the musculus adductor mandibulae here has its insertion on the ventral surface of that bone. In my 75 mm. specimen, and in that described by Lehn, the cartilage of the chondrocranium is also here perforated, but in Budgett's 30 mm. larva it is shown as simply hollowed out on its ventral surface, but not perforated, the definitive perforation thus apparently being caused by the insertion of the musculus temporalis.

In Budgett's 30 mm. larva the highest point of the median line of the dorsal surface of the chondrocranium lies between the postorbital processes, in Lehn's 76 mm. specimen it lies somewhat posterior to that point, and in my adults still farther posteriorly, at the hind end of the dorsal surface of the chondrocranium; this change in position of this highest point apparently being caused by a gradual thickening of the cartilage from the hind end of the supra-cranial fontanelle to the hind end of the dorsal surface of the chondrocranium. From this highest point in the adult, the dorsal surface slopes antero-ventrally at a slight angle, the posterior surface sloping postero-ventrally at an angle of about 30° to the horizontal plane. From the hind edge of the dorsal surface a small flat crista occipitalis, which is horizontal instead of vertical in position, projects posteriorly and slightly overhangs the dorsal edge of the posterior surface.

In the otic region, the median portion of the dorsal surface of the chondrocranium is nearly flat, and on either side of this flat portion there is a large, but non-functional temporal groove. Each postero-lateral corner of the flat surface forms the hind end of the mesial bounding edge of the temporal groove of its side, and corresponds exactly, in topographical position, to the epiotic process of *Amia* and certain of the Teleostei. The temporal groove has a Y-shaped hind end, one limb of this Y running postero-laterally onto the dorsal surface of the postero-lateral portion of the opisthotic, and the other limb running postero-mesially and then postero-ventrally onto the posterior surface of the chondrocranium. The lateral limb of the Y is a slight depression, only, and lies antero-lateral to the posterior semicircular canal, the mesial limb crossing that canal; the two limbs thus corresponding to the two branch depressions described by me (Allis, 1920a) at the hind end of the temporal depression on the dorsal surface of the chondrocrania of *Lepidosteus* and *Rana*. The slight depression of the lateral limb lodges the postero-lateral corner of the parieto-dermopterotic, that part of that bone enclosing the hind end of the main latero-sensory canal. The depression of the mesial limb lodges a postero-ventral process of the parieto-dermopterotic, and between this limb and the lateral one, the posterior process of the parieto-dermopterotic projects directly posteriorly. The temporal groove, itself, is almost completely filled by a rounded ridge on the ventral surface of the parieto-dermopterotic.

The dorsal end of the sinus utriculus superior lies considerably mesial to the temporal groove, not far from its fellow of the opposite side. The anterior semicircular canal runs antero-laterally from there, lying mesial to the temporal groove and always enclosed in the cartilage of the chondrocranium.

The posterior semicircular canal runs postero-laterally, anterior to the epiotic process, and then beneath and across the base of the mesial limb of the Y-shaped prolongation of the temporal groove, its course there being marked by a low rounded ridge which forms the boundary between the dorsal and posterior surfaces of the chondrocranium, and the canal lying partly in the cartilage of the chondrocranium and partly in the opisthotic bone. The lateral semicircular canal lies in part internal to, and in part ventro-posterior to the articular facet for the hyomandibula, and traverses both the cartilage of the lateral wall of the chondrocranium and the opisthotic bone, its canal in the latter bone lying internal to the descending arm of the posterior semicircular canal and being in part confluent with that canal.

The anterior end of the lateral semicircular canal lies posterior to the curved descending limb of the anterior semicircular canal, and between these two portions of these two canals there is a marked re-entrant angle in the dorso-lateral edge of the chondrocranium. The anterior edge of the spiracular canal lies in the point of this angle, and the ramus oticus lateralis issues on the dorsal surface of the chondrocranium almost directly mesial to it. The angle is thus a fossa spiracularis, and corresponds to that depressed region on the dorso-lateral edge of the chondrocranium of 14 mm. embryos of *Lepidosteus* to which I have referred (Allis, 1920*a*) as probably lodging the recessus dorsalis spiracularis. This depressed region of the chondrocranium of embryos of *Lepidosteus* later becomes spanned by cartilage, and so gives rise to the spiracular canal, the lateral edge of this spanning cartilage forming a connection between the primarily independent sphenotic and pterotic ridges. The chondrocranium of *Polypterus* thus here remains in the stage of development shown in the 14 mm. *Lepidosteus*, and a spheno-pterotic ridge such as is found in the adults of the *Holostei* and *Teleostei*, is never developed, its two component parts persisting as independent ridges; and this is apparently the condition in mammals, the fossa spiracularis of *Polypterus* corresponding to some portion of the fossa epitympanica of mammals.

The dorsal portion of the posterior surface of the chondrocranium extends from the hind edge of its dorsal surface to the dorsal edge of the foramen magnum, sloping postero-ventrally at an angle of about 30° to the horizontal plane. This part of the posterior surface is, in reality, the dorsal surface of the occipital portion of the chondrocranium, and its lateral edge, which separates it from the lateral surface of the chondrocranium, is formed by a lateral occipital ridge similar to that found in many of the *Teleostei*, this ridge starting from the base of the posterior process of the opisthotic, and running along the dorsal margin of the foramen vagum to the ventro-posterior portion of the exoccipital part of the basi-exoccipital. Dorso-mesial to this ridge is a ridge which forms the lateral boundary of the postero-mesial prolongation of the temporal groove, and mesial to this latter ridge is another ridge which forms the mesial boundary of the same prolongation, this latter ridge running dorso-anteriorly into the epiotic process. Between this latter ridge and its fellow of

the opposite side the dorsal surface of the chondrocranium is slightly concave. The conditions in *Polypterus* thus here resemble those in *Amia* (Allis, 1897), *Scomber* (Allis, 1903), and the mail-cheeked fishes (Allis, 1909), excepting in that, in all these latter fishes, the lateral bounding ridge of the posterior prolongation of the temporal groove is confluent with the lateral occipital ridge, the two together forming the bounding edge between the posterior and lateral surfaces of the chondrocranium.

On the lateral surface of the postorbital portion of the neurocranium there is a large articular facet for the hyomandibula, the antero-ventral portion of this facet lying on the lateral surface of the chondrocranium, but its dorso-posterior portion on the lateral edge of the parieto-dermopterotic, and hence actually above the chondrocranium. The antero-ventral end of the facet lies external (lateral) to the anterior portion of the lateral semicircular canal, but its posterior portion dorsal to that canal. The dorsal edge of the facet is formed by a sharp curved ridge which, as described in an earlier work (Allis, 1920*a*), lies partly on the cartilage of the chondrocranium but mainly on the lateral edge of the parieto-dermopterotic, the hollow of the curve presented ventro-posteriorly. That part of this ridge that lies on the chondrocranium is continued posteriorly, on that cranium, internal to the parieto-dermopterotic, and is continuous with the lateral edge of the dorsal surface of the opisthotic, the entire ridge thus forming the pterotic portion of the sphenopterotic ridge of the chondrocranium. Ventral to the posterior portion of the facet for the hyomandibula there is another ridge, which lies wholly on the opisthotic, and ventral to it is the opisthotic ridge, which begins at about the middle of the lateral edge of the postorbital process, immediately dorsal to the definitive foramen faciale, and runs postero-dorsally across the opisthotic to the hind end of the posterior process of that bone. Between these two ridges there is, on the opisthotic, a concave and roughened surface which gives insertion to the muscoli adductor hyomandibularis, adductor operculi, and levatores arcuum branchialium. Ventral to the opisthotic ridge there is a groove, the sulcus jugularis, which lodges the vena jugularis after it issues from the definitive foramen faciale; and ventral to this sulcus there is a large bulla acustica. From the bulla acustica a broad but low ridge runs posteriorly and slightly ventrally, ventral to the foramen vagum and parallel to the lateral occipital ridge, and between these two ridges there is a deep groove which lodges the nervus vagus after it issues from its foramen.

In Budgett's 30 mm. larva the dorso-lateral edge of the otic portion of the chondrocranium is formed by a large ridge, which is said to enclose the lateral semicircular canal and is hence a *prominentia semicircularis lateralis*. It is called by Budgett the pterotic ridge, and the hyomandibula articulates with its lateral surface. In my 75 mm. specimen this prominentia is found in similar position, and the hyomandibula here also articulates with its lateral surface, but a secondary ridge of cartilage forms the dorsal boundary of the surface of articulation, and it is this secondary ridge that forms the dorso-lateral edge

of this part of the chondrocranium, and is, therefore, the pterotic ridge properly so called, the hyomandibula at no place extending dorsal to it. Mesial to this pterotic ridge, the dorsal surface of the prominentia semicircularis lateralis forms a low and rounded ridge which separates the temporal groove into lateral and mesial portions, the mesial portion lodging the main latero-sensory canal. The parieto-dermopterotic extends laterally beyond this part of the prominentia, its lateral edge resting upon the summit of the pterotic ridge and at no place forming part of the articular facet for the hyomandibula, as it does in the adult. Immediately posterior to the facet for the hyomandibula, the prominentia semicircularis lateralis becomes narrower and more rounded in serial transverse sections, and the pterotic ridge on its dorso-lateral corner gradually vanishes. The prominentia still forms the dorsal boundary of the jugular groove, and the anterior edge of the adductor hyomandibularis is now cut in the sections, this muscle being inserted on the prominentia dorsal to the vena jugularis, between that vein and a large lymph space which extends forward internal to the hyomandibula. Proceeding posteriorly in the sections, a ridge develops on the summit of the prominentia, immediately dorsal to the lymph space above mentioned, this ridge lying ventral to the line prolonged of the pterotic ridge and evidently being, notwithstanding that it lies posterior to the facet for the hyomandibula, that marked ridge on the opisthotic of the adult that forms the ventral boundary of the posterior portion of that articular facet; this ridge vanishing, in the 75 mm. specimen, on the dorsal surface of a posteriorly projecting portion of the otic capsule which lodges the vertically descending portion of the posterior semicircular canal. In the adult the hind end of this ridge forms a slight process on the lateral surface of the posterior process of the opisthotic, as seen in the posterior view of the chondrocranium (fig. 14). The dorsal, or supratemporal branch of the nervus glossopharyngeus runs upward across the surface of insertion of the musculus adductor hyomandibularis, there traversing that muscle, and then perforates the ridge just above described, to reach the dorsal surface of the chondrocranium. In the adult, that part of this nerve that, in this embryo, lies along the external surface of the surface of insertion of the adductor hyomandibularis has become entirely enclosed in the opisthotic.

Lehn (1918, p. 365) considers the ridge just above described on the dorsal surface of the prominentia semicircularis lateralis to be the crista parotica, but as the ridge to which Gaupp (1893) first gave that name, in *Rana*, forms the dorsal edge of the jugular groove, it seems more probable that it is represented in the entire posterior portion of the opisthotic ridge of *Polypterus*, as already suggested in an earlier work (Allis, 1920*a*, p. 264).

The cranial cavity occupies about two-thirds of the full length of the chondrocranium, extending from the foramen magnum forward between the orbits to a median wall that separates the foramina olfactoria from each other and that is formed by the mesial portions of the articulating anterior ends of the vertical laminae of the sphenoid. In the orbito-temporal and occipital

regions the bounding walls are entirely of bone, but in the auditory region entirely of cartilage excepting where they are perforated by the large openings that lead into the labyrinth recesses, these openings doubtless being closed by membrane though none could be detected in the dissections. The anterior and posterior portions of the floor of the cavity lie in approximately the same horizontal level, and between them, extending from the foramina optica to the postelinoid wall (proötic bridge), is the large pituitary fossa, this fossa lodging the lobi inferiores in its anterior portion, the hypophysis in its middle portion, and the saccus vasculosus, called by Waldschmidt (1887) the glandular portion of the hypophysis, in its posterior portion, beneath the proötic bridge. The floor of the fossa is perforated, its full length, by the basicranial fontanelle, which is closed ventrally by the parasphenoid. At about the middle of the length of the fontanelle there is, on the dorsal surface of the parasphenoid, a slight median hypophysial depression. The sides of the fontanelle are nearly parallel, and are formed, in the adult, by the basal portions of the vertical laminae of the sphenoid, but in the 75 mm. larva by the cartilaginous trabeculae. The cranial cavity is of approximately equal width throughout the auditory and orbito-temporal regions, and the brain extends its full length. Dorsal to the foramen opticum of either side there is a large but slight depression in the lateral wall, this depression marking the position of the fore-brain.

The ventral portion of the labyrinth recess of either side is occupied by a deep fossa which runs postero-laterally and is separated by a slight and rounded transverse ridge into a small anterior and a large posterior portion. The former lodges the sacculus and the latter the lagena, the thin ventral wall of the latter fossa bulging outward and forming the bulla acustica on the external surface of the chondrocranium. Dorsal to the fossa lagenae there is a fossa in the postero-lateral wall of the recess, this fossa lying in the opisthotic, in the hollow of the curve of that portion of the lateral semicircular canal that projects posteriorly into the hollow of the curve of the posterior semicircular canal, as described by Retzius (1881). The dorsal end of the lagena doubtless lies in this fossa, but I could not definitely determine this in my specimens. Dorsal to the anterior portion of this fossa lagenae there is a small depression which doubtless lodges the saccus endolymphaticus. Antero-lateral to the dorsal edge of the fossa sacculi there is a fossa, slightly double, which lodges the recessus utriculi and the ampullae anterior and lateralis, and antero-lateral and postero-lateral to this fossa are the openings, respectively, of the anterior and lateral semicircular canals. Postero-mesial to the dorsal edge of the fossa lagenae there is a small fossa which lodges the ampulla posterior, and dorso-lateral to this is the ventral opening of the posterior semicircular canal. Two little grooves, which diverge anteriorly and posteriorly from near the median line of the roof of the labyrinth recess, lead into the dorsal ends of the canals for the anterior and posterior semicircular canals, and the little fossa that lodges the dorsal end of the saccus endolymphaticus lies ventro-lateral to the posterior one of these two grooves.

The walls of the labyrinth recess are traversed by all three of the semi-circular canals, the part so traversed by the anterior canal lying wholly in the cartilage, internal to the postfronto-sphenotic, while the parts traversed by the lateral and posterior canals are in part enclosed in the opisthotic. The nervi facialis, glossopharyngeus, and ophthalmicus superficialis all enter the labyrinth recess before perforating the cartilaginous wall of the cranium. The nervus facialis, having entered the recess, perforates its cartilaginous wall near the mesial end of the ridge between the fossa sacculi and the fossa that lodges the recessus utriculi and the ampullae anterior and lateralis, and passing ventral to the recessus utriculi opens into the jugular canal, which will be described in connection with the parasphenoid. The foramen for the ophthalmicus superficialis lies slightly anterior to the foramen faciale, close against the ridge of cartilage that forms the mesial wall of the anterior portion of the labyrinth recess, and traverses the cartilage ventro-mesial to the ampulla anterior. The canal for the nervus glossopharyngeus begins in the ventral wall of the labyrinth recess mesial to the mesial end of the ridge between the fossa lagenae and the fossa for the ampulla posterior, and running ventral to the latter ampulla issues at the ventro-posterior edge of the bulla acustica.

Retzius did not find a canalis utriculo-saccularis in the adult specimens he examined. In my 75 mm. larva the large sac formed by the sacculus and lagena was connected by a narrow canal with the basal portion of the sinus utriculi superior, the canal opening into the sacculus-lagena on its mesial surface close to the base of the ductus endolymphaticus.

From the above general description it is seen that the cranium of *Polypterus* is strictly platybasic in type. The cavum cranii differs markedly, in its general lines, from that of *Amia* and all of the Teleostei I know of excepting only *Amiurus* and *Silurus*, and it as markedly resembles that of many of the Selachii. The resemblance is particularly marked with that of *Scymnus*, as shown by Gegenbaur (1872, fig. 3, Pl. 4), and slightly less so with that of *Chlamydoselachus* as described by me (Allis, 1914). In both these latter fishes there is, as in *Polypterus*, a large pituitary fossa which lodges the lobi inferiores and the pituitary body, the anterior end of the fossa being formed by a presphenoid bolster and the posterior end by a postelinoid wall. The nervus opticus perforates the cranial wall dorsal to the presphenoid bolster in *Chlamydoselachus*, as it does in *Polypterus*, and but slightly posterior to that bolster in *Scymnus*. The pituitary foramen perforates the side wall of the fossa in all three fishes, but differs slightly in position in each of them, perforating the side wall near the middle of the length of the fossa in *Polypterus*, at its hind end in *Chlamydoselachus*, and apparently perforating the hind wall in *Scymnus*. The arteria carotis interna perforates the floor of the fossa by a median foramen, in *Chlamydoselachus* and *Scymnus*, while in *Polypterus* it enters the cranial cavity anterior to the fossa, through the foramen opticum, but this is probably not an important difference, for as the artery in *Chlamydoselachus* and *Scymnus* quite undoubtedly runs forward a certain distance

between the cartilage of the fossa and its lining membrane, it lies morphologically anterior to the fossa. In *Chlamydoselachus* the brain extends forward nearly to the level of the presphenoid bolster, and in embryos doubtless extended onto the bolster, as it does in the adult *Polypterus*. In *Scymnus* there is a large presphenoid shelf, as in *Polypterus*, but it is not said how far forward the brain extends. The anterior end of the *cavum cranii* is formed, in all three fishes, by a narrow median column which separates the *foramina olfactoria* from each other, and in the *Selachii* this column is said by Sewertzoff (1899) to be formed by the *trabeculae* fused to form what he has called the rostral stalk. A *septum nasi*, where found, as in *Galeus* and *Mustelus*, lies ventral to that stalk. In *Polypterus* the *septum* apparently lies dorsal to the *trabeculae*. But, however this may be, it is evident that the nasal capsules must lie morphologically dorsal to the *trabeculae* in all these fishes, for the *nervi olfactorii* always run outward dorsal to the latter cartilages.

NASAL SAC AND NASAL APERTURES

In my 75 mm. larva of *Polypterus senegalus*, and also in one adult specimen from Abyssinia, the only ones examined in this respect, the nasal sac is divided into five sectors by five longitudinal septa which radiate outward from the axis of the sac. Waldschmidt (1887) also found but five sectors and septa in the 25 cm. to 30 cm. specimens of *Polypterus bichir* examined by him, as did also J. Müller (1846) in what were probably older specimens of the same fish. Wiedersheim (1906), however, says that there are six sectors and six septa in this fish.

In my 75 mm. larva, one of the five septa is horizontal in position and extends mesially from the horizontal axis of the sac to its periphery, the other septa extending dorso- and ventro-mesially and dorso- and ventro-laterally. The *nervus olfactorius* lies in the horizontal axis of the sac, but it does not enter the sac in the line of that axis, entering it by passing ventro-antero-laterally across the hind end of that sector of the sac that lies immediately dorsal to the horizontal septum, that sector not extending as far posteriorly as the others. The two mesial sectors both extend forward slightly beyond the other three, and there lie mesial to an open space into which they and the other three sectors all open. The ventral one of the two mesial sectors is prolonged anteriorly beyond this space, and there lies in a slight recess in the nasal cartilage. In the adult this projecting anterior end of this sector becomes somewhat separated from the remainder of the nasal organ and forms the "Nebenriechorgan" said by Waldschmidt to have been described by Wiedersheim in a work I have not been able to consult. It is innervated, as Waldschmidt says, by a simple terminal branch of the *nervus olfactorius*.

Into the open space, above referred to, that lies lateral to the anterior ends of the two mesial sectors of the nasal sac, the anterior nasal tube opens, the base of the tube projecting a certain distance into the space, and being slit a certain distance upward along its lateral surface. Slightly posterior to this

tube, in the lateral portion of the space into which it opens, the posterior nasal passage begins, and runs posteriorly in a slight depression on the lateral surface of the antorbital process of the premaxillary bone. This depression lies between the lateral edge of the nasal bone above and tube 5 of the infra-orbital latero-sensory canal below, and the nasal passage opens posteriorly in a crescentic and slit-like aperture which lies slightly anterior to the anterior edge of the orbit. The anterior nasal tube was, in certain of my preserved specimens, folded back onto the external wall of this posterior nasal passage, and, pushing in that wall, was half imbedded in the groove that lodges the passage.

In one of my large specimens, the only one examined in this connection, the two nasal passages had the same relations to each other and to the nasal sac that they had in the 75 mm. larva, but in a 30 cm. specimen the two nasal apertures both opened into a space that was partially separated from the nasal chamber by a membranous partition, and that was apparently the "Vorhöhle" of Waldschmidt's (1887) description. A large opening led from this atrial chamber into the nasal chamber, and was incompletely bridged by a process of membrane which projected dorso-posteriorly from its antero-ventral edge and touched, but was not fused with, the opposite edge of the opening. Nothing resembling the arrangement here described by Waldschmidt was found in either of the three specimens examined.

The nasal epithelium of *Polypterus* would thus seem to be a special development of the rosette form found in certain of the Teleostei and in *Chimaera*, and it is usually assumed that it has arisen from that form as a result of a thickening of the sensory epithelium and a concomitant deepening of the nasal sac. The nasal capsule cannot, however, have arisen by the simple deepening of a shallow pit, for the terminal branches of the *nervi ophthalmicus* and *maxillaris trigemini* both perforate the wall of that capsule and then run forward between it and the nasal sac to issue through the *fenestra nasalis*. These terminal branches of these nerves both contain latero-sensory fibres, and hence must necessarily have primarily passed external to the nasal capsule, and a simple deepening of the capsule could not have included them within it. There must then have been a forward growth of the lateral wall of the capsule, and it is possible that a similar growth of the primitive sac and nasal epithelium has also taken place.

OSTEOLOGY

The bones that form the skull of *Polypterus* are, as is well known, in part so-called primary ones (*ossa substituentia*) and in part secondary, or dermal ones (*ossa investiantia*), and certain of them are apparently the equivalents of two or more bones usually found separate and independent in the *Holostei* and *Teleostei*. Whether this is due to the invasion, by one bone, of the territory usually occupied by one or more other bones, or is due to the actual fusion of two or more primarily independent bones, cannot be determined from my

material, for, even in my 75 mm. specimen, there is no positive indication, in any of the bones concerned, of two or more separate centres of ossification. It nevertheless seems proper, in certain cases, to assume the fusion of two bones, and to indicate the two components by the use of a compound term.

Parieto-dermopterotic. This bone was called by both J. Müller (1846) and Traquair (1871) the parietal. Van Wijhe (1882) later called it the squamosoparietal, because of its assumed formation by the fusion of the squamosal and parietal bones of the Teleostei, and I adopted this term in my work on the latero-sensory canals of this fish. The bone, however, only includes the dermal component of the squamosal of the Teleostei, and as the latter bone is currently called by English authors the pterotic, I shall call the bone of *Polypterus* the parieto-dermopterotic.

The two parieto-dermopterotics, one on either side of the head, are each somewhat rectangular in shape, and they together form the posterior portion of the flat dorsal surface of the neurocranium, extending from the orbitotemporal to the occipital regions and lying upon the otic portion of the chondrocranium. Each bone articulates, in the median line, with its fellow of the opposite side, and articulates anteriorly either with the frontal of its side, alone, or with both that bone and the postero-mesial corner of the frontal of the opposite side, the sutural line between the frontals not always being in line with the suture between the parieto-dermopterotics. The anterior end of each bone rests upon the dorsal surfaces of the postfronto-sphenotic and the vertical plate of the sphenoid, and between these two bones it roofs the hind end of the supraorbital fontanelle. Mesial to the sphenoid it roofs one half of the hind end of the median supracranial fontanelle.

Along the lateral edge of the anterior portion of the bone there is a depressed region which extends forward slightly onto the hind end of the frontal. The anterior portion of this depression lodges the mesial half of the anterior spiracular ossicle. The posterior portion of the depression is deeper than the anterior portion, and lodges the anterior portion of the dorsal end of the spiracular canal, this part of the depression extending downward across the lateral edge of the bone. Posterior to this there is, on the lateral edge of the bone, a concave depression which forms the dorsal portion of the articular facet for the hyomandibula, the dorsal edge of this depression forming a sharp ridge which runs dorso-posteriorly in a curved line from the ventral edge of the lateral edge of the bone, at about the middle of its length, to the posterior end of its dorsal edge.

The postero-lateral corner of the bone rests upon the dorsal surface of the opisthotic, and from the deeper layers of this part of the bone a stout process, directed posteriorly along the dorso-lateral surface of the trunk muscles, gives insertion to a fascia-like formation related to the muscle fibres of the most anterior segment of the trunk muscles that is seen in dorsal views. This process apparently belongs wholly to the dermopterotic portion of the bone, and corresponds to that posterior process of the pterotic that is found in many of

the Teleostei. In *Salmo* this process is said by Gaupp (1905, p. 678) to be developed in relation to the primary, and not the dermal component of the pterotic, and, furthermore, in all of the Teleostei it is with what is considered to be the primary component of this bone, and not the dermal one, that the hyomandibula articulates. The process of *Polypterus* is, nevertheless, certainly not of primary origin, and it has quite certainly been developed, like the corresponding process of *Scomber* (Allis, 1899, p. 55), in relation to the fibrous tissues to which it gives insertion. From the base of this process of *Polypterus*, and from the ventral surface of the parieto-dermopterotic immediately mesial to it, another process arises which is directed ventro-posteriorly and slightly mesially and lies in that shallow depression on the posterior surface of the chondrocranium that forms a postero-ventral continuation of the mesial arm of the Y-shaped temporal groove. This depression lies immediately lateral to the epiotic ridge, its lateral half lying upon the dorso-posterior surface of the opisthotic, and its mesial half in part upon the cartilage of the chondrocranium and in part upon the dorsal surface of the single median basi-exoccipital bone. Mesial to this ventro-posterior process of the parieto-dermopterotic, the hind end of that bone projects posteriorly somewhat beyond the hind edge of the dorsal surface of the chondrocranium, and there lies upon the dorsal surface of the trunk muscles. The hind edge of the bone is nearly transverse in position, and is slightly bevelled where it is overlapped externally by the anterior edges of the two mesial ones of the three supratemporal bones of its side.

The pterotic portion of the bone is traversed its full length by the main infraorbital latero-sensory canal, the part of the bone so traversed forming a rounded ridge on the ventral surface of the bone which completely fills the temporal groove on the dorsal surface of the chondrocranium. The bone lodges two sense organs of the canal that traverses it, and a tube of the canal issues through the bone slightly posterior to the middle of its length. Immediately posterior to the opening of this tube there is a slight depression which lodges the middle head-line of pit organs.

Frontal. The frontal lies immediately anterior to the parieto-dermopterotic and is the largest bone on the dorsal surface of the cranium. Its mesial edge is nearly straight, and articulates with the corresponding edge of the frontal of the opposite side. Its anterior edge is deeply cut out by a rounded or angular incisure into which the hind end of the nasal fits, the latter bone overlapping externally the frontal. The frontal thus has pointed antero-mesial and antero-lateral corners. The antero-mesial corner rests upon the hind end of the dorsal surface of the median ethmoid. The antero-lateral corner rests upon the flattened dorsal edge of the antorbital process of the premaxillary. Posterior to the latter process the frontal rests upon a portion of the dorsal edge of the ectethmoid, the surface of contact with the latter bone lying slightly mesial to the lateral edge of the frontal. Mesial to these two surfaces of articulation the frontal rests directly upon the cartilage of the chondrocranium, but between the frontal and the cartilage there is, along the lateral

edge of the chondrocranium and underlying the supraorbital latero-sensory canal, a shallow groove which lodges the nerves that supply the sensory organs of that canal.

Posterior to the antorbital process of the premaxillary, the lateral edge of the frontal runs postero-laterally in a more or less wavy line, about one half of the width of the bone here overhanging the orbit. When the bone reaches the postfronto-sphenotic it rests upon and is firmly bound to the dorsal surface of that bone, the lateral edge of the frontal here turning postero-mesially in a rounded angle. The larger, mesial portion of the dorsal surface of the postfronto-sphenotic is slightly hollowed out to receive the frontal, the remaining, lateral portion of the bone forming a slight ridge along the lateral edge of the frontal. On the lateral edge of this part of the frontal there is a small rounded incisure which gives passage to the double tube infraorbital 10—supraorbital 7 of the latero-sensory system (Allis, 1900*a*). Posterior to this tube the frontal roofs for a short distance the main infraorbital latero-sensory canal, that canal lying in a groove on the dorsal surface of the postfronto-sphenotic. The frontal then overlaps externally the anterior edge of the parieto-dermopterotic, and is itself overlapped externally by the anterior corner of the anterior spiracular ossicle, the latter ossicle lying in a slight depression on the hind end of the frontal and being loosely bound to it by tough dermal tissues. Anterior to this spiracular ossicle the lateral edge of the frontal is in articular contact with the posterior one or two prespiracular ossicles, and anterior to all of the prespiracular ossicles it is in articular contact with the postorbital bone.

Mesial to the postfronto-sphenotic the frontal roofs the large supraorbital fontanelle, then rests upon the dorsal edge of the vertical plate of the sphenoid, and mesial to the latter bone, roofs, with its fellow of the opposite side, the median supracranial fontanelle. Along the line where the frontal rests upon the dorsal edge of the vertical plate of the sphenoid, there is a ridge on its ventral surface, this ridge being Y-shaped at its anterior end. Beneath the hind ends of the frontals, in the membrane that closes the supracranial fontanelle, there is the small, round and thin median plate of cartilage already referred to.

The frontal is traversed, the greater part of its length, by the supraorbital latero-sensory canal, but is not traversed by any part of the main infraorbital canal. It lodges three sense organs of the supraorbital canal, and two of the tubes of that canal issue on the dorsal surface of the bone. Beginning mesial to the posterior one of these two tubes, and extending postero-mesially, there is a short and slight depression on the dorsal surface of the bone, which lodges the anterior head-line of pit organs.

Nasal. The nasal is a somewhat oval bone which lies upon the cartilaginous roof of the nasal capsule. Its posterior end is bluntly pointed and lies in the re-entrant angle in the anterior edge of the frontal, overlapping that bone externally and being firmly bound to it by dermal tissues. Its mesial edge overlaps externally, and rests upon the dorsal surface of the posterior process

of the median ethmoid, and is there in contact with, or closely approaches, the corresponding edge of its fellow of the opposite side. Its lateral edge is free, and lies upon the dorsal surface of the antorbital process of the premaxillary. The anterior edge of the bone is straight, or slightly re-entrant, and articulates with the accessory nasal bone.

The nasal is traversed by the supraorbital latero-sensory canal, and lodges the third sense organ of that line. The third supraorbital tubule traverses a notch in the anterior edge of the bone, the fourth tubule traversing a notch in its latero-posterior edge.

Accessory nasal. This bone is a small and somewhat triangular one, immovably bound to the anterior end of the nasal. Its small anterior end rests upon and is bound to the dorso-posterior end of the ascending process of the premaxillary. Its mesial edge fits into a slight groove on the postero-lateral surface of the thickened anterior portion of the median ethmoid, and lateral to the latter bone it rests directly upon the cartilaginous roof of the nasal capsule. Its lateral edge is in contact with the movable os terminale of Traquair's descriptions. The bone is traversed by the supraorbital latero-sensory canal, and lodges the second sense organ of that line. The external surface of the bone lies deeper than the corresponding surface of the nasal, and has not the rugous markings of the latter bone. On one side of the head of the two specimens examined it was found in two pieces.

Os terminale. This bone is a small, curved, somewhat comma-shaped bone traversed by the supraorbital latero-sensory canal and lodging the first sense organ of that line. It is a movable bone, lies in the tough dermis along the postero-mesial edge of the base of the nasal tube, and overhangs the dorsal edge of the fenestra nasalis. It lies along the lateral edge of the accessory nasal, its antero-mesial end resting upon, or adjoining, the dorsal end of the ascending process of the premaxillary. Like the accessory nasal it lies deep in the dermis, and has not the rugous markings of the nasal.

The nasal, accessory nasal and os terminale, together, quite certainly represent the single nasal bone of *Amia*, as fully explained in my work on the latero-sensory canals of this fish (Allis, 1900a).

Ethmoid. The ethmoid is a median bone and is included by Traquair among the primary ossifications. It is said by him to be "a median ossification in the front of the septum narium," and to send "backwards beneath the nasal bones a flat narrow process which is ossified in the membrane superficial to the cartilage." Pollard (1892, p. 400), without making reference to Traquair, says that, "There is no ossification of the cartilage in front of the nasal septum." In all my specimens, from the 75 mm. larva to the largest adult, the bone is strictly a dermal one, lying everywhere external to the cartilage and separated from it by a layer of connective tissue.

The bone has a thickened anterior end and a thinner, plate-like posterior portion, and lies on the dorsal surface of the chondrocranium, in a median depression between the nasal capsules which is much more pronounced beneath

the anterior portion of the bone than beneath its posterior portion. The thickened anterior end of the bone lodges the anterior section of the infraorbital latero-sensory canal of either side of the head, the two canals anastomosing with each other in this bone, in the median line, but without leaving the slightest indication, even in the 75 mm. larva, of a median tube where the anastomosis has taken place. The bone lodges two sense organs, one belonging to either canal, and the thickened portion of the bone that is traversed by this so-formed cross-commissural canal lies in a groove that has a curved course, convex posteriorly, and crosses transversely the dorsal surface of the rostral process of the chondrocranium immediately anterior to the fenestrae nasales. The rostral process of my adult specimens projects forward slightly beyond the anterior edge of the ethmoid and abuts against the slightly concave posterior surfaces of the premaxillaries. The ethmoid is accordingly not exposed on the ventral surface of the chondrocranium, between the premaxillaries, as Traquair says that it was in his specimen.

Each half of the anterior edge of the ethmoid abuts against and is firmly bound to the premaxillary of its side, and immediately lateral to this surface of contact, the short ascending process of the premaxillary projects posteromesially in a groove on the lateral surface of the ethmoid, the latter bone thus being held between the two premaxillaries. The ascending process of the premaxillary does not extend the full length of the groove on the lateral surface of the ethmoid, the groove posterior to that process lodging the lateral edge of the accessory nasal, the anterior end of the latter bone resting upon the dorso-posterior end of the ascending process of the premaxillary. The frontal and nasal of either side both overlap externally the hind end of the ethmoid, this being the relations that these bones have to the ethmoid in the Characidae and Cyprinidae (Sagemehl, 1884 and 1891), but the reverse of the relations that the frontals have to the supra-ethmoid of Parker's (1873) descriptions of *Salmo salar*.

The ethmoid of *Polypterus* thus corresponds to that middle portion of the dermal ethmoid of *Amia* that lodges the anterior sense organ of the main infraorbital canal of either side. The lateral portions of the bone of *Amia*, each of which lodges a second sense organ of the related infraorbital canal, have each fused, in *Polypterus*, with the premaxillary of its side, as fully explained in my work on the premaxillary and maxillary bones of this fish (Allis, 1900b).

Infranasal and infraorbital bones. These bones are usually all described as the infraorbital chain, but the anterior ones are definitely preorbital and infranasal in position and not infraorbital, and they are developed in relation to a definitely preorbital part of the main infraorbital latero-sensory line. The infranasal bones, which correspond to the lateral portion of the median ethmoid and the antorbital bone of *Amia*, have both fused with the premaxillary, and the infraorbital bones, excepting the anterior and posterior ones, have fused with the maxillary (Allis, 1900b).

The anterior infraorbital bone corresponds to the lachrymal of *Amia*, but is called by Traquair the anterior suborbital. It is a triangular bone the base of which is directed anteriorly and abuts in large part against the hind edge of the antorbital process of the premaxillary, but partly also against the lateral border of the anterior edge of the ectethmoid. Its dorsal edge forms the antero-ventral margin of the orbit. Its ventral edge rests upon the dorsal edge of the maxillary. It is traversed by the main infraorbital latero-sensory canal and lodges one sense organ of that canal.

The next two bones of the chain are suborbital ones, each containing a single sensory organ of the line, and they have both completely fused with the maxillary.

The next, or posterior bone of the chain is called by Traquair the posterior suborbital, but as it forms the posterior margin of the orbit it is a postorbital. Its dorsal edge is in contact with the lateral edges of the frontal and post-fronto-sphenotic, its ventral edge in contact with the dorsal edge of the posterior portion of the maxillary, and its hind edge overlapped externally by the one or two anterior prespiracular ossicles. It is traversed by the main infraorbital canal and lodges one sense organ of that canal.

Spiracular ossicles. In my 49 cm. specimen of *Polypterus bichir* (figs. 5 and 6) there were 7-8 prespiracular ossicles, 2 spiracular ossicles, and 3-5 postspiracular ones, this agreeing approximately with the number of these ossicles shown by J. Müller (1846) in his figure of this fish, and with the number described by Bridge (1888) in that one of his two specimens that had fourteen dorsal finlets. In one of my small specimens, which had 8-12 finlets, there were nine of these ossicles in all, on either side of the head, this agreeing approximately with the number in the specimens described by Traquair, which also had 8-12 finlets, and with the number in that one of two specimens described by Bridge that also had this same number of finlets. This difference in the number of these spiracular ossicles is thus probably a specific character.

Supratemporals and posttemporal. There are three supratemporal bones on either side of the head in all of my specimens, two of them lying in transverse line immediately posterior to the parieto-dermopterotic, and the third one lying posterior to the lateral portion of the lateral one of the other two. The two bones transversely placed are traversed by the supratemporal latero-sensory canal and each lodges one sense organ of that canal, the postero-lateral bone being traversed by the main infraorbital canal and lodging one sense organ of that canal. These three bones, together, thus correspond to the single large supratemporal (extrascapular, Sagemehl) bone of *Amia*, as fully explained in my work on the latero-sensory canals of this fish.

The posttemporal is a relatively large, plate-like bone in contact anteriorly with the hind edges of the two transversely placed supratemporals, and laterally with the median edges of the postero-lateral supratemporal and the posterior postspiracular ossicle. From the ventral surface of the lateral edge of the bone, at about the middle of its length, a short stout rod-like process

projects antero-ventrally and slightly mesially and gives insertion to a stout ligament which has its origin on the posterior process of the opisthotic. From the base of this process of the posttemporal a slight ridge runs postero-mesially across the ventral surface of the bone, and on reaching its mesial edge turns posteriorly and becomes a stout posterior process which gives insertion to a large fascia-like tendon related to the muscle fibres of that segment of the trunk muscles that is the third one seen in dorsal view of the adult.

Basi-exoccipital. The basi-exoccipital, the occipital bone of earlier descriptions, is, as Traquair has stated, formed by the fusion of the median basioccipital and the two exoccipitals of the Holostei and Teleostei. It has exposed dorsal, ventral, lateral, posterior, and cerebral surfaces. Anteriorly it is everywhere bounded by cartilage. Its dorsal and lateral surfaces are separated from each other by the lateral occipital ridge, already described, this ridge lying wholly on the exoccipital portion of the bone. Its lateral and ventral surfaces are separated by a rounded edge which starts posteriorly on the lateral edge of the vertebra-like hind end of the bone and, lying wholly on the basioccipital portion of the bone, runs anteriorly and slightly ventrally to its anterior end. This edge of the bone is not exposed in the prepared cranium, being covered, throughout its entire length, by the lateral edge of the parasphenoid.

The posterior surface of the bone is formed by the hind end of its basioccipital portion and the hind edges of its exoccipital portions. The hind end of the basioccipital portion is oval in shape, the vertical axis of the oval being slightly less than half as long as its horizontal axis. It is slightly concave, and gives articulation to the first free vertebra. The hind edges of the exoccipital portions of the bone form the lateral and dorsal boundaries of the foramen magnum, and are bound by membrane to the anterior edges of the occipital vertebral arch.

The lateral surface of the bone, formed largely by its exoccipital portion, is about twice as tall at its anterior as at its posterior end. Its anterior edge is deeply notched, at about the middle of its height, to form the posterior border of the foramen vagum, and from this foramen a deep groove runs postero-ventrally and gradually vanishes toward the hind edge of the lateral surface of the bone. The dorsal edge of this groove is formed by the lateral occipital ridge, its ventral edge by the ridge, already described, that runs posteriorly from the bulla acustica. Both dorsal and ventral to the foramen vagum the anterior edge of the bone is overlapped externally by, and articulates with, projecting processes of the opisthotic, these processes extending posteriorly along the external surfaces of the anterior ends of the lateral occipital and subvagus ridges.

Posterior to and in line with the foramen vagum there are two foramina, one of which transmits, as Lehn has stated, the posterior occipital nerve (z^v) of Fürbringer's (1897) descriptions and the other the ventral root of his anterior occipito-spinal nerve (a^v); the internal openings of these two foramina lying considerably anterior to their external openings. The external opening of the

anterior one of the two foramina lies in the vagus groove on both sides of the head of the one specimen examined, the posterior foramen lying at the dorsal edge of that groove on one side of the head, but, on the other side, definitely on the lateral occipital ridge. A slight groove runs postero-ventrally from each foramen, and ends, postero-ventrally, either in a slight depression, in a relatively deep pit, or in a short canal leading into the bone. Each groove lodges the related nerve for a short distance after it issues from its foramen, the pit, or canal, at its hind end apparently giving passage to an artery, as explained below. Dorsal to and slightly anterior to the posterior one of these two foramina, and dorso-mesial to the lateral occipital ridge, there is a small foramen for the dorsal root of the anterior occipito-spinal nerve (a^d), the internal opening of this foramen lying considerably posterior to the internal opening of the foramen for the ventral root of the same nerve.

The two ventral occipital foramina above described thus correspond almost exactly, in general position, to the foramina for the first and second occipital nerves of my descriptions of *Amia*, and as the nerves that issue through these foramina in *Amia* are called by Fürbringer the nerves z and a , as are also the corresponding nerves in *Lepidosteus*, the two nerves and their foramina in these three fishes are, in all probability, homologous. The foramina in these fishes are, however, apparently not the homologues of the occipital foramina of *Scomber* (Allis, 1903) and the mail-cheeked fishes (Allis, 1909), for the foramina in these latter fishes all lie either directly on the lateral occipital ridge, or definitely dorso-posterior to that ridge, this being in accord with Fürbringer's conclusion that the nerve that issues through the anterior one of the foramina in these fishes is the second occipito-spinal one (nerve b), and hence the nerve next posterior to the one that issues through the posterior foramen in *Polypterus* and *Amia*.

Antero-ventral to the anterior occipital foramen, between it and the transverse plane of the foramen vagum, there is on each side of the head what appears like a simple imperfection in the bone, but a bristle can be pushed into it for a considerable distance. This canal lies in the line prolonged of the two little pits, or canals, at the hind ends of the two grooves that lead postero-ventrally from the two occipital foramina, and in the adult nothing could be found entering either of them. In the 75 mm. larva a branch of an intervertebral artery penetrated the bone in a position corresponding to that of each of the two posterior canals, but nothing was found entering the bone in the position of the anterior canal. The two intervertebral arteries here concerned arose as a single artery from the dorsal aorta immediately after that artery issued from the hind end of the aortic canal, each artery first sending a branch into the canal in the basioccipital, then one into the cranial cavity through the foramen for the related occipital nerve, and then continuing onward, doubtless in relation to a muscle septum, but this was not traced. From the posterior one of these two intervertebral arteries, previous to the branch sent into the cranial cavity, a branch was sent posteriorly, and from this branch a branch

was sent into the cranial cavity through that foramen in the occipital neural arch that gives passage to the ventral root of the related spinal nerve (nerve *b*ⁿ). No separate artery arising directly from the aorta was found in relation to this neural arch, but one was found in relation to the first, third and fourth free vertebrae. Between the arteries sent to the first and third vertebrae an artery arose from the dorsal aorta, but it was apparently not distributed to the segment of the second vertebra, this vertebra being supplied by a posterior branch from the artery to the first vertebra.

The dorsal surface of the basi-exoccipital forms the ventral portion of the gently sloping posterior surface of the chondrocranium. For a short distance immediately anterior to the foramen magnum, the mid-dorsal line of this surface is nearly horizontal in position, the bone here forming an arch above the medulla. Anterior to this short horizontal portion the surface widens gradually and slopes gently upward to the anterior edge of the bone. The two epiotic ridges, one on either side, are prolonged slightly onto the basi-exoccipital, and separate the exposed portion of its dorsal surface into three regions, one median and two lateral, each of which is slightly concave and is prolonged dorso-anteriorly in a corresponding depression on the cartilaginous portion of the posterior surface of the chondrocranium. Each lateral depression forms the mesial portion of that shallow depression on the posterior surface of the cranium that forms the ventro-mesial arm of the Y-shaped temporal groove and lodges the ventro-posterior process of the parieto-dermosphenotic. The median depression is apparently formed by what Lehn (1918, p. 360) calls the supratemporal grooves, but as the depression ends dorso-anteriorly at the hind edges of the parieto-dermosphenotics it corresponds to the postero-ventral prolongations of the supratemporal grooves of my descriptions of Scomber (Allis, 1903) and not to those grooves themselves, the grooves lying on the dorsal surface of the cranium.

The hind edges of the exoccipital portions of the basi-exoccipital form the lateral and dorsal boundaries of the foramen magnum, the lateral edges of the foramen inclining upward and forward. The basioccipital portion of the bone projects posteriorly, beyond its exoccipital portions, a distance equal to about one half the thickness of the first free vertebra, and its dorsal surface is here slightly concave, transversely, on either side of the median line. In these concavities the rounded bases of a pair of free dorsal neural arches rest, the anterior edges of the arches resting against and being connected by membrane with the hind edges of the exoccipital portions of the basi-exoccipital. These two arches, one on either side, are fused with each other in the median line dorsal to the spinal cord, and a short dorsal neural spine articulates with, and is firmly bound to, the dorsal portions of their posterior edges. The neural arch of either side is perforated by the ventral root of a spinal nerve, and either perforated, or notched on its anterior edge, by the dorsal root of the same nerve. The next posterior, or second pair of dorsal neural arches are fused with the first free vertebral centrum, the arch of either side being perforated

by both roots of the related spinal nerve. The first neural arch is accordingly an occipital arch, related to a vertebral centrum that has fused with the basi-exoccipital, and the nerve that perforates it is actually the posterior occipital nerve. It is however called by Fürbringer (1897) the second spinal nerve.

The rounded edge that separates the lateral and ventral surfaces of the basi-exoccipital, and the larger portion of the ventral surface of that bone, are covered externally by the hind end of the parasphenoid, the two bones being so firmly ankylosed that they could not be separated without breakage even in an alcoholic specimen that had been long macerated. In a fresh specimen they could probably be separated, for the two bones are wholly separate and distinct in my 75 mm. larva. In the hind edge of the parasphenoid there is a large and deep V-shaped incisure, which extends about one half the length of the basi-exoccipital, and a corresponding portion of the ventral surface of the basi-exoccipital is exposed between the limbs of the V. In the middle line of this exposed surface there is a large foramen which leads into the aortic canal, and on either side of this foramen there is a round depression which lies partly on the basi-exoccipital and partly on the parasphenoid and gives origin to a stout ligament which runs almost directly laterally and is inserted on the shoulder girdle.

Aortic canal. The aortic canal of *Polypterus* was, so far as I know, first particularly described by Bridge (1888), and he refers to it, in the plural, as the basicranial canals. Of these canals he says: "In both specimens the somewhat massive bone occupying the basioccipital region and continuously surrounding the foramen magnum, and possibly including also the centrum of the first vertebra, is perforated near the posterior end of its under surface, at the extremity of the parasphenoid, by a small median foramen. Traced forwards this foramen leads into two divergent canals, which at first lie between the basioccipital above and the parasphenoid below, but more anteriorly, between the last mentioned bone and the cartilaginous basis cranii. Finally, after perforating the roots of the lateral wings of the parasphenoid, the canals open into the orbit near the postero-inferior angles of the lateral plates of the sphenethmoid, and below the notch for the second and third divisions of the fifth nerve. The median foramen apparently transmits the dorsal aorta, and it is probable that the divergent canals are traversed by either the internal or external carotids, or possibly by both arteries during a portion of their course. Although the eye muscles in *Polypterus* are not in any way related to these canals, it is by no means improbable that the latter represent the orbital canals so characteristic of many Teleostean fishes."

Pollard (1892) says of this canal: "The dorsal aorta runs both forwards and backwards. The precardiac portion penetrates immediately into the skull passing into the body of the last vertebra which takes part in the formation of the cranium. Further forwards it lies between the cranium and the parasphenoid dividing and passing out with each wing of the latter to join the efferent 1st branchial. The common trunk thus formed runs on as the oph-

thalmic artery on each side." In one of his figures (fig. 12, Pl. 28) he shows the canal lying between the basi-exoccipital and the parasphenoid, while in another (fig. 23, Pl. 28) he shows it wholly enclosed in the basi-exoccipital.

Budgett (1902) does not particularly describe this canal in his 30 mm. larva of *Polypterus senegalus*, but he describes a so-called subaortic bridge of cartilage which projects ventrally beneath the hind ends of the parachordals and encloses a short section of the aorta. Of this bridge he says: "The basi-occipital region does not completely envelope the anterior end of the notochord, but is composed of two halves (the parachordal cartilages) abutting on two sides of the front end of this structure. Posteriorly these two masses of cartilage send wings ventrally which meet and fuse beneath the dorsal aorta, enclosing it in a short canal which is roofed in by the notochord itself. Anteriorly to the bifurcation of the aorta, the basioccipital cartilages fuse below the notochord, sending forward a narrow medial plate of cartilage which underlies the tip of the notochord."

In a figure giving a lateral view of the occipital portion of a reconstructed skull, Budgett (*l.c.* fig. 4, Pl. 33) shows the aorta turning dorso-anteriorly immediately anterior to his subaortic bridge and there being immediately hidden from view by the parachordal cartilage, and as the parachordals are said, in the quotation just above given, to be here separated from each other by the anterior end of the notochord, it would seem as if the aorta must lie in a deep groove on the ventral surface of the basal plate. The descriptions and figures are, however, not in accord as to this, and it would furthermore seem as if there must be some error either in the figures or in the descriptions of them. In the fig. 4 above referred to, the subaortic bridge is shown lying considerably posterior to the hind end of the otic capsule, and, anterior to the bridge, the parachordals run dorso-anteriorly at a considerable angle to the ventral surface of the notochord. Fig. 1 on the same plate is said to give a lateral view of the same reconstructed primordial cranium with the exoccipital region cut off, and figs. 2 and 3 to give posterior and anterior views of the same. The subaortic bridge of fig. 4 should accordingly be excluded from figs. 1, 2 and 3. The aorta is however shown, in each of these three figures, enclosed within an arch of cartilage, and in figs. 2 and 3 this arch is said, by index letters, to be the subaortic bridge. It must then be that the aorta is again enclosed in a canal in the parachordal cartilage after it has traversed the canal formed by the bridge at its hind end, but this is in no way indicated in the descriptions. In fig. 4 the notochord is shown decreasing rapidly in size as it approaches the subaortic bridge, but in a cross-section through it, shown in fig. 2, and hence presumably close to the hind end of the otic capsule, the notochord has not diminished in size and is even approximately as tall, in cross-section, as it is in the region of the aortic bridge.

In the adult *Polypterus*, I find the aortic canal penetrating the ventral surface of the basioccipital immediately anterior to its vertebra-like hind end, between the diverging hind ends of the parasphenoid. The canal then turns

forward and, wholly enclosed in the basioccipital, extends to the anterior end of that bone. There it bifurcates, the bifurcations passing outward, on either side, in the cartilage of the basis cranii and opening in the canal enclosed between the lateral, ventral and mesial plates of the lateral wings of the parasphenoid. The cartilage in which these bifurcations lie extends the full length of the basal portion of the labyrinth region, and separates the anterior end of the aortic canal from the hind end of the pituitary fossa. This cartilage is thick in the median line, but thinner on either side, and raised portions of the parasphenoid there support the anterior walls of the bifurcations of the aortic canal.

The aortic canal and occipital region in the 75 mm. Polypterus senegalus. In my 75 mm. specimen of *Polypterus senegalus* I find no trace of the cartilaginous subaortic bridge of Budgett's descriptions, nor does Lehn describe it in her 76 mm. one. There is, however, on the ventral surface of the basal plate of the chondrocranium, a groove, with ventro-laterally projecting edges, which lodges the dorsal aorta and its diverging branches (the lateral dorsal aortae), and hence is an aortic groove.

The floor of the postpituitary portion of the cavum cerebrale cranii begins anteriorly in a narrow transverse bridge of cartilage which extends from one cranial wall to the other and is the homologue of the cartilago acrochordalis of Sonies's (1907) descriptions of embryos of the chick and duck. It represents, at this age, the proötic bridge of the adult and has concave anterior and posterior edges, the widened base of the bridge forming, on either side, a ridge on the cerebral surface of the lateral wall of the cranium. Anteriorly this ridge vanishes on the cranial wall opposite the line of the cerebral sulcus that lies along the dorsal edge of the lobus inferior. Posteriorly it descends gradually and becomes continuous with the dorsal edge of the thick cartilage that forms the lateral boundary of the posterior portion of the basicranial fontanelle, and this posterior part of the ridge is connected by membrane, throughout its entire extent, with its fellow of the opposite side, this membrane and the cartilaginous proötic bridge forming the roof of the posterior portion of a dorsal, but non-functional myodomic cavity (Allis, 1919*b*) which lodges the large pituitary body. The dorsal portion of the thick cartilage that forms the posterior boundary of the basicranial fontanelle thus forms the posterior boundary of a fenestra basicranialis posterior, the ventral portion of the cartilage forming the posterior boundary of a fenestra ventralis myodomus (Allis, 1919*b*). What Waldschmidt (1887) calls the nervous portion of the hypophysis lies beneath the cartilaginous proötic bridge, the glandular portion lying beneath the membrane posterior to that bridge. Waldschmidt says that this so-called glandular portion of the hypophysis of this fish is in no sense a saccus vasculosus such as is found in the Teleostei, but as the two structures evidently are, as Waldschmidt says, genetically related, it may be called the saccus. The pituitary vein of either side perforates the lateral wall of the myodomic cavity beneath the anterior portion of the proötic bridge and

immediately falls into the infraorbital branch of the vena jugularis. The perforation of the roof of the cavum sacci vasculosi, the fenestra basicranialis posterior above referred to, is described by Lehn (1918, p. 364) in her 76 mm. specimen, but it is not the fenestra basicranialis posterior of her descriptions, which lies posterior to this and will be referred to later.

The basicranial fontanelle ends slightly posterior to the hind end of the saccus vasculosus, and from there as far back as the tip of the notochord, the basal plate is an unbroken plate of cartilage. From that point, posteriorly, to the point of bifurcation of the aortic groove, the basal plate encloses the anterior end of the notochord and is somewhat thickened in the median line, but the cartilage is imperfect in places both dorsal and ventral to the notochord, the parachordal plates of opposite sides not yet having completely fused around it. This thickening of the cartilage here forms a median ridge on the ventral surface of the basal plate, this ridge increasing in height posteriorly and, at the point of bifurcation of the aortic groove, projecting ventrally below the level of the ventral surface of the aorta. The lateral surfaces of the ridge are here scooped out to form grooves which are directed postero-mesially and lodge the lateral dorsal aortae, and when these grooves unite with each other in the median line, the ventral portion of the ridge is pinched off and projects posteriorly as a short process which extends to the point where the lateral dorsal aortae join the median aorta. This little process may be called the median subaortic process. It is not shown or mentioned by Budgett in his descriptions either of his 30 mm. larva or of the older ones examined by him, but is described by Lehn (1918, p. 257) in her 76 mm. specimen. Pollard (1892) shows it in two of the sectional views of his 21 cm. specimen, and of it he says: "In front of the vertebral elements which have been drawn into the base of the skull there occurred in the youngest specimen of *Polypterus* a small oval block of cartilage curiously surrounded by a thin shell of bone and above it lay the thread-like termination of the notochord." This would seem to mean that Pollard found the projecting hind end of the process of my larva as an independent piece of cartilage, but Winslow (1898), who examined drawings made by Kingsley of Pollard's sections of this same specimen says: "A peculiar rod of cartilage projects a short distance backward from beneath the middle of the basilar plate."

Anterior to the median subaortic process, the lateral aortic groove of either side diverges from the median ridge on the ventral surface of the basal plate, and its mesial boundary is then formed by a sharp cartilaginous ridge which diverges from the median one. The lateral boundary of the groove is here at first formed by an anterior prolongation of the lateral bounding ridge of the median, posterior portion of the aortic groove, but this ridge gradually vanishes on the rounded ventro-mesial edge of the otic capsule, the groove then lying in the angle formed where that capsule is joined by the parachordal plate, and there gradually vanishing anteriorly. Posterior to the subaortic process, the lateral aortic grooves of opposite sides fuse to form a median groove which lies directly

beneath the notochord, the notochord here lying against the ventral surface of the basal plate and projecting ventrally beneath it into the groove. Proceeding posteriorly, the ventrally projecting ridge that forms, on either side, the lateral boundary of the groove gradually diminishes in height, and the parachordal cartilages there recede slightly from the notochord, thus leaving a small fenestration in the parachordal plate which lies approximately in the transverse plane of the anterior edge of the foramen vagum, and hence in that of the hind ends of the otic capsules, and is the fenestra basicranialis posterior of Lehn's descriptions. This fenestra is spanned, at about the middle of its length, by a bridge of membrane bone which encloses the notochord. Posterior to the fenestra the dorsal edge of the mesial edge of each parachordal is in contact with the lateral surface of the notochord, the notochord, enclosed in bone, lying between the parachordals with exposed dorsal and ventral surfaces which form, respectively, the median portion of the floor of this part of the cavum cranii, and the roof of the here shallow aortic groove on the ventral surface of the basal plate.

Up to the point where the lateral aortic canals unite with each other in the median line, there is no indication of ossification in relation to the cartilage that surrounds the notochord, and even in the adult the cartilage still persists in this region. In my sections, which were double stained in Weigert and magdala-red fluids, a superficial layer of the cartilage is everywhere stained a reddish colour which is much deeper in certain regions than in others. This layer contains occasional cells, found singly and somewhat separated from each other, and coloured lines extend inward from it between the cells of the deeper portion of the cartilage, certain of these lines occupying the entire space between adjoining cells, while others are completely surrounded by a less deeply staining matrix which separates the cells. In certain places these lines seem to be fibrous, but in others they are certainly simply a staining of the matrix of the cartilage. Superficial to this layer there is, on the cerebral surface of the cartilage, a thin membranous layer which is in most places closely applied to the cartilage, but in certain places separated from it. This membrane is quite certainly the dura mater, or a part of it, and where it has separated from the cartilage scattered cells are found in the intervening space. On the external surface of the cranium fibrous lines separate, in certain places, from the external surface of the deeply staining superficial layer of the cartilage and are continuous with the perichondrial fibrous tissues that lie external to it. Throughout the notochordal portion of the region there is, internal to and concentric with the superficial reddish layer on the cerebral surface of the cartilage, a second layer of strictly similar appearance, and between the two layers there is a layer of cells which look like the cartilage cells found in places where the cartilage is undergoing resorption. Beginning somewhat anterior to the base of the median subaortic process, the cells in that portion of the cartilage of the basis cranii that lies dorsal (cerebral) to the notochord are encircled, in groups of one or more, by the reddish lines above described, and in the transverse

plane of the tip of the subaortic process these cells all become separated from the remainder of the cartilage by a prolongation of the inner one of the two reddish layers above referred to. A median portion of the cartilage, which lies directly upon the dorsal surface of the notochord and which is concavo-convex in transverse section is thus here incompletely separated from the parachordals, and as the latter cartilages do not here reach the notochord, and as the fenestra basicranialis posterior of Lehn's descriptions begins immediately posterior to the median cartilage, the latter cartilage fills the anterior end of the fenestra and apparently represents a stage in the occlusion of it. This little cartilage is described by Lehn (1918, p. 363) in her specimen, and is there said to be continuous anteriorly with the cartilage of the basis cranii.

In the basioccipital region resorption cavities are forming in the cartilage, and they lie, in certain places, internal to the reddish superficial layer of the cartilage, but in others include that layer. Where perichondrial bone has been formed it occupies exactly the place of this reddish layer, and it is difficult to tell where bone ends and the unossified tissue begins. The tissue thus cannot be cartilage, for perichondrial bone is said never to be formed by direct ossification of cartilage. It is however skeletogenous tissue of some sort, and it lies directly upon the cartilage without a recognisable intervening layer of tissue of any sort, the conditions here thus seeming to be similar to those described by Schauinsland (1906, p. 445) in the neural arches of *Amia*, where the first-formed bone is said to develop in the perichondrium (im Perichondrium). Nowikoff (1909) says that, in the tibia of the new-born mouse, the first-formed bone develops external to the perichondrium, but Schäfer (1893, p. 275) makes the general statement that true membrane-bone (that is, perichondrial bone), "lies underneath the perichondrium, and closely investing the surface of the cartilage." There is thus difference of opinion as to how this bone develops.

The parasphenoid, in the region of the subaortic process, underlies the cartilage of the basis cranii, separated from it by dense fibrous tissue, and its lateral edges project laterally on either side so as to partly floor the related diverging branch of the aortic groove. Posterior to the point where these diverging branches unite with each other in the median line, and as far back as the point where the lateral dorsal aortae fuse with each other to form the median dorsal aorta, the notochord lies on the ventral surface of the cartilage of the basis cranii, directly dorsal to the median subaortic process. Around the subaortic process a layer of perichondrial bone is forming, and laminae of bone are sent outward from it to the inner surface of the dense fibrous tissue that lies between it and the parasphenoid, this perichondrial bone and the related laminae forming part of the basioccipital. The lateral edges of the parasphenoid here extend upward, on either side, to the cartilaginous lateral edge of the aortic groove and abut directly against that cartilage, with a somewhat broad and flattened edge, the aortic groove of more anterior sections

thus becoming a canal the ventral portions of the walls of which are formed by the parasphenoid. From here the aortic groove extends posteriorly to the hind end of the parachordal cartilage, the cartilaginous lateral edges of the groove projecting ventrally as slight ridges which increase somewhat in height at the hind end of the cartilage.

Posterior to the hind end of the median aortic process, that portion of the basioccipital bone that develops in relation to that process still continues, but it is here a purely membrane bone, developed internal to the dense fibrous tissues in which the parasphenoid is imbedded, and having no relations whatever to the cartilage of the chondrocranium. Farther posteriorly, in the transverse plane of the anterior edge of the foramen vagum, this portion of the basioccipital extends upward on either side, internal to the parasphenoid, until it reaches the cartilage of the basis cranii, where it fuses with the layer of perichondrial bone developed in relation to that cartilage, the dorsal aorta thus here being wholly enclosed in the basioccipital, that part of the bone that forms the roof of the canal being developed in relation to the parachordal cartilages, but the part that forms the floor and lateral walls of the canal being developed in relation to fibrous tissue and in no relation whatever to existing cartilage.

At the hind end of the otic capsule, the parachordal of either side, as seen in transverse sections, is directed dorso-laterally, and immediately posterior to the capsule its dorsal edge forms the ventral boundary of the foramen vagum. From that point it diminishes gradually in height and ends slightly posterior to the foramen for the anterior occipital nerve (the nerve z'' of Fürbringer's descriptions), that foramen lying immediately dorsal to the hind end of the cartilage, in membrane bone that forms part of the exoccipital. Posterior to this the notochord increases rapidly in size, is circular in transverse section, and is completely surrounded by a layer of deeply staining tissue that looks like bone and includes the outer layer of the fibrous portion of the notochordal sheath. From this deeply staining layer, processes of bone of membrane origin project outward along the dorso-lateral and ventro-lateral lines of the notochord. The dorso-lateral processes extend posteriorly to the hind end of the skull, form the posterior portions of the exoccipitals, and end dorsally in connective tissues that here form the roof of the cranial cavity. The ventro-lateral processes are short, and correspond in position to the aortic supports of Budgett's descriptions of the vertebrae in his 90 mm. larva of this fish. They are continuous, at their outer ends, with that portion of the basioccipital, of membrane origin, that forms the lateral and ventral bounding walls of the aortic canal, and this bone is now beginning to break through on its ventral surface preparatory to the exit of the aorta from its canal. This portion of the basioccipital still lies wholly internal to the dense fibrous tissue that separates it from the parasphenoid, the latter bone here being represented only by its two projecting hind ends, one on either side, these ends lying external to thickened portions of the basioccipital that correspond to those slightly

raised and pad-like portions of the bone which, in *Amia* (Allis, 1897), give support to the parasphenoid. Irregular laminae of membrane bone extend between the dorso-lateral and ventro-lateral processes of either side.

Slightly posterior (7 sections) to the hind ends of the parachordals, cartilage appears within the basal portions of the dorso-lateral bony processes and extends posteriorly through about 25 sections, the bases of these cartilaginous processes resting directly upon the deeply staining outer layer of the notochord and their sides being lined by perichondrial bone which is continuous with that layer, and is prolonged dorsally beyond the cartilaginous processes to form the dorsal portions of the exoccipitals. The ventral roots of the second pair of occipital nerves (nerves α^2 , Fürbringer) issue from the cranial cavity immediately dorsal to these cartilaginous processes, there perforating the membrane-bone portions of the exoccipitals, the dorsal roots of these nerves issuing, almost directly dorsal to the ventral roots, across the hind edges of the exoccipitals. These cartilaginous processes are thus evidently the dorso-lateral vertebral processes of a vertebra that has fused with this part of the cranium. They are described by Lehn (1918, p. 351) in her 76 mm. specimen, and are said to be continuous, in a 55 mm. specimen, with the parachordal cartilages anterior to them. The processes are continuous posteriorly, as Lehn has stated, with a thin cartilaginous ring which surrounds the notochord, lying between its deeply staining outer layer and a concentric ring of bone that develops external to it. This thin ring of cartilage would seem to be similar to the one described by Schauinsland (1906, p. 444) in *Amia* and there called by him the skeletoblastic layer. Immediately posterior to this ring, there is a second pair of dorso-lateral cartilaginous processes, and they form the basal portions of the free occipital arches. Their bases break through the ring of bone concentric with the notochord and rest directly upon its outer, deeply staining layer. The third, and posterior, pair of occipital nerves, the second spinal nerves of Fürbringer's descriptions, perforate the membrane-bone portions of these arches.

Comparing the conditions above described in my 75 mm. larva with those described and figured by Budgett in his 30 mm. one, it is first to be remarked that the notochord, as shown in Budgett's fig. 4, Pl. 33, would seem to end considerably posterior to the otic capsules. Its mid-dorsal line is shown curving rapidly ventrally, and as Budgett says that the notochord tapers "suddenly...anteriorly...towards its termination," one naturally concludes that this tapering is here represented, and that it continues uninterruptedly to the anterior end of the chord. This is however not the case, for Budgett says that the tip of the notochord reaches the hind end of the membrane that closes the "very large fontanelle in the posterior end of which lies the hypophysis." The notochord must accordingly extend forward a considerable distance beyond the point where it is shown, in Budgett's figure, passing between the hind ends of the parachordal cartilages, and it must there run upward and forward at a considerable angle to the vertebral part of the chord. The post-

auditory portions of the parachordals also run dorso-anteriorly at a considerable angle to the auditory portions, thus leaving a marked depression in the mid-dorsal line between the hind ends of the otic capsules and the second neural arch of this larva. No such depression can be noticed in my transverse sections, and it is not shown in the median section of Lehn's specimen (1918, fig. 4).

The subaortic bridge of Budgett's descriptions is shown by him lying immediately posterior to the point where the notochord passes upward between the hind ends of the parachordals, and directly beneath the expanded base of the exoccipital cartilage of his descriptions. The nerve XI of his descriptions, my anterior occipital nerve, issues across the anterior edge of the exoccipital cartilage, the first spinal nerve of his descriptions, my second occipital, issuing across the posterior edge of that cartilage. The subaortic bridge of this 30 mm. larva must then be represented, in my 75 mm. larva, by the little ventrally projecting processes on the extreme hind ends of the parachordal cartilages, and as these little processes do not extend ventrally beyond the level of the dorsal surface of the aorta, the bridge of Budgett's larva must have undergone considerable resorption, the part so resorbed being replaced by membrane bone that forms part of the basioccipital. Anterior to this point, a similar resorption of cartilage, and its replacement by membrane bone, must also have taken place, for at no place does cartilage bound the entire lateral surface of the aorta.

Anterior to the bifurcation of the aorta, the parachordal cartilages of opposite sides are said by Budgett to fuse with each other beneath the notochord, this apparently being represented, in my larva, by the basal portion of the median subaortic process. From this point Budgett says that a narrow median plate of cartilage is sent forward as far as the tip of the notochord. There must then be an open space on either side of this median band, between it and the ventral edge of the otic capsule of its side. No such space exists in my larva, the cartilage of the basis cranii here being complete, and the tip of the notochord lies at a considerable distance (40 sections of 15μ thickness) posterior to the hind edge of the basicranial fontanelle.

The so-called exoccipital cartilage of Budgett's larva is evidently represented, in my larva, by the anterior dorso-lateral vertebral process, for these two cartilages have similar relations of the nerves. In Budgett's larva the so-called first lateral vertebral process is shown by him attached to the base of the exoccipital cartilage, and there is no corresponding so-called ventral vertebral process. The second lateral process of his larva lies postero-ventral to the base of the first free spinal neural arch, and there is a corresponding ventral process. In my larva the first dorsal rib is attached to the second dorso-lateral vertebral process, in relation to which the free occipital arch is developed, and there is no corresponding ventral rib. The second dorsal rib and the first ventral one are both attached to the first free vertebra. The anterior lateral and anterior ventral vertebral processes of Budgett's larva are

accordingly not represented by ribs in my larva, and must either have both disappeared or be represented, one or both, in the large ligament which, in the adult, extends from the ventral surface of the hind end of the basioccipital to the shoulder-girdle. This ligament is well developed in my 75 mm. larva, arising from the lateral surface of that portion of the basioccipital that forms the hind end of the aortic canal and there being continuous with the tough fibrous tissue that lies between the basioccipital and the parasphenoid.

The first free neural arch of Budgett's larva is thus the free occipital arch of the adult, and the related lateral vertebral process must have acquired connection with it by a continuation of the dorsal shifting of these lateral processes that is evident in Budgett's larva. Two vertebral centra and one neural arch have then fused with the hind end of the cranium during the ontogenetic development of this fish. In my 75 mm. larva the wholly enclosed portion of the aortic canal lies anterior to the anterior one of these two vertebrae, the posterior opening of the canal lying ventral to that vertebra and in a nearly horizontal position. In transverse sections through this opening, the processes of the basioccipital closely resemble the haemal processes shown by Budgett in sections through both the anterior and posterior portions of the body of his 90 mm. and 130 mm. specimens of this fish, and the raised, pad-like portions of the basioccipital which, both in my larva and in the adult, support the lateral margins of the parasphenoid, lie dorsal to these processes of the basioccipital and hence in the positions of the bases of the lateral vertebral processes.

Opisthotic. The opisthotic, so named by Traquair, was considered by him to represent both the opisthotic and epiotic of the Teleostei. It has both primary and membrane components and is a much more important bone than in any of the Holostei and Teleostei. It is of irregular shape, forms the dorso-postero-lateral corner of the chondrocranium, and has both external and internal surfaces, the latter forming a posterior portion of the labyrinth recess of the cranial cavity. Its dorsal surface is in articular contact with the ventral surface of the postero-lateral portion of the parieto-dermopterotic, the mesial portion of its posterior surface in contact with the internal surface of the ventro-posterior process of the same bone, and the stout posterior process of the parieto-dermopterotic projects posteriorly between these two articular surfaces. The anterior portion of the dorsal surface of the bone forms the floor of the posterior portion of the temporal groove, and the anterior edge of the bone here shows two directions of growth, one forward along the ridge that forms the lateral wall of the temporal groove and the other anteromesially across the hind end of that groove and along the outer surface of a slightly raised portion of the chondrocranium which marks the course of the posterior semicircular canal.

Postero-ventrally the opisthotic articulates with the external surface of the basi-exoccipital, a deep and rounded incisure in this edge of the bone forming the anterior boundary of the vagus foramen. The anterior edge of the

bone articulates, in its middle third, with the proötic portion of the ascending process of the parasphenoid, and there forms the posterior boundary of the foramen faciale. The dorsal and ventral thirds of this edge of the bone are both continuous with the cartilage of the chondrocranium, the ventral third being thin and covering the dorso-posterior portion of the small but pronounced swelling of the bulla acustica. This latter part of the bone is perforated, not far from its ventral edge and at the ventro-posterior edge of the bulla, by the foramen glossopharyngeum. A strongly developed opisthotic ridge extends dorso-posteriorly from the anterior edge of the bone to the hind end of its posterior process, and apparently corresponds to the crista facialis and crista parotica, combined, of mammals (Allis, 1920*a*). Dorsal to this ridge there is another, which forms the ventral boundary of the posterior portion of the articular facet for the hyomandibula, this ridge ending posteriorly in a slight process which apparently corresponds to the hind end of the pterotic ridge of the Holostei and Teleostei. Between this ridge and the opisthotic ridge there is a large and slightly concave surface which gives origin to the muscoli adductor hyomandibularis, adductor operculi, and levatores arcuum branchialium. The stout posterior process of the bone projects posteriorly in the line prolonged of this concave surface, and gives origin to a stout ligamentous formation which is in part inserted on the distal end of the ventro-anterior process, or so-called pedicel, of the suprascapula, and in part on the dorsal end of the supraclavicula. Ventral to the opisthotic ridge, between it and the bulla acustica, is the large jugular groove. Dorsal to the anterior portion of the opisthotic ridge the lateral surface of the opisthotic forms the ventral portion of the articular facet for the hyomandibula.

On the internal, or cerebral, surface of the opisthotic there are two recesses, a small ventro-posterior one which lodges the hind end of the sinus utriculi posterior, and a large dorso-anterior one which lies in the hollow of the curve of the hind end of the lateral semicircular canal. The lateral and posterior semicircular canals both traverse the bone, the bony canals being in communication with each other at the point where the lateral membranous canal passes internal to the posterior canal. The bone is also traversed by the dorsal, or supratemporal branch of the nervus glossopharyngeus, this nerve entering the bone immediately ventral to the opisthotic ridge and leaving it on its dorsal surface.

In my 75 mm. specimen the opisthotic is but slightly developed. The primary portion of the bone is represented by a thin layer of perichondrial bone which covers that projecting hind end of the otic capsule that lodges the vertically descending portion of the posterior semicircular canal. A few short laminae of bone, of membrane origin, project outward from this perichondrial bone into the surrounding tissues, and on its hind end there is a short posterior process, of membrane origin, which is imbedded in fibrous tissues which extend from there to the overlying dermal bones.

The opisthotic of *Polypterus* thus has the topographical position of the

opisthotic of other fishes, but it has a much greater extent than that bone has in any other recent fish I know of, having invaded the regions occupied, in those fishes, by the autopterotic, proötic, and epiotic. Pollard (1891) says of this bone that: "In brief the bone is not an opisthotic or intercalare of fish but corresponds to the 'Petrosum' of Urodeles." In a later work, he (1892) still calls this bone the Petrosum in his text, but refers to it in a figure given as the opisthotic. In *Wimania sinuosa*, one of the Coelacanthidae, it is an even larger and more important bone than in *Polypterus*, and it has been fully described and discussed by Stensiö (1921) both in that fish and in *Bergeria mougeoti*, one of the Palaeoniscidae, Stensiö considering it to be there formed by the fusion of the opisthotic and proötic of the Teleostei and calling it the proötico-opisthotic. Stensiö also discusses (1921, p. 156) the bone in *Polypterus*, but does not consider that it there contains the proötic.

There is no epiotic in this fish.

What I consider to represent the proötic will be discussed when describing the parasphenoid.

Postfronto-sphenotic. This bone was called by Traquair the postfrontal, and by Bridge and Pollard the sphenotic. It is said by Traquair to consist of two portions, "a posterior, yellowish and spongy-looking, placed like a little vertical plate projecting down from the posterior external angle of the frontal bone; and an anterior part, white and compact, flattened horizontally, and closely applied to the lower part of the frontal, along its external margin behind the orbit." All three of these authors show the bone in figures said to give dorsal views of the cranium with the dermal (investing) bones removed, the bone thus being considered, by all of them, to be a primary ossification.

In my adult specimens the bone is as shown by Traquair, but there is a distinctly evident line along its lateral surface, between the two components noted by Traquair, this line vanishing near the anterior edge of the bone beneath a projecting corner of its superficial component. That part of the bone that lies ventral to this line is of primary origin and represents the sphenotic bone of the Holostei and Teleostei, the part that lies dorsal to the line being of dermal origin and representing the postfrontal of those fishes. Anterior to the anterior end of the line separating these two components, the long anterior process of the bone is also partly of primary and partly of dermal origin, but there is no line of demarcation between the two components.

In my 75 mm. larva the supraorbital band of cartilage forms, as in Budgett's and Lehn's larvae, the entire lateral boundary of the large supraorbital fontanelle. In its posterior portion it is V-shaped in transverse section, as shown in Budgett's figure, the hollow of the V directed dorsally and lodging the anterior end of the otic portion of the main infraorbital latero-sensory canal, which here lies beneath the overhanging lateral edge of the frontal. Posterior to the base of the supraorbital band, the latero-sensory canal is roofed by the anterior end of the parieto-dermopterotic, short laminae of bone being sent down on either side of the canal, thus partly enclosing it. The

parieto-dermopterotic is here completely covered, externally, by the hind end of the lateral edge of the frontal. Immediately anterior to the parieto-dermopterotic, at the base of the supraorbital band, a layer of perichondrial bone has formed on the dorsal edge of the lateral arm of the V-shaped band. From this perichondrial layer, bony laminae, of membrane origin, are sent upward and give insertion, on their lateral surface, to the anterior edge of the musculus levator arcus palatini. These laminae belong to the dermal, or postfrontal component of the bone, and bound laterally the main infraorbital canal, that canal here lying on the dorsal surface of the supraorbital band and being roofed by the lateral edge of the frontal. Continuing forward, in the sections, the main infraorbital canal is soon joined by the hind end of the supraorbital canal (Allis, 1900*a*), and at this point a nerve perforates the supraorbital band and sends a branch to a sense organ that lies in the main infraorbital canal anterior to the point where it is joined by the supraorbital canal, the infraorbital canal here still lying on the dorsal surface of the supraorbital band and not yet being wholly enclosed in the postfrontal component of the postfronto-sphenotic. Continuing forward, the infraorbital canal leaves the dorsal surface of the supraorbital band and acquires a position along its ventrolateral edge, and it is now wholly enclosed in dermal bone which is continuous with the perichondrial layer developed in relation to the supraorbital band. The supraorbital canal here lies in the frontal, directly above the supraorbital fontanelle. From here forward the infraorbital canal always lies ventrolateral to the supraorbital band, enclosed in dermal bone that is continuous with the perichondrial layer enclosing that band, and the lateral edge of the frontal overlaps the band externally. The infraorbital canal then leaves the postfronto-sphenotic, to run downward posterior to the orbit, but the supraorbital band continues onward, lying beneath the frontal and without either dermal or perichondrial bone related to it. The two components of the postfronto-sphenotic are thus apparently completely fused with each other from their very inception, and not simply ankylosed in later stages of development.

In the adult *Polypterus* the sphenotic component of the postfronto-sphenotic has roughly the shape of a tetrahedron, the base of the tetrahedron directed dorsally and its posterior surface directed postero-mesially and everywhere in primary relation to the cartilage of the chondrocranium. The latter surface nowhere comes into direct relation to the labyrinth recess, but it lies dorso-anterior to the dorso-anterior portion of the anterior semicircular canal. The other two surfaces of the bone are directed the one antero-ventro-mesially and the other laterally, the angle that separates them being presented antero-ventrally and forming the dorso-posterior boundary of the orbital fossa. This edge of the bone is continued forward, as a slight rounded ridge, along the ventral surface of the anteriorly projecting portion of the bone, the latter portion of the bone lying along the lateral edge of the roof of that posterior part of the orbital fossa that is filled by the musculus adductor mandibulae, its anterior end reaching almost to the hind edge of the external opening of the

fossa. The dorsal surface of the bone is large, and has a slightly raised portion along its lateral edge, the deeper-lying portion of the surface lodging and giving support to both the frontal and the parieto-dermopterotic, the former bone occupying approximately the anterior three-quarters of the surface and the latter bone its posterior quarter. The raised and thickened lateral edge of the bone projects laterally slightly beyond the edges of the frontal and parieto-dermopterotic and forms part of the dorsal surface of the skull. Anterior to this raised edge, the bone is entirely covered by the frontal, the lateral edges of the two bones coinciding. The main infraorbital canal, coming up from its course beneath the orbit, enters the bone on its lateral edge at about the anterior quarter of its entire length, and issues from it on its dorsal surface slightly posterior to the middle of the length of that surface. At this point the compound tube 10 infraorbital-7 supraorbital is given off, this tube running antero-laterally, in a curved line, in a groove on the dorsal surface of the bone and issuing through a notch in the lateral edge of the frontal. From the point where this tube is given off, nearly to the hind edge of the bone, the infraorbital canal lies in a deep groove on its dorsal surface, roofed dorsally, in its anterior portion, by the frontal, and posteriorly by the antero-lateral corner of the parieto-dermopterotic, both of these bones resting on the dorsal surface of the postfronto-sphenotic on either side of the canal. In a specimen used in relation to my earlier work on this fish, I found the infraorbital canal enclosed in the postfronto-sphenotic for a short distance posterior to the infraorbital tube 10, a point of bone projecting mesially from the lateral edge of the groove that lodges the canal and fusing with the mesial edge of the groove, thus forming a narrow bridge across it.

Parasphenoid. The parasphenoid is a large and complex bone, and Traquair says that it has been considered to contain, in its anterior portion, the vomer, and in its ascending processes both the proötics and the alisphenoids. He himself concludes that it does not contain either of these three bones, and that it is strictly comparable to the parasphenoid of other fishes. The proötic is said by him to be wholly wanting.

The parasphenoid consists, as in the Holostei and Teleostei, of what may be called a body, and an ascending process on either side, but each ascending process encloses a large canal which, as stated in an earlier work (Allis, 1919*b*, p. 313), corresponds to the canalis parabasalis of the Teleostei. The mesial wall of this canal corresponds to the ascending process of the parasphenoid of *Amiurus*, and the ventral and lateral walls to the ascending process of *Amia* and *Scomber*, and as the process is triangular in transverse section, these three walls may be called the mesial, ventral and lateral plates of the process.

The body of the parasphenoid is a large flat horizontal plate which covers the larger part of the ventral surface of the chondrocranium, the ventral plate of each ascending process projecting laterally and slightly ventrally from it at about the posterior third of its length. Anterior to these processes the lateral edges of the bone converge slightly throughout the full length of

the orbital region, the lateral portions of the bone here forming the floor of the deeper portions of the orbits. Anterior to the orbits the bone widens slightly, and, lying upon the ventral surface of the ethmoidal cartilage, articulates with the hind ends of the palatal plates of the premaxillaries. The extreme anterior end of the bone varies in width in different specimens, and there may here be, on either side, bits of bone that have not yet fused with it. Posterior to the ascending processes, the body of the bone widens slightly to its hind end, and in that end there is a large V-shaped incisure which extends about half the length of this part of the bone. The posterior portion of the basi-exoccipital projects ventrally between the two arms of this incisure, the arms lying along the rounded lateral edges of the basi-exoccipital and extending posteriorly slightly beyond them, there appearing as short processes which project posteriorly along the lateral edges of the first vertebra.

Extending from close to the anterior end of the bone to the level of its ascending processes, there is a well-defined pad of minute thickly-set teeth. This pad has a large anterior end, with an evenly rounded anterior edge, and there occupies the full width of the parasphenoid, but it tapers rapidly and evenly from there to its hind end, where it forms a narrow median band which separates into two curved bands, one on either side, each band running latero-posteriorly along the ventral surface of the curved anterior edge of the ventral plate of the ascending process of its side, and extending nearly to the outer end of that plate. This pad has evidently been developed in relation to the teeth it bears, and the dermal bone so formed has apparently fused with an underlying bone of distinctly different, membrane origin. Between the lateral edges of these two parts of the bone there is a large and rounded groove which receives and gives movable articulation to the dorso-mesial edge of the entopterygoid.

On the dorsal surface of the body of the parasphenoid there is a large median groove, which extends its full length but is somewhat constricted in the pituitary region. At the middle of the length of the pituitary fossa there is a slight median pit, and in a specimen that had been long macerated the bone was here perforated, this thus probably indicating where the epidermal stalk of the hypophysis formerly passed. In the region of the aortic groove the bone is thin in the median line, and in the macerated specimen above referred to this part of it had disintegrated, leaving two long diverging hind ends to the bone. The anterior end of the space between these two ends lies beneath the point where the aortic canal separates into its diverging anterior ends, and hence represents the point where the subaortic process is found in the 75 mm. specimen. For a short distance anterior to this point the parasphenoid is considerably thickened on either side, and this thickened portion is traversed by a deep groove which lodges the basal portion of the related lateral dorsal aorta, the anterior edge of the groove arching posteriorly and forming a partial roof to the groove. This groove runs antero-laterally and opens into the posterior portion of the large canal through the ascending process of the bone.

From near the postero-mesial end of the groove, a small groove leads postero-laterally and opens on the lateral edge of the bone. Anterior to the ascending processes of the bone, each lateral edge of the median groove on its dorsal surface forms a thin ridge which articulates, in its anterior portion with the ectethmoid, and posteriorly with the ventral edge of the sphenoid. At its hind end this ridge curves postero-laterally and is continuous with the anterior edge of the mesial plate of the ascending process of the bone, a large and rounded notch in the latter edge forming the ventral boundary of the anterior opening of a canal in the chondrocranium which I have called, in earlier works, the facialis portion of a trigemino-facialis chamber, but which is more properly called the jugular canal.

The ventral plate of the ascending process of the parasphenoid is triangular in shape, with a convex anterior edge and a concave posterior one. The anterior portion of the anterior edge of the plate is attached by tough connective tissues to the dorsal surface of the dorso-mesial border of the entopterygoid, and it and the lateral edge of the body of the bone anterior to it form the mesial wall and roof of a groove in the dorsal surface of the buccal cavity which leads posteriorly into the oral opening of the spiracular canal, the posterior portion of the edge of the process forming the mesial boundary of the latter opening. The lateral plate of the ascending process rises from the dorsal surface of the anterior edge of the ventral plate, and, projecting dorso-mesially, abuts against and fuses with the external surface of the mesial plate of the process. The mesial plate lies directly upon the cartilage of the chondrocranium, and, in the 75 mm. specimen, is much wider at its base than at its dorsal end, the latter end extending upward along the external surface of the outer wall of the jugular canal and being but slightly wider than it, its hind edge projecting posteriorly slightly beyond the opening of the canal. In the adult this plate still lies along the outer surface of the cartilage that encloses the jugular canal, and, after its fusion with the lateral plate, extends upward until it nearly reaches the ventral edge of the sphenotic portion of the postfronto-sphenotic, the two bones there being separated by a narrow band of cartilage with which they both, apparently, have similar primary relations. In the ventral portion of the hind edge of the plate there is a large incisure, which embraces the anterior edge of the bulla acustica, and anterior to this incisure, or confluent with it, the plate is perforated by a foramen which bounds the anterior opening of the lateral aortic canal of its side. On the mesial surface of the posterior half or two-thirds of the plate, along the line where it fuses with the lateral plate, two flanges of bone have developed, one projecting dorso-mesially along the ventro-mesial surface of the posterior half of the jugular canal and the other dorso-mesially along its lateral and dorsal surfaces, the two flanges arching toward each other and nearly enclosing this portion of the canal (fig. 15). The hind end of each of these flanges projects posteriorly and overlaps externally, and articulates with, the anterior edge of the opisthotic, thus forming the lateral boundary of the foramen faciale. The mesial surface of the

ventro-mesial flange, and the dorsal and lateral surfaces of the dorso-mesial flange, are both in direct contact with the cartilage of the cranial wall, and between the dorso-mesial flange and the dorsal portion of the entire ascending process there is a thick mass of cartilage, that portion of this cartilage that lies anterior to the two flanges being traversed by the anterior portion of the jugular canal. No layer of connective tissue could anywhere be distinguished between these several parts of the bone and the cartilage upon which they lie,

The ascending process of the parasphenoid of the adult *Polypterus* thus differs greatly from that of the 75 mm. specimen. In the latter specimen all parts of the process are definitely of either membrane or dermal origin, whichever it may be, for the mesial plate of the process is everywhere separated from the cartilage of the chondrocranium by connective tissue, and the ventral and lateral plates have no relations to the cartilage, lying, respectively, internal to the lining membrane of the buccal cavity and to that of the spiracular canal. In the adult, the mesial plate has apparently, in places, acquired primary relations to the cartilage, and the flanges that partly enclose the jugular canal replace, if they do not actually represent the proötic of other fishes, and they probably represent the small and independent bone which both van Wijhe (1882, p. 257) and Stensiö (1921, p. 157) find in this region and which they consider to be a proötic. No part of the bone would seem to contain any part of the alisphenoid.

The canal through the ascending process of the parasphenoid transmits the common carotid artery, a lymph vessel, pharyngeal branches of the *nervi glossopharyngeus* and *vagus* and a sympathetic nerve, and the *ramus palatinus facialis*, after issuing from the jugular canal, runs antero-ventrally across its anterior opening. The canal is thus not the strict homologue of the *canalis parabasalis* of *Amia* and the *Teleostei*, but it certainly represents a part of that canal. The dorsal ends of the efferent arteries of the external hyal gill and the first branchial arch enter the posterior portion of the canal and there fall into the lateral dorsal aorta. The dorsal end of the pharyngo-branchial of the first branchial arch enters the hind end of the angle between the lateral and ventral plates of the process, and is there strongly attached by fibrous tissues; and the pointed posterior corner of this angle gives attachment to a stout ligament which runs posteriorly and is inserted on the dorsal end of the first *ceratobranchial*. The *bulla acustica* projects laterally beyond the level of the external opening of the aortic canal, and there closely approaches, and in certain cases touches, the dorsal surface of the parasphenoid, enclosing, in the latter case, a canal between the otic capsule and the parasphenoid. No vessel or nerve was found traversing this canal in the adult, but it is possible that it may be traversed by small arteries related to the thymus. What I consider to be the *suprapharyngeal process* of the *epibranchial* of the first branchial arch articulates with the dorsal surface of the *bulla*, this branchial cartilage being called by Lehn (1918, p. 365) the "*Pharyngobranchiale inferius*."

The jugular canal is a canal through the cartilaginous postorbital process

which transmits the jugular vein and also a general sensory branch of the nervus trigeminus which joins the truncus hyomandibularis facialis. The primary foramen of the nervus facialis opens into this canal near its hind end, and there may be, anterior to this foramen, an independent foramen for the ramus palatinus facialis. The ramus hyomandibularis issues from the canal through its hind end, the ramus palatinus through its anterior end. The canal thus lies approximately between the primary foramina of the trigeminus and facialis nerves, and hence corresponds to the posttrigeminus portion of some part of the trigemino-facialis chamber of other fishes, and probably to some part of the pars jugularis only of that chamber. The trigeminus part of the chamber lies immediately anterior to this canal, in a recess in the cranial wall that lies beneath the anterior end of the anterior semicircular canal and opens directly into the hind end of the orbital fossa, the posterior portion of the recess being closed externally by the anterior edge of the ascending process of the parasphenoid. The conditions here thus closely agree with those described by Stensiö (1921, p. 177) in *Bergeria mougeoti*—but somewhat differently interpreted by him (see Allis, 1922)—excepting in that the ascending process of the parasphenoid of *Bergeria* consists of but a single plate of bone, and hence corresponds either to the mesial plate alone of the process of *Polypterus*, or to the three plates fused so as to appear as a single one. The trigeminus chamber and the jugular canal are both described by Lehn in her 76 mm. specimen, and I, still earlier, described them in a work relating to the arteries of this fish (Allis, 1908*b*).

Sphenoid. The sphenoid bone of *Polypterus* was so named by Traquair, and was considered by him to be a median bone which occupied the space filled, in the teleostean skull, by the bones called by Huxley the orbitosphenoids, the postsphenoids, and the wings of the latter bones. The bone was said to consist of two vertical laminae connected with each other, posteriorly, by a narrow horizontal plate which formed part of the floor of the cranial cavity. Bridge accepted for this bone the name given to it by Traquair, but Pollard called it the orbitosphenoid. As it certainly contains more than the latter bone, I retain the name given by Traquair.

The internal surface of each vertical lamina of the bone is slightly concave, its outer surface slightly convex. The dorsal edge of the lamina flares slightly (fig. 10), and articulates by dentated suture with the ventral edge of a longitudinal ridge on the ventral surface of the frontal, this latter ridge beginning at the posterior end of the frontal and extending forward, along its mesial third or quarter, nearly its full length. At about the middle of its length this ridge gives off a mesial branch which extends forward a short distance and then curves abruptly to the mesial edge of the bone. When the dorsal edge of the sphenoid reaches the point where this ridge is given off, it expands both laterally and mesially, the lateral portion extending forward but a short distance and there ending abruptly with a straight transverse edge, while the mesial portion curves mesially, widens antero-posteriorly, and, after completely

encircling the nervus olfactorius, meets in the median line its fellow of the opposite side, the two laminae, one on either side of the head, here suturing with each other their full heights. The anterior end of the dorsal edge of each lamina, as seen in the prepared skull, lies on a level with, and is continuous with, the cartilage of the chondrocranium, but ventral to this visible edge the bone continues onward, beneath the cartilage, in an antero-lateral direction, and articulates by suture, at its anterior end and lateral to the canalis olfactorius, with the hind end of the ectethmoid (prefrontal, Traquair). The anterior surface of the bone is everywhere bounded by cartilage, excepting only where it articulates with the ectethmoid.

The surface by which each vertical lamina of the bone articulates, anteriorly, with its fellow of the opposite side is somewhat V-shaped, the V placed horizontally, with its point directed forward (fig. 11). The ventral arm of this V is longer than the dorsal one, and extends to the transverse plane of the foramen opticum, where it curves ventrally and ends in a straight horizontal edge which rests upon the dorsal surface of the parasphenoid. The articulation of the two laminae with each other forms a narrow median wall which lies between the nervi olfactorii and forms the anterior boundary of the median portion of the cranial cavity. Immediately lateral to both the dorsal and ventral arms of this V-shaped median wall, the cerebral surface of each lamina of the bone is slightly hollowed out, this hollow lodging the lobus olfactorius and leading forward to the canalis olfactorius. The floor of this hollow lies above the level of the floor of the pituitary fossa, in the level of the floor of the postpituitary portion of the cranial cavity, and the hind edge of the floor forms, with its fellow of the opposite side, the anterior wall of the pituitary fossa, this raised portion of the cranial floor thus being the homologue of the presphenoid bolster of Gegenbaur's (1872) descriptions of the Selachii.

The ventral edge of each vertical lamina flares somewhat, as its dorsal edge does, but this edge is grooved to form an inverted V, the mesial arm of which is considerably longer than the lateral arm. The hollow of this V rests upon the longitudinal ridge that forms the lateral boundary of the median groove on the dorsal surface of the parasphenoid, the long mesial arm of the V everywhere reaching and resting upon the dorsal surface of that bone, but its external arm not everywhere reaching that surface, the lateral surface of the ridge on the parasphenoid forming, in places, a ventral portion of the mesial wall of the orbital fossa. The lateral arm of the V extends forward to the anterior end of the bone. The mesial arm is abruptly tenoned in the transverse plane of the external opening of the foramen opticum, the V in the ventral edge of the bone anterior to this point being much larger and deeper than it is posterior to it.

The hind edge of each vertical lamina is nearly vertical, inclining slightly anteriorly, and it is everywhere continuous with the cartilage of the chondrocranium excepting at its ventro-posterior corner, where it articulates with the

anterior edge of the mesial plate of the ascending process of the parasphenoid. In this hind edge of the lamina there are two rounded incisures, the dorsal one of which may become entirely enclosed in the bone. The dorsal incisure forms the anterior margin of a foramen which transmits a meningeal vein coming from the dorsal surface of the brain. The ventral incisure forms the anterior margin of the foramen trigeminum, this foramen opening in the cranial cavity dorsal to the proötic bridge (postclinoid wall), slightly anterior to the middle of its width, and being frequently almost entirely, but never entirely, enclosed in the bone. This foramen lies immediately anterior to the anterior wall of the labyrinth recess, and there is here a slight recess on the cerebral surface of the sphenoid. Dorso-posterior to this foramen, the foramen ophthalmicum perforates the cartilage that lies between the sphenoid and the postfronto-sphenotic, and enters the anterior end of the labyrinth recess. From the latter foramen a groove runs dorso-anteriorly along the external surface of the orbital wall, between the sphenoid anteriorly and the postfronto-sphenotic posteriorly, and lodges the ramus ophthalmicus superficialis trigemini, that nerve giving off, while in the groove, the ramus oticus, which pierces the overhanging end of the otic capsule, traverses the canal for the anterior semicircular canal of the ear, and then again perforates the cartilage to issue on the roof of the chondrocranium. Immediately ventral to the ventral edge of the foramen trigeminum, there is a more or less pronounced and rounded notch on the outer surface of the hind edge of the sphenoid, and the nervus abducens, coming from the orbit, traverses this notch and enters a relatively long canal in the cartilage, this canal opening on the floor of the cranial cavity immediately posterior to the base of the postclinoid wall. Anterior to the foramen trigeminum, and in line with it, the sphenoid is perforated by a foramen which transmits the nervi oculomotorius and ophthalmicus profundus, and in a line running dorso-anteriorly from this foramen there are two foramina, the ventral one transmitting the nervus trochlearis and the dorsal one a second meningeal vein from the dorsal surface of the brain. Postero-ventral to the foramen profundo-oculomotorium is the foramen for the pituitary vein, this foramen lying near the ventral edge of the sphenoid and entering the cranial cavity slightly anterior to the anterior edge of the postclinoid wall. In the specimen that was macerated this foramen could not be found on either side of the head. These several foramina were all described in an earlier work (Allis, 1908*b*), and Lehn (1918) describes them in her 76 mm. specimen.

Slightly anterior to the middle of the orbital fossa, at the hind edge of that part of the fossa that is occupied by the eyeball, there is a large notch in the ventral edge of each vertical lamina of the sphenoid. This notch is imperfectly divided into anterior and posterior portions, and it lies beneath a slight swelling on the external surface of the sphenoid. From this notch a canal leads inward in the bone and opens on its cerebral surface dorsal to the hind edge of the presphenoid bolster. This canal transmits the nervus opticus

and the internal carotid artery, and a groove on the internal surface of the sphenoid leads posteriorly from it and marks the further course of the nervus opticus. On both sides of the head of the macerated specimen, a small canal perforated the mesial wall of this canal for the nervus opticus and opened on the internal surface of the sphenoid immediately anterior to the opening of the main canal, this small canal doubtless being traversed by one of the two divisions of the internal carotid. This little canal did not exist in the specimen used for the figures.

Anterior to the anterior end of that portion of each vertical lamina of the sphenoid that lies lateral to the canalis olfactorius, there are, on each side of the head of the specimen used for illustration, two little plates of bone which lie between the sphenoid and the ectethmoid, and there is nothing to definitely show to which one of these two bones they belong. Traquair shows them forming part of the ectethmoid (prefrontal, Traquair), and, following him, I have already referred to the dorsal one of the two as forming part of the ectethmoid. Both plates will accordingly be considered when describing the latter bone.

The hind ends of the two vertical laminae of the sphenoid are connected by the horizontal plate described by both Traquair and Bridge, this plate forming the postclinoid wall and corresponding to the proötic bridge of the *Holostei* and *Teleostei*. The dorsal surface of this bridge inclines slightly postero-ventrally, and its ventral surface still more so, the bridge being thicker at its posterior than at its anterior end. Its anterior edge is concave and its posterior edge convex, as Bridge has stated, the hind edge of the bridge projecting posteriorly beyond the hind edges of the vertical laminae of the bone and there being everywhere bounded by cartilage. The hind ends of the vertical laminae are not in contact with each other beneath this bridge, being there separated from each other by cartilage that forms the posterior boundary of the basicranial fontanelle. This fontanelle is large, extends the full length of the pituitary fossa, and corresponds to the fenestra ventralis myodomi of *Amia*.

In my 75 mm. larva the non-cartilaginous portion of the orbital wall has practically the extent that is shown in Budgett's figure of his 30 mm. larva, extending from near the hind edge of the nasal capsule to a certain distance posterior to the foramen opticum. In Budgett's specimen this portion of the wall was wholly membranous. In my specimen, the posterior and larger portion of this membranous wall has already undergone ossification as membrane bone, and where this membrane bone adjoins the surrounding cartilage, the cartilage is breaking down preparatory to being replaced by bone. There is nowhere any indication either of calcification or of direct ossification of the cartilage. The proötic bridge is, in this larva, a narrow transverse bridge of cartilage which extends the full length of the nervous portion of the pituitary body but does not cover its glandular portion, that portion of the organ being separated from the cranial cavity by membrane only. The conditions in this larva are thus here similar to those in embryos of

Amia, *Lepidosteus* and certain of the *Teleostei* (Allis, 1919*b*). The glandular portion of the pituitary body extends to the hind end of the basicranial fontanelle, this hind end lying considerably anterior to the tip of the notochord. In Budgett's 30 mm. larva the fontanelle extended to the tip of the notochord, and the proötic bridge was wholly of membrane. In Budgett's 90 mm. specimen this bridge had become entirely chondrified, and he says that in this specimen the tubules of the glandular portion of the hypophysis are still in communication, by a duct, with the cavity of the mouth. No indication of such a duct was found in my 75 mm. larva, but there is, in the adult, as already stated, a median depression on the dorsal surface of the parasphenoid slightly anterior to the anterior edge of the proötic bridge which doubtless represents the place where the duct has disappeared. Lehn describes (1918, p. 364) this duct in her 76 mm. specimen.

The so-called sphenoid of this fish thus occupies approximately the region of the orbitosphenoids, alisphenoids and median basisphenoid of the *Ganoidei* and *Teleostei*, and in addition forms the proötic bridge, which in the *Ganoidei* and *Teleostei* is usually (always?) formed by processes of the proötics. What seems to be a strictly similar bone is found in *Bergeria mougeoti* (Stensiö, 1921), one of the *Palaeoniscidae*, but, singularly enough, is not found in the *Coelacanthidae*, which are supposed to be much more closely allied to *Polypterus*. In the *Coelacanthidae* the proötic bridge is formed by what were formerly considered to be the paired proötics but which Stensiö considers to be a median basisphenoid comparable to that bone of higher vertebrates and hence in no way comparable to the similarly named bone of the *Teleostei*. *Polypterus* further resembles the *Palaeoniscidae*, and differs from the *Coelacanthidae*, in that its parasphenoid has well-developed ascending processes which lie external to a trigeminus chamber and jugular canal.

Ectethmoid. The ectethmoid (prefrontal, Traquair) is, in the specimen used for illustration, formed by a large and irregular bone which forms the anterior wall of the orbital fossa, and two smaller bones which lie posterior to it. In Traquair's specimen these three bones were apparently fused to form a single bone. The larger bone forms part of the lateral wall of the nasal cavity, and its dorsal surface forms part of the dorsal surface of the primordial cranium, but as the dorso-posterior end of the antorbital process of the premaxillary rests upon it and conceals it, it is not seen in the accompanying fig. 10. The dorsal one of the two smaller bones also forms part of the dorsal surface of the primordial cranium, there lying directly posterior to the larger bone and posterior also to the antorbital process of the premaxillary. Between this small bone and the larger one the preorbital canal leads from the dorso-anterior end of the orbital fossa into the hind end of a short groove on the dorsal surface of the nasal capsule along the mesial edge of the antorbital process of the premaxillary, this groove lodging the ramus ophthalmicus superficialis trigemini, the ramus ophthalmicus profundus, and an accompanying vein and artery. Between the ventral one of the two smaller bones and the ventro-

anterior corner of the vertical lamina of the sphenoid dorsally, and the parasphenoid ventrally, there is the external opening of a small canal which leads into the canalis olfactorius as it leaves the sphenoid bone to enter the nasal capsule, this canal transmitting the terminal portion of the orbito-nasal artery. The ventral surfaces of the ectethmoid and the ventral one of the two smaller bones are covered by cartilage, these bones thus not being exposed on the ventral surface of the chondrocranium. Along the orbital edge of this covering cartilage there is a groove which is continuous with the groove along the lateral edge of the parasphenoid and gives articulation to the articular surface on the anterior edge of the autopalatine.

Visceral arches. There are in *Polypterus* a mandibular, a hyal, and four branchial arches, and they have been figured and described, in all or in part, by Agassiz (1833-43), Müller (1846), Traquair (1871), van Wijhe (1882) and Pollard (1892). Budgett (1902) has described these arches in a 30 mm. embryo, and I have described the maxillary and premaxillary bones and the labial cartilages in the adult (Allis, 1900*b*, 1919*c*).

Basal line. There is but one piece in the basal line of this fish, the basi-branchial of van Wijhe's (1882) descriptions. It is relatively large, and has a flat dorsal and a somewhat concave and irregular ventral surface (figs. 16-19). Its posterior quarter, approximately, is of cartilage and gives articulation to the third and fourth branchial arches. The remainder of the element has become entirely ossified excepting at its anterior end, where it gives articulation to the hyal arch, and at two points on each lateral edge, where it gives articulation to the first and second branchial arches.

The articular facets for the hyal arches occupy the entire anterior end of the element, excepting a narrow median line which separates them. They are oval in shape, the long axis of each facet directed dorso-anteriorly, and they give articulation, through the intermediation of a pad of tough connective tissue, to the hypohyals. The basibranchial is considerably thickened, dorso-ventrally, in the planes of the long axes of these facets, and it is similarly, but less pronouncedly thickened in relation to the articular facets for the second and third branchial arches. Ridges on the ventral surface of the bone run from each of these thickened points toward the middle portion of its anterior third, and there vanish, the ventral surface of the bone thus being concave both longitudinally and transversely. Between the ridges of opposite sides there is a longitudinal groove, which is relatively deep both anteriorly and posteriorly but vanishes in the middle of the length of the bone. Lateral to the ridges of either side, the lateral edge of the bone is much thinner than in its middle portion, and the articular cap for the first branchial arch lies on this thin lateral edge, between the caps for the hyal and second branchial arches; the cap having a shallow facet which is presented laterally and slightly antero-ventrally and gives articulation to the postero-mesial corner of the first hypobranchial. In the specimen used for illustration, this cap was connected with the cap for the hypohyal by a narrow line of cartilage along the

lateral edge of the element. The articular cap for the second branchial arch lies at about the middle of the length of the element, extends from the dorsal to the ventral surface of the element, is slightly 8-shaped, and the facet on its outer surface is presented postero-laterally and gives articulation to the distal end of the second hypobranchial. The posterior, cartilaginous portion of the element is twice as broad and thick in its anterior portion as in its posterior, and is concave transversely on its ventral surface. On either side of its hind end it gives articulation to the fourth ceratobranchial, and on either side of its thickened anterior portion there are two articular facets, separated by a slight groove, which gives articulation to the two articular ends at the distal end of the third hypobranchial.

Branchial arches (figs. 16-21). The hypobranchial of the first branchial arch is, roughly speaking, a thick flat semicircular plate with a stout process arising from the straight edge that forms the diameter of the semicircle, and it is shown in dorsal and ventral views in figs. 20-21. The straight edge forms the distal edge of the element, and the postero-mesial half of the curved edge articulates in part with the ceratobranchial of its arch and in part with the related articular facet on the basibranchial. The process of the element arises from the ventral edge of its straight distal edge, and the ossification of the entire element has apparently proceeded from this point as a centre, semicircular plates of perichondrial bone developing on both sides of the element and giving to it its semicircular appearance. The process is capped with cartilage and strongly attached by ligamentous tissues to the edge of the pad of connective tissue that lies between the articulating surfaces of the hypohyal and basibranchial.

The second hypobranchial has enlarged distal and proximal ends, the longer axes of these ends lying at right angles to each other. The anterior end of the element articulates with the 8-shaped articular facet at the middle of the length of the basibranchial, its posterior end articulating with the ceratobranchial of the arch.

The third hypobranchial resembles the second one in general shape, but has two articular heads on its distal end, these two heads corresponding to the two parts of the 8-shaped articular head of the second hypobranchial, and articulating with the two articular facets at the anterior end of the posterior, cartilaginous portion of the basibranchial.

There is no fourth hypobranchial, as van Wijhe has stated, but the distal portion of the ceratobranchial of this arch forms, in general appearance, a serial continuation of the preceding hypobranchials.

The first ceratobranchial is a stout, strongly curved and flattened bone, capped at each end with articular cartilage. Its distal end lies in a nearly horizontal position, and articulates with the hypobranchial of the arch. Its ventro-lateral (external) edge is not grooved in my large specimens, but is grooved in the 30 cm. ones, and on either side of this edge of the bone there is a row of branchial rays which are wholly of cartilage in my 75 mm. speci-

men, but partly calcified in the adult. The bases of these branchial rays tend to fuse with each other, as shown in fig. 22, and the presence of a double row of rays in this fish, and of but a single row in the Selachii, suggests that the extrabranchials of the latter fishes have been derived either from the basal portions of the anterior row of branchial rays, or from those dorsal and ventral rays of the posterior row that were primarily related to the pharyngeal and hyal elements of the arch. This was explained in a recent work (Allis, 1918c, p. 264), but by typographical error a part of the sentence was omitted.

The second ceratobranchial is only about two-thirds as long as the first one, and is less strongly curved. The outer surface of the curve is presented ventrally and is deeply grooved throughout the larger part of its length, the groove lying postero-mesial to an angular process on the antero-lateral edge of the bone, near its distal end. This process is capped with cartilage, and is related to the surface of insertion of the *musculus interarcualis ventralis* of its arch. The groove on the ventral (external) edge of the bone lodges the afferent artery of the arch.

The third ceratobranchial has much the shape of the second one, but is somewhat shorter and more slender, and the ventro-anteriorly directed process near its distal end is less strongly developed.

The fourth ceratobranchial has strikingly the appearance of being formed by a ceratobranchial and hypobranchial which have not been separated from each other by transverse segmentation. There is no process, capped with cartilage, near the distal end of the ceratobranchial part of the bone, but there is, at that point, a rounded angle on the anterior edge of the bone. Both ends of the bone are capped with cartilage, the distal end articulating with the facet on the hind end of the cartilaginous portion of the basibranchial, and the proximal end articulating, by its anterior corner, with the posterior corner of the cartilaginous cap on the proximal end of the third ceratobranchial. The ceratobranchial part of the bone is grooved on its external edge, exactly as the other ceratobranchials are, but in order to reach this groove the afferent artery of the arch runs postero-laterally across the dorsal surface of the bone, in a groove on that surface, and then turns upward across the posterior surface of the bone, passing through a large opening between it and a series of dermal toothed plates which have fused with it, along the posterior edge of its dorsal surface. The probable explanation of this twisting of the artery around the ceratobranchial is given on a later page.

The epibranchial of the first arch is the bone called by both van Wijhe and Pollard (1891) the *suprapharyngobranchial* of that arch. Both ends of the element are capped with cartilage, the cap on the distal end being large and articulating by one corner with the proximal end of the ceratobranchial of the arch, and by the other with the so-called *infrapharyngobranchial* of the arch. An independent bit of cartilage interposed between the epibranchial and ceratobranchial, such as is shown by van Wijhe in his figure and called by him the *epibranchial* of the arch, was found in certain of the adult specimens

but not in others. In the 75 mm. specimen there is here a little process of the epibranchial, and it is probable that the head of this process sometimes becomes detached, and is found as an independent piece.

The large cartilaginous cap on the distal end of the epibranchial quite unquestionably represents the primitive element, the ossified portion being a process on its postero-mesial edge which corresponds to the suprpharyngobranchial process of the epibranchial of the first branchial arch of *Amia* (Allis, 1897). This process of the epibranchial of *Polypterus* forms the principal portion of the element, and it articulates, by its proximal end, with the bulla acustica, there lying in normal position ventral to the vena jugularis. The so-called infrapharyngobranchial is quite certainly simply the pharyngeal element of the arch and is, in the adult, a slender rod of bone which is frequently immovably ankylosed with the epibranchial and apparently has primary relations to the proximal corner of the cartilage that caps that bone and which I consider to represent the primary epibranchial. Between it and the epibranchial, on the external surface of the arch, there is a deep groove, which lies wholly on the epibranchial and lodges the efferent artery of the arch. In the 75 mm. larva, the pharyngobranchial is a slender and wholly independent rod of cartilage which articulates movably with the epibranchial. It lies imbedded in the lateral surface of the thymus, its anterior end extending into the hind end of the angle between the lateral and horizontal plates of the ascending process of the parasphenoid, and there being attached by fibrous tissues. A stout ligament has its origin on the point of that angle, and running postero-laterally, parallel to and slightly ventral to the pharyngobranchial, is inserted on the dorsal end of the ceratobranchial of the arch. In the middle of its length this ligament is, for a short distance, wholly muscular, thus apparently corresponding to that interarcualis dorsalis muscle of the *Selachii* that extends between the first branchial and hyal arches. The levator muscle of the arch is inserted mostly on the pharyngobranchial, but partly also on adjacent portions of the epibranchial. Comparison of these two elements of this arch of *Polypterus* with the similarly named elements of the arch in *Amia* (Allis, 1897), would seem to leave no possible doubt as to their being respectively homologous, the posterior corner of the proximal end of the epibranchial of *Amia* having, in *Polypterus*, acquired articulation with the cranial wall instead of with the proximal end of the infrapharyngobranchial of the second branchial arch.

In the second and third branchial arches of *Polypterus* the epibranchial and pharyngobranchial have fused with each other and are usually both wholly of cartilage. The part that corresponds, in position and in its relations to the efferent artery of the arch, to the epibranchial of the first arch is greatly reduced in length, and its dorso-anterior and dorso-posterior edges have arched toward each other dorsal to the efferent artery of the arch and fused, so forming a short canal through which the efferent artery passes. The pharyngobranchials of these two arches are directed antero-mesially, approximately parallel to

the bony process on the epibranchial of the first branchial arch, and not, as van Wijhe says, posteriorly. In the specimen used for illustration the pharyngobranchial of the second arch had undergone partial ossification.

In the fourth arch there is neither epibranchial nor pharyngobranchial, the anterior corner of the cap of cartilage on the proximal end of the ceratobranchial simply forming a slight process which articulates with the proximal end of the third ceratobranchial.

The branchial arches of this fish are thus strictly comparable to those in *Amia*. In both fishes the so-called infrapharyngobranchials are simply pharyngobranchials, and there are no independent suprapharyngobranchials in either fish.

The cartilaginous branchial rays (fig. 22) have been referred to in an earlier work (Allis, 1918c), and the probable significance of the dorsal ends of the rods formed by the fusion of their bases there considered.

Hyal arch. The hyal arch of *Polypterus* consists, as currently described, of a hypohyal, ceratohyal, interhyal, and hyomandibula. The symplectic is always said to be wanting. The so-called accessory hyomandibula of certain descriptions was considered by van Wijhe, and since him by other authors, to be one of the series of spiracular ossicles that has become secondarily attached to the hyomandibula.

The hypohyal is a disk-shaped piece, the antero-mesial surface of which is slightly convex and the postero-lateral surface slightly concave. It lies in a nearly vertical plane and its distal edge, which is directed postero-mesially, articulates with the facet on its side of the anterior end of the basibranchial. On its ventral edge, and the postero-lateral surface of that edge, the deeper part of the stout tendon of the musculus sternohyoideus has its insertion, and ossification of the element takes place from the point of attachment of this tendon as a centre, perichondrial plates of bone developing on both surfaces of the element and advancing toward its dorsal edge, the latter edge remaining cartilaginous even in my adult specimens. The superficial portion of the tendon of the sternohyoideus runs forward across the ventral edge of the basihyal and becomes a tough ligamentous formation which envelops the distal end of the ceratohyal, and attached to this ligamentous formation there is a little circular pad of tough tissue which lies between the antero-lateral edge of the hypohyal and the mesial corner of the distal end of the ceratohyal and forms an articular pad between the articulating surfaces of the two elements.

The ceratohyal is a stout flat slightly curved bone with a large distal end, triangular in cross section, and a flat and expanded proximal end which has a long and convex edge. The proximal end of the bone lies in a nearly horizontal position, immediately mesial to and in the horizontal plane of the ventral edge of the hind end of the mandible, but not extending quite to the hind end of that bone. The anterior end of the bone curves slightly dorsally, the ventral surface of the bone thus being slightly convex longitudinally.

Both ends of the bone are capped with cartilage in my small specimens, but in the larger ones ossification tends to extend over the middle portion of the long convex proximal edge of the bone, cartilage persisting only at either end of the edge. The mesial portion of the proximal edge of the bone is covered by a tough pad of fibrous tissue which extends laterally and envelops the distal end of the interhyal of current descriptions, a bone which must represent either the epihyal alone, or both that element and the pharyngohyal (Allis, 1918c), and which I shall hereafter call the epihyal. This tissue binds these two bones firmly, but flexibly, together, and certain ligaments have their origins or insertions in it. One of these ligaments is a short one which extends to the internal surface of the gular plate. Another is a relatively narrow band which arises from the ventral portion of the hind edge of the dentary and from the dermarticlar immediately posterior to it, and from there runs posteriorly across the ventral surface of the pad on the proximal end of the ceratohyal, there being strongly attached to it. It then turns proximally (here laterally) along the dorsal (internal) surface of the epihyal, and running along that bone, strongly attached to it, reaches and is inserted on the internal surface of the hyomandibula. Beneath (internal to) this ligament is a wider and stouter one which arises from the ventral surface of the dermarticlar and running postero-mesially separates into two parts, the mesial one of which is inserted in the pad of fibrous tissue on the proximal end of the ceratohyal, while the lateral one turns dorso-mesially over the lateral portion of the proximal end of the ceratohyal, is there strongly attached to it, and then continues onward and is inserted on the internal surface of the metapterygoid. Beneath this ligament, the hind edge of the fold of epithelial tissue that lies between the floor of the buccal cavity and the ventral surface of the tongue of the fish, is attached, by connective tissue, to the proximal end of the ceratohyal. Beneath the deeper one of the two ligaments above described, and as a part of it, a stout ligament arises from the ventral surface of the articular, and, turning dorsally over its hind edge, is in part inserted on the internal surface of the mandible, but in part continues upward as a short stout ligament which has its insertion on an angular ridge on the internal surface of the quadrate. This ligament and the one inserted on the internal surface of the metapterygoid both pass between the external and internal branches of the ramus mandibularis facialis.

The epihyal is, as shown in figs. 50-52, a small and somewhat cylindrical bone, both ends of which are capped with cartilage. It lies, when the mouth is closed, in a nearly horizontal position, directed postero-laterally and slightly dorsally immediately posterior to the hind end of the mandible. The distal end of the element articulates with the lateral portion of the proximal end of the ceratohyal, and slightly proximal to this articular end of the epihyal there is, on its hind edge, a slight process which gives attachment to the ligamentous formation that binds the two elements together. The summit of this process was of cartilage in one specimen, this seeming to indicate that this process and the actual articular end of the bone together form its distal

end, and that this entire end articulated with the ceratohyal before the two elements acquired the inclined relations to each other that they actually have. The proximal end of the element articulates with the ventro-mesial surface of a process of the cartilage that caps the ventral end of the hyomandibula, the two elements there lying nearly at right angles to each other.

The hyomandibula is, as shown in figs. 29 and 30, a stout flat bone, with two portions which lie nearly at right angles to each other, the dorsal portion directed, from above, ventro-posteriorly, and the ventral portion ventrally and slightly anteriorly. Slightly dorsal to the angle between these two portions, the opercular process projects posteriorly and slightly dorsally, is capped with cartilage, and articulates with an articular facet on the internal surface of the operculum, this facet being lined with cartilage, as van Wijhe has stated. A stout ligament arises from the dorsal edge of the process and is inserted on the ventral edge of the large posteriorly projecting portion of the accessory hyomandibula of Traquair's descriptions. A large depressed region on the anterior portion of the lateral surface of the hyomandibula marks the surface of insertion of the musculus adductor mandibulae. Posterior to this depressed region, the preoperculum lies upon the lateral surface of the bone, and is bound to it by connective tissues.

Both ends of the hyomandibula are capped with cartilage. The dorsal cap articulates with the lateral surface of the cranium in the large hyomandibular facet, the dorsal end of the bone there projecting dorsally beyond the level of the dorsal edge of the large cheek-plate and lying directly internal to the dorsal end of the spiracular canal. The ventral cap has two articular surfaces, one on the ventro-mesial surface of a short pointed process on the posterior end of the cap, and the other on the anterior edge of the anterior end of the cap. The former surface gives articulation to the proximal end of the epihyal. The other surface is a facet which gives articulation to a short process, capped with cartilage, which projects posteriorly from the internal surface of the posterior portion of the quadrate. Dorsal to this latter articulation, the ventral portion of the anterior edge of the hyomandibula fits into a slight groove on the hind edge of the metapterygoid and is bound to it by connective tissues.

There is no independent symplectic, but it is possible that that element is represented in that short articular process of the quadrate that articulates with the anterior surface of the cartilaginous cap on the ventral end of the hyomandibula. This will be discussed when describing the quadrate.

The so-called accessory hyomandibula is a small bone which sits saddle-like on the hind edge of the dorsal arm of the hyomandibula, extending downward from the dorsal end of the arm to the base of the opercular process. The two bones are tightly bound together, and cannot be separated in my non-macerated specimens. The posterior portion of the dorsal end of the bone is exposed on the outer surface of the skull, there lying immediately anterior to the anterior postspiracular ossicle. The dorsal edge of the bone articulates

with the skull in the dorso-posterior portion of the large hyomandibular facet, the articulation being wholly with the lateral edge of the parieto-dermopterotic. The articulating edge of the process was not capped with cartilage on one side of the head of the one adult specimen examined, this being as van Wijhe found it in his specimen. On the other side of the head of my specimen the process was capped with cartilage, this being as Traquair shows it in his figure. On both sides of the head of my 75 mm. specimen there was here a little independent piece of cartilage lying along the dorsal edge of the bone.

The accessory hyomandibula bounds part of the hind end of the spiracular opening, as van Wijhe has stated, and it was considered by him to be one of the series of spiracular ossicles, a conclusion that has been accepted by both Bridge and Pollard. The presence of a bit of cartilage in the articular edge of the bone is decidedly against this supposition, and, as fully discussed in an earlier work (Allis, 1918c), I consider this bit of cartilage to represent the dorsal end of the bar formed by the fusion of the bases of the posterior row of branchial rays of the hyal arch, here not completely differentiated to form a posterior articular head to the hyomandibula such as is found in the Teleostei. The ligament that connects the bone that encloses this cartilage with the opercular process represents the ventral portion of the posterior articular head of the teleostean hyomandibula, and the shank of the accessory hyomandibula is a secondary formation of membrane origin. The articular head of the hyomandibula is the homologue of the anterior articular head of the teleostean hyomandibula, and it is derived from the dorsal end of the bar formed by the fusion of the bases of the anterior row of branchial rays of the hyal arch. The ramus hyoideus facialis runs outward between these two heads of the hyomandibula, thus having normal relations to them, but the ramus mandibularis facialis runs outward anterior to the anterior head, which is, so far as I know, an exceptional position in fishes.

Opercular and cheek bones. The larger part of the cheek of this fish is covered by a large and irregular dermal plate which was called by both Müller (1846) and Agassiz (1833-43) the preoperculum. Huxley (1861) says that this bone has two parts, one of which he calls the supratemporal and the other the hyomandibula, and he says that he is much inclined to doubt the existence of a true preoperculum in any crossopterygian fish. Traquair (1871) calls the bone the cheek-plate, and says that the presence of anything corresponding to the preoperculum is somewhat doubtful. Collinge (1893) considers it to be the homologue of the infraorbital bones of *Lepidosteus* grafted upon the preoperculum, and says that in young skulls these two components of the bone are separated dorsally by a distinct groove, and ventrally by a suture. Pollard (1892) adopts the name preoperculum, but says that the bone consists, as Agassiz first showed, of two parts which correspond to the preoperculum and the lower postorbital of *Amia*.

This bone of my adult specimens has, as Huxley, Pollard and Collinge all say, decidedly the appearance of being formed of two components, a large

plate-like superficial one, and a deeper one which lies along the mesial surface of the hind edge of the superficial component and projects ventrally beyond it as a stout flat process. There is, however, no suture, at any place in any of my several specimens, separating the two components from each other.

The superficial component is less wide anteriorly than it is posteriorly, its dorsal and ventral edges inclining forward toward the dorsal and ventral edges of the hind end of the maxillary. The more or less convex dorsal edge of the bone is overlapped externally by the series of spiracular ossicles. In the anterior edge of the bone there is a V-shaped incisure which varies in depth but occupies the full length of the edge, the anterior end of the bone thus having two pointed processes, the dorsal one of which overlaps externally the hind end of the maxillary, while the ventral one is overlapped externally by the latter bone. Immediately posterior to the point of the angle in this edge of the bone there is, on the external surface of the bone, a short oval groove which lodges the anterior horizontal cheek-line of pit organs, and both dorsal and ventral to this groove there are slight depressions which, in the fresh specimen, are filled with dermal tissues. In the horizontal line of this groove there is, at the hind edge of the bone, another short groove, which lodges the posterior horizontal cheek-line of pit organs, and perpendicular to the ventral edge of this groove there is a short groove for the vertical line of pit organs. The hind edge of the superficial component forms a slight ledge which runs postero-dorsally in a curved line along the external surface of the deeper component, the dorsal end of the ledge running either into the groove that lodges the vertical cheek-line of pit organs, or, posterior to that groove, into the hind end of the groove that lodges the posterior horizontal cheek-line. The conditions here vary greatly, and it is probably these vertical and horizontal grooves that led Collinge to say that the two components of the bone were separated from each other by a groove. The superficial component of the bone is not traversed by the infraorbital latero-sensory canal and is accordingly the homologue of the so-called squamosal of *Glyptopomus* and *Osteolepis*, and not of the postorbitals of *Amia* (Allis, 1919*e*).

The deeper component of the bone corresponds to the preoperculum of *Amia* and the Teleostei. Its ventral end is formed by the ventral process of the entire bone, and from there it extends upward along the mesial surface of the superficial component to about one third the distance between the posterior horizontal cheek-line of pit organs and the dorsal edge of the entire bone, where it has the appearance of ending abruptly, with a concave dorsal edge which lies approximately in the level of the axis of the opercular process of the hyomandibula. Up to this point the hind edge of this deeper component lies upon, and is bound by dermal tissues to, the hind edge of the lateral surface of the hyomandibula, and its hind edge is grooved to receive the anterior edges of the operculum and suboperculum. Dorsal to this point the internal surface of the cheek-plate is hollowed out to receive the articular end of the operculum and to give passage to the *museculus dilatator operculi*, and dorsal to this

hollow, the dorsal edge of the entire bone is somewhat thickened, and forms an eminence, or short process, which is directed dorso-postero-mesially and gives attachment to tissues of the region.

The preoperculo-mandibular latero-sensory canal enters the ventral end of the process-like ventral end of the cheek-plate, and runs upward in the plate to its dorsal edge, thus passing upward beyond its thickened, preopercular portion. At the dorsal end of the ventral, process-like portion of the bone, tube No. 7 of the line is given off, tube No. 8 being given off directly posterior to the posterior horizontal cheek-line of pit organs. Dorsal to the thickened, preopercular portion of the bone, the canal turns dorso-anteriorly and traverses the superficial, plate-like portion of the bone, approximately along the bottom of the hollow that lodges the articular end of the operculum and the musculus dilatator operculi. This part of the canal contains no sensory organ, the dorsal organ of the line lying in the dorsal end of the deeper, thickened part of the bone. That part of the canal that lies dorsal to this thickened portion has thus apparently been secondarily enclosed in a part of the entire bone that does not belong to the preoperculum.

The bone *Y'* of Traquair's descriptions I do not find in any of my specimens, unless it be that it is represented in the anterior prespiracular ossicle.

The bone *Y''* is always present, and in all my large specimens there is a second and similar bone posterior to it, as shown in Müller's (1846) figure of this fish, the external surfaces of both bones being tuberculated. In the small specimens of *Polypterus Lapradei* the anterior bone, only, was found, this being as shown in Traquair's figure of his specimen of *Polypterus senegalus*. The two bones usually lie ventral to the ventral edge of the cheek-plate, but may somewhat overlap that edge.

The operculum (fig. 33) is a large bone with a rounded hind edge marked with concentric lines. The ventral portion of the anterior end of the bone fits into the groove on the hind edge of the deeper component of the cheek-plate, and immediately dorsal to this part of the bone is the facet for the opercular process of the hyomandibula. This facet is lined with cartilage and is presented antero-mesially, this being the only bony fish I know of in which this facet is said to be lined with cartilage, excepting only *Alepocephalus* (Gegenbaur, 1878). The operculum projects anteriorly somewhat beyond this facet, and is there hollowed out on its internal surface. On the internal surface of the anterior edge of this part of the bone the tendon of the musculus dilatator operculi has its insertion. The dorsal edge of the operculum is overlapped externally by the ventral edges of the postspiracular ossicles, the dorsal edge of the operculum being slightly grooved, on its external surface, to receive them.

The suboperculum articulates, along its anterior edge, with the hind edge of the cheek-plate, its dorso-posterior edge being overlapped externally by the antero-ventral edge of the operculum.

Palatoquadrate. The palatoquadrate (figs. 29 and 30) is an elongated struc-

ture, traversed its full length by a band of cartilage which is bounded dorsally, ventrally and internally by bone, its external surface alone being exposed. The dorsal edge of the apparatus is strongly convex and lies in a nearly horizontal position, its anterior two-thirds fitting into the groove on the lateral edge of the orbital portion of the parasphenoid, between its membrane and tooth-bearing components, and being bound to it by connective tissues, and its posterior third turning outward and lying along the lateral surface of the ventral end of the spiracular canal. The hind end of the apparatus is double, the two ends being parallel and separated by a slight groove, but their hind edges lying at a considerable angle to each other. The internal one of these two edges extends downward from the dorsal edge of the apparatus to about the middle of its width, and abuts against and is firmly bound to the anterior edge of the ventral portion of the hyomandibula. The external one of the two edges extends the full width of the apparatus, inclining antero-ventrally and overlapping externally, at its dorsal end, the anterior edge of the hyomandibula. The posterior portion of the ventral edge of the apparatus is bent outward at approximately a right angle to the anterior portion, lies in a transverse position, and forms the articular surface for the mandible. Starting from the outer end of this bent-out edge, a ridge runs upward on the external surface of the apparatus, approximately in the transverse plane of the anterior edge of the postorbital process of the chondrocranium, and marks both the posterior limit of the surface of origin of the deeper portion of the *musculus adductor mandibulae*, and the anterior limit of the surface of origin of the superficial portion. Immediately anterior to this ridge, and slightly ventral to the middle of its length, there was, in two of the four specimens examined, but not in the other two, the external opening of a canal which ran dorso-posteriorly in the apparatus. It did not issue on the internal surface of the apparatus, and nothing was found entering it. The bending outward of the ventral edge of the apparatus forms a deep depression on its external surface, the anterior edge of the depression being marked by a lateral process on the ectopterygoid. The transverse plane of the angle of the gape lies immediately posterior to this process, between it and the anterior edge of the ascending process of the splenial, and when the mouth opens and shuts, the splenial, with the attached labial cartilage and related tissues, has a sliding dorso-ventral motion on the hind edge of the lateral process of the ectopterygoid. The anterior end of the cartilaginous core of the apparatus has ossified as the autopalatine, and this bone, capped with cartilage, articulates with the cartilage that covers the ventral border of the orbital surface of the ectethmoid.

The quadrate was, in the specimen particularly examined, so firmly bound to the metapterygoid that the two bones could not be separated without breakage. The bone is quadrantal in shape, with one edge lying in a horizontal plane and the other directed dorso-postero-mesially, and its external surface is crossed by the ridge, above described, that forms the boundary between the surfaces of insertion of the deeper and superficial portions of

the adductor mandibulae. The ventral edge of the bone is curved, with its posterior portion transverse in position, and this part of the edge articulates with the autarticular in a transverse groove on the dorsal surface of that bone, neither of the articular surfaces being capped with cartilage so far as could be determined from my specimens.

On the internal surface of the bone there is a pronounced ridge which begins, ventrally, at the mesial end of the articular edge of the bone, and runs dorso-posteriorly nearly to its dorsal edge. There it turns posteriorly, or postero-ventrally, and extends to the hind edge of the bone, there forming the ventral end of the mesial one of the two diverging hind edges of the dorsal portion of the entire apparatus. Between this ridge and the hind edge of the bone there is a deep depression which receives the hind end of the autarticular when the mouth is widely opened. That part of the ridge that forms the ventral end of the mesial one of the diverging hind edges of the apparatus is capped with cartilage that is continuous with the cartilaginous core of the apparatus, and, as already stated, it articulates with the anterior edge of the cartilaginous cap on the ventral end of the hyomandibula. The ramus mandibularis externus facialis passes external to this process-like part of the quadrate, the ramus mandibularis internus passing internal to it, the process thus having to these two nerves and to the hyomandibula and quadrate, the relations that the teleostean symplectic would have if it were to fuse with the quadrate instead of with the hyomandibula; and it is quite probable that it represents some part of that element of the hyal arch.

The convex dorsal edge of the quadrate is everywhere bounded by cartilage. Its internal surface, anterior to the ridge across it, is completely covered by the metapterygoid and ectopterygoid, these two bones resting directly upon it, and the metapterygoid being firmly ankylosed with it in the one specimen examined.

The metapterygoid has, in my adult specimens, decidedly the appearance of being wholly an investing bone, and in the 75 mm. specimen it at no place has primary relations to the cartilage of the apparatus, this thus confirming van Wijhe's and Pollard's conclusions regarding it. It lies mainly upon the internal surface of the apparatus, but its dorsal edge embraces the dorsal edge of the cartilaginous core and projects somewhat above it, there being exposed on the lateral surface of the apparatus. The anterior portion of this dorsal edge is grooved on its dorso-lateral surface, and there receives and articulates with the hind end of the entopterygoid. On the mesial surface of the apparatus the bone articulates anteriorly with both the ectopterygoid and entopterygoid, and ventrally with the quadrate, overlapping the mesial surface of the latter bone to a considerable extent and being itself overlapped mesially by the entopterygoid, the latter bone fitting into a sharply marked depression on the mesial surface of the metapterygoid.

The hind edge of the bone is slightly thickened and grooved, and lodges part of the cartilage, already referred to, that forms the ventral portion of the

mesial one of the two hind edges of the entire apparatus. The dorso-posterior corner of that part of the bone that overlaps externally the dorsal edge of the cartilage of the apparatus is either perforated by a foramen, or deeply notched in its hind edge. This foramen, or notch, is traversed by the ramus mandibularis internus facialis, that nerve then running downward between the cartilage of the apparatus and the internal plate of the metapterygoid and issuing at the ventral edge of the latter bone, between it and that process of the quadrate that apparently corresponds to the symplectic. The dorso-anterior portion of the mesial surface of the bone is roughened with minute tooth-like eminences.

The entopterygoid is a long thin dermal bone which forms the larger part of the dorso-mesial edge of the apparatus, there projecting considerably beyond the cartilage of the apparatus. Ventral to this wide projecting edge, the bone rests upon the mesial surfaces of the metapterygoid and ectopterygoid, lying in a sharply marked depression along the dorsal edges of those bones, and being separated, by them, from all contact with the cartilaginous portion of the palatoquadrate. The anterior half of the dorso-mesial edge of the bone is loosely bound to the lateral edge of the parasphenoid, between its membrane and tooth-bearing components, the posterior half lying against the external surface of the spiracular canal. The anterior end of the bone is thin, and extends forward onto the ventral surface of the posterior portion of the ethmoidal cartilage, there being covered by tough connective tissues. Its hind end is somewhat pointed, curves postero-laterally, and rests upon the dorso-external surface of the dorsal edge of the metapterygoid. Its mesial surface is completely covered with small tooth-like eminences, excepting that part of its anterior end that extends forward beneath the ethmoidal cartilage.

The ectopterygoid is a thin dermal bone which lies directly upon the mesial surface of the cartilage of the palatoquadrate, its dorsal edge coinciding with the dorsal edge of that cartilage, but its ventral edge extending ventrally beyond the cartilage. The mesial surface of the bone is everywhere covered with small tooth-like eminences, these eminences becoming small sharp teeth along the anterior half of its ventral edge and there forming a posterior continuation of the teeth on the oral surface of the mesial dermo-palatine, the so-called vomer of earlier descriptions. The dorsal edge of the bone is overlapped to a considerable extent by the ventral edge of the entopterygoid, as just above explained. Its hind end overlaps slightly the anterior edges of the metapterygoid and quadrate.

The anterior end of the ventro-lateral edge of the ectopterygoid is somewhat thickened, apparently by dermal accretions to its external surface, this giving rise to what appears like a short antero-laterally projecting process, this process and the remainder of the bone being separated by a narrow V-shaped space which receives the hind edge of the palatine process of the maxillary. The anterior end of the body of the ectopterygoid, which forms the ventro-mesial boundary of this V-shaped space, articulates with the hind end

of the mesial dermopalatine, the antero-laterally projecting process giving support, on its dorsal surface, to the autopalatine. This little process may accordingly be called the palatine process of the ectopterygoid, and posterior to it, at the hind end of the row of small sharp teeth on the anterior portion of the ventral edge of the bone, there is a second process, which I have above referred to as the lateral process of the bone. This process is directed laterally and has a flat and somewhat spreading outer end which abuts against, and is firmly bound to, the ventral portion of the internal surface of the maxillary, immediately posterior to the toothed part of that bone (Allis, 1900*b*). The posterior edge of the process is slightly hollowed and gives sliding articulation to tissues attached to the anterior edge of the ascending process of the splenial. Dorso-anterior to the base of this process there is a large semicircular notch in the ventral edge of the cartilage of the palatoquadrate, the lateral surface of the ectopterygoid there being exposed. This notch lies beneath the eyeball, and is apparently caused by the wearing action of that organ. The bone is here traversed by a small canal which begins at the dorsal edge of the palatoquadrate cartilage and issues near the ventral edge of the ectopterygoid, the canal transmitting a branch of the ramus palatinus facialis, which thus has the course of the ramus palatinus posterior facialis of *Amia*. In *Amia* that nerve runs antero-ventrally across the external (dorso-lateral) surface of the ectopterygoid, passes internal to the cartilage of the palatoquadrate, and then internal to the autopalatine, between it and the dermopalatine, sometimes perforating the autopalatine in part of its course. The conditions in *Polypterus* would accordingly arise if the autopalatine of *Amia* were to be pushed forward beyond this nerve, and the nerve were then to become enclosed in the dermopalatine, this suggesting that the dermopalatine of *Amia* is represented in the anterior portion of the ectopterygoid of *Polypterus*.

The autopalatine is a small bone of primary origin which develops in the anterior end of the palatoquadrate cartilage, that end of the cartilage here turning slightly antero-laterally. The bone rests upon the dorsal surface of the palatine process of the ectopterygoid, and was not, as van Wijhe found it, fused with that process in any of my specimens. Its slightly concave dorsal surface is capped with cartilage and articulates with the cartilage that covers the ventral surface of the ectethmoid. The ethmopalatine ligament of Pollard's descriptions (1892, p. 413) arises from the cranium posterior to this articular surface and, running postero-laterally and spreading considerably, is inserted along the dorso-mesial edge of the cartilaginous core of the palatoquadrate. Pollard says that this cartilaginous core projects forward beyond the autopalatine, and that this anterior portion is the homologue of the prepalatine cartilage of his descriptions of the Siluridae. No such projecting portion of the cartilage was found in any of my specimens.

Van Wijhe (1882, p. 253) found the autopalatine fused with the anterior end of the ectopterygoid, as above stated, and because of this he concluded that this anterior portion of the latter bone fulfilled the function of a dermo-

palatine, and was hence probably, genetically (in der Entwicklungsgeschichte), an independent bone, the equivalent of the dermopalatine of the Ganoidei, a conclusion which the relation of the ramus palatinus posterior facialis to the bone seems to fully confirm, as just above explained.

The mesial dermopalatine (figs. 23-27), the so-called vomer of earlier authors, forms a direct anterior prolongation of the ventro-lateral portion of the ectopterygoid. It is furnished with small sharp teeth, and its posterior portion lies upon and is firmly bound to the ventral (oral) surface of the palatine process of the maxillary, its anterior end projecting forward beyond that process and lying upon the ventral (oral) surface of the palatine process of the premaxillary, but only loosely bound to it. This end of the bone is somewhat wider than its posterior portion, and curving mesially meets and articulates, in the median line, with its fellow of the opposite side. The curved external edge of the bone is concentric with the line of the premaxillo-maxillary teeth, and separated from them by a groove which I have called the primary alveololabial sulcus (Allis, 1919c). Along the postero-mesial edge of the bone there is a slight furrow in the lining membrane of the roof of the buccal cavity, and I formerly, but erroneously, considered the anterior edge of this groove to represent the maxillary breathing-valve of the Teleostei. This bone thus being a mesial dermopalatine, the dermopalatine of *Amia*, which is represented in the anterior portion of the ectopterygoid of *Polypterus*, must be a lateral dermopalatine.

Mandible. The mandible contains the four bones described by Traquair, and also the mento-Meckelian ossicle described by van Wijhe. No bone corresponding to the angular of van Wijhe's descriptions was found in any of the specimens examined, nor was there any indication of such a bone having fused with the dermarticular.

The dentary is a long and rather slender bone, the anterior end of which curves mesially. It bears on its dorsal edge a single row of sharp stout teeth. Its mesial surface is deeply grooved its entire length, the anterior half of this groove being relatively narrow, with an enlarged anterior end, and lodging the anterior portion of Meckel's cartilage and the mento-Meckelian ossicle. The posterior portion of the groove is deeper than the anterior portion, and widens gradually to the hind end of the bone, there occupying its entire width and lodging the anterior portion of the dermarticular. The mesial surface of the dorsal edge of the groove is flat and articulates with the lateral (aboral) surface of the ventral half of the anterior portion of the splenial, the latter bone projecting dorsally above the articulating surface with the dentary and forming a pronounced ridge which lies parallel to the outer, tooth-bearing edge of the dentary and is separated from it by a deep groove which lodges the ramus mandibularis internus facialis and a branch of the ramus mandibularis trigemini that I consider to represent part of the ramus posttrematicus internus of the nerve. In the hind edge of the dentary there is a large V-shaped incisure, the sharp dorsal and ventral edges of the incisure resting upon the

external (lateral) surface of the dermarticlar. The anterior end of the bone is thickened, turns slightly mesially, and has a large flat surface which articulates with its fellow of the opposite side. The ventral edge of this part of the bone is flattened and projects slightly ventrally as a sharp ridge, but there is no indication that this part of the bone was, as van Wijhe suggests, a primarily independent predentary that has fused with the dentary.

The dentary is traversed its full length by the mandibular latero-sensory canal, the canal entering the bone on its external surface, close to the symphysis, and leaving it at the re-entrant point of the large V-shaped incisure in its hind edge. Two tubes leave the canal as it traverses the bone, and the bone lodges three sense organs of the line. The ramus mandibularis externus facialis runs forward ventral to the groove that lodges Meckel's cartilage, and three short canals give passage to the branches sent to the three sense organs lodged in the bone.

The dermarticlar is a stout dermal bone, with a long and sharply pointed anterior end which fits into the posterior portion of the groove on the mesial surface of the dentary, the outer surface of the dermarticlar being excavated to receive the diverging hind ends of the dentary. Posterior to the dentary the ventral edge of the bone is thin, and on the external surface of this edge, immediately posterior to the hind end of the dentary, there is a small pit-like depression which is presented ventrally and forms part of the surface of origin of the long ligament that has its insertion on the proximal (posterior) end of the ceratohyal. On the mesial surface of the bone there is a groove to receive the posterior portion of Meckel's cartilage, and this groove is crossed by a smaller groove which lodges the ramus mandibularis externus facialis and the ramus mandibularis trigemini as those two nerves run forward onto the mesial surface of the dentary. Dorsal to the posterior portion of this latter groove there is a depression which forms the surface of insertion of a part of the musculus adductor mandibulae. Ventral to the hind end of Meckel's cartilage the ventral edge of the groove that lodges it rises as a ridge-like process, the mesial surface of which is flat and roughened and articulates with the aboral surface of the ventral edge of the splenial. Posterior to this, the mesial surface of the dermarticlar articulates with the lateral surface of the autarticlar, the dorsal edge of the bone projecting upward beyond this surface of articulation and there articulating with the ventral edge of the lateral plate of the ascending process of the splenial.

The dermarticlar is traversed by the posterior portion of the mandibular latero-sensory canal, and lodges two organs of that line. The canal enters the bone on its external surface at the point of the V-shaped incisure in the dentary, and leaves it near its dorsal edge close to its hind end, one tube leaving the canal as it traverses the bone. Slightly dorso-anterior to the opening by which the canal leaves the hind end of the bone, there is a notch in the edge of the bone, this notch leading into a canal which runs forward, at first between the dermarticlar and the autarticlar and then through a portion of the former

bone to reach and enter the little groove that crosses the groove that lodges Meckel's cartilage, this canal transmitting the ramus mandibularis externus facialis.

The autarticular (figs. 38 and 39) is an irregular bone which lies between the hind ends of the dermarticlar and splenial, articulating with the former bone by its entire lateral surface excepting only a narrow dorso-posterior edge, and with the splenial by the anterior third or half of its mesial surface. The hind end of Meckel's cartilage abuts against the anterior end of the bone, and is in primary relations to it. At about the middle of the length of the dorsal surface of the bone there is a transverse hour-glass shaped groove which is lined with connective tissue and not with cartilage and gives articulation to the articular edge of the quadrate. These two articulating surfaces are thus neither of them lined with cartilage. Anterior to this articular groove, the dorsal surface of the autarticular is deeply grooved, this groove occupying the entire dorsal surface of the bone and inclining antero-ventrally into the hollow of the mandible. Posterior to the articular groove the bone narrows abruptly and then tapers to a rounded hind end which is capped with a pad of tough connective tissue which looks somewhat like cartilage and rubs against the anterior edge of the epiphyal. On the mesial surface of the bone, immediately ventral to the mesial end of the articular facet for the quadrate, there is the external opening of a short canal which traverses the bone and transmits the ramus mandibularis internus facialis.

The mento-Meckelian ossicle is a small cylindrical, or knob-shaped bone which extends from the anterior end of Meckel's cartilage forward to the symphysis, where it articulates with its fellow of the opposite side. It lies in the enlarged anterior end of the longitudinal groove on the mesial surface of the dentary and is not seen in either lateral or anterior views of the latter bone.

Meckel's cartilage is a rod-shaped piece which extends from the autarticular to the mento-Meckelian ossicle. In its posterior portion it is flat, and there lies against the mesial surface of the dermarticlar. Anteriorly it becomes gradually rounded, and there lies in the longitudinal groove on the mesial surface of the dentary.

The splenial (fig. 28) is a long dermal bone which is best described as formed of two thin plates, one lateral and the other mesial, the lateral plate being narrower than the mesial one and not extending as far posteriorly. In the anterior half of the bone the two plates have a common dorsal edge and are completely fused with each other. Posteriorly the ventral portions of the two plates diverge from each other, but their dorsal edges remain fused, and the two plates are produced dorsally to form the tall ascending process of the bone. The lateral surface of the mesial plate here rests upon the flattened mesial surfaces of the autarticular and dermarticlar, the ventral edge of the lateral plate resting upon the dorsal edges of the lateral surfaces of those same bones. The ascending process is thus deeply grooved both ventrally and posteriorly, and straddles the posterior opening of the ramus of the mandible,

the floor of that opening being formed by the concave dorsal surface of the prearticular portion of the autarticular. Anterior to the ascending process, the mesial plate of the splenial rests against the mesial surface of the ridge that forms the dorsal edge of the groove in the dentary that lodges Meekel's cartilage, the ventral edge of the lateral plate resting upon the dorsal surface of that ridge. Anterior to the anterior end of the splenial there are the two little dermal and toothed plates described by van Wijhe, and these plates and the dorsal edge of the splenial form the mesial boundary of the deep groove that is bounded laterally by the tooth-bearing edge of the dentary, that groove extending from the anterior edge of the base of the ascending process forward to the symphysis and there being continuous with the groove of the opposite side. The mesial surface of the splenial, and the base of its ascending process are covered with minute tuberosities.

The ascending process of the splenial, together with the labial cartilage and related tissues, has sliding articulation with the posterior edge of the lateral process at the middle of the length of the ectopterygoid. On its dorsal and posterior edges it gives insertion to the masseter division of the musculus adductor mandibulae, and anterior to that muscle to the tough connective tissues that envelop the labial cartilage. There is no cartilage whatever in the process, even in my 75 mm. specimen, and I can see no reason to assume, as van Wijhe has suggested was probable, that any part of it is, or has been derived from, a primary ossification. The process would seem to correspond strictly to the coronoid (operculum) bone of certain reptiles (Baur, 1895, fig. 3), and is certainly in no way related to the cartilaginous coronoid process of *Amia*.

Maxillary. This bone of the adult *Polypterus* has been formed by the fusion of two suborbital latero-sensory ossicles with a dental bone that quite certainly corresponds to the maxillary component of the superior maxillary bone of mammals (Allis, 1900*b* and 1919*c*). Projecting mesially from the mesial surface of the anterior portion of the bone there is a long and thin palatine process which rests directly upon the ventral surface of the ethmoidal cartilage, but is only loosely bound to it. The mesial half of the ventral (oral) surface of this process supports, and is immovably attached to, the posterior two-thirds, approximately, of the mesial dermopalatine and to the anterior end of the ectopterygoid. The bone bears a single row of stout sharp teeth, and the hind end of this tooth-bearing part of the bone rests against the antero-ventral edge of the lateral process of the ectopterygoid, the lateral end of the latter process resting against the mesial surface of the maxillary dorso-posterior to this point, and being firmly but not immovably bound to it by a short stout ligament. All movements of the palatoquadrate are thus impressed upon the maxillary, and *vice versa*.

The maxillary articulates anteriorly with the premaxillary and lachrymal, and posterior to those bones forms the larger part of the ventral boundary of the orbit. Its dorso-posterior corner is overlapped externally by, and loosely attached to, the postorbital bone and the anterior spiracular ossicle.

The dorsal portion of the hind end of the bone projects posteriorly as a long and pointed process which fits against the internal surface of the large cheek-plate, the ventral portion of the bone projecting as a shorter process which lies against the external surface of the cheek-plate. These two bones and the palatoquadrate and hyomandibula are thus all firmly but apparently not immovably bound together. The anterior one of the two bones *Y''* lies external to the ventro-posterior corner of the maxillary.

The dorsal portion of the maxillary is traversed by the infraorbital latero-sensory canal, that canal entering the bone close to its dorsal edge, at the hind end of the lachrymal, and issuing from it on its external surface near its dorsal edge and immediately ventral to the postorbital bone. One primary tube is given off as the canal traverses the bone, and issues from it dorsal to the hind end of the line of maxillary teeth. The bone lodges two sensory organs of the line.

Premaxillary. This bone, like the maxillary, is formed by the fusion of latero-sensory and dental components, and also like the maxillary it has a flat palatine process, of membrane origin, which rests upon the ventral surface of the ethmoidal cartilage. This palatine process projects posteriorly and articulates with the anterior edge of the parasphenoid, and between it and its fellow of the opposite side there is a small exposed portion of the ventral surface of the rostral process of the chondrocranium. The internal surface of the premaxillary rests against the anterior edge of the rostral process, the bone projecting dorso-posteriorly above that process, and the internal (here posterior) portion of its dorsal edge there articulating with the anterior edge of the median ethmoid. Lateral to the latter bone the premaxillary sends a small ascending process dorso-postero-mesially, this process lying in the groove along the lateral surface of the head of the ethmoid and giving support, on its dorsal end, to the antero-mesial corner of the nasal, and partly also to the mesial end of the os terminale. Lateral to this process, the dorsal surface of the premaxillary is slightly hollowed out and forms the ventral edge of the fenestra nasalis, this part of the premaxillary lying beneath the antero-lateral portion of that atrial chamber of the nasal sac from which the anterior and posterior nasal tubes have their origins. Lateral and posterior to the fenestra nasalis the premaxillary has a stout antorbital process which projects dorso-posteriorly along the lateral edge of the fenestra nasalis, there lying against the lateral surface of the nasal capsule and giving support, on its dorsal end, to the lateral edge of the nasal and the antero-lateral corner of the frontal. Postero-ventrally the process articulates both with the ectethmoid and the lachrymal, and ventral to the latter bone with the anterior end of the maxillary. The bone has a single row of stout sharp teeth which apparently correspond to the premaxillary teeth of mammals (Allis, 1919*c*).

The premaxillary is traversed by the preorbital portion of the infraorbital latero-sensory canal, that canal entering it on its dorsal surface at the lateral edge of the median ethmoid, and leaving it at the anterior edge of the lachry-

mal. Two primary tubes leave the canal as it traverses the bone, the lateral one lying dorsal to the hind end of the row of premaxillary teeth. The bone lodges three organs of the infraorbital line, which correspond to those in the antorbital and the lateral half of the median ethmoid of *Amia*.

LATERO-SENSORY CANALS

These canals were fully described in an earlier work (Allis, 1900*a*), and as their relations to the individual cranial bones have already been given in the present work, and the manner of their innervation will be given when describing the nerves, it will suffice to here give simply their general course and disposition.

The accompanying fig. 1 gives a full length view of a 44 cm. specimen of *Polypterus bichir*, and shows the external openings of the primary tubes of the cranial canals, the line of little grooves that mark the positions of the sensory organs of the lateral line of the body, and other similar grooves that mark the positions of other lines of surface organs. Figs. 2, 3 and 4 give enlarged lateral, dorsal and ventral views of the same specimen. Comparing these figures with those of the prepared skull of the 49 cm. specimen (figs. 5 and 6), it is seen that most of the surface pores of the canals lie in a thick dermis which completely covers all those bones the external surfaces of which are without rugous markings, and also the smooth and bevelled edges of certain of the other bones.

The supraorbital canal begins at a pore that lies immediately posterior to the base of the nasal tube, approximately in the line prolonged of the three suborbital pores of the main infraorbital line. From there the canal enters and traverses the os terminale, and at its antero-mesial end anastomoses with the second primary tube of the main infraorbital canal, there forming the double tube and pore 2 inf.-2 sup. Turning posteriorly from there the supraorbital canal enters and traverses, successively, the accessory nasal, nasal and frontal, issuing from the latter bone near the hind end of its lateral edge and there anastomosing with the main infraorbital canal to form the double tube and pore 10 inf.-7 sup. There are six sensory organs in the line, and seven primary tubes and pores.

The main infraorbital canal begins in the median line on the top of the snout, and is there in direct continuation with its fellow of the opposite side of the head. There is no median pore marking the point of fusion of these two canals, this probably being due to the fact that the anterior sensory organ of each line lies so close to the median line, that the two organs were enclosed simultaneously in the process of involution that gave origin to the canal, no primary tube ever forming between them. Starting from this point the canal traverses the ethmoid, and on issuing from that bone anastomoses with the supraorbital canal to form the double tube and pore 2 inf.-2 sup. The canal then enters and traverses, successively, the premaxillary, lachrymal, maxillary, postorbital and postfronto-sphenotic, and on the dorsal surface of the latter bone becomes a groove which is roofed in its anterior portion by the frontal

and in its posterior portion by the parieto-dermopterotic. Slightly anterior to the line between these two latter bones the canal anastomoses with the hind end of the supraorbital canal, a single double tube and pore, 10 inf.-7 sup. marking the point of fusion. Posterior to this point the canal enters the parieto-dermopterotic, traverses that bone and then the second and first supratemporals and the posttemporal, at the hind end of which it comes to the surface and ends. While traversing the second supratemporal, or between that bone and the first supratemporal, it anastomoses with the lateral end of the supratemporal cross-commissure, so forming the double tube and pore 12 inf.-1 supratemporal. There are 13 sense organs in all in the line, and 13 primary tubes and pores, the anterior tube and pore of the line not being present.

The supratemporal commissure traverses the second and third supratemporal bones, and anastomoses in the median line with its fellow of the opposite side, a single median pore marking the point of fusion. There are two sense organs in the line, and three primary tubes and pores, counting the two terminal ones.

The preoperculo-mandibular canal begins at the symphysis of the mandibles, at a median pore common to it and its fellow of the opposite side. From there the canal runs posteriorly through the dentary and dermarticlar, traverses the dermis between the latter bone and the ventral end of the preoperculum, and then turns upward in the latter bone, traversing it and ending at a pore that lies on the external surface of the cheek-plate near its dorsal edge. The canal does not reach and anastomose with the main infraorbital canal, this doubtless being related to the presence of the line of spiracular ossicles. There are eight sense organs in the line, five in the mandible and three in the preoperculum, and there are nine primary tubes, but in the specimen used for illustration the external openings of the fifth and sixth tubes had fused to form a single pore, there thus being but eight surface pores along the line. In an adult specimen of *Polypterus ornatipinnis* this anastomosis of these two pores had not taken place, and there were accordingly nine primary pores related to the line. In the specimen used for fig. 30, there were four nerves entering the canal as it traversed the preoperculum, but whether there were three or four sensory organs was not determined.

The lateral line of the body begins posterior to the posttemporal bone, and is represented by longitudinal grooves on the external surfaces of successive scales, the grooves on the first seven rows of scales forming three short lines, the first one of which lies in the line of the hind end of the cranial canal, the next one slightly ventral to the first one, and the third one still farther ventrally. The next groove lies slightly ventral to the third short line, and from there the line of grooves continues in an unbroken line to the base of the tail fin, there being one groove on each successive scale. Dorsal to this line, approximately in the line of the dorso-anterior one of the three short lines, there is another line of sense organs, the positions of which are indicated by

a somewhat irregular line of grooves placed transversely on every third or fourth scale; and dorsal to this line there is, along the ventral edge of the dorsal fin, a line of short longitudinal grooves, approximately one on each successive scale.

On the head there are six short lines of surface organs, each marked by a slight depression on the external surface of the underlying bone: an anterior head-line on the dorsal surface of the frontal, mesial, or postero-mesial to pore 6 supraorbital; a middle head-line on the parieto-dermopterotic, mesial, or postero-mesial to pore 11 infraorbital; an anterior horizontal cheek-line on the cheek-plate somewhat posterior to pore 8 infraorbital; a posterior horizontal cheek-line on the cheek-plate immediately anterior to pore 8 preoperculo-mandibular; a vertical cheek-line on the cheek-plate immediately ventral to the posterior horizontal cheek-line; and a transverse line on the ventral surface of the gular plate.

MYOLOGY

Eye muscles. The recti superior, inferior and externus arise from a short tendinous stalk that has its origin on the sphenoid, near its ventral edge and immediately posterior to the foramen opticum, its position and its relation to these muscles suggesting the eye stalk of the Selachii. The rectus internus has its origin directly upon the sphenoid, near its ventral edge and anterior to the foramen opticum, between that foramen and the foramen for the orbito-nasal artery. The obliquus superior arises from the ectethmoid, on the edge of, and partly within, the preorbital canal, the obliquus inferior arising from that same bone, near its ventral edge.

The innervation of these muscles is as in *Amia* (Allis, 1897), excepting in that the inferior division of the nervus oculomotorius passes dorsal, instead of ventral, to the rectus inferior.

Muscles innervated by the nervus trigeminus. These muscles have been described by both Pollard (1892) and Luther (1913).

The musculus adductor mandibulae, the masseter of Pollard's and Luther's descriptions, has, in my adult specimens, the superficial (upper) and deeper (lower) portions described by Pollard but not found by Luther. In the 75 mm. specimen both portions are also found, but not so distinctly separated from each other as in the adult. The superficial portion is the larger, and has its origin in part on a line of tough connective tissue that is attached to the internal surface of the dorsal border of the cheek-plate, in part on the external surface of the dorsal portion of the hyomandibula, and in part on the external surface of that part of the palatoquadrate that lies posterior to the ridge that runs upward across the quadrate from the outer end of its articular edge. The dorsal edge of the muscle is thin, and along a part of this edge is the line of tough connective tissue, above referred to, which is firmly attached to the dorsal edge of the cheek-plate and hence serves in part as surface of origin of the muscle, and in the 75 mm. specimen this is the only origin that the muscle has. The surface of origin on the palatoquadrate covers

parts of the quadrate, entopterygoid and metapterygoid, and that on the hyomandibula the anterior portion of that bone from the dorsal edge of the palatoquadrate upward to the line of the opercular process, the fibres of the muscle all having their origins on a tough membrane that covers these several bones, and not directly on the bones themselves. A slip of that part of the membrane that covers the surface of origin on the palatoquadrate extends posteriorly, external to the ramus mandibularis facialis, and is inserted on the hyomandibula posterior to that nerve (fig. 46). The fibres of the muscle converge toward the ascending process of the splenial, running antero-ventrally, anteriorly, and even antero-dorsally, and the dorsal and larger part of them are inserted on the dorsal edge of that process and along the internal surface of its hind edge, the ventral fibres passing directly into the ramus of the mandible and there being inserted on the internal surface of the dermarticlar.

The deeper portion of the adductor arises from that part of the quadrate that lies anterior to the ridge that runs upward from the outer end of its articular edge, these fibres, like those of the superficial portion of the muscle, arising from a membrane that covers the quadrate and not directly from that bone. The fibres of this portion of the muscle run antero-ventrally and are inserted, mostly tendinous, on the internal surface of the dermarticlar, the tendinous ends of the muscle passing mesial, or in part lateral and in part mesial, to the ramus mandibularis trigemini. Associated with this part of the adductor there is a short muscle which corresponds to the mandibular portion of the muscle of *Amia* and certain of the Teleostei. The fibres of this latter muscle arise from the stout flat tendon of the musculus temporalis and pterygoideus, to be described below, and running ventro-anteriorly are inserted on the dorsal surface of the hind end of Meckel's cartilage.

The musculus temporalis has its origin from the ventral surface of the postfronto-sphenotic, from the supraorbital band of cartilage, and from that part of the ventral surface of the frontal that roofs the supraorbital fontanelle, the surface of origin of the muscle extending forward to the transverse plane of the foramen opticum. From this long surface of origin, the fibres of the muscle run postero-ventrally, ventrally and antero-ventrally, and passing external to the rami ophthalmicus profundus and ophthalmicus superficialis trigemini, and internal to the rami maxillaris and buccalis trigemini, are all inserted on the external surface of a tendinous band which lies between it and the musculus pterygoideus and which gives insertion, on its internal surface, to the fibres of the latter muscle. This tendinous band passes internal to the ramus mandibularis trigemini and, diminishing in width, is inserted on the internal surface of the dermarticlar.

The musculus pterygoideus arises from the postero-ventral portion of the lateral surface of the sphenoid and from adjacent portions of the mesial plate of the ascending process of the parasphenoid, there lying between the nervus trigeminus dorsally and the common carotid artery, the ramus palatinus

facialis, and the vena orbitalis inferior ventrally. It is a wide stout muscle, runs ventro-laterally and slightly anteriorly along the external surface of the palatoquadrate, and has its insertion on the tendinous band, just above described, that gives insertion on its external surface to the musculus temporalis.

The musculi temporalis and pterygoideus apparently together correspond to the first and second divisions of the levator maxillae superioris of my descriptions of *Amia* (Allis, 1897).

The single primitive levator arcus palatini has been more or less completely differentiated into four muscles; the levator arcus palatini of Luther's descriptions (levator maxillae superioris of Pollard), the protractor hyomandibularis of Pollard's descriptions, the dilatator operculi, and the musculus spiracularis (Luther). These muscles, excepting the spiracularis, all arise together from the lateral surface of the postfronto-sphenotic, there forming practically a single muscle but separated from each other by an aponeurotic formation. The fibres of the levator arcus palatini run postero-ventrally and, spreading somewhat, are inserted on a curved tendinous band which is concave postero-ventrally. This band crosses the external surface of the protractor hyomandibularis at about the middle of its length, and has its ventro-anterior end inserted on the dorsal edge of the entopterygoid, and its dorso-posterior end on the external surface of the hyomandibula in the horizontal line of its opercular process. The dilatator operculi lies along the dorsal edge of the levator arcus palatini, and runs posteriorly and slightly laterally. Its fibres are all inserted on a long tendinous formation which extends the full length of the muscle, along the middle line of its external surface, and has its insertion on the internal surface of the anterior edge of the operculum. The musculus spiracularis lies along the dorsal edge of the dilatator operculi, and in the adult has its origin on the hind edge of the frontal bone, as Luther states. Pollard calls it a slip of the dilatator, but even in my 75 mm. specimen it is wholly independent of that muscle. It runs posteriorly along the lateral edge of the spiracular opening, and apparently has its insertion on the wall of that opening. It lies directly beneath the spiracular ossicles and is attached to them by fibrous tissues, but not inserted on them. The protractor hyomandibularis lies internal to the levator arcus palatini, and is a much stouter muscle. Its fibres run postero-ventrally and most of them are inserted on a membrane that covers and forms part of the lateral wall of the spiracular canal, that membrane having its attachment, ventrally, to the dorsal edge of the palatoquadrate and, posteriorly, to the anterior edge of the hyomandibula, the longest fibres of the muscle, which are the external ones, only extending to the edges of those two skeletal elements and not overlapping them. The muscle thus has an action upon the suspensorial apparatus that is strictly similar to that of the so-called levator arcus palatini, and, in addition, an action of some sort on the spiracular canal.

There is no muscle comparable to the intermandibularis of *Amia*, but

there are two muscles strictly comparable to the geniohyoidei inferior and superior of that fish, and I have described them in an earlier work (Allis, 1919*d*). The geniohyoidei inferior and superior of this fish are called by Pollard the intermaxillares anterior and posterior, the former being said to be innervated by the ramus mandibularis trigemini and the latter by the ramus hyoideus facialis.* Holmqvist (1910) calls the anterior one of these two muscles the intermandibularis, and the posterior one the protractor hyoidei, and he says that the latter muscle, as an independent structure, is found only in the bony fishes and in *Amia*, the term bony fishes, as employed by him, evidently meaning the Teleostei only. In a later work (1911), Holmqvist calls the intermandibularis of his earlier descriptions of *Polypterus* the intermandibularis II, in order to distinguish it from an intermandibularis such as is found in *Amia*, which latter muscle is called the intermandibularis I; and these two muscles, where found, are both considered by him to be innervated by the ramus mandibularis trigemini. The protractor hyoidei, which is the geniohyoideus superior of my descriptions of *Amia*, is, on the contrary, considered by him to be innervated by the ramus hyoideus facialis. In the Teleostei the homologue of this latter muscle of *Polypterus* is said (1910, p. 12) to have added to it certain fibres derived from the constrictor of the mandibular arch, the anterior portion of the muscle then being innervated by the nervus trigeminus and its posterior portion by the nervus facialis. It is said that, in both *Polypterus* and *Lepidosteus*, none, or but few, of these trigeminus fibres have as yet been acquired by the protractor, and Holmqvist's descriptions would seem to indicate that he did not consider them, where found, to have been derived from the intermandibularis II (geniohyoideus inferior). Where they are considered to have come from is not clear. Luther (1913), following Holmqvist's earlier work, calls the two muscles of *Polypterus* the intermandibularis and protractor hyoidei, and he says that the former muscle is derived from the ventral portion of the constrictor of the mandibular arch, and is innervated by the ramus mandibularis trigemini, while the protractor hyoidei is derived from the ventral portion of the constrictor of the hyal arch and is innervated by the ramus hyoideus facialis.

The contraction of either of these two muscles would evidently have similar effect upon either the mandible or the hyal arch, and in my work on *Amia*, I said (Allis, 1897, p. 562) that this action must be either that of an adductor (more properly protractor) of the hyal arch or a retractor of the mandible, according as the one or the other of these two structures was fixed and stationary. If then the principal action of the posterior muscle is that of a protractor hyoidei, as Holmqvist's descriptions would seem to establish, that must be the action also of the anterior muscle. The two muscles, in fact, become, in certain of the Teleostei described by Holmqvist, simply anterior and posterior portions of a single muscle, but apparently always separated from each other by a more or less developed aponeurotic line. If one of them is called a protractor hyoidei, the other should then also be so called, one being

an anterior protractor and the other a posterior one. I have however thought best, for the sake of conformity in my several works, to continue to use for them the names employed in my descriptions of *Amia* and *Scomber*.

The geniohyoideus inferior, thus defined, is a muscle strictly similar to that of *Amia*, arising in the median line from a median aponeurotic raphe common to it and its fellow of the opposite side, and running antero-laterally to be inserted mainly upon the mesial surface of Meckel's cartilage, immediately ventral to the ventral edge of the splenial, but partly also along the ventral edge of the latter bone. The geniohyoideus superior arises, as in *Amia*, from the proximal (posterior) end of the ceratohyal, and, running anteriorly and somewhat mesially, has its mesial fibres inserted on a posterior continuation of the median raphe that gives insertion to the geniohyoideus inferior, while the lateral fibres pass internal (dorsal) to the geniohyoideus inferior and are inserted on the dorsal portion of the raphe that gives insertion to the fibres of that muscle. The fold of the mucous membrane of the mouth cavity that lies beneath the tongue, lies between the lateral portions of the two geniohyoidei.

The mesial edge of the geniohyoideus superior is in contact with the lateral edge of the hyohyoideus inferior, the two muscles there forming a single and practically continuous sheet. The two muscles are however certainly innervated, as fully explained in my recent work (Allis, 1919*d*), the one by the nervus trigeminus, and the other by the nervus facialis, and the fibres of the one pass ventral, and those of the other dorsal, to a fold of the dermal tissues that extends inward between the two muscles and spreads laterally on either side, thus forming a short fold, or pocket, between the two muscles. This pocket opens, superficially, into a long and narrow median space formed by the infolding of the dermis inward and laterally beneath the mesial edge of each gular plate, this space extending anteriorly nearly to the anterior edge of the geniohyoideus inferior.

Muscles innervated by the nervus facialis. The adductor hyomandibularis and adductor operculi, called by Pollard the retractor hyomandibularis and the opercularis, form a single continuous muscle which has its origin on the large concave surface on the dorso-lateral surface of the posterior portion of the opisthotic ridge, and the anterior portion of the muscle is inserted on the internal surface of the hyomandibula and the posterior portion on the internal surface of the operculum.

The hyohyoideus has inferior and superior portions similar to those of *Amia*, the inferior portion being called by Pollard both the mantle muscle and the muscle of the jugular plate. Of it he says: "Behind the intermaxillaris is a separate muscle which arises from a median raphe of its own, and proceeds to the postero-internal angle of the jugular plate. Some fibres pass on into the mantle." Starting from this median aponeurotic raphe, which is common to it and its fellow of the opposite side and lies internal to the raphe of the geniohyoidei, the muscle runs posteriorly in the gill cover and becomes a wide

thin sheet the lateral edge of which is contiguous with the mesial edge of the geniohyoideus superior, as already explained. Slightly posterior to the hind end of the latter muscle, the hyohyoideus ends as a continuous muscle sheet, but separate bundles are continued onward in the gill cover and form the hyohyoideus superior. No fibres of either division of the muscle have any attachment to the gular plate. The hyohyoideus superior continues upward in the gill cover, as a series of small and somewhat stringy muscle bundles, the anterior bundles all ending at the ventral edge of the operculum, but the posterior ones extending the full length of the gill cover, as shown in fig. 45. In my 75 mm. specimen certain bundles of these fibres have undergone specialisation in relation to the external gill, and form a relatively large muscle which lies ventral to the external gill and sends branches into it. The hind end of the ventral edge of the adductor operculi lies dorsal to the external gill, and doubtless also acts upon it, the base of the gill lying between it and the large bundle of the hyohyoideus above referred to.

Muscles innervated by the nervi glossopharyngeus and vagus. The levator muscle of the first branchial arch arises by two independent heads, one of which has its origin on the opisthotic ridge immediately dorsal to the foramen faciale and the other on the lateral plate of the ascending process of the parasphenoid ventral to the latter foramen. The truncus hyomandibularis facialis and the efferent artery of the hyal arch pass between these two heads, the one to enter the jugular canal and the other the canalis parabasalis. Beyond this nerve and artery the two heads of the muscle unite to form a single muscle, which runs postero-ventrally and has its insertion in part on the pharyngobranchial of the first branchial arch and in part on the epibranchial of that arch. The stout ligament that extends from the ventro-postero-lateral corner of the ascending process of the parasphenoid to the dorsal end of the ceratobranchial of the first branchial arch passes across the external surface of that part of the muscle that is inserted on the pharyngobranchial.

Posterior to this muscle there are four levator muscles, all of which have their origins on the large concave surface on the dorso-lateral aspect of the posterior portion of the opisthotic ridge, their surfaces of origin lying ventral to those of the adductores hyomandibularis and operculi. The levatores all run postero-ventrally, each one overlapping externally, to a considerable extent, the next posterior muscle. The levators of the second and third branchial arches are each inserted on the epi-pharyngobranchial of their arch, the levator of the fourth arch being inserted on the dorsal end of the ceratobranchial of its arch. Wiedersheim (1904) says that this latter levator is in large part inserted on a tendinous line which separates it from part of the transversus ventralis, but it was not so found in my specimens. The fifth, and last levator is inserted on the anterior edge of the clavicle, and varies considerably in importance in different specimens, being wholly wanting in certain of them. The first four levators are each innervated by a branch of the nerve of its arch. The innervation of the fifth levator was not determined in the

one fish examined in which the muscle was well developed. In a second fish, in which the muscle had the appearance of being a small slip of the fourth levator, it was innervated by a branch of the nerve of that arch. It represents the *musculus trapezius* of the *Plagiostomi* (Allis, 1917). The dorsal end of the clavicle is enclosed in a sheath-like formation of connective tissue, and certain fibres of the trunk muscles, inserted on it, have somewhat the appearance of a rudimentary *trapezius*, but they do not represent that muscle.

There are, as Pollard states, no *interarcuales dorsales* and no *adductores arcuum branchialium*.

The *interarcualis ventralis* of the first branchial arch arises from the ventral surface of the *ceratobranchial* of its arch, near its distal end, and running almost directly forward is inserted, by tendon, on the dorsal surface of the *ceratohyal*, near its distal end.

The *interarcualis ventralis* of the second branchial arch is somewhat separated, at its origin, into two parts. One of these parts forms the postero-mesial portion of the entire muscle and has its origin immediately distal to the little process, capped with cartilage, near the distal end of the *ceratobranchial* of its arch. The other part forms a wide muscle-sheet which has its origin partly on the distal end of the *ceratobranchial* and partly on the *hypo-branchial* of the arch, but mostly on a ligamentous band which has its origin on the *ceratobranchial* of the first arch and from there extends postero-mesially and is in part inserted on the second arch, and in part either passes between the two parts of the *interarcualis* of that arch, or passes ventral to both of them, and reaches the ventral wall of the pericardial chamber, where it continues onward in that wall and, entering the tough connective tissue that lies between the two *sternohyoidei*, is inserted on the clavicle. From these several surfaces of origin, the fibres of the muscle run anteriorly and antero-mesially and are all inserted on a ligamentous band which is attached, anteriorly, to the dorsal edge of the distal end of the *ceratohyal*, contiguous to and continuous with the tendon of the *interarcualis* of the first arch. From there the band extends postero-mesially dorsal to the afferent arteries of the *hyal* and first branchial arches, and, posterior to the common trunk of those two arteries, turns mesially ventral to the *truncus arteriosus* and is continuous with its fellow of the opposite side.

The *interarcualis ventralis* of the third arch has its origin on the *ceratobranchial* of its arch immediately distal to the little process, capped with cartilage, near the distal end of that element. It lies internal (dorsal) to the *interarcualis* of the fourth arch, and is largely concealed from view until that muscle is removed. It runs antero-mesially and is inserted on the lateral edge of the posterior, cartilaginous portion of the large *basibranchial*. It is innervated by branches of the nerve of its arch.

The *interarcualis ventralis* of the fourth arch has its origin on the *ceratobranchial* of its arch, dorsal to that distal portion of the bone that corresponds to the *hypo-branchials* of the more anterior arches. Running forward and but

slightly mesially, ventral and hence superficial to the interarcualis of the third arch, it is inserted on the ligamentous formation that serves as surface of origin for the anterior portion of the interarcualis of the second arch. It is innervated by the nerve of its arch, and not by the nervus hypoglossus, as Pollard thought probable.

The pharyngo-clavicularis is, at its origin, a single continuous muscle which arises from the anterior edge of the ventral portion of the clavicle. It runs almost directly forward, but slightly dorsally and mesially, and separates into two parts which are inserted, one on that part of the fourth ceratobranchial that corresponds to the ceratobranchial of the more anterior arches and the other on the part that corresponds to the hypobranchial, the two parts straddling the afferent artery of the arch. In *Polypterus ornatipinnis* the muscle fibres are inserted directly on the ceratobranchial. In *Polypterus bichir* the two parts each become tendinous and the tendons are inserted on the ceratobranchial at a considerable distance from each other. The muscle is innervated by branches of the pharyngeal branch of the nervus vagus, as stated in one of my earlier works (Allis, 1917, p. 358). This muscle is not described by Pollard.

The transversus ventralis is a large muscle-sheet which arises, on either side, from the fourth ceratobranchial and has its insertion in a median aponeurotic raphe common to it and its fellow of the opposite side, as Pollard states. It lies directly internal (dorsal) to the pericardial chamber, and is continuous, posteriorly, with the constrictor oesophagei. It is innervated by branches of the pharyngeal branch of the nervus vagus. Wiedersheim (1904) calls it the constrictor pharyngis, and says that its anterior portion is an adductor of the fourth branchial arches.

Longitudinal ventral muscles. There are but two of these muscles, the sternohyoideus and branchiomandibularis.

The sternohyoideus, called by Pollard (1892) the coracohyoideus, has its origin on the dorso-anterior surface of the ventral portion of the clavicle. It is a stout muscle crossed by two aponeurotic septa which extend entirely through it. It ends anteriorly in a stout tendon which passes dorsal to the afferent arteries of the hyal and first branchial arches and is inserted mainly on the hypohyal, but partly also in the tough connective tissues that cover the ventral surface of the tongue. The tendon of the muscle encloses, near its mesial edge, a small bone, and a slender median Y-shaped bone lies between the muscles of opposite sides, enclosed in tough connective tissue that lies between the muscles near their dorsal surfaces. This tough tissue is attached to the ventral surface of the pericardial chamber and encloses the two ligaments, one on either side and already described, that have their origins on the ventral ends of the ceratobranchials of the first and second branchial arches.

The branchiomandibularis, called by Pollard the "branchiomandibularis sui geniohyoideus," arises mostly from the distal end of that part of the third

hypobranchial that forms the ventral one of the two heads by which it articulates with the basibranchial, but certain of its fibres have their origins on the anterior wall of the pericardial chamber. It runs at first ventro-anteromesially and passes, with its fellow of the opposite side, between the basal portions of the tendons of the sternohyoidei, the two branchiomandibulares there being closely pressed together. The muscle then passes ventral to the afferent arteries of the hyal and first branchial arches, and, spreading somewhat, runs directly forward, dorsal (internal) to the hyohyoideus inferior and to both divisions of the geniohyoideus, and is inserted on the dentary close to the symphysis. Near their insertions, the muscles of opposite sides are separated by a tough median septum of fibrous tissue which spreads laterally, on either side, both dorsal and ventral to the muscles, there lying between them and the adjacent portions of the external epidermis and the lining membrane of the mouth cavity.

The muscle is innervated by a branch of the spino-occipital nerves.

ANGIOLOGY

Vena jugularis. The vena jugularis of *Polypterus* is formed by the union of two veins, one of which is supraorbital and the other infraorbital in position. The former corresponds to the orbito-nasal vein of Allen's (1905) descriptions of the mail-checked fishes, but as it closely accompanies the ophthalmic artery and the ramus ophthalmicus superficialis trigemini it may be called the ophthalmic vein. The infraorbital vein closely accompanies the orbito-nasal artery, and it might, accordingly, be called the orbito-nasal vein, but to avoid confusion it seems best to call it simply the infraorbital vein. It apparently has no homologue in Allen's descriptions, for the vein called by him the facialis-maxillaris is said to accompany the ramus maxillaris trigemini in the posterior portion of its course through the orbit. These veins and their several branches were traced in the 75 mm. specimen, and not in the adult, and the following descriptions relate to them as there found.

The ophthalmic vein has its origin in numerous little branches on the dorsal surface of the anterior end of the snout, some of these branches running posteriorly along the dorsal surface of the nasal capsule and others entering that capsule through the fenestra nasalis. These latter branches unite to form a single vein which runs posteriorly along the dorsal surface of the nasal sac, between it and the roof of the nasal capsule, there being accompanied by a branch of the ophthalmic artery, a branch of the ramus ophthalmicus profundus, and the terminal portion of the ramus ophthalmicus superficialis trigemini, the latter nerve containing the latero-sensory fibres that innervate the sense organs in the os terminale and the accessory nasal bone. While in this position the vein receives one large, and possibly other smaller branches coming from the nasal sac, and the vein so formed, together with the accompanying nerves and artery, perforates the roof of the nasal capsule and issues at the anterior end of a groove on its dorsal surface. This groove is short,

leads posteriorly into the preorbital foramen, and through that foramen into the dorso-anterior portion of the orbit. While in this short groove the vein receives a vein formed by the fusion of the branches, above referred to, that arise on the anterior end of the snout and run posteriorly along the external surface of the nasal capsule, and the so-formed vein then traverses the foramen preorbitalis and enters the orbit along with the accompanying nerves and artery.

The short groove above described is shown in the accompanying fig. 10, of the chondrocranium of the adult; is shown in Pollard's figure giving a dorsal view of the chondrocranium of his 21 cm. specimen of *Polypterus*; is apparently shown in Budgett's figure of his 30 mm. larva as a slit-like opening that lies immediately anterior to the preorbital foramen; and is described by Lehn (1918, p. 388) as a large opening (*grosse Öffnung*) which leads into a canal which opens into the orbit and is considered by her to be an anterior eye-muscle canal. Pollard shows a foramen at the anterior end of the groove and calls it the *canalis ethmoidalis*, this name seeming to indicate that he here found a canal and that he considered it to be the homologue of the similarly named canal in Gegenbaur's (1872) descriptions of the *Selachii*. There is no canal here in my 75 mm. specimen, but conditions found in the adult indicate that the anterior end of the groove might become roofed by cartilage and so be converted into a short canal. This canal would, however, not be the homologue of the *canalis ethmoidalis* of Gegenbaur's descriptions of the *Selachii*, for that canal simply traverses the cartilage of the nasal capsule from its dorsal to its ventro-lateral surface without at any point entering or communicating with the cavity of the capsule. In *Heptanchus* I find this canal traversed by an important vein which connects the ophthalmic and infra-orbital veins, but the canal is not traversed either by the ophthalmic artery or by the lateralis branches of the ophthalmicus superficialis trigemini, these latter structures running forward on the dorsal surface of the nasal capsule without at any point perforating it. The canal of *Heptanchus* and the groove or canal of *Polypterus* are thus not homologous, and I have accordingly called the groove of *Polypterus* the antero-mesial ethmoidal groove, to distinguish it from the postero-laterally situated canal of *Heptanchus*.

Having entered the orbit, the ophthalmic vein runs posteriorly in its dorsal portion and, in the 75 mm. specimen, receives several branches: one from the *musculus obliquus superior*; two from the dorsal surface of the cranium through foramina that perforate the roof of the orbit; two from the cranial cavity, each branch issuing through an independent foramen in the cartilaginous portion of the orbital wall; a branch formed by the fusion of one vein coming from the *musculus rectus superior* and another from the eyeball, accompanying the *nervus ciliaris longus*; a branch from the temporal and pterygoid divisions of the *musculus adductor mandibulae*; and one that is formed by branches from the *masseter* division of the adductor, from the *levator maxillae superioris*, and from the mandible. The latter one of these

several branches is evidently the mandibular vein, for it is the only branch from the mandible that reaches the jugular vein. It accompanies, in its course, the ramus mandibularis trigemini, and receives a branch that accompanies the ramus maxillaris trigemini. It is accordingly a maxillo-mandibular vein, and will be so referred to.

After receiving these several branches, the ophthalmic vein has become what I wrongly called, in an earlier work (Allis, 1908*b*), the external jugular, and the posterior one of the two branches received from the cranial cavity was there said to probably be the encephalic vein of Allen's (1905) descriptions of the Loricati. In favour of the latter assumption is the fact that the vein receives branches from the region of the hypophysis, but, as noted in my earlier work, its foramen of exit has a markedly different position from that of the encephalic vein of the Loricati.

The ophthalmic vein, in its course through the orbit, lies along the mesial wall of the orbit, internal to the musculus temporalis and dorsal to the nervi opticus, oculomotorius and profundus. When it reaches the hind end of the orbit it lies beneath the overhanging anterior portion of the postorbital process, and there passes between the ganglia formed on the lateralis-communis and general sensory-motor roots of the nervus trigeminus, ventral to the former and dorsal to the latter. These ganglia are both extracranial in position, and they and the ophthalmic vein all lie beneath the overhanging postorbital process, that process here enclosing the dorso-anterior portion of the anterior semicircular canal. Posterior to this, the vein and ganglia lie in a recess in the cranial wall, closed externally by the lateral plate of the ascending process of the parasphenoid, the chamber so formed being "the trigeminus portion of a perfectly typical trigemino-facialis chamber" (Allis, 1908*b*, p. 220), and strictly similar to the trigemino-facialis chamber of Stensiö's (1921) descriptions of *Birgeria mougeoti*. The general sensory-motor root of the trigeminus now soon perforates the mesial wall of this chamber, its foramen lying, in the adult, at the bottom of a small but marked recess on the cerebral surface of the cranial wall. Posterior to this, the lateralis-communis root traverses the cranial wall through a short canal which opens into the anterior end of the labyrinth recess, the ophthalmic vein continuing posteriorly external to the cranial wall and dorsal to the general sensory-motor root, and being joined, posterior to the latter root, by the infraorbital vein to form the vena jugularis.

The infraorbital vein arises in the tissues at the anterior end of the snout, and runs posteriorly along the ventral surface of the nasal capsule, no branches, so far as could be traced, entering the nasal capsule and running posteriorly between that capsule and the nasal sac, as is the case with the ophthalmic vein. Near the hind end of the nasal capsule it receives a large branch from the nasal sac, and another from the labial fold. The branch from the nasal sac traverses a foramen in the floor of the nasal capsule together with a branch of the maxillary artery and a branch of the ramus maxillaris trigemini, and in the nasal sac it forms anastomoses both with the ophthalmic vein and with

a vein that comes from the cranial cavity through the foramen olfactorium. The infraorbital and ophthalmic veins are thus here connected with each other, but this connection is by branches that traverse the nasal sac, instead of, as in the Selachii, by a branch that passes outside the nasal capsule.

The infraorbital vein, after receiving these two branches, runs posteriorly along the floor of the orbit, receiving branches from the maxillary region, from the musculus obliquus inferior, rectus internus, rectus inferior and rectus externus, and one from the eyeball that accompanies the nervus ciliaris brevis. Close to this latter vein it apparently receives a branch that comes from the large orbital lymph sinus, that sinus also apparently being connected with that branch of the ophthalmic vein that accompanies the nervus ciliaris longus. The infraorbital vein here lies ventral to the musculus pterygoideus, along the lateral edge of the parasphenoid and immediately dorsal to the common carotid artery, and when it reaches the hind end of the orbit, it passes dorsal to the anterior edge of the horizontal plate of the ascending process of the parasphenoid, and, lying in the angle between that plate and the mesial plate of the process, receives the pituitary vein, which issues from the pituitary fossa through the pituitary foramen. The infraorbital vein then runs upward posterior to the general sensory-motor root and ganglion of the trigeminus, and falls into the ophthalmic vein, as above described.

From this description of these two veins it is evident that, in this fish, the basal portion of the vena ophthalmica is formed by that portion of the vena capitis lateralis that lies anterior to the nervus facialis, and the vena infraorbitalis by the corresponding portion of the vena capitis media plus the posttrigeminus commissure between that vein and the vena capitis lateralis. The conditions seem to indicate that a pretrigeminus commissure between the venae capitis media and lateralis primarily existed, and that the vena maxillo-mandibularis acquired connection with it. The commissure then lost its connection with the vena capitis media, but retained that with the vena capitis lateralis and so became the basal portion of the vena maxillo-mandibularis. The vena infraorbitalis retained its connection with the primitive vein (cardinalis anterior), as did also the pituitary vein. This would fully explain the conditions actually found, and the vena jugularis, instead of beginning anterior and ventral to the nervus trigeminus, begins posterior and dorsal to it, this being, so far as I know, exceptional in fishes, and an excellent example of how difficult it is to give names to these veins of fishes that will definitely indicate their homologies.

The vena jugularis, formed, as above set forth, by the union of the ophthalmic and infraorbital veins, at first lies internal to that portion of the lateral plate of the ascending process of the parasphenoid that lies dorso-anterior to the line of fusion with the mesial plate of that process, and then enters that short canal in the cartilaginous side wall of the cranium that has been already referred to as the jugular canal. Posterior to the anterior opening of this jugular canal, the lateral and mesial plates of the ascending

process of the parasphenoid fuse with each other, and the projecting dorsal end of the so-formed plate lies against the outer wall of the jugular canal. The jugular vein is accompanied, as it enters its canal, by the ramus palatinus facialis and a general sensory branch sent from the trigeminus ganglion to the truncus hyomandibularis facialis. The ramus palatinus facialis soon falls into the communis root of the nervus facialis, that root perforating the mesial wall of the jugular canal along with the lateralis and motor roots of the nerve. This foramen is thus the foramen primitivum faciale, and it lies ventral to the vena jugularis. Shortly posterior to this foramen, the jugular canal opens on the external surface of the chondrocranium, but it is still, for a few sections, closed externally by the fused dorsal ends of the mesial and lateral plates of the ascending process of the parasphenoid. The mesial plate of the ascending process then vanishes in the sections, and the vein and the nervus hyomandibularis facialis lie in a groove in the cartilaginous lateral wall of the cranium, still enclosed externally, for a short distance, by the hind edge of the lateral plate of the process. The posterior opening of the jugular canal is accordingly the foramen faciale of the skull of the adult. Posterior to this foramen the vein lies in the jugular groove on the lateral surface of the cranium, and there receives venous vessels from the hyal and each of the branchial arches, and also the vena jugularis interna, which issues from the cranial cavity through the foramen vagum.

Afferent and efferent arteries. The truncus arteriosus (figs. 51-54) gives off, immediately after issuing from the pericardial chamber, a large vessel on either side which runs laterally anterior to the musculus branchiomandibularis, at its point of origin, and immediately separates into two parts, one ventral to the other, which are, respectively, the afferent artery of the second branchial arch and the united trunks of the afferent arteries of the third and fourth arches.

The afferent artery of the second branchial arch runs outward internal (dorsal) to the interarcualis ventralis of the fourth arch, and posterior both to the head of the hypobranchial of its own arch and to the interarcualis ventralis, and reaches the ventral surface of the ceratobranchial of its arch.

The trunk formed by the united afferent arteries of the third and fourth branchial arches turns posteriorly, passes between the two articular heads at the distal end of the third hypobranchial, then internal (dorsal) to the interarcualis ventralis of the third arch, at its insertion, and at the hind edge of that muscle separates into its two parts, the afferent arteries of the third and fourth arches. The afferent artery of the third arch turns laterally and reaches the ventral surface of the ceratobranchial of its arch. The afferent artery of the fourth arch continues posteriorly, passes across the dorsal (internal) surface of the fourth ceratobranchial, in the marked groove on that surface and between that bone and the related dermal plates, and turning dorso-laterally across the hind edge of the ceratobranchial, passes between the inferior and superior divisions of the musculus pharyngo-clavicularis and reaches the

ventral (external) surface of its ceratobranchial. This artery thus has the relations to the distal end of its ceratobranchial that the artery of the third arch has to the ventral one of the two articular heads at the distal end of its hypobranchial, which suggests that these parts of these two bones may be homologous, for otherwise it would be difficult to explain how the artery has come to twist completely around the branchial bar of its arch in order to reach its ventral (external) surface.

After giving off this large branch on either side, the truncus arteriosus continues forward, and approximately in the level of the articular head of the hypobranchial of the first arch gives off a large branch on either side and then continues onward as a small and unimportant median artery which could be traced a short distance in the adult, but was not even evident in the 75 mm. specimen. The large branch on either side lies dorsal (internal) to the musculus branchiomandibularis, and soon separates into the afferent arteries of the hyal and first branchial arches. The latter (fig. 52) runs laterally across the ventral surface of the tendon of the musculus sternohyoideus and ventral to the interarcualis of its arch, and reaches the ventral surface of the ceratobranchial of its arch. The afferent hyal artery runs posteriorly along the ventral surface of the musculus sternohyoideus and reaches the ventro-mesial edge of the ceratohyal, near its proximal end, where it turns dorso-laterally along the posterior surface of the epihyal and the corresponding edge of the hyomandibula, and becomes the efferent artery of the arch.

The median dorsal aorta, running forward, reaches the hind end of the cranium, and there enters the aortic canal in the basis cranii. Running forward in that canal it separates into its two branches, the lateral dorsal aortae, each of which issues from the aortic canal into the canalis parabasalis in the ascending process of the parasphenoid. Immediately before entering the aortic canal, the dorsal aorta receives the efferent artery of the second branchial arch, and immediately posterior to that artery the efferent arteries of the third and fourth branchial arches, these two latter arteries usually being fused to form a single trunk. Posterior to these several arteries the dorsal aorta gives off a single artery which runs posteriorly beyond the head region and was not traced, and then the subclavian arteries. Immediately after issuing from the aortic canal, the lateral dorsal aorta of either side receives, close together, the efferent arteries of the hyal and first branchial arches, and then continues onward as the common carotid.

The afferent and efferent arteries of the branchial arches all lie between the two rows of branchial rays of their respective arches, the efferent artery lying internal to the afferent artery and each of them receiving, at the level of the dorsal end of the ceratobranchial, a relatively large branch which comes from those branchiae that lie dorsal to this point. The efferent artery of the hyal arch comes upward along the hind edge of the hyomandibula, and passes, with the ramus hyoideus facialis, between the hyomandibula and the ligament that extends from its opercular process to the accessory hyomandibula.

The efferent arteries were not farther traced in the adult, but in the 75 mm. specimen the artery of each of the first three branchial arches falls, at the ventral end of its arch, into a ventral longitudinal commissure which lies internal to all the afferent arteries and hence is an internal lateral hypobranchial artery (Allis, 1912). The efferent artery of the fourth arch does not fall into this commissure, but the subclavian artery does, this latter artery being, in fact, a direct posterior continuation of the commissure. From the efferent artery of the fourth arch a large branch is given off near the proximal end of the ceratobranchial of the arch, and sends branches to the oesophagus, to the air-bladder and to the heart. Between the roots of the second and third afferent branchial arteries, the lateral hypobranchial receives a small branch from the truncus arteriosus, and, continuing onward beyond the first efferent artery, passes internal to the afferent hyal artery and, turning mesially, enters the thyroid gland. There it separates into two parts, one of which continues mesially and joins its fellow of the opposite side, the other turning anteriorly and forming an anterior prolongation of the hypobranchial. The latter artery soon gives off two branches, one of which runs upward along the ventromesial (morphologically external) edge of the ceratohyal, and the other in similar relation to Meckel's cartilage, the former lying posterior to the ramus mandibularis internus facialis and the other anterior to that nerve. These two arteries are, the one the anterior efferent hyal artery and the other either the afferent mandibular artery, or the posterior efferent artery of that arch (Allis, 1916), and dorsal to the ramus mandibularis internus facialis they fuse with each other, and then immediately fall into a cross-commissural vein which extends from the efferent hyal artery to the mandibular branch of the carotid artery, the anterior portion of this commissure running forward along the external surface of the ventro-lateral edge of the palatoquadrate. Dorsal to the commissure the anterior efferent hyal artery continues upward, accompanies the ramus hyoideus facialis as it passes inward across the hind edge of the hyomandibula, and internal to the latter element falls into the epibranchial longitudinal commissure, described immediately below. Anterior to this artery a small artery arises from the cross-commissure and runs upward along the external surface of the palatoquadrate, between it and the overlying muscles, and apparently represents a dorsal continuation of the afferent mandibular artery.

Anterior to the afferent mandibular artery, the lateral hypobranchial artery continues onward, is joined by the terminal branches of the mandibular branch of the carotid, and then ends in a cross-commissural vessel which connects it with its fellow of the opposite side.

A dorsal, or epibranchial longitudinal commissure arises, in my 75 mm. specimen, by three roots, two from the median dorsal aorta before it enters the aortic canal, and one from the lateral dorsal aorta after it issues from that canal, a branch of this latter root going to the thymus.

Carotid arteries. The main branches of the carotid arteries were described

by me in 1908, and brief reference to them was made in a later work (Allis, 1916). In the work published in 1908, and also in a work published in that same year on the pseudobranchial and carotid arteries of *Amiurus* (Allis, 1908*a*), the descriptions are, in certain places, greatly confused, and I am unable to account for it excepting on the assumption that there was some resetting of the type after the proofs had been corrected. I was unfortunately absent from my laboratory at the time, and the proofs were corrected and returned by an assistant.

In my 75 mm. specimen the lateral dorsal aorta of either side issues from the aortic canal into the posterior portion of the canalis parabasalis, and there immediately receives the efferent arteries of the hyal and first branchial arches. It then becomes the common carotid, and runs forward in the canalis parabasalis accompanied by a lymph vessel, a sympathetic nerve, and a communicating branch from the nervus glossopharyngeus to the ramus palatinus facialis which would seem to represent, in this fish, Jacobson's anastomosis. No branch of the common carotid is sent into the jugular canal, but immediately anterior to the anterior opening of that canal a branch is sent upward posterior to the general sensory ganglion of the nervus trigeminus and then forward dorsal to that ganglion but ventral to the related lateralis-communis ganglion, this branch corresponding to the ophthalmic branch of the external carotid of *Amia* and the Teleostei. A branch is sent upward from this artery along the anterior surface of the spiracular canal, and other branches to the muscoli pterygoideus, masseter, temporalis and obliquus superior, and to the dorsal surface of the head, the artery then traversing the foramen pre-orbitalis and accompanying the branches of the vena ophthalmica, as already described. Approximately in the transverse plane where this ophthalmic artery separates from the common carotid, the communicating branch from the nervus glossopharyngeus falls into the ramus palatinus facialis, the latter nerve then passing dorso-lateral, and hence posterior, to the ophthalmic artery.

After giving off this ophthalmic branch the remainder of the common carotid issues from the canalis parabasalis and then runs forward in the groove on the lateral edge of the body of the parasphenoid, accompanied by the lymph vessel that traverses the canalis parabasalis with it, and also by the ramus palatinus facialis, and when it reaches the hind edge of the foramen opticum it gives off the maxillo-mandibularis artery. That part of the carotid that lies between the latter artery and the ophthalmic artery thus contains both the internal carotid and a large part of the external carotid of the non-siluroid Teleostei, but, because of its position, so similar to that of the internal carotid of *Amiurus* (Allis, 1908*a*), it was given that name in my earlier work. It seems, however, better to consider it as still a part of the common carotid, the internal carotid being that part of the artery that remains after the maxillo-mandibular artery is given off.

The maxillo-mandibular artery runs ventro-laterally and soon separates into its maxillary and mandibular portions. The maxillary artery runs for-

ward through the orbit, giving off certain branches, and then traverses the foramen by which the nasal branch of the vena maxillaris issues from the nasal capsule. Inside that capsule a branch is sent into the nasal sac to join and fuse with a terminal branch of the orbito-nasal artery, the remainder of the artery running forward between the sac and the wall of the nasal capsule to issue through the fenestra nasalis. The mandibular artery runs ventrally and reaches a point that lies slightly posterior to the angle of the gape of the mouth, where it gives off a number of little branches which form the "much vasculated tissue" referred to in my earlier work (Allis, 1916, p. 116), one of these branches being the hyomandibular cross-commissural vessel there described. The mandibular artery then sends a branch into the labial fold, where it supplies both external and internal surfaces of the labial cartilage, and itself continues onward into the mandible and separates into two terminal branches, both of which fall into the lateral hypobranchial artery. The much vasculated tissue above referred to lies somewhat dorsal to the ventro-lateral edge of the palatoquadrate, and mesial to the bottom of the longitudinal groove on the dorsal surface of the buccal cavity that I have recently described as the secondary superior alveolo-labial furrow (Allis, 1919c).

The internal carotid artery, after it separates from the maxillo-mandibular artery, immediately gives off two branches, arising close together, one of which goes to the choroid gland and hence corresponds to the arteria ophthalmica magna of other fishes. The other branch is the posterior cerebral artery, which perforates the cranial wall immediately posterior to the nervus opticus and turns posteriorly in the cranial cavity, giving off as it traverses the cranial wall, a branch which goes to the eyeball and is apparently the arteria centralis retinae. The internal carotid artery then immediately gives off the anterior cerebral artery, which perforates the cranial wall between the posterior cerebral artery and the nervus opticus and supplies the anterior portion of the cranial cavity, a terminal branch traversing the foramen olfactorium and entering the nasal sac. The remainder of the artery is now the orbito-nasal artery, which continues onward, sends a branch to the choroid gland, another to accompany the ramus palatinus facialis and others to certain of the muscles of the eyeball, and then itself passes over the lateral edge of the cartilage of the basis cranii and penetrates the basal portion of the membranous lateral wall of the cranial cavity. Running forward in this membrane, it enters the cranial cavity, and then, always lying in, or external to the lining membrane of that cavity, and hence never entering the cavum cerebrale cranii, it reaches and enters the nasal capsule through the foramen olfactorium.

The internal carotid of my 75 mm. specimen of this fish, like that artery of *Amiurus*, thus passes lateral and then dorsal to the trabecula in order to enter the cranial cavity, instead of passing ventral and then mesial to the trabecula as it does in all other fishes that I know of.

Trigemino-facialis chamber. From the above descriptions of the veins,

arteries and nerves of this region, it is evident that the canal in the cranial wall traversed by the vena jugularis represents some part of a trigemino-facialis chamber, and it is probable that it represents the pars jugularis, and that part only of the posttrigeminal portion of the chamber. The pars ganglionaris of this part of the chamber must then be represented either in the short canal by which the nervus facialis traverses the cartilage of the cranium, or in some part of the anterior portion of the labyrinth recess. The trigeminal part of the chamber is represented in the space, between the lateral wall of the chondrocranium and the ascending process of the parasphenoid, that lodges both the trigeminal ganglion and the vena jugularis, and it would seem as if it must represent the entire chamber notwithstanding that it is not closed externally by cartilage. This condition of the chamber is apparently primitive, for it closely resembles that described by Stensiö in the Palaeoniscidae, as already stated.

NEUROLOGY

Nervus and lobus olfactorius. The nervus olfactorius of the adult is long, has a long intracranial course, and arises from a bulbus olfactorius that is separated from the remainder of the telencephalon by a slight constriction only, as Bing and Burckhardt (1905) have stated. The rhinocele extends about half the length of the bulbus.

In my 75 mm. specimen the nervus olfactorius is short, while the bulbus is relatively long, as it is shown to be in Bing and Burckhardt's figure of a 16.5 cm. specimen. The bulbus extends forward to the foramen olfactorium, and from its anterior end two bundles of fibres arise, one from its dorsal and the other from its ventral half, the dorsal half of the bulbus projecting forward slightly beyond the ventral one. These two bundles form the nervus olfactorius, which runs ventrally and but slightly antero-laterally, and enters the nasal capsule on the dorso-mesial aspect of its hind end. The bulbus is entirely separate from its fellow of the opposite side, but closely pressed against it, as far back as the line of attachment of the anterior edge of the tela choroidea.

There is, as shown in Bing and Burckhardt's figure of a median sagittal section of an 18 cm. specimen, a deep median fold in the tela choroidea, but the anterior end of the bottom of that fold, as there shown, lies at a much higher level than in my 75 mm. specimen, where it descends almost to the level of the floor of the third ventricle. The floor of the latter ventricle is here thin, and in the transverse plane of the foramen interventriculare rises slightly in the median line, so that it has, in transverse sections, the shape of an inverted V, the top of this inverted V meeting the bottom of the median fold of the tela. Anterior to this point there is, on either side, a tall and narrow anterior prolongation of the ventricle, which forms a sort of diverticulum extending through 10 sections of 15μ each. The dorsal end of each diverticulum is enlarged, and is prolonged anteriorly as a short projecting pocket which lies on the dorsal surface of the related bulbus. Venous vessels that come from the nasal sacs with the nervi olfactorii lie, some in the dorsal and some in the

ventral angle between the bulbi of opposite sides, and becoming united at the hind ends of the diverticula by dorso-ventral commissures, continue posteriorly in the hollow of the fold of the tela, and form the choroid plexus. The conditions in my 75 mm. specimen thus here so closely resemble those shown by Johnston (1911, figs. 1 and 45) both in a median view of the brain of the adult *Amia* and in a median sagittal section of a 25 mm. embryo of the same fish, that it is probable that the lamina supraneuroporica has a similar position in each of them, and if Johnston is correct in placing this lamina ventro-posterior to the anterior end of the bottom of the median fold of the tela in his 25 mm. *Amia*, it must form the anterior portion of what is actually the floor of the third ventricle of *Polypterus*, and not, as Bing and Burckhardt (1905) concluded, the anterior portion of the bottom of the median fold of the tela, which forms the median line of the roof of the third ventricle.

The dorsal edge of the lateral wall of the telencephalon has been everted, and there is an external sulcus extending the full length of the primordium hippocampi, approximately at the middle of the height of the lateral wall of the telencephalon, and it is particularly deep in its middle portion. The lateral edge of the tela choroidea is everywhere attached to the ventral edge of this everted portion of the lateral wall.

Nervus terminalis. What seems to be the nervus terminalis of either side is found, in my 75 mm. specimen, as two nervous strands which are wholly separate and independent of each other up to the point where they enter the nasal capsule. One of these strands arises from the dorso-lateral surface of the bulbus olfactorius, and the other from its ventral and ventro-lateral surfaces. Each strand arises by two or more rootlets which look, in sections, like protruding portions of the superficial layer of the bulbus, and each strand runs forward along the related surface of the bulbus to its anterior end. Each strand then follows the related root of the nervus olfactorius, and, as it enters the nasal capsule, fuses with its fellow. No ganglion cells could be recognised in any part of the nerve.

Nervus opticus. There is a well developed optic chiasma which lies upon the dorsal surface of the parasphenoid slightly anterior to the slight depression that lodges the hypophysis. The chiasma forms the anterior end of a marked ridge, formed by the hypothalamus, on the ventral surface of the brain, and the base of the ascending tract of the opticus is, in lateral view, separated from the chiasma by a slight furrow. From there the nervus opticus runs antero-laterally and slightly dorsally and traverses the sphenoid bone through the foramen opticum, passing, in my 75 mm. specimen, dorsal to the cartilaginous trabecula. The nerve then gradually curves somewhat more laterally and penetrates the sclerotic ventro-posterior to its central point. It is a solid nerve, without any indication of folding of any sort.

Nervus oculomotorius. This nerve, after its origin from the base of the brain, runs antero-laterally and issues from the cranial cavity through a foramen in the sphenoid common to it and the radix profundi (Allis, 1908b;

Lehn, 1918), the oculomotorius there lying anterior to the radix profundus. The oculomotorius then runs forward between the profundus ganglion and the cranial wall, closely pressed against the dorso-mesial surface of the ganglion, and there separates into its superior and inferior divisions. There is no slightest indication of an anastomosis with the profundus, such as Lehn found in her specimen. The superior division runs upward mesial to the ramus ophthalmicus profundus and innervates the rectus superior. The inferior division runs forward ventral to the nervus profundus and comes into intimate contact with the ciliary ganglion, there unquestionably being connected with that ganglion by strands which form the radix brevis. The nerve then continues onward, passing ventro-lateral to the rectus superior and mesial to the rectus externus and sends a branch to the rectus inferior. It then passes dorsal to the latter muscle and ventral to the nervus opticus, sends one or two branches to the rectus internus, and then passes ventral to the latter muscle and terminates in the obliquus inferior.

The course and distribution of this nerve is thus as it is in *Amia* excepting in that the inferior division of the nerve passes dorsal instead of ventral to the rectus inferior, this relation of the nerve to the latter muscle being, so far as I know, exceptional in the gnathostome fishes. The recti inferior and externus arise close together from the tendinous stalk that gives origin to them and also to the rectus superior, and the oculomotorius passes close to their points of origin from that stalk. A slight shifting of the point of origin of the inferior muscle would make it creep, at its origin, across the nerve, and it would then lie dorsal to it, as it does in *Amia*, without having either cut through the nerve or been cut through by it.

Nervus trochlearis. This nerve has the usual origin, and after a relatively long intracranial course issues from the cranial cavity through its foramen in the sphenoid. It then runs forward and becomes closely applied to the ventro-mesial surface of the ramus ophthalmicus superficialis trigemini, passes ventral to that nerve but dorsal to all the other nerves of the orbit, and enters the obliquus superior near its point of origin from the cranium.

Nervus abducens. This nerve arises, in the 75 mm. specimen, by two rootlets quite near the mid-ventral line of the brain, and from there runs antero-laterally and issues from the cranium with the nervus trigeminus through a large perforation of the cranial wall which is closed by fibrous tissue which surrounds the nerves and completely separates them from each other. That part of this tissue that encloses the abducens later undergoes chondrification, and the nerve then traverses a short canal in the cranial wall which lies postero-ventral to the foramen trigeminum and opens on the floor of the cranial cavity immediately posterior to the base of the postclinoid wall.

After issuing from its foramen the nerve runs antero-laterally ventral to the nervus trigeminus and enters and supplies the musculus rectus externus.

Nervus profundus. The root of the nervus profundus issues from the medulla, in the adult, anterior to but in contact with the root of the trigeminus,

while in the 75 mm. specimen it issues from the medulla slightly anterior to the anterior rootlet of the trigeminus. Its point of origin from the medulla indicates that its fibres are quite certainly all general cutaneous ones. The root runs forward in the cranial cavity and, in the 75 mm. specimen, traverses a perforation of the cartilaginous cranial wall that is common to it and the nervus oculomotorius and that lies anterior to the foramen trigeminum. As the two nerves traverse this perforation of the cranial wall, they are separated from each other by membrane, their two foramina, at this age, thus not being actually confluent, the primordial membranous cranial wall simply not having undergone either chondrification or ossification between the two nerves. Having issued through this foramen, a ganglion immediately forms on the root of the profundus, the nervus oculomotorius lying between this ganglion and the cranial wall and the nervus abducens lying immediately ventral to the ganglion. No communicating branch is received from the trigeminus ganglion, and no sympathetic nerve could be traced to it. There is, as already stated, no anastomosis with the nervus oculomotorius.

The radix longa arises, in the 75 mm. specimen, from the ventral surface of the profundus ganglion, and running forward enters a small ciliary ganglion which lies directly against the inferior division of the nervus oculomotorius, at the point where the branch of that nerve to the musculus rectus inferior is given off, and is there unquestionably connected with the oculomotorius by fibres that represent the radix brevis. The radix longa is not described by Lehn, but it is probably represented in that anastomosis of the profundus and oculomotorius to which she refers. From the ciliary ganglion the ramus ciliaris brevis arises, and passing between the recti superior and externus and dorsal to the rectus inferior, has a course approximately parallel to the latter muscle and perforates the sclerotic between the point of insertion of that muscle and the point where the nervus opticus enters the eyeball. Close to, or coincident with, the point where this nerve perforates the sclerotic, that cartilage is also traversed by a branch of the orbito-nasal artery and a branch of the infraorbital vein.

Anterior to the point of origin of the radix longa from the profundus ganglion, either a single branch arises from that ganglion, or two branches arise close together, the one or two branches forming the portio ophthalmici profundus shown by van Wijhe (1882) in his figure of this fish. Branches of this nerve, or nerves, run upward and forward, some passing mesial and others lateral to the ramus ophthalmicus superficialis trigemini, and, accompanying branches of the latter nerve, are distributed to tissues on the dorsal surface of the head in the region of organs 5 and 6 supraorbital. No complete anastomosis of any of these branches with the ramus ophthalmicus superficialis was noticed.

From the anterior end of the profundus ganglion the ramus ophthalmicus profundus and the ramus ciliaris longa arise, either close together or as a single trunk. The ciliaris longa runs forward between the recti superior and

externus, and passing dorsal to the nervus opticus perforates the sclerotic dorso-lateral to that nerve, between it and the point of insertion of the rectus superior, there being accompanied by a branch of the orbito-nasal artery. Lehn found this nerve arising from the ramus ophthalmicus in the transverse plane of the foramen opticum.

The ramus ophthalmicus profundus runs forward between the recti superior and externus, there lying between the superior and inferior divisions of the nervus oculomotorius, and then continues onward dorsal to the nervus opticus. A branch is here sent upward to join, but not fuse with, the ramus ophthalmicus superficialis trigemini, this branch and the main nerve both traversing a large orbital lymphatic space. Branches of this branch of the profundus perforate the roof of the orbit and are distributed to tissues on the dorsal surface of the head in the region of organ 4 supraorbital, one branch accompanying the lateralis branch to that organ. After giving off this branch the ramus ophthalmicus profundus continues onward and upward, passes ventral to the nervus trochlearis, and, in the 75 mm. specimen, ventral to the musculus obliquus superior, close to its origin in the preorbital canal. In one adult specimen that was examined the nerve also passed ventral to the obliquus superior, but in the specimen used for illustration, the nerve passes ventral to the trochlearis but dorsal to the obliquus superior. Beyond this point the nerve traverses the preorbital canal with the ophthalmicus superficialis trigemini, and on issuing from that canal lies in the antero-mesial ethmoidal groove. A branch is there sent to tissues in the region of organ 3 supraorbital, the terminal portion of the nerve then traversing the perforation in the roof of the nasal capsule at the anterior end of the ethmoidal groove and running forward in the nasal capsule accompanied by the terminal portion of the ophthalmicus superficialis trigemini and a vein and artery, as already described. As the nerve traverses the capsule one or two branches are sent upward through its roof to the region of organ 2 supraorbital, and on issuing from the capsule through the fenestra nasalis the remainder of the nerve is distributed to tissues in the region of organ 1 supraorbital, and to the extreme anterior end of the snout.

The nervus profundus of this fish thus sends branches to the entire region that, in most teleosts, is innervated by general cutaneous branches of the ramus ophthalmicus superficialis trigemini. This has been fully discussed in an earlier work (Allis, 1918*b*), and it was there said that the portio ophthalmici profundus and the ramus ophthalmicus profundus of this fish were quite certainly the homologues, respectively, of the frontal and nasal branches of the ophthalmic nerve of higher vertebrates.

Nervus trigeminus. The nervus trigeminus is currently considered to contain only general sensory and motor fibres, the communis and lateralis fibres that are associated with it being assigned to the nervus facialis. As so conceived, this nerve of the adult *Polypterus* arises from the medulla by a single root common to it and the nervus profundus. In the 75 mm. specimen these two

roots are wholly independent, and the nervus trigeminus arises by two rootlets, one of which is motor and the other apparently wholly general cutaneous. The root of the trigeminus, so formed, runs antero-laterally, traverses the foramen trigeminum, and then immediately swells into a large ganglion which is apparently wholly general cutaneous, the motor component of the nerve lying imbedded in the ventral surface of the ganglion. The root of the nerve, as it traverses its foramen, is accompanied by the nervus abducens, but not by any recognisable vein or artery. The ganglion lies in the trigeminus portion of the trigemino-facialis chamber, immediately anterior to that portion of the infraorbital vein that runs upward between the nervi trigeminus and facialis to fall into the ophthalmic vein, the latter vein passing dorsal to the ganglion. Dorsal to this ganglion and separated from it by the ophthalmic vein, is a ganglion formed by the fusion of two ganglia, one of which is formed on a lateralis root and the other on an intracranial branch from the communis root of the nervus facialis. The larger part of the ganglion on the lateralis root lies in the trigemino-facialis chamber, while the ganglion of the communis root is largely intracranial in position and is continuous with the intracranial portion of the facialis ganglion. The roots and ganglia of this fish thus resemble those in *Scorpaena* (Allis, 1909, p. 81), excepting in that the communis fibres issue from the cranial cavity with the lateralis fibres instead of with the general cutaneous ones.

From the lateralis-communis ganglion three nerves arise, the rami ophthalmicus superficialis, buccalis, and oticus, and in addition to these nerves two separate bundles of fibres are sent to the general cutaneous ganglion. The ramus ophthalmicus superficialis contains both lateralis and communis fibres, but no general cutaneous ones could be traced to it either from the general cutaneous ganglion itself, or from any of its branches. The nerve is accordingly neither an ophthalmicus facialis, an ophthalmicus lateralis, nor an ophthalmicus superficialis trigemini, as those terms are currently employed, for the two former terms are considered to designate a nerve formed exclusively of lateralis fibres, and the latter a nerve that contains a considerable proportion, at least, of general cutaneous fibres. There is also the further question as to whether the lateralis and communis fibres contained in this nerve belonged primarily to the trigeminus or to the facialis. I have accordingly thought best, as fully explained in an earlier work (Allis, 1918*b*), to readopt for this nerve the time-honoured term ramus ophthalmicus superficialis trigemini, referring, when necessary, to the lateralis or communis fibres as the lateralis or communis trigemini. Lehn calls this nerve the ramus supraorbitalis ophthalmici lateralis, and considers it to be a branch of a nerve which she calls the nervus ophthalmicus lateralis, the other branches of which are the rami infraorbitalis ophthalmici lateralis, maxillaris ophthalmici lateralis, and mandibularis externus ophthalmici lateralis. She says that an independent ramus ophthalmicus superficialis trigemini, comparable to that found in other fishes, is wanting in *Polypterus*.

The ramus ophthalmicus superficialis trigemini, thus defined, runs forward internal to the musculus temporalis and dorsal to all the nerves of the orbit, traverses the preorbital canal at the dorso-anterior corner of the orbit, and enters the antero-mesial ethmoidal groove on the dorsal surface of the nasal capsule. At the anterior end of that groove the nerve traverses the foramen that there perforates the roof of the nasal capsule, and runs forward in that capsule between its cartilaginous roof and the lining membrane of the nasal sac. As it traverses the orbit branches are sent upward through its roof to supply the anterior head-line of pit organs and organs 6, 5 and 4 of the supra-orbital latero-sensory canal, these organs all lying on, or in, the frontal bone. As the nerve traverses the ethmoidal groove a branch is sent to organ 3 supra-orbital, which lies in the nasal bone, and as it traverses the nasal capsule a branch is sent upward through the roof of the capsule to organ 2 supraorbital, which lies in the accessory nasal. The nerve then issues through the fenestra nasalis, and its lateralis component terminates in organ 1 supraorbital, which lies in the os terminale. Communis fibres doubtless accompany the lateralis fibres in all these branches of the nerve, and the branches are accompanied by general cutaneous branches of the nervus ophthalmicus profundus, as already described.

The ramus buccalis trigemini arises, like the ramus ophthalmicus superficialis, from the lateralis-communis ganglion and contains both lateralis and communis fibres. The nerve runs forward external to the musculus temporalis and then along the floor of the orbit until it reaches its anterior end. There it perforates the ventro-lateral portion of the wall of the nasal capsule, runs forward in that capsule, between its cartilaginous wall and the lining membrane of the nasal sac, passes along the dorsal surface of the ventral border of the fenestra nasalis, and, mesial to that fenestra, perforates the wall of the capsule and issues on its external surface.

Seven branches are given off by the ramus buccalis after its origin from its ganglion, this making, with the terminal branch, eight branches in all to the nerve. Two other branches, which arise directly from the lateralis-communis ganglion, belong morphologically to it, and each of these ten branches doubtless contains both lateralis and communis fibres. The terminal branch of the nerve, the one that issues from the nasal capsule antero-mesial to the fenestra nasalis, innervates organ 1 infraorbital, which lies in the median ethmoid bone. The second and third branches issue through the fenestra nasalis and innervate organs 2 and 3 infraorbital, both of which lie in the premaxillary. The fourth branch is given off just before the nerve leaves the orbit to enter the nasal capsule, and running outward innervates organ 4 infraorbital, which also lies in the premaxillary. The fifth, sixth, seventh, and eighth branches innervate the corresponding infraorbital organs, which lie, organ 5 in the lachrymal, organs 6 and 7 in the maxillary, and organ 8 in the post-orbital bone. The ninth branch arises from the anterior portion of the lateralis-communis ganglion, and running upward perforates, in my 75 mm.

specimen, that overhanging portion of the dorsal end of the postorbital process of the chondrocranium that later ossifies as the sphenotic portion of the postfronto-sphenotic, and innervates organ 9 infraorbital, that organ lying in the postfrontal portion of the postfronto-sphenotic. The tenth branch of the nerve is the so-called ramus oticus facialis. It arises from the lateralis-communis ganglion, and, running upward, immediately perforates the cranial wall and enters the auditory capsule beneath the ampulla of the anterior semicircular canal. Passing ventro-lateral to that ampulla, it again enters the cartilage of the chondrocranium and issues on its dorsal surface to enter the parieto-dermopterotic bone and innervate organ 10 infraorbital, which lies in the anterior portion of the latter bone. This ramus oticus contains communis as well as lateralis fibres, but no general cutaneous ones could be traced to it, and it is not accompanied by any branch arising from the general cutaneous ganglion of the nerve.

The general cutaneous ganglion receives two bundles of communis fibres from the lateralis-communis ganglion, as above described, and still another bundle of similar fibres from a part of the facialis ganglion that lies at the base of the ramus palatinus facialis, this latter bundle forming the anastomosis described by Lehn and running upward ventro-mesial to the maxillo-mandibular vein. All of these communis fibres apparently traverse the general cutaneous ganglion and go both to the ramus mandibularis trigemini and to certain branches that have independent origin from the ganglion but belong morphologically to that nerve.

From the proximal end of the ganglion a bundle of general cutaneous fibres is sent posteriorly into the jugular canal to there join the truncus hyomandibularis facialis, and issue with it through the posterior opening of the canal. This bundle of fibres thus has a course which lies morphologically posterior to the outer wall of the jugular canal, and as that wall is probably formed (Allis, 1918*a*) by the posterior branchial-ray bar of the mandibular arch, the nerve has to the bar the relations of a facialis nerve and not of a trigeminus one. This bundle of fibres thus probably belongs to the nervus facialis, and must, accordingly, represent the primitive general cutaneous component of that nerve, a component which is otherwise wanting, and its issuing from the medulla with the general cutaneous fibres of the trigeminus, instead of as a part of the root of the facialis, is of secondary origin, and due to central condensations.

The rami maxillaris and mandibularis trigemini arise from the anterior end of the general cutaneous ganglion, and from the ganglion, close to the bases of these nerves, several small branches have their origin, these branches all containing motor fibres and hence undoubtedly belonging, morphologically, to the ramus mandibularis.

The ramus maxillaris contains only general cutaneous fibres, and runs forward through the orbit, closely accompanying the ramus buccalis throughout its entire course. Branches are sent from it to tissues of the region traversed,

and they apparently present no features of special importance. One branch enters the maxillary portion of the labial fold, toward its anterior end, and sends branches anteriorly and posteriorly in it.

The ramus mandibularis and the several smaller associated branches all contain motor, communis and general cutaneous fibres. The proximal one of the smaller branches runs antero-dorsally and in large part penetrates, on its internal surface, the muscle-mass formed by the levator arcus palatini and its derivatives, certain of the branches, however, passing outward across the anterior edge of the levator and then posteriorly a short distance along its external surface. The next one or two branches arise in the angle between the rami maxillaris and mandibularis and are sent the one to the musculus temporalis and the other to the pterygoideus, the branch to the temporalis penetrating it on its internal surface and that to the pterygoideus penetrating it on its dorso-external surface. The next two branches arise from the base of the ramus mandibularis and not directly from the ganglion, and are the one largely motor and the other wholly sensory. The motor branch goes to the large superficial portion of the adductor mandibulae, entering it on its internal surface. The sensory branch runs outward across the anterior edge of the superficial portion of the adductor and then postero-ventrally along its external surface, some of its branches penetrating the muscle, this branch thus apparently corresponding to the ramus posttrematicus externus anticus of the more posterior arches.

After giving off these several branches, which doubtless vary somewhat in different specimens, the ramus mandibularis runs downward along the dorso-external surface of the musculus pterygoideus, and while in that position sends a branch to the deeper portion of the adductor, the branch entering the muscle on its external surface. The nerve then passes internal to the deeper portion of the adductor, crosses the internal surface of that muscle, and then turns forward, there either passing over the hind edge of the muscle, onto its external surface, or traversing the muscle near its hind edge and close to its origin (figs. 42-44). The nerve then enters the ramus of the mandible, there lying, in my 75 mm. specimen, internal to those fibres of the superficial portion of the adductor that pass directly into the ramus of the mandible, but external to the tendon of insertion of the muscoli temporalis and pterygoideus, and also external to those fibres of the mandibular portion of the adductor that have their insertions on the latter tendon. Luther (1913, p. 21) shows this nerve passing internal to this tendon and muscle, but it was not so found in any of my specimens. No motor fibres going to the mandibular portion of the adductor could be traced in the sections of my 75 mm. specimen, but the nerve, in this part of its course, sends a small sensory branch outward to join the ramus mandibularis internus facialis as that nerve traverses its canal in the dermarticlar.

As the ramus mandibularis here passes between the two parts of the adductor, it gives off a branch which is wholly sensory and soon separates into

two parts. One of these parts runs forward dorsal to that ridge on the internal surface of the dentary that forms the dorsal edge of the groove that lodges Meckel's cartilage and gives support to the dorsal edge of the splenial, and is there joined by the ramus mandibularis internus facialis, not shown in the figures, the two nerves lying in the groove between the dentigerous edges of the dentary and splenial. The other part of the branch runs forward ventral to the ridge, above referred to, on the mesial surface of the dentary, there lying along the dorsal surface of Meckel's cartilage and soon entering a canal in the dentary which begins at about the anterior quarter of the entire length of the mandible. A branch is there at once sent outward through the bone, and entering the mandibular portion of the labial fold turns posteriorly in it. The remainder of the nerve then continues onward in the canal in the dentary, accompanied by an arterial vessel, and sends branches to the dentary teeth. Both portions of this branch of the ramus mandibularis thus have a course dorsal to Meckel's cartilage, that is, morphologically along its internal surface. The branch is accordingly the ramus posttrematicus internus trigemini and corresponds strictly in its relations to the dentary and to Meckel's cartilage to the inferior dental nerve of human anatomy (Bryce, 1915, fig. 92).

After giving off this branch, the remainder of the ramus mandibularis runs antero-ventrally across the external (morphologically anterior) surface of Meckel's cartilage, in the groove on the internal surface of the dermcartilage that was described when describing that bone, and is there joined by the ramus mandibularis externus facialis, the two nerves then running forward ventral (morphologically external) to Meckel's cartilage, in a groove on the mesial surfaces of the dermcartilage and dentary, and being accompanied by a branch of the mandibular artery. The two nerves here pass ventral to the musculus geniohyoideus inferior, close to its line of origin, but are not seen in ventral views because of the underhanging ventral edge of the mandible. As the ramus mandibularis passes over the hind edge of the geniohyoideus inferior it gives off either a single branch which immediately separates into two branches, or two branches arising close together. These two branches contain some sensory fibres and all the remaining motor fibres of the nerve, and they run antero-mesially along the ventral surface of the geniohyoideus inferior, and then turn, the one anteriorly and the other posteriorly, each of them sending branches into the muscle to innervate it. The anterior branch does not continue beyond the muscle. The posterior branch continues posteriorly beyond it and reaches the ventral surface of the geniohyoideus superior, where it breaks up into branches which penetrate that muscle and innervate it. The terminal branch of the nerve usually, but not always, runs directly into a branch of the ramus hyoideus facialis, the two nerves there forming a continuous circuit, as the corresponding nerves do in *Amia* and *Scomber*. This has been fully discussed in a recent work (Allis, 1919*d*), and it was there shown that the fibres of the ramus mandibularis trigemini are all sent to the geniohyoideus, and that the musculus hyohyoideus is innervated wholly by the

nervus facialis. After giving off this important branch to the two divisions of the geniohyoideus, the ramus mandibularis continues onward in the groove on the mesial surface of the dentary, sending branches outward with each of the branches of the mandibularis externus facialis to the latero-sensory organs of the mandibular canal, the branches of the trigeminus innervating the general sensory tissues of the region.

This terminal portion of the ramus mandibularis thus corresponds, in its relations to Meckel's cartilage and its terminal distribution, to the nervus mylohyoideus of human anatomy (Bryce, 1915, fig. 92), but there is no branch that corresponds to the nervus lingualis unless it be that part of the ramus posttrematicus internus that runs forward in the groove between the dorsal (oral) edges of the dentary and splenial; and the fact that that part of the nerve is accompanied by the mandibularis internus facialis seems to indicate that it is the lingualis.

Nervus facialis. The nervus facialis arises, in the adult, by a single root which issues from the medulla slightly posterior to the root of the trigeminus and in contact, posteriorly, with the root of the nervus acusticus. In the 75 mm. specimen it arises by four rootlets, two lateralis, one communis, and one motor, the two lateralis rootlets furnishing, the one the lateralis fibres to the nervus trigeminus and the other those to the nervus facialis. The communis root soon becomes ganglionated, and then separates into two parts, one destined to the nervus trigeminus and the other to the nervus facialis. Those parts of the lateralis and communis roots that are destined to the nervus trigeminus run forward in the cranial cavity, and, joining the root of the latter nerve, issue with it through the trigeminus foramen. These two bundles of fibres thus here definitely belong, both in their point of exit from the cranial cavity and in their peripheral distribution, to the nervus trigeminus, and, as already stated, I consider them to belong to that nerve and not to the nervus facialis.

After giving off these two bundles of fibres to the nervus trigeminus, the remainder of the facialis root, composed of lateralis, communis and motor fibres, traverses the primary facialis foramen and enters the jugular canal in the lateral wall of the cranium, there lying ventral to the vena jugularis. Ganglion cells then immediately appear in the lateralis component of the root, and the communis component, which is still ganglionated, separates into two parts, one of which extends forward in the jugular canal and the other posteriorly in it. The anterior portion of this communis ganglion gives origin to the ramus palatinus, and to the bundle of communis fibres, already referred to, that is sent to the general cutaneous ganglion of the nervus trigeminus, and it is connected, by an extracranial communicating branch, with the communis ganglion of the nervus glossopharyngeus. The fibres that arise from the posterior portion of the ganglion join the lateralis and motor fibres of the nervus, and together form the truncus hyomandibularis, this truncus receiving the communicating branch from the general cutaneous ganglion

of the trigeminus, already described. Sympathetic fibres are sent from the main sympathetic chain both to that portion of the communis ganglion that is related to the truncus hyomandibularis and to the part related to the ramus palatinus.

The ramus palatinus, or more properly ramus anterior facialis, issues through the anterior opening of the jugular canal and enters the trigeminus chamber, where it turns sharply downward onto the dorsal surface of the horizontal plate of the ascending process of the parasphenoid, passing dorso-lateral to the ophthalmic branch of the common carotid artery, close to its point of separation from the latter artery. The nerve, still containing ganglion cells, then runs forward dorso-lateral to the common carotid artery, and after receiving the communicating branch from the nervus glossopharyngeus, gives off the communicating branch to the general cutaneous ganglion of the nervus trigeminus. The latter branch runs upward, dorso-lateral to the infra-orbital branch of the vena jugularis, and as its fibres apparently all go to the ramus mandibularis trigemini, as already stated, it is the ramus pretrematicus externus of the facialis. The ramus palatinus, still ganglionated, here becomes slightly enlarged, thus forming a slight ganglion at the base of the nerve, and ganglion cells are not continued forward beyond this point. From the anterior end of this small ganglion, or from the base of the ramus palatinus immediately anterior to it, a branch is given off which runs forward a short distance parallel to the palatinus, in the dense connective tissues that bind the palatoquadrate to the ventral surface of the lateral edge of the parasphenoid, there lying dorso-lateral to the dorso-mesial edge of the entopterygoid. It then separates into two branches both of which run ventrally between the entopterygoid and the palatoquadrate cartilage and are distributed to the ventro-mesial surface of the latter cartilage. This branch must therefore be a ramus pretrematicus internus facialis, as that nerve is defined by Sewertzoff (1911), but if it contains fibres derived from the communicating branch from the nervus glossopharyngeus, it would be, in part, also a ramus pharyngeus glossopharyngei corresponding to that nerve as described by me in *Amia* (Allis, 1897, p. 685).

The ramus palatinus then continues onward along the dorsal surface of the lateral edge of the parasphenoid, lateral to the common carotid artery and ventral to the musculus pterygoideus, until it reaches the anterior edge of the latter muscle. There it passes downward over the lateral edge of the parasphenoid, and runs forward, at first immediately dorsal to the connective tissue that binds the palatoquadrate to the parasphenoid, and then enclosed within that tissue, there lying considerably dorso-mesial to the dorso-mesial edge of the palatoquadrate cartilage. The nerve then gives off a branch which runs antero-latero-ventrally along the internal surface of the palatoquadrate cartilage, between it and the entopterygoid and ectopterygoid, and, beyond the lateral edge of the palatoquadrate cartilage, enters a canal in the entopterygoid and issues from that bone near its lateral edge. There it continues forward

and can be traced a certain distance, communicating branches connecting it with the ramus maxillaris trigemini. This branch of the palatinus thus corresponds to the ramus palatinus posterior of *Amia*, and as it lies internal to the palatoquadrate cartilage it would seem as if it must be a ramus pretrematicus internus facialis, there thus being two of these nerves in this fish, one anterior and the other posterior.

After giving off this branch, the remainder of the nerve becomes the ramus palatinus anterior, or ramus pharyngeus facialis, and runs forward, in the tissues dorsal to the entopterygoid, to the anterior end of that bone. It then passes beneath the nasal capsule, there lying at first in the tissues immediately mesial to the mesial dermopalatine (the so-called vomer), and then dorsal to the latter bone. It is accompanied, throughout this part of its course, by a small vein and artery.

The truncus hyomandibularis facialis runs posteriorly in the jugular canal and issues through its posterior opening, being joined, while in the canal, by the communicating branch of general cutaneous fibres from the trigeminus ganglion. The truncus then runs outward ventral to the vena jugularis, and soon separates into its rami mandibularis and hyoideus, the ramus opercularis being a branch of the latter nerve.

The ramus mandibularis contains all of the lateralis fibres of the nerve, some of the communis fibres, and, so far as could be judged from my sections, a considerable portion of the general cutaneous fibres received from the trigeminus ganglion, but no motor fibres. The nerve runs postero-ventrally along the mesial wall of the spiracular canal, there lying at first dorsal and then lateral to the efferent artery of the hyal arch, the nerve and artery both lying in a fold of the mucous tissues that projects ventrally between the posterior portion of the spiracular canal, externally, and the dorso-anterior end of the first gill cleft internally. At the hind edge of the spiracular canal the nerve turns ventro-laterally across that edge, between it and the anterior edge of the hyomandibula and then downward along the lateral surface of the canal, there lying along the line of insertion of the musculus protractor hyomandibularis, and internal to the superficial division of the adductor mandibulae, between the latter muscle and the external wall of the dorso-anterior diverticulum of the first gill cleft. There the nerve gives off its first branch, which runs ventro-posteriorly and supplies both the dorsal one of the three latero-sensory organs in the preoperculum, and the organs of the posterior horizontal and vertical cheek-lines of pit organs. Fibres that are not lateralis ones certainly form part of this branch and go to tissues of the region, but whether they are communis or general cutaneous ones could not be definitely determined, and the same is true for the other branches of the nerve. A second and similar branch is then sent to the seventh preoperculo-mandibular organ, and approximately at the point of origin of this branch the ramus mandibularis separates into its external and internal branches.

The ramus mandibularis externus contains all of the lateralis fibres of the

ramus mandibularis and also some of the other fibres of that nerve and is apparently the ramus posttrematicus externus anticus facialis (Allis, 1920*b*). It runs downward internal to that part of the superficial division of the adductor mandibulae that has its origin on the hyomandibula, but external to the tough membrane that here covers the latter bone, and then passes internal to that slip of the tough membrane that covers the external surface of the palatoquadrate that has its insertion on the hyomandibula. Ventral to that slip it sends a branch to the sixth preoperculo-mandibular organ, the non-lateralis fibres related to this branch sometimes appearing as a separate and independent branch. The main nerve then turns ventro-anteriorly along the hind edge of the palatoquadrate, and passing external to the quadrato-hyomandibular articulation, and posterior and external to the quadrato-mandibular articulation, reaches the hind end of the mandible, where it enters the canal that lies, at first, between the dermarticlar and autarticlar, but farther forward entirely in the former bone. While in that canal two branches are sent outward, one going to the fifth and the other to the fourth preoperculo-mandibular organs, these two organs both lying in the dermarticlar. The nerve then issues from the canal in the dermarticlar and enters that groove on the mesial surface of the dentary that first passes external to Meckel's cartilage and then forward along the ventral edge of that cartilage and lodges also the ramus mandibularis trigemini. There branches are sent to the third and second organs of the preoperculo-mandibular canal, the terminal branch of the nerve going to the first organ of that canal.

The ramus mandibularis internus, which is the posttrematicus internus facialis, turns antero-ventrally after its separation from the ramus externus and either passes through a notch, or a foramen, at the dorso-posterior corner of the metapterygoid. It then continues onward along the hind edge of the palatoquadrate, passing internal to the quadrato-hyomandibular articulation and postero-ventral to the quadrato-mandibular articulation, and reaches the mandible. There it enters the short canal that begins on the mesial surface of the autarticlar, directly ventral to the mesial end of the articular facet for the quadrate, and issues from that canal onto the mesial surface of the hind end of Meckel's cartilage. There it runs antero-dorsally across Meckel's cartilage and enters the groove between the splenial and the dentigerous edge of the dentary, where it runs forward to the anterior end of the mandible, accompanying that branch of the ramus mandibularis internus trigemini that also occupies that groove. This nerve of *Polypterus* thus has to Meckel's cartilage the relations of the chorda tympani of human anatomy (Bryce, 1915, fig. 92), which is further evidence that it is the homologue of that nerve.

The ramus hyoideus facialis runs posteriorly internal to the hyomandibula, and immediately gives off its ramus opercularis, which contains both sensory and motor fibres, the former apparently being communis ones. This ramus runs posteriorly mesial to the hyomandibula and dorsal to the opercular process of that bone, receives a communicating branch from the ramus anterior

glossopharyngei, and then reaches the external surfaces of the muscoli adductor hyomandibularis and adductor operculi, where it runs posteriorly, sending branches to both those muscles and to tissues of the region. A terminal branch of the nerve runs directly into a terminal branch of the supra-temporal branch of the nervus vagus, the two nerves forming a continuous circuit which is topographically similar to that in *Amia* (Allis, 1897), but different from that in *Menidia* (Herrick, 1899). Lehn found this nerve lying ventral to the opercular process of the hyomandibula.

After giving off the ramus opercularis, the ramus hyoideus turns outward across the dorsal edge of the opercular process of the hyomandibula, there passing between the hind edge of the latter bone and the stout ligament that extends from the opercular process upward to the accessory hyomandibula. The nerve then runs ventrally in the gill cover, lying slightly posterior to the hyomandibula and epihyal and sending branches posteriorly and postero-ventrally internal to the opercular bones, these branches innervating the musculus hyohyoideus superior and tissues of the region. At the level of the proximal (posterior) end of the ceratohyal the nerve passes onto the external surface of the hyohyoideus inferior, and is distributed to that muscle and adjacent tissues. One branch of the nerve passes onto the external surface of the geniohyoideus superior and usually there anastomoses with that terminal branch of the trigeminus that innervates the latter muscle, another branch passing internal to the geniohyoideus superior and anastomising with a branch of the ramus posttrematicus glossopharyngei.

Nervus acusticus. This nerve arises by a large root which lies immediately posterior to, and in contact with, the lateralis root of the nervus facialis. In the adult this root may issue from the medulla as two separate roots, a ramus anterior (vestibularis) and a ramus posterior (cochlearis). The ramus anterior, when found as a separate root, separates into two parts, one of which supplies the maculae of the ampulla anterior, ampulla externa, and recessus utriculi, and the other the maculae sacculi and neglecta. The ramus posterior supplies first the macula lagenae and then the macula of the ampulla posterior. I thus find this nerve as described by Retzius (1881), excepting in that the ramuli said by him to go to the maculae sacculi and neglecta form part of the anterior, instead of the posterior ramus of the nerve.

Nervus glossopharyngeus. This nerve arises, in the adult, as well as in the 75 mm. specimen, by two rootlets which lie close together, ventral and slightly posterior to the root of the nervus lineae lateralis vagi. One of the rootlets contains the motor, and the other the sensory fibres of the nerve, the latter fibres apparently all being communis ones. This root soon receives a bundle of lateralis fibres from the root of the nervus lineae lateralis vagi, and, running postero-laterally, enters and traverses the recessus sacculi, there passing ventral to all parts of the membranous ear and to all branches of the nervus acusticus. The nerve then issues from the cranium through the glossopharyngeus foramen, there lying ventral to the vena jugularis and being

accompanied, as it traverses its foramen, by a delicate branch of that vein, a similar but much larger branch issuing with the nervus vagus through its foramen.

Immediately after issuing from its foramen the nervus glossopharyngeus gives off, in the 75 mm. specimen, a branch which contains both communis and lateralis fibres, and an independent ganglion, involving both components, immediately forms upon it. From this ganglion a ramus supratemporalis arises, this nerve containing all the lateralis fibres of the glossopharyngeus and a part of the communis fibres. It runs dorsally along the lateral surface of the cranium, passes mesial to the vena jugularis, and then traverses a canal in the opisthotic and issues on the dorsal surface of that bone. There it separates into two branches, one of which penetrates the parieto-dermopterotic and innervates organ 11 of the main infraorbital canal, the other anastomosing with two branches of the ramus supratemporalis vagi and going to the organs of the middle head-line of pit organs. The latter branch of the glossopharyngeus apparently contains only communis fibres, while the vagus branches apparently contain lateralis fibres, and if this be correct the middle head-line of pit organs would be innervated by the vagus.

After giving off this branch, the nervus glossopharyngeus receives a communicating branch from the first vagus ganglion and then runs dorso-laterally across the postero-mesial edge of the epibranchial of the first branchial arch, and reaches the dorsal surface of that element. There it swells into an elongated ganglion which lies along the lateral surface of the cranium, ventral to the vena jugularis. From the hind end of this ganglion the ramus posttrematicus glossopharyngei arises, and from its anterior end the ramus anterior glossopharyngei.

The ramus anterior lies, in the 75 mm. specimen, along the dorsal surface of the thymus, but gives off a small branch which traverses that gland and rejoins the main nerve at its anterior end. The ramus anterior there gives off a branch which runs posteriorly between the two heads of the levator muscle of the first branchial arch and then along the external surface of that muscle, and reaches the external surface of the ceratobranchial of its arch, where it runs downward in the arch, always lying anterior to the ramus posttrematicus glossopharyngei. This branch of the ramus anterior is accordingly the ramus posttrematicus externus anticus. As it passes over the hind edge of the levator of the arch, it crosses, externally, a ramus posttrematicus internus, to be later described, and may there anastomose with that nerve, these nerves and the ramus anterior then forming a loop around the levator. After giving off this branch, the ramus anterior gives off, in the 75 mm. specimen, two branches, both of which run postero-ventrally, one lying along the ventral surface of the musculus adductor hyomandibularis and dorsal to the efferent artery of the hyal arch, and the other ventral to that artery, close to the ramus mandibularis facialis. The dorsal one of these two branches is connected, by an anastomosing branch, with the ramus opercularis facialis, the anastomosing

branch passing across the anterior edge of the adductor hyomandibularis. These two branches of the nerve both lie immediately lateral (internal) to the mucous lining membrane of the lateral wall of the dorsal, pocket-like end of the first branchial cleft, and hence are both pretrematic nerves, the ventral one being a pretrematicus internus and the other apparently a pretrematicus externus. The remainder of the ramus anterior, which is now the ramus pharyngeus glossopharyngei, runs forward through the canalis parabasalis in the ascending process of the parasphenoid—there lying ventral to the efferent artery of the hyal arch and lateral to the common carotid artery—and fuses with the small ganglion at the base of the ramus palatinus facialis, slightly proximal to the point of origin of the communicating branch from that ganglion to the general cutaneous ganglion of the nervus trigeminus. This branch of the glossopharyngeus is described by Lehn as the ramus palatinus, and it would seem to represent Jacobson's nerve, but it fuses entirely with the palatinus portion of the geniculate ganglion, instead of receiving a branch from that ganglion and then continuing onward to end in an otic ganglion. Furthermore, the nerve apparently contains only communis fibres, and Norris says (1908, p. 547) that Jacobson's nerve is largely composed, in the Amphibia, of general cutaneous fibres, with but few communis and sympathetic ones.

The ramus posttrematicus, immediately after its origin from the hind end of the glossopharyngeus ganglion, sends a motor branch to the levator muscle of the first branchial arch, and then runs outward posterior to that levator. It then immediately gives off a sensory branch which passes internal to the ramus posttrematicus externus anticus, and may, as already stated, anastomose with that nerve. This branch then perforates, from its external surface and near its dorsal edge, the stout ligament that extends from the latero-ventro-posterior corner of the ascending process of the parasphenoid to the dorsal end of the first ceratobranchial, and reaches the internal edge of the latter ceratobranchial, where it runs downward in its arch, lying close to, or fusing with, the ramus pretrematicus internus of the first vagus nerve. This branch of the glossopharyngeus is thus a ramus posttrematicus internus. Soon after giving off this sensory branch, the ramus posttrematicus crosses the external surface of the epibranchial of the first branchial arch, there lying in the groove between that element of the arch and the pharyngobranchial, and reaches the external surface of the ceratobranchial, where it lies between the bases of the two rows of cartilaginous branchial rays. There it is joined by the ramus pretrematicus externus of the first vagus nerve, this branch apparently being a general cutaneous one and fusing completely with the ramus posttrematicus glossopharyngei. The trunk so formed continues downward in the arch, and soon sends a branch to the tissues of the arch, this branch apparently containing motor fibres destined to innervate certain small muscles related to the gill filaments. Near the ventral end of the arch two branches are sent to the musculus interarcualis ventralis of the arch, and between these two branches the ramus posttrematicus forms an anastomosis with a branch of

the ramus hyoideus facialis, as already described. Beyond this point the nerve anastomoses completely with the terminal portion of the ramus pretrematicus internus of the first vagus, the nerve so formed continuing onward along the internal surface of the tissues that form the floor of the buccal cavity.

Nervus lineae lateralis vagi. This nerve arises from the medulla slightly dorsal and anterior to the root of the glossopharyngeus, and immediately sends a branch to the latter root. The root then becomes imbedded in the lateral surface of the large intracranial vagus ganglion and issues from the cranial cavity through the vagus foramen with the vagus nerve and a large venous vessel which joins the vena jugularis. As the root issues through the vagus foramen it separates into two parts and a ganglion forms on each of them, one being the ganglion of the ramus supratemporalis and the other that of the nervus lineae lateralis. The latter nerve was not further traced. The ramus supratemporalis passes ventro-anterior to the venous vessel that issues through the vagus foramen, and then runs dorso-laterally mesial to the posterior process of the opisthotic, in the hollow between that process and the body of the bone. Branches are sent by it to organs 12 and 13 of the main infraorbital latero-sensory canal, which lie the one in the first supratemporal bone and the other in the posttemporal (suprascapular), then two separate branches to the middle head-line of pit organs, and the nerve then terminates in branches to the two supratemporal organs, which lie in the second and third supratemporal bones.

Nervus vagus. The nervus vagus arises by several rootlets which contain motor, communis and general cutaneous fibres. A large intracranial ganglion forms on the general cutaneous fibres and protrudes partly through the vagus foramen, and two extracranial ganglia are formed on the communis fibres of the nerve, one in relation to the fibres destined to the first vagus nerve and the other on the remaining fibres of the nervus.

The ramus supratemporalis vagi of the 75 mm. specimen arises by two roots from the dorsal surface of the protruding, extracranial portion of the general cutaneous ganglion, each root receiving a bundle of communis fibres. One root runs upward dorso-posterior, and the other ventro-anterior to the vein that issues through the vagus foramen, the two then fusing with each other and joining the ramus supratemporalis of the nervus lineae lateralis. The nerve is in part distributed to tissues on the dorsal surface of the head, but two important branches run laterally over the dorsal edge of the musculus adductor operculi, and then ventrally along the external surface of that muscle. One of these branches fuses with the ramus opercularis facialis, the other passing external to that nerve and being distributed to tissues in the gill cover, this distribution of this branch of the vagus evidently showing that that cover was not developed wholly in relation to the hyal arch.

The first vagus nerve arises, with the other vagus nerves, from the ventral portion of the intracranial ganglion, and separates from the other vagus nerves while they are all traversing the vagus foramen, the first vagus there lying ventral to the other nerves, and all of them lying ventral to the distal

end of the general cutaneous ganglion of the complex. The nerve consists mainly of motor and communis fibres, but some general cutaneous fibres must certainly enter it, for, as there are certainly general cutaneous tissues in the arch the nerve traverses, there must be nerve fibres to innervate them. Furthermore, although no general cutaneous fibres could be definitely traced into this nerve, they were traced into the nerves sent to the more posterior arches. After the nerve has separated from the other nerves of the complex, a small and independent ganglion is formed in relation to its communis fibres, this ganglion forming, as in *Amia* (Allis, 1897, fig. 59), a knob-like swelling on the anterior surface of the main trunk of the nerve. From this ganglion, in the 75 mm. specimen, four nerves arise, and the descriptions that follow, of this nerve and the other vagus nerve, apply largely to this specimen.

One of the nerves that arise from the first vagus ganglion is a communicating branch to the *nervus glossopharyngeus*, and it has already been referred to when describing that nerve.

A second nerve separates into two parts. One of these parts immediately joins and fuses with the main sympathetic nerve, but the nerve so formed soon separates into two parts, one of which is certainly largely composed of sympathetic fibres and the other largely of communis fibres. Both of these nerves run forward and traverse the *canalis parabasalis* in the ascending process of the *parasphenoid*, the sympathetic nerve then falling into the *trigeminus ganglion* and the communis one joining and closely accompanying the *ramus palatinus facialis proximal* to the point where the communicating branch is sent from that nerve to the *trigeminus ganglion*, this nerve thus being the *ramus pharyngeus* of the first vagus nerve. The other part of this second nerve of the first vagus perforates the *thymus*, and while in that gland receives a communicating branch from the communis nerve just above described. The nerve so formed then enters the first branchial arch and reaches the internal surface of that arch, where it joins and fuses with the *ramus posttrematicus internus glossopharyngei*. This branch of the first vagus is thus the *ramus pretrematicus internus* of that nerve, and the nerve formed by its fusion with the *ramus posttrematicus internus glossopharyngei* is the *ramus internus* of the first branchial arch. This nerve runs downward along the internal surface of the arch, and, at its ventral end, joins and fuses with the terminal portion of the *ramus posttrematicus glossopharyngei*, as already described.

The third nerve that arises from the first vagus ganglion runs outward between the *levator muscles* of the first and second branchial arches, and separates into two parts. One of these parts is the *ramus pretrematicus externus* of the first vagus, and joins the *ramus posttrematicus glossopharyngei* on the external surface of the first arch. The other part is the *ramus posttrematicus externus anticus* of the first vagus, and it has a course, in its arch, similar to that of the corresponding branch in the *glossopharyngeus arch*.

The remaining branch that arises from the first vagus ganglion is the *ramus posttrematicus*. This nerve first sends a motor branch to the *levator muscle*

of its arch, and then both in my 75 mm. specimen and in one adult that was examined, runs outward through that muscle. On issuing from the muscle it gives off its ramus posttrematicus internus, which immediately joins and fuses with the ramus pretrematicus internus of the second vagus. The main nerve then receives, and fuses with, the ramus pretrematicus externus of the second vagus, and, running downward in its arch, gives off first a branch which contains motor fibres, apparently destined to muscle fibres related to the gill filaments, then a branch which is apparently wholly sensory, and then a third branch which innervates the musculus interarcualis ventralis of its arch. The remainder of the nerve then separates into two branches, each of which anastomoses with the ramus internus of the arch.

The second vagus nerve arises from the main extracranial ganglion of the vagus complex, and contains motor, communis, and a few general cutaneous fibres. It immediately gives off a motor branch to the levator muscle of its arch, and a communis branch which goes to the dorsal surface of the branchial chamber in the region of the basioccipital, and then runs outward anterior to the levator muscle of its arch. The nerve then gives off, in succession, a ramus pretrematicus internus, a ramus pretrematicus externus, a ramus posttrematicus externus anticus, and a ramus posttrematicus internus; all of these nerves having courses similar to those of the corresponding nerves in the preceding arches. The remainder of the nerve is then the definitive ramus posttrematicus, which runs downward in its arch, gives off branches similar to those of the first vagus, and then separates into two parts, each of which fuses with one of two terminal branches of the ramus internus of the arch.

The third vagus nerve arises from the extracranial ganglion of the complex and soon sends a motor branch to the levator muscle of its arch. It then runs outward anterior to that levator and gives off, in succession, a ramus pretrematicus internus, a ramus pretrematicus externus, a ramus posttrematicus externus anticus, and a ramus posttrematicus internus, these nerves all having courses similar to those in the preceding arches, excepting in that the ramus posttrematicus externus anticus fuses completely with the ramus posttrematicus throughout the larger part of its course. The ramus posttrematicus runs downward in its arch giving off branches similar to those in the preceding arches, and finally anastomosing with the ramus posttrematicus internus of its own arch, exactly as, in the more anterior arches, it anastomoses with that nerve fused with the ramus posttrematicus internus of the next posterior arch. No pharyngeal branch was found related to this nerve.

The remaining vagus nerve, the ramus intestinalis, was not traced beyond its origin from the extracranial ganglion of the complex, but branches of the nerve innervate the superior and inferior pharyngo-claviculares, and the transversus ventralis.

SUMMARY

The cranium of *Polypterus* is platybasic, and several of the cranial bones correspond, in topographical position and relations, to two or more of the bones of recent Holostei and Teleostei. These several bones are the basi-exoccipital (basioccipital + exoccipitals), the parieto-dermopterotic (parietal + dermopterotic), the postfronto-sphenotic (autosphenotic + dermosphenotic), the premaxillary (premaxillary + antorbital + $\frac{1}{2}$ dermoethmoid), the maxillary (maxillary + suborbitals), the cheek-plate (preoperculum + cheek-plate), and the sphenoid (orbitosphenoids + alisphenoids + piscine basisphenoid + proötic bridge). The nasal, accessory nasal and os terminale, found wholly separate in this fish, are usually represented by a single bone in other fishes. There is a large opisthotic, which is partly of primary and partly of secondary origin and invades somewhat the regions occupied, in other fishes, by the epiotic, autopterotic and proötic, the two former bones, as independent ossifications, being wholly wanting in this fish, and the proötic either also wanting, being found as a small and unimportant bone, or, possibly, found fused with the ascending process of the parasphenoid.

The opisthotic, so well developed in this fish, is found as a dermal, and often unimportant, bone in the Holostei and most of the Teleostei; the epiotic, absent in *Polypterus*, is found in both the Holostei and Teleostei; and the autopterotic, also absent in *Polypterus*, is found in the Teleostei but not in the Holostei. In the Teleostei there are thus five otic bones, the sphenotic, pterotic, epiotic, proötic and opisthotic, but the opisthotic is tending to disappear, this apparently being correlated to the development of the autopterotic. In the Tetrapoda, a proötic, alone, is found in the Batrachia (Gaupp, 1905), a proötic and opisthotic in Reptilia, a proötic, opisthotic and epiotic in Aves, and several otic bones in the Mammalia, Huxley giving three, but Vrolik six. A sphenotic, found in *Polypterus* and in the Holostei and Teleostei, is not described as such in any of the Tetrapoda, but one of the centres of ossification ascribed to the proötic in man has markedly the position of the piscine auto-sphenotic, for it is said to appear on the dorso-lateral aspect of the otic capsule, over the superior (anterior) semicircular canal, to form the "border" over the nervus facialis, and to extend into the tegmen tympani from above, all of which would be characteristics of an enlarged autosphenotic and not of the piscine proötic.

The dental arcade is apparently similar to that in the Mammalia, and, in fishes, this arcade is known only in the Crossopterygii. The superior maxillary bone has certain striking resemblances to that of the Mammalia.

The trigemino-facialis chamber consists of a trigeminus chamber and a jugular canal, the latter canal apparently representing a primitive condition of the facialis part of the entire chamber. The lateral wall of the trigeminus chamber is formed by the ascending process of the parasphenoid, instead of, as in the Holostei and Teleostei, by the proötic.

The hyomandibula corresponds to the prefacialis portion of the holostean and teleostean hyomandibula, the postfacialis portion of the latter element being represented by ligament.

The common carotid artery traverses the canalis parabasalis through the ascending process of the parasphenoid and enters the ventral portion of the trigeminus chamber, where it gives off an ophthalmic branch, which accompanies the ramus ophthalmicus superficialis trigemini. The remainder of the artery issues into the orbit and there runs forward along the lateral edge of the parasphenoid, in the position of the orbito-nasal artery of the Teleostei, but the artery still contains the equivalents of the internal carotid, of a part of the external carotid, and of the orbito-nasal artery of the latter fishes. As this artery approaches the foramen opticum it gives off first a maxillo-mandibularis branch, and then two branches which enter the cranial cavity posterior to the nervus opticus and are, the one the arteria cerebralis posterior and the other the arteria cerebralis anterior. The remainder of the artery is then the orbito-nasal artery. The internal carotid of this fish thus enters the cranial cavity by passing dorsal, instead of ventral, to the trabecula, a condition which is also found in *Amiurus* (and hence probably in others of the Siluridae) but in no other fish that I know of.

The jugular vein is formed by the union of supraorbital and infraorbital veins, the supraorbital one accompanying the ramus ophthalmicus superficialis trigemini, and receiving, at its base, the maxillo-mandibularis vein, while the infraorbital one accompanies the common carotid and orbito-nasal arteries.

The nervus terminalis is apparently represented by two nervous strands that arise from the bulbus olfactorius and accompany the nervus olfactorius into the nasal sac.

The eye-muscles are innervated as they are in the Ganoidei and Siluridae, excepting in that the inferior division of the nervus oculomotorius passes dorsal, instead of ventral, to the musculus rectus inferior.

The radix profundus, which apparently contains only general sensory fibres, issues from the cranial cavity with the nervus oculomotorius, and a ganglion then immediately forms upon it. No branches from other nerves could be traced to this ganglion, and from it three nerves arise: the radix longa, which runs forward with the nervus oculomotorius and enters the ciliary ganglion, which is sessile on the inferior division of the nervus oculomotorius; a ramus ophthalmicus profundus, which runs forward between the two divisions of the oculomotorius and then ventral to the nervus trochlearis and joins, but does not fuse with, the ramus ophthalmicus superficialis trigemini as it traverses the preorbital foramen; and a portio ophthalmici profundi, which runs forward in the orbit, but not beyond it, lying ventral to the ramus ophthalmicus superficialis trigemini and sending branches to the dorsal surface of the head, accompanying branches of the latter nerve. The profundus nerve of this fish thus sends branches to the entire region that, in most teleosts, is innervated by branches of the ramus ophthalmicus superficialis trigemini,

its ramus ophthalmicus corresponding to the ophthalmic nerve of man and its portio ophthalmici to the frontal branch of that nerve.

The nervus trigeminus contains motor, general sensory, communis, and lateralis fibres, the communis and lateralis fibres arising from the medulla with the corresponding roots of the nervus facialis. These fibres all issue from the cranial cavity through the foramen trigeminum and enter the trigeminus chamber, where two separate ganglia form, one on the general sensory fibres and the other on the lateralis-communis ones. From the lateralis-communis ganglion the rami oticus, ophthalmicus superficialis and buccalis arise, all of which contain both lateralis and communis fibres, and important bundles of communis fibres are also sent to the general sensory ganglion. The latter ganglion also receives communis fibres from the ramus palatinus facialis, and it sends a bundle of general sensory fibres into the jugular canal to there join and fuse with the truncus hyomandibularis facialis. From the general sensory ganglion the rami maxillaris and mandibularis arise, the former apparently containing only general sensory fibres, and the latter motor, general sensory and communis ones.

The radix facialis apparently contains only motor, lateralis, and communis fibres, but it receives the bundle of general sensory fibres just above mentioned from the nervus trigeminus. The radix issues from the cranial cavity into the jugular canal, and a ganglion forms on it which is partly intracranial and partly extracranial in position. From this ganglion the rami palatinus and hyomandibularis arise, the palatinus containing only communis fibres and running forward in the jugular canal, while the hyomandibularis contains motor, communis and lateralis fibres and runs posteriorly in that canal. The ramus palatinus sends a communicating branch to the general sensory ganglion of the trigeminus, and receives one from the nervus glossopharyngeus. The ramus hyomandibularis receives a general sensory bundle from the trigeminus ganglion, and sends its ramus mandibularis outward anterior to the hyomandibula and its ramus hyoideus outward posterior to that element, between it and a ligament that represents its postfacialis portion.

The nervus glossopharyngeus contains motor, communis and lateralis fibres, and apparently no general sensory ones, and it has a dorsal branch and all the ventral branches typical of a branchial nerve.

The nervus vagus contains motor, general sensory, communis, and lateralis fibres, the latter fibres all entering the ramus supratemporalis vagi and the nervus lineae lateralis. The first and second vagus nerves each has all the typical ventral branches, but in the third nerve these branches are less definitely evident.

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ABBREVIATIONS IN PLATES

*aa*¹⁻⁴, afferent arteries of first to fourth branchial arches; *ab*, nervus abducens; *abfr*, foramen for nervus abducens; *ac*, aortic canal; *A.HM*, accessory hyomandibula; *ah*, afferent artery of hyal arch; *Am*¹, superficial division of musculus adductor mandibulae; *Am*², deeper division of musculus adductor mandibulae; *Am*³, mandibular division of musculus adductor mandibulae; *ANA*, accessory nasal; *Ao*, musculus adductor operculi; *ART*^a, autarticular; *ART*^d, dermarticular; *AUP*, autopalatine; *ba*, bulla acustica; *BB*, basibranchial; *BEO*, basi-exoccipital; *Bm*, musculus branchiomandibularis; *CB*¹⁻⁵, ceratobranchials of first to fifth arches; *cf*, canal for nervus hyomandibularis facialis; *CH*, ceratohyal; *cj*, canal for vena jugularis; *cl*, ramus ciliaris longus; *CP*, cheek plate; *cpf*, canal for ramus palatinus facialis; *D*, dentary; *dl*, dorsal body-line of pit organs; *Do*, musculus dilatator operculi; *EB*¹, epibranchial of first branchial arch; *ECP*, ectopterygoid; *ECT*, ectethmoid; *eg*, antero-mesial ectethmoidal groove; *EH*, epihyal; *ENP*, entopterygoid; *ETH*, ethmoid; *ffr*, foramen for nervus facialis; *Ghi*, musculus geniohyoideus inferior; *Ghs*, musculus geniohyoideus superior; *glfr*, foramen for nervus glossopharyngeus; *HB*¹⁻², hypobranchials of first and second branchial arches; *hf*, ramus hyoideus facialis; *HH*, hypohyal; *Hhi*, musculus hyohyoideus inferior; *Hhs*, musculus hyohyoideus superior; *HM*, hyomandibula; *il*, intermediate body-line of pit organs; *ioc*, infraorbital latero-sensory canal; *ip*¹⁻¹¹, pores of infraorbital line; *i²s²p*, double pore at point of union of supraorbital and infraorbital canals; *i¹⁰s¹p*, double pore at point of union of supraorbital and infraorbital canals; *Iv*¹⁻⁴, musculi interarcuales ventrales; *LA*, lachrymal; *Lab*¹⁻⁵, levator muscles of first to fifth arches; *Lap*, musculus levator arcus palatini; *ll*, lateral line of body; *M*, Meckel's cartilage; *MDP*, mesial dermopalatini; *mdt*, ramus mandibularis trigemini; *mef*, ramus mandibularis externus facialis; *mj*, ramus mandibularis facialis; *mif*, ramus mandibularis internus facialis; *MM*, mentomeckelian ossicle; *MP*, metapterygoid; *MX*, maxillary; *mxt*, ramus maxillaris trigemini; *NA*, nasal; *nl*, nervus lineae lateralis; *nt*, nasal tube; *o*, nervus opticus; *ocfr*, foramen for oculomotorius and ophthalmicus profundus; *ocm*, nervus oculomotorius; *ofr*, foramen for nervus opticus and internal carotid artery; *oi*, musculus obliquus inferior; *onfr*, foramen for orbito-nasal artery; *opf*, ramus opercularis facialis; *opp*, nervus ophthalmicus profundus; *OPS*, opisthotic; *opt*, ramus ophthalmicus trigemini; *os*, musculus obliquus superior; *OT*, Os terminale; *otfr*, foramen for ramus ophthalmicus trigemini; *PA*, parieto-dermopterotic; *PB*¹, pharyngobranchial of first branchial arch; *Pc*, musculus pharyngo-clavicularis; *pf*, foramen for pituitary vein; *Pg*, musculus pterygoideus; *Ph*, musculus protractor hyomandibularis; *pmp*, preoperculo-mandibular pores; *PMX*, premaxillary; *pna*, posterior nasal aperture; *pq*, palatoquadrate; *PS*, parasphenoid; *PSF*, postfrontosphenotic; *PT*, posttemporal; *Q*, quadrate; *re*, musculus rectus externus; *rif*, musculus rectus inferior; *rit*, musculus rectus internus; *rs*, musculus rectus superior; *s*, spiracle; *Sh*, musculus sternohyoideus; *SP*, sphenoid; *Sp*, musculus spiracularis; *sp*¹⁻⁶, pores of supraorbital canal; *SPL*, splenial; *ST*, supratemporals; *ta*, truncus arteriosus; *tfr*, foramen for nervus trigeminus; *Tp*, musculus temporalis; *trfr*, foramen for nervus trochlearis; *Tv*, musculus transversus ventralis; *vfr*, foramen for nervus vagus.

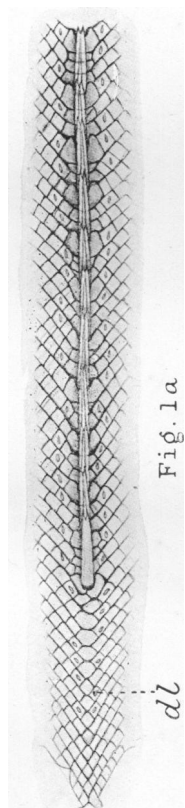


Fig. 1a

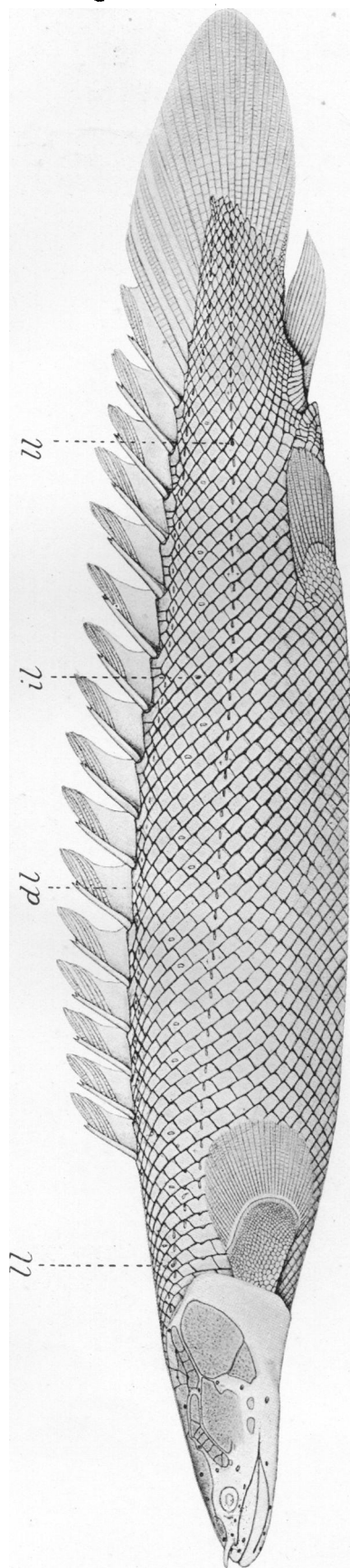


Fig. 1

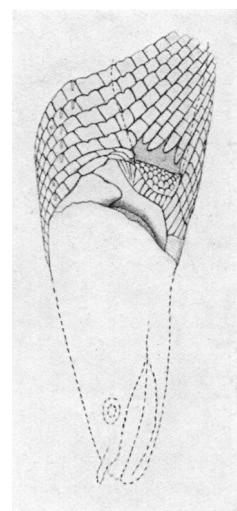


Fig. 1b

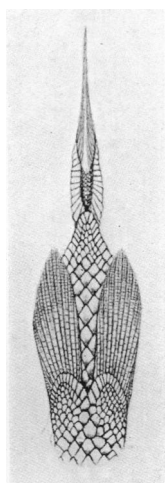


Fig. 1c

Fig. 1. Full length lateral view of 44 cm. *Polypterus bichir*. x 1.

Fig. 1a. Dorsal view of mid-dorsal line of same. x 1.

Fig. 1b. Lateral view of anterior portion of trunk of same, with pectoral fin removed. x 1.

Fig. 1c. Ventral view of anal fins of same. x 1.

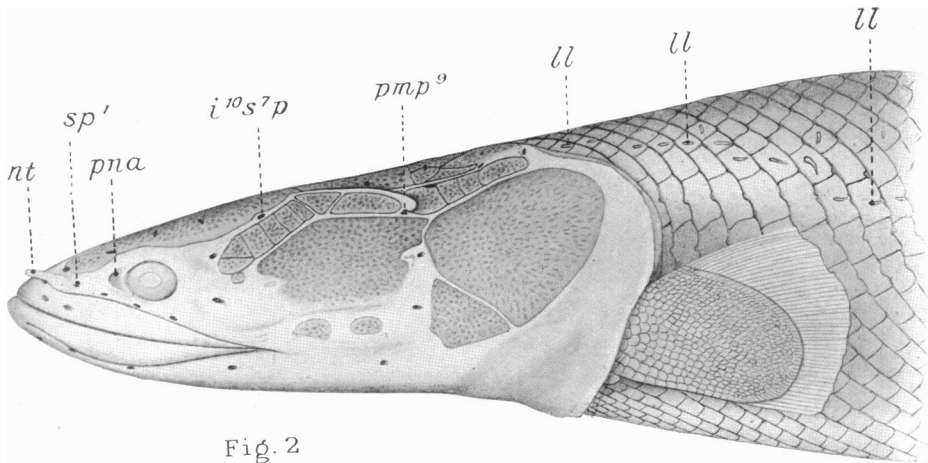


Fig. 2

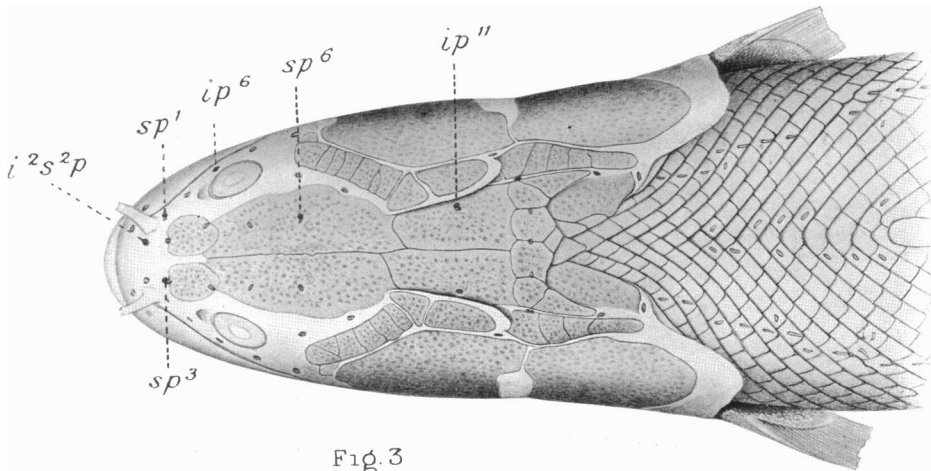


Fig. 3

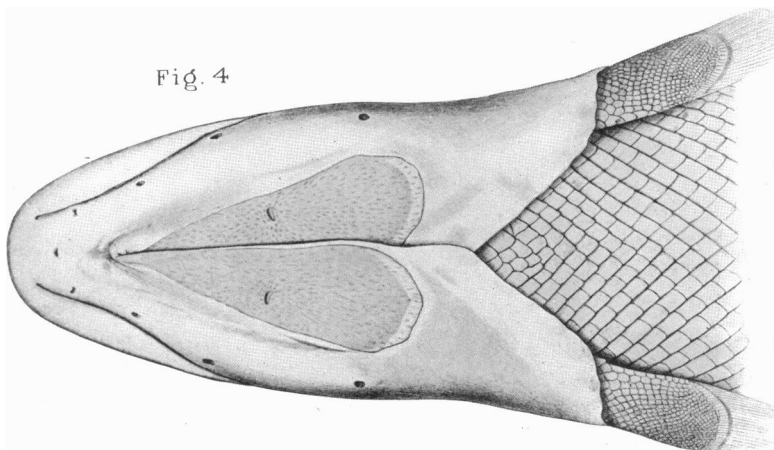


Fig. 4

Fig. 2. Lateral view of head of 44 cm. *Polypterus bichir*. $\times 2$.
Fig. 3. Dorsal view of head of same. $\times 2$.
Fig. 4. Ventral view of head of same. $\times 2$.

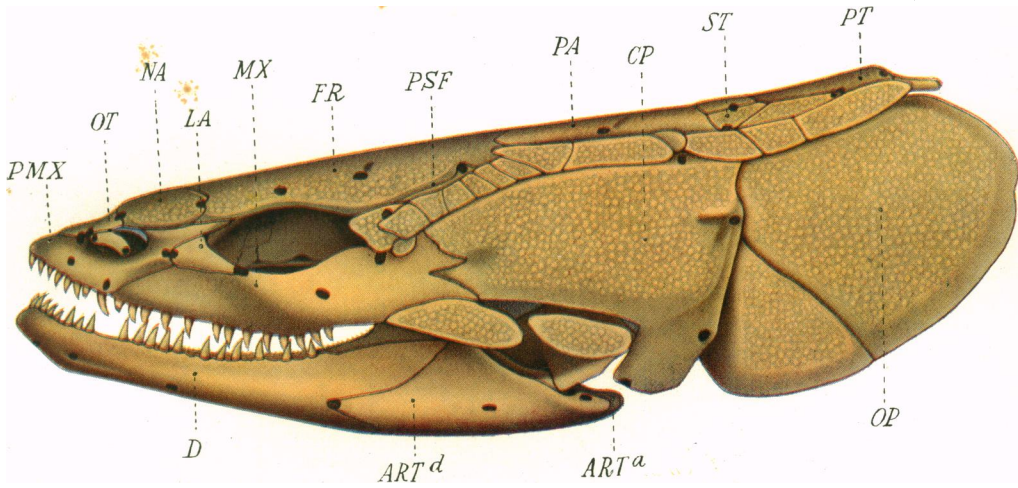


Fig. 5

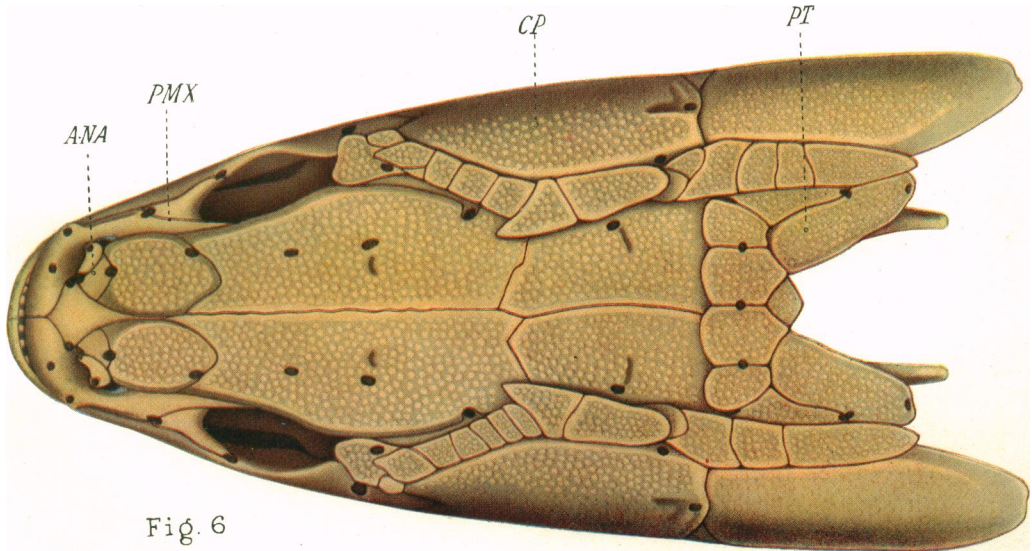


Fig. 6

Fig. 5. Lateral view of entire skull of a 49 cm. *Polypterus bichir*. $\times 2$.
Fig. 6. Dorsal view of same. $\times 2$.

Fig. 7

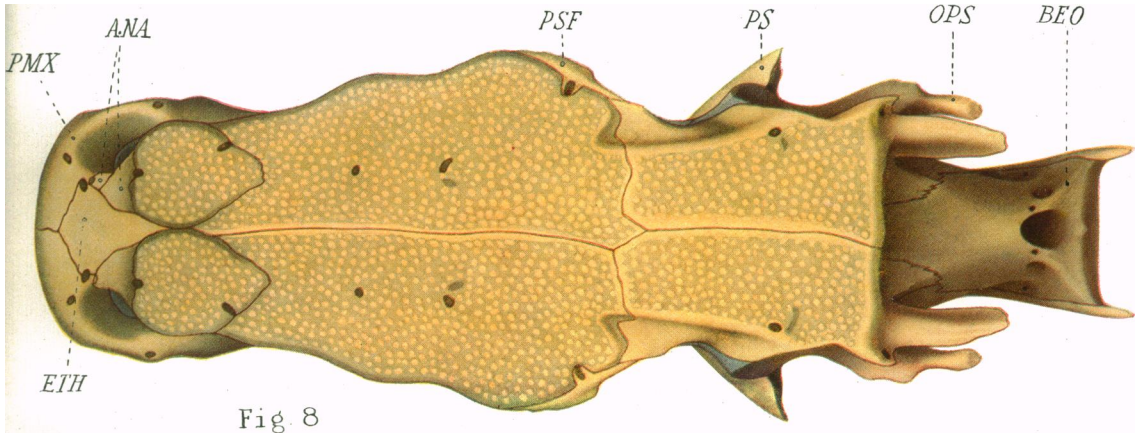
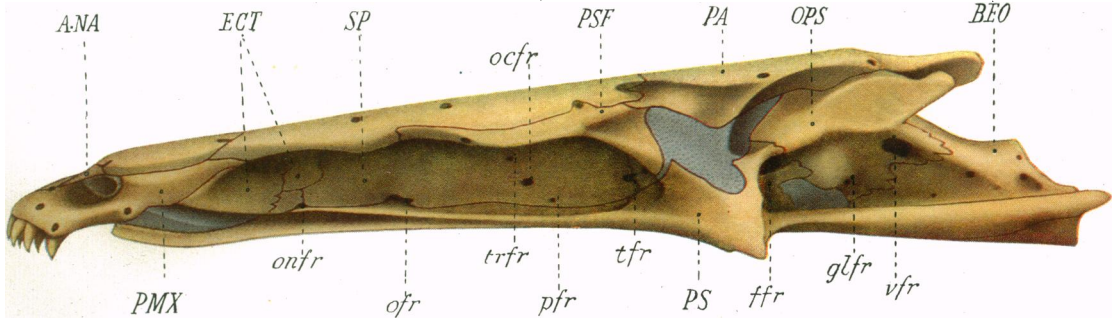


Fig. 8

Fig. 9

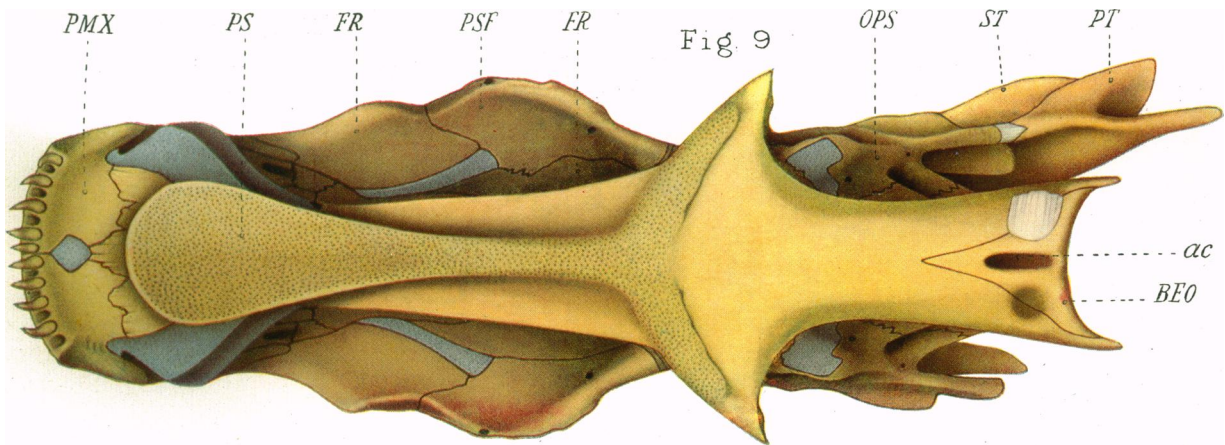


Fig. 7. Lateral view of neurocranium of large specimen of *Polypterus bichir* from Abyssinia. $\times 2$.

Fig. 8. Dorsal view of same. $\times 2$.

Fig. 9. Ventral view of same. $\times 2$.

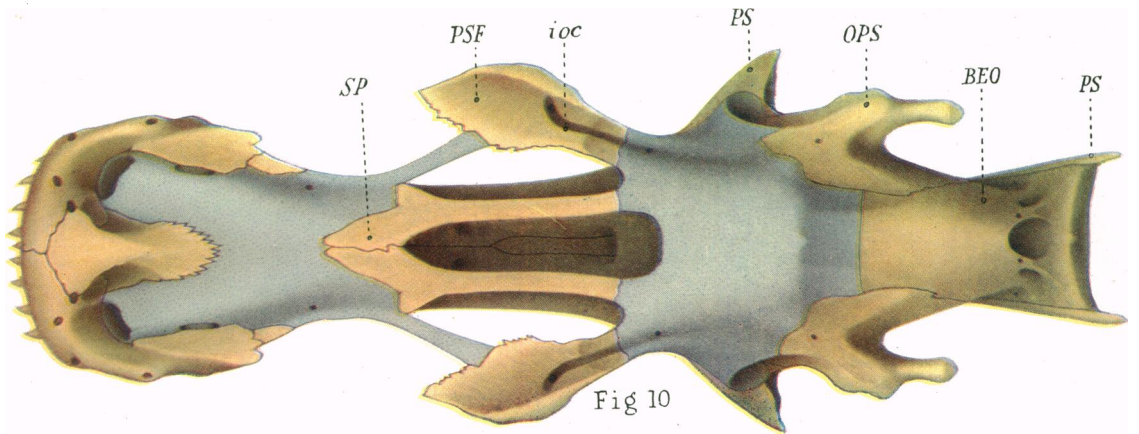


Fig. 10

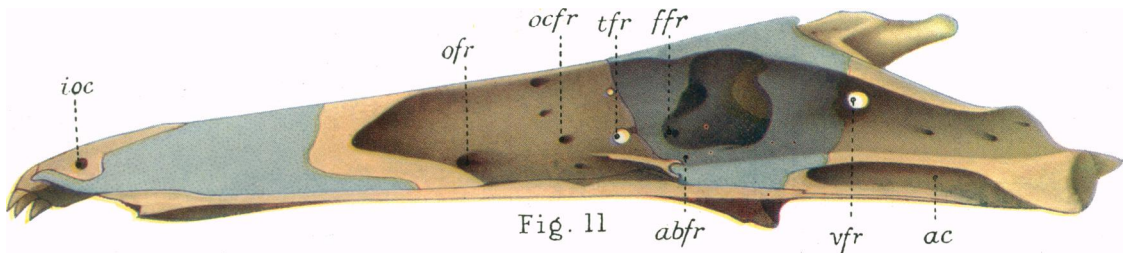


Fig. 11

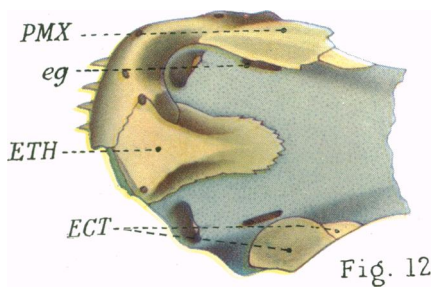


Fig. 12

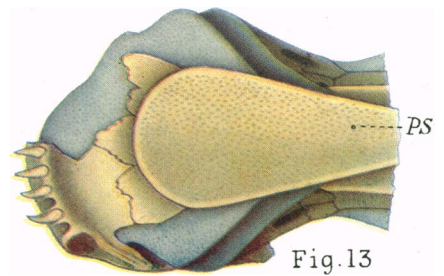


Fig. 13

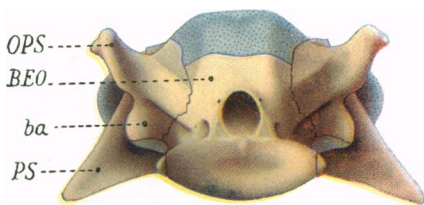


Fig. 14

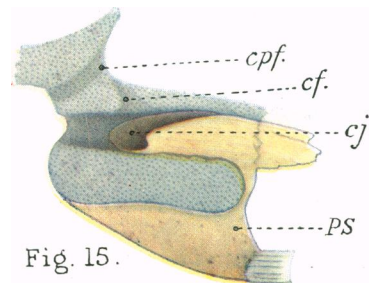


Fig. 15.

Fig. 10. Dorsal view of neurocranium of large specimen of *Polypterus bichir* from Abyssinia with dermal bones removed. $\times 2$.

Fig. 11. Median view of bisected skull of same. $\times 2$.

Fig. 12. Dorsal view of ethmoidal region of same, with left premaxillary removed. $\times 2$.

Fig. 13. Ventral view of same. $\times 2$.

Fig. 14. Posterior view of neurocranium of same. $\times 2$.

Fig. 15. Dorsal view of section through jugular canal. $\times 3$.



Fig. 16

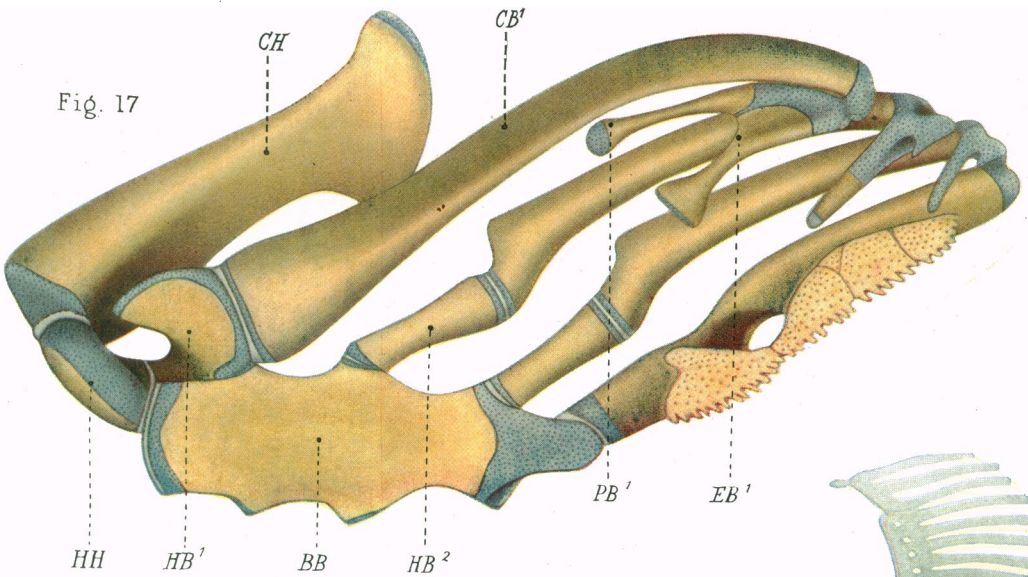


Fig. 17



Fig. 18.



Fig. 20

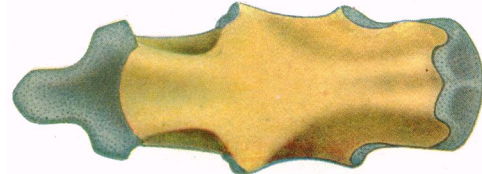


Fig. 19



Fig. 21.

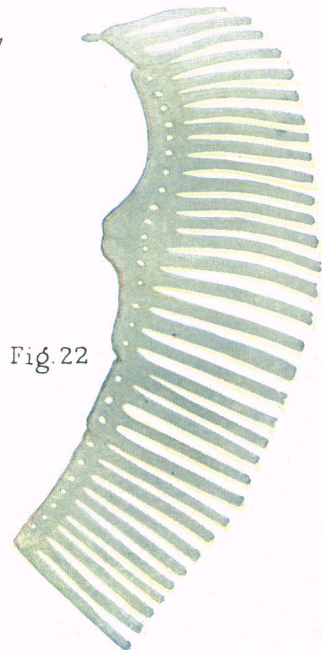


Fig. 22

Fig. 16. Ventral view of hyal and branchial arches of large specimen of *Polypterus bichir* from Abyssinia. $\times 2$.
 Fig. 17. Dorsal view of same. $\times 2$. Fig. 18. Lateral view (right side) of basibranchial of same. $\times 2$. Fig. 19. Ventral view of same. $\times 2$.
 Fig. 20. Ventral view of first hypobranchial of same. $\times 2$. Fig. 21. Dorsal view of same. $\times 2$.
 Fig. 22. Lateral view of branchial rays of second branchial arch. $\times 4$.

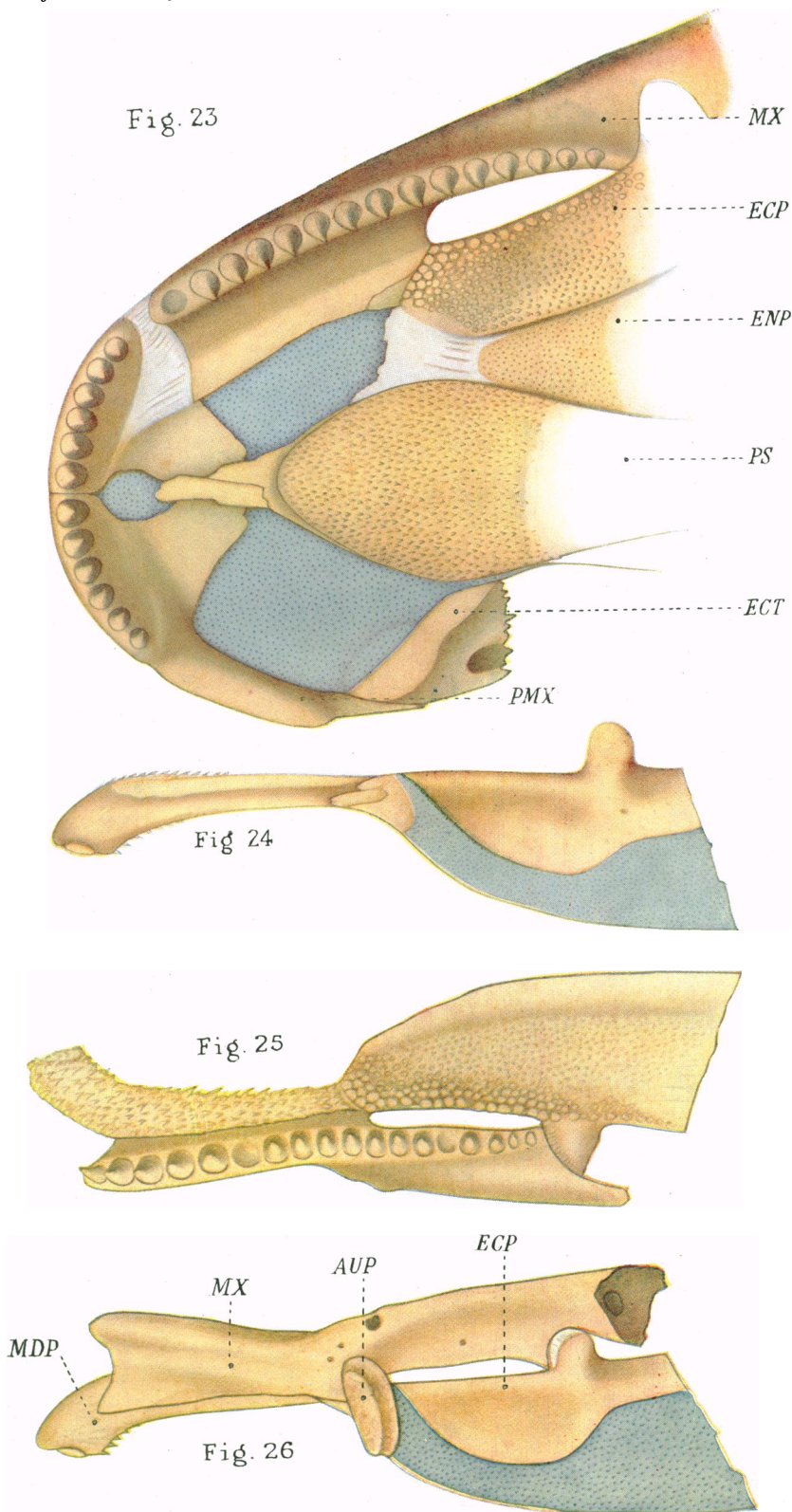


Fig. 23. Ventral view of anterior portion of roof of mouth of a 27 cm. specimen of *Polypterus Lapradei*, with right maxillary bone and both median dermopalatines removed. $\times 6$.

Fig. 24. Dorsal view of right median dermopalatine and anterior end of palatoquadrate. $\times 6$.

Fig. 25. Ventral view of same, with maxillary attached. $\times 6$.

Fig. 26. Dorsal view of same. $\times 6$.

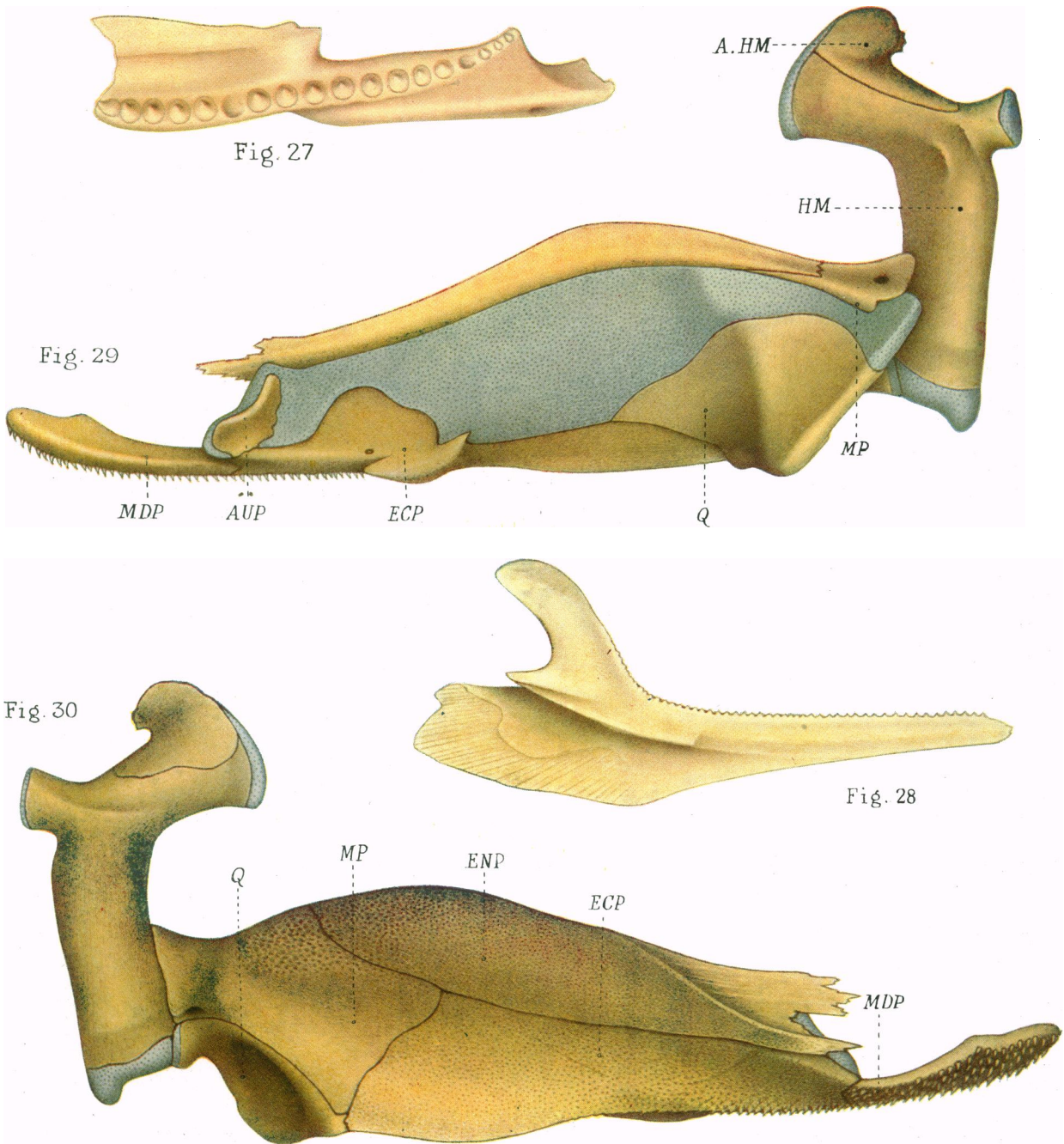


Fig. 27

Fig. 29

Fig. 30

Fig. 28

- Fig. 27. Ventral view of right maxillary of a 27 cm. specimen of *Polypterus Lapradei*. $\times 6$.
Fig. 28. Lateral view of splenial of large specimen of *Polypterus bichir* from Abyssinia. $\times 2$.
Fig. 29. Lateral view of hyomandibula and palatoquadrate of same. $\times 2$.
Fig. 30. Median view of same. $\times 2$.

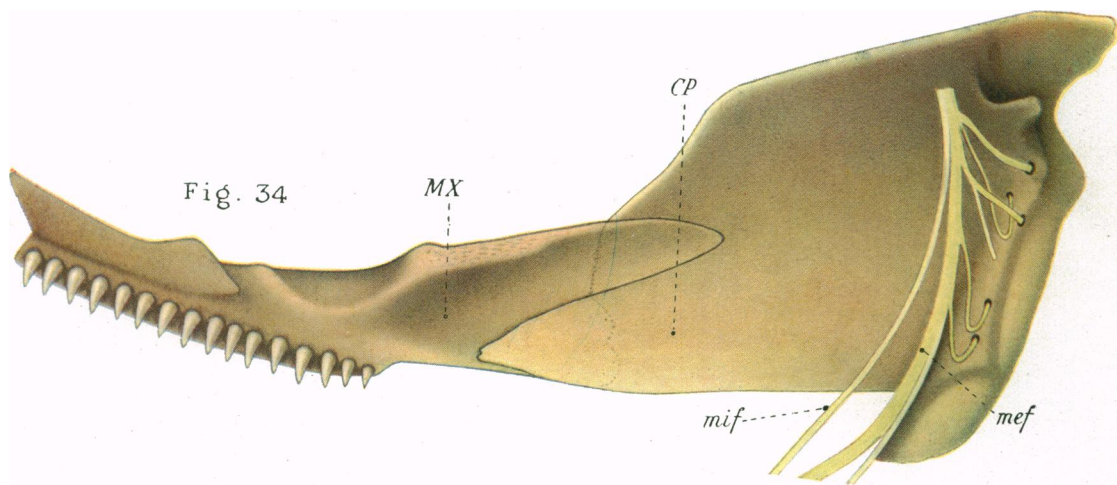
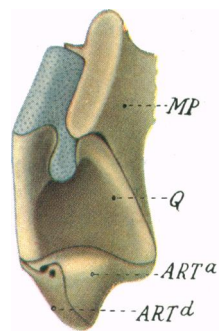
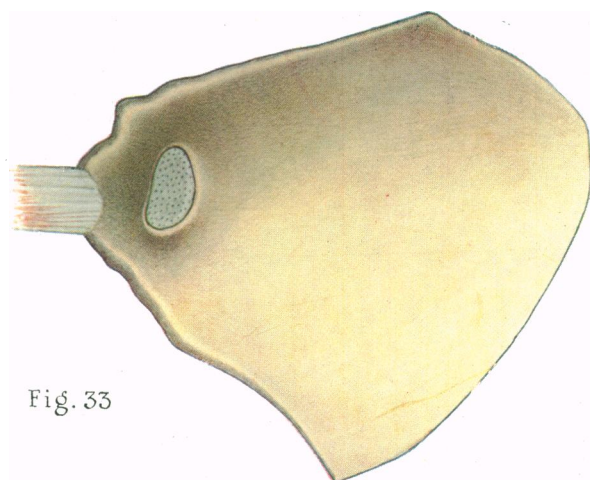
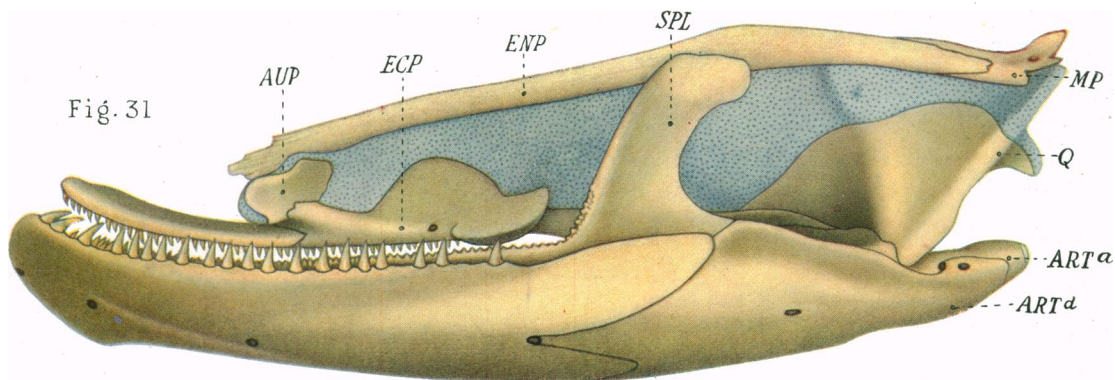


Fig. 31. Lateral view of palatoquadrate and mandible of large specimen of *Polypterus bichir* from Abyssinia. $\times 2$.
 Fig. 32. Posterior view of same. $\times 2$.
 Fig. 33. Internal view of operculum of same specimen. $\times 2$.
 Fig. 34. Internal view of cheek-plate and maxillary of same specimen. $\times 2$.

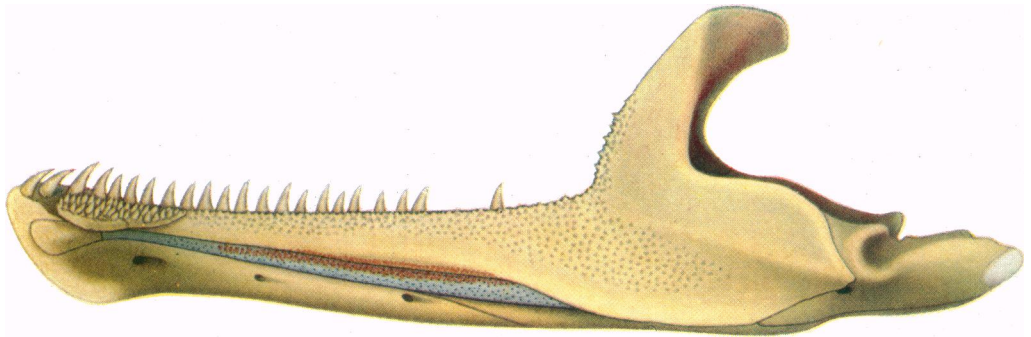


Fig. 35

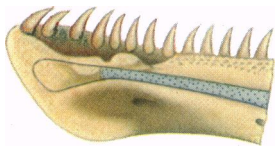


Fig. 35a

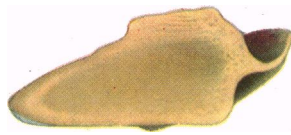


Fig. 39

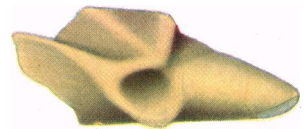


Fig. 38

Fig. 36

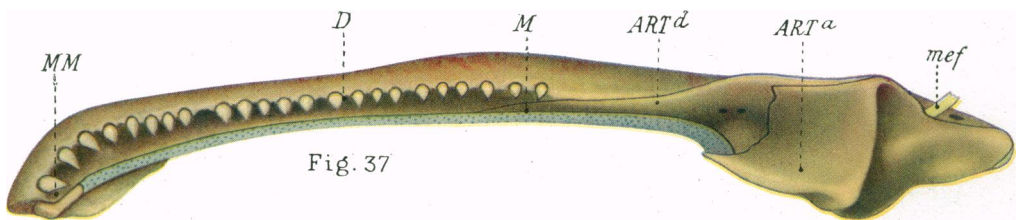
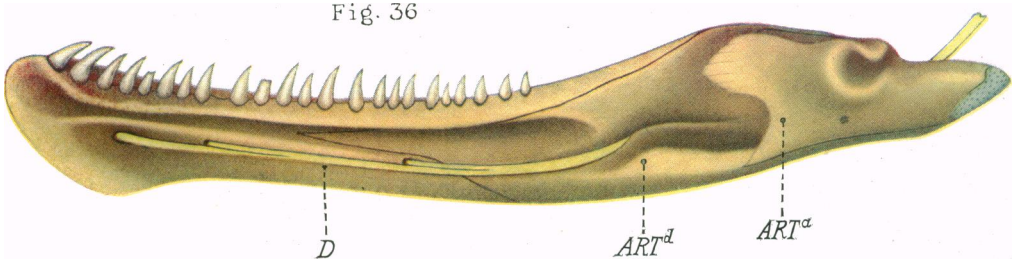


Fig. 37

- Fig. 35. Internal view of left mandible of large specimen of *Polypterus bichir* from Abyssinia. $\times 2$.
 Fig. 35a. Anterior end of the same with dermal ossicles removed. $\times 2$.
 Fig. 36. The same with splenial removed. $\times 2$.
 Fig. 37. Dorsal view of the same. $\times 2$.
 Fig. 38. Dorso-mesial view of the autarticular. $\times 2$.
 Fig. 39. Lateral view of the same. $\times 2$.

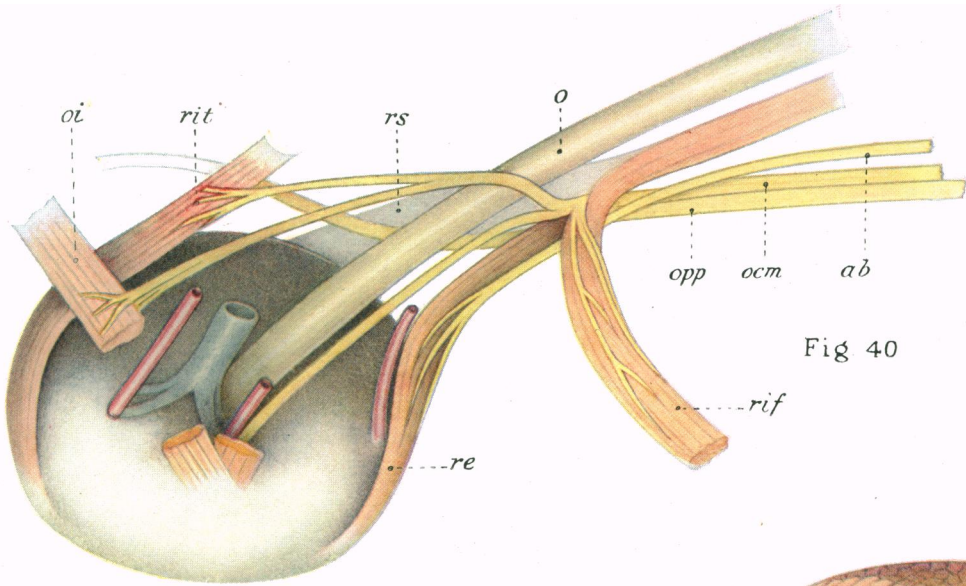


Fig 40

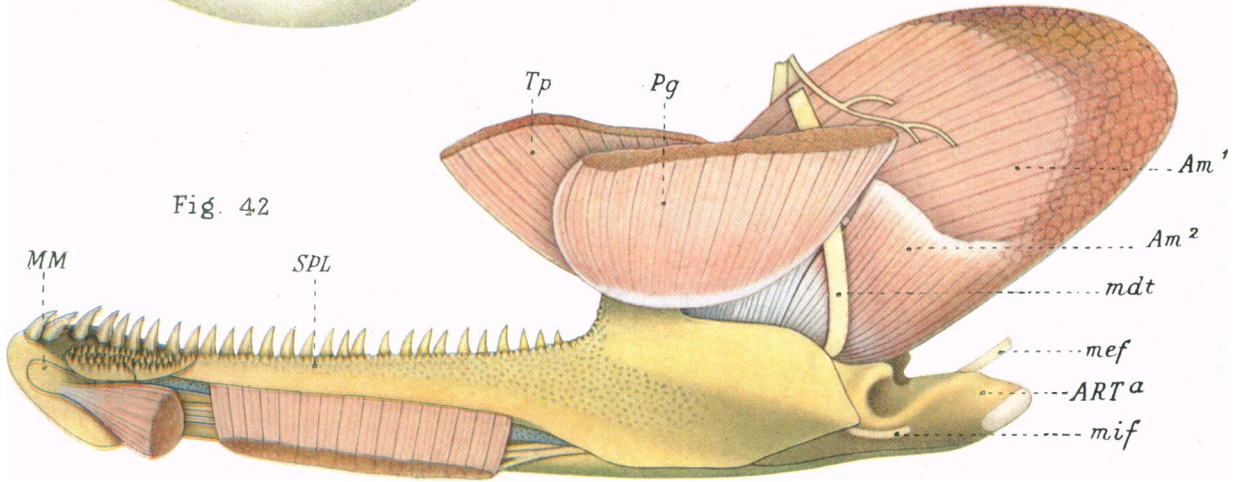


Fig. 42

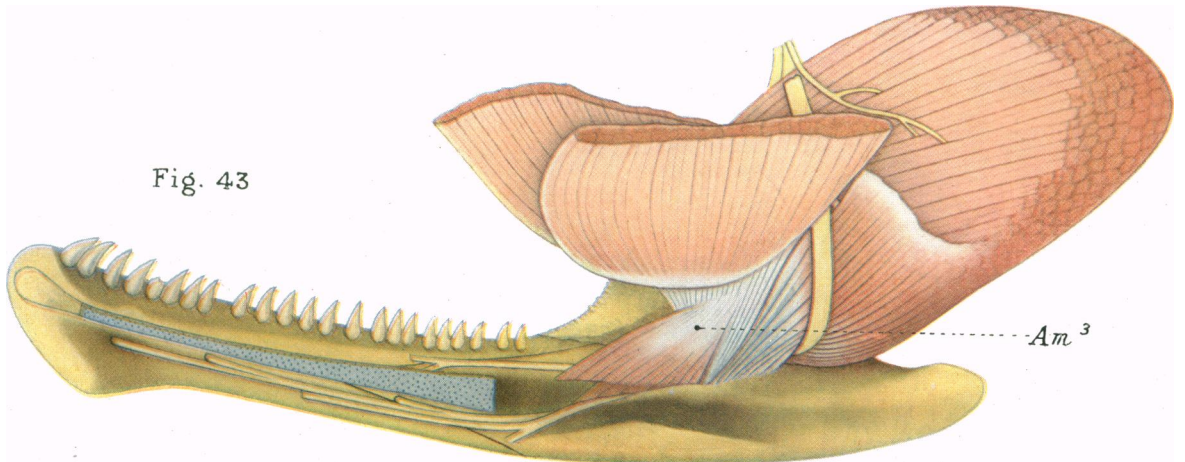


Fig. 43

- Fig. 40. Ventral view of right eyeball of large specimen of *Pclypterus bichir* from Abyssinia. $\times 6$.
 Fig. 42. Internal view of mandible with muscles attached. $\times 2$.
 Fig. 43. The same, with splenial removed. $\times 2$.

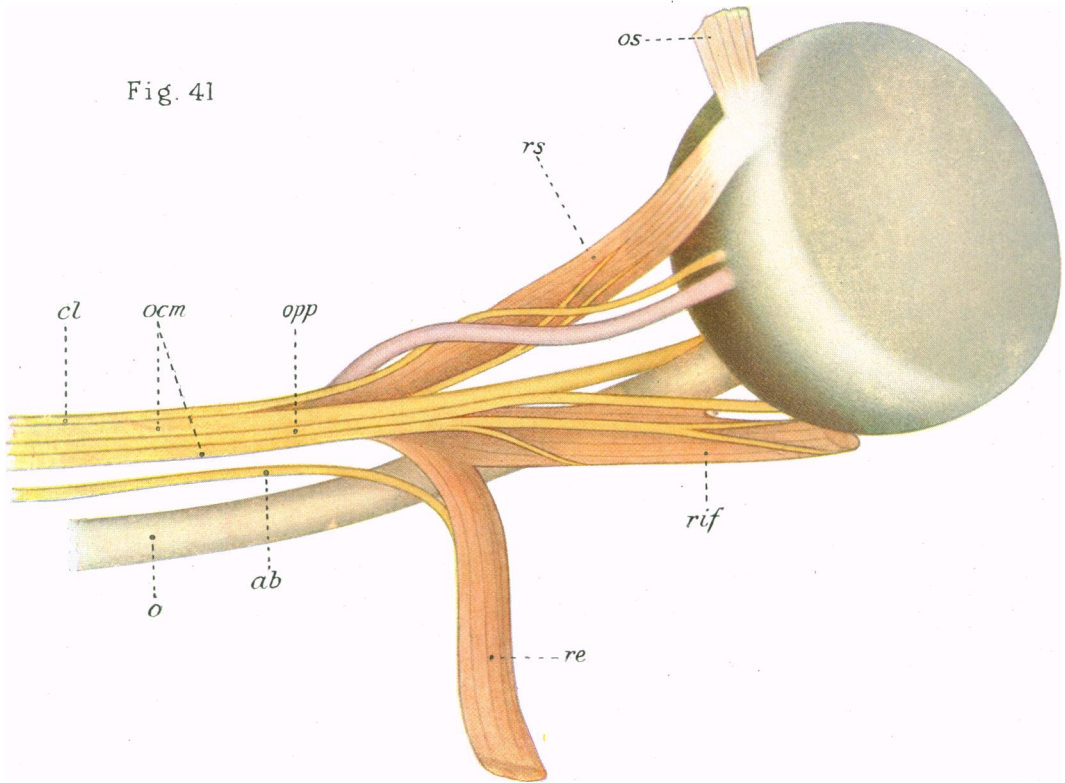


Fig. 41

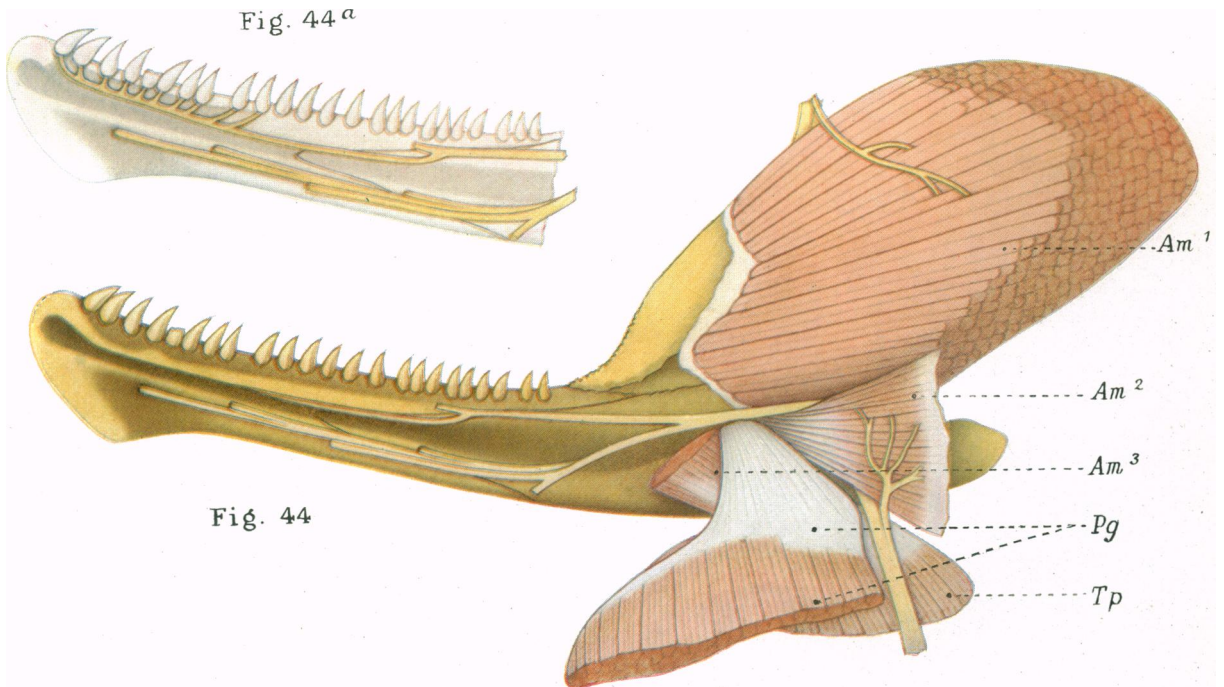


Fig. 44^a

Fig. 44

Fig. 41. Lateral view of right eyeball of large specimen of *Polypterus bichir* from Abyssinia. $\times 6$.
 Fig. 44. Internal view of mandible with musculi temporalis and pterygoideus turned downward. $\times 2$.
 Fig. 44a. Anterior end of the same, showing innervation of the teeth. $\times 2$.

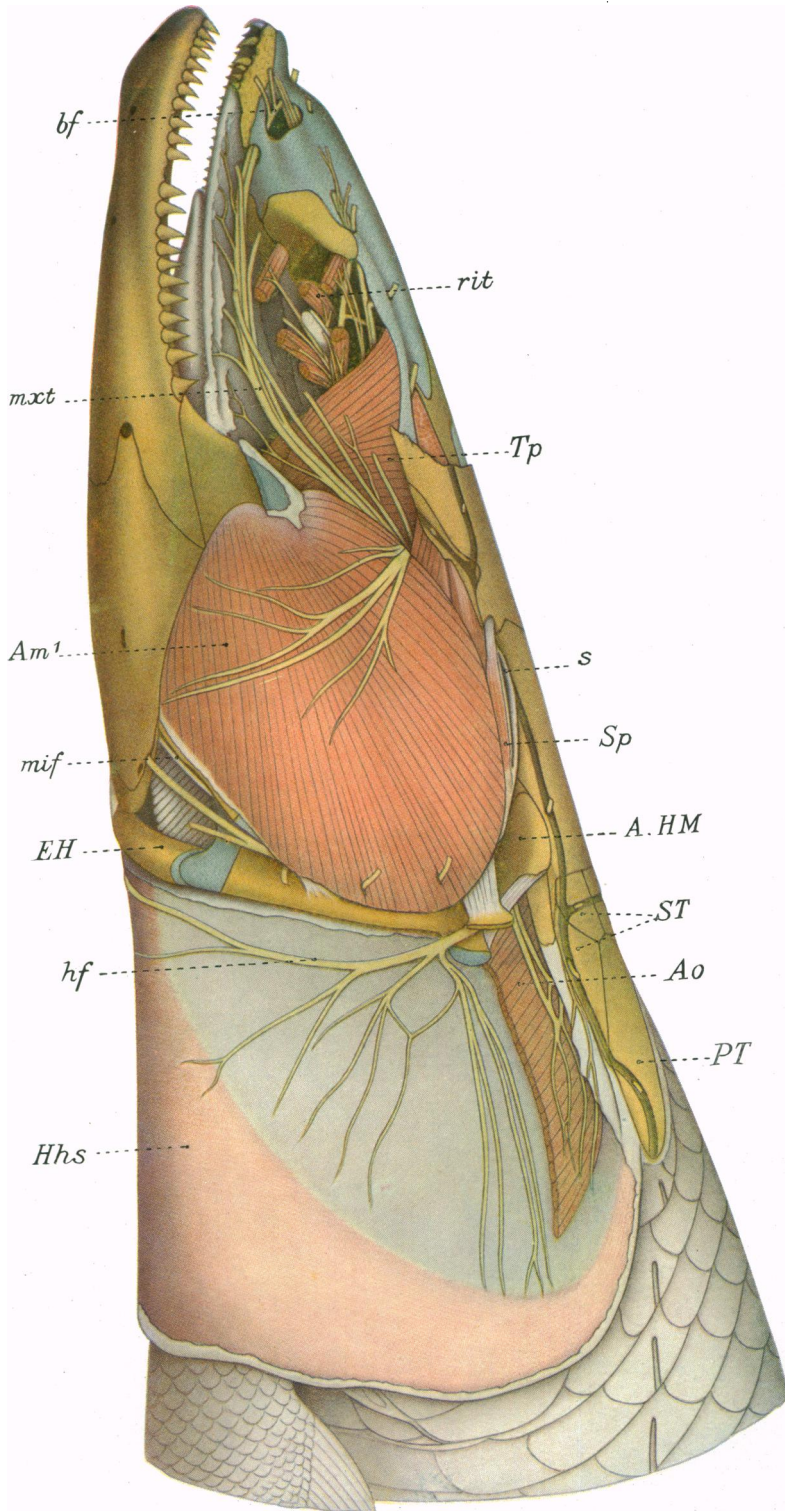


Fig. 45. Lateral view of head of large *Polypterus bichir* from Abyssinia, with skin and eyeball removed. $\times 2$.

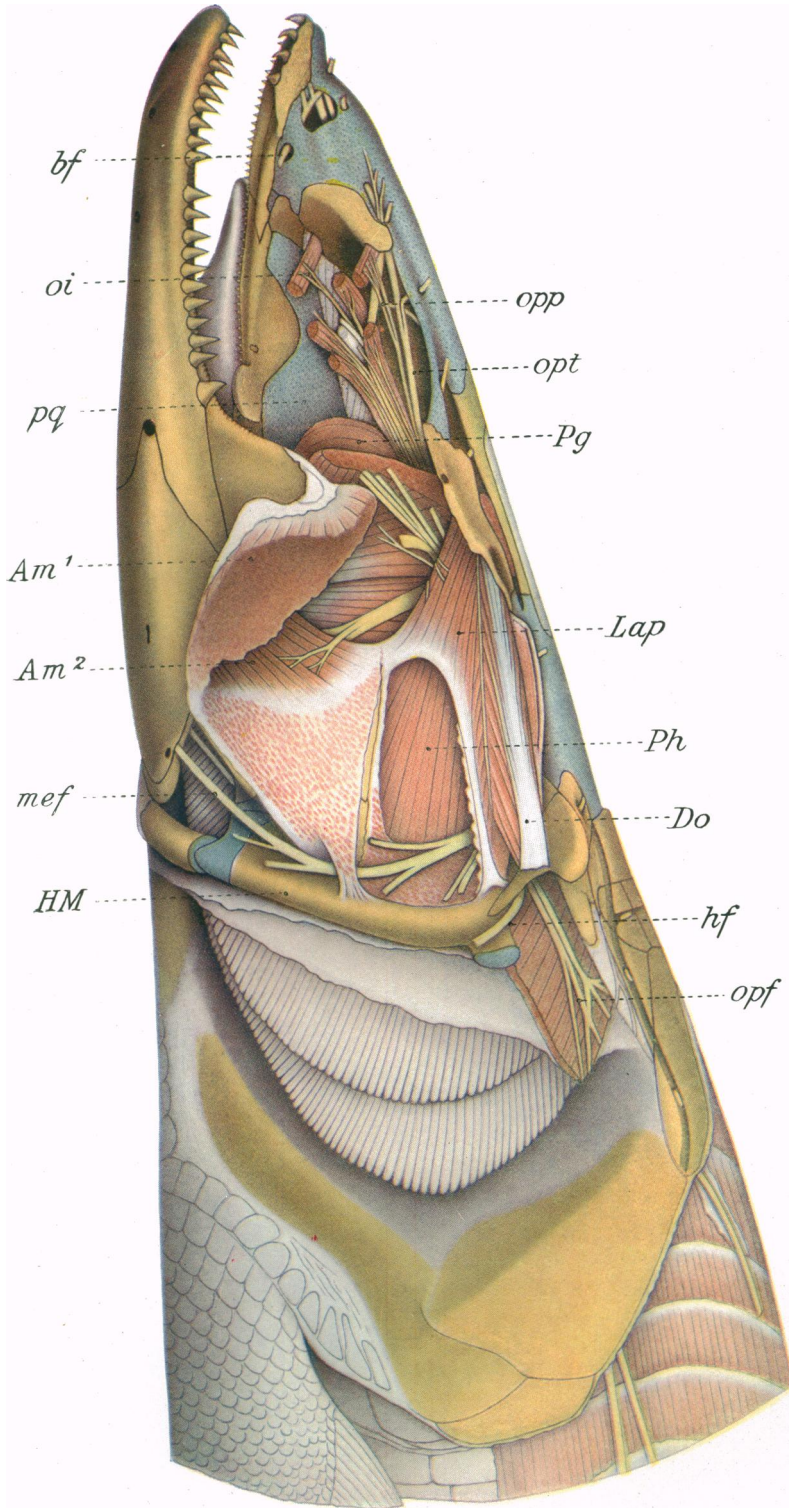


Fig. 46. Lateral view of head of large *Polypterus bichir* from Abyssinia, with musculus masseter removed. $\times 2$.

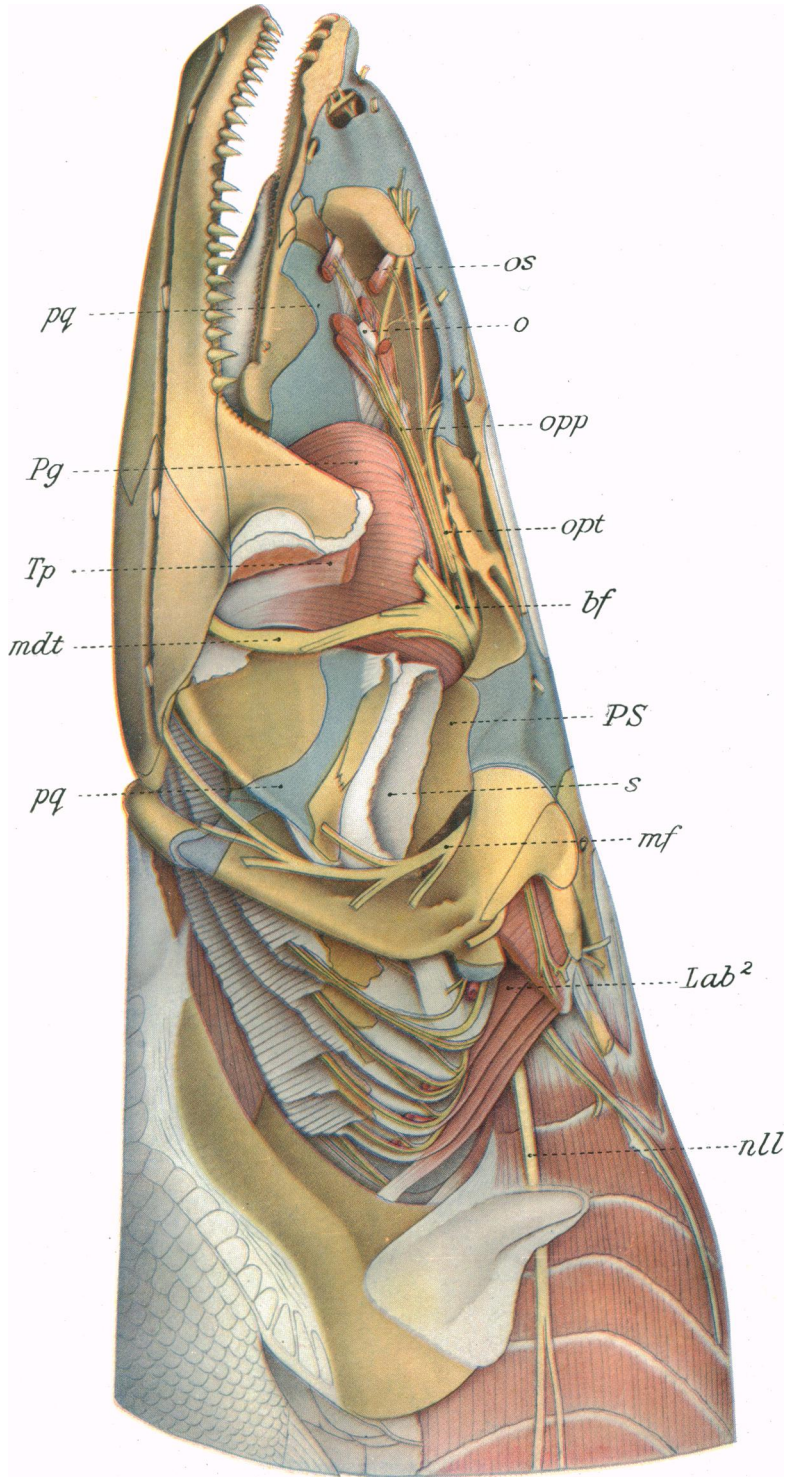


Fig. 47. A deeper dissection of head of large *Polypterus bichir* from Abyssinia. $\times 2$.

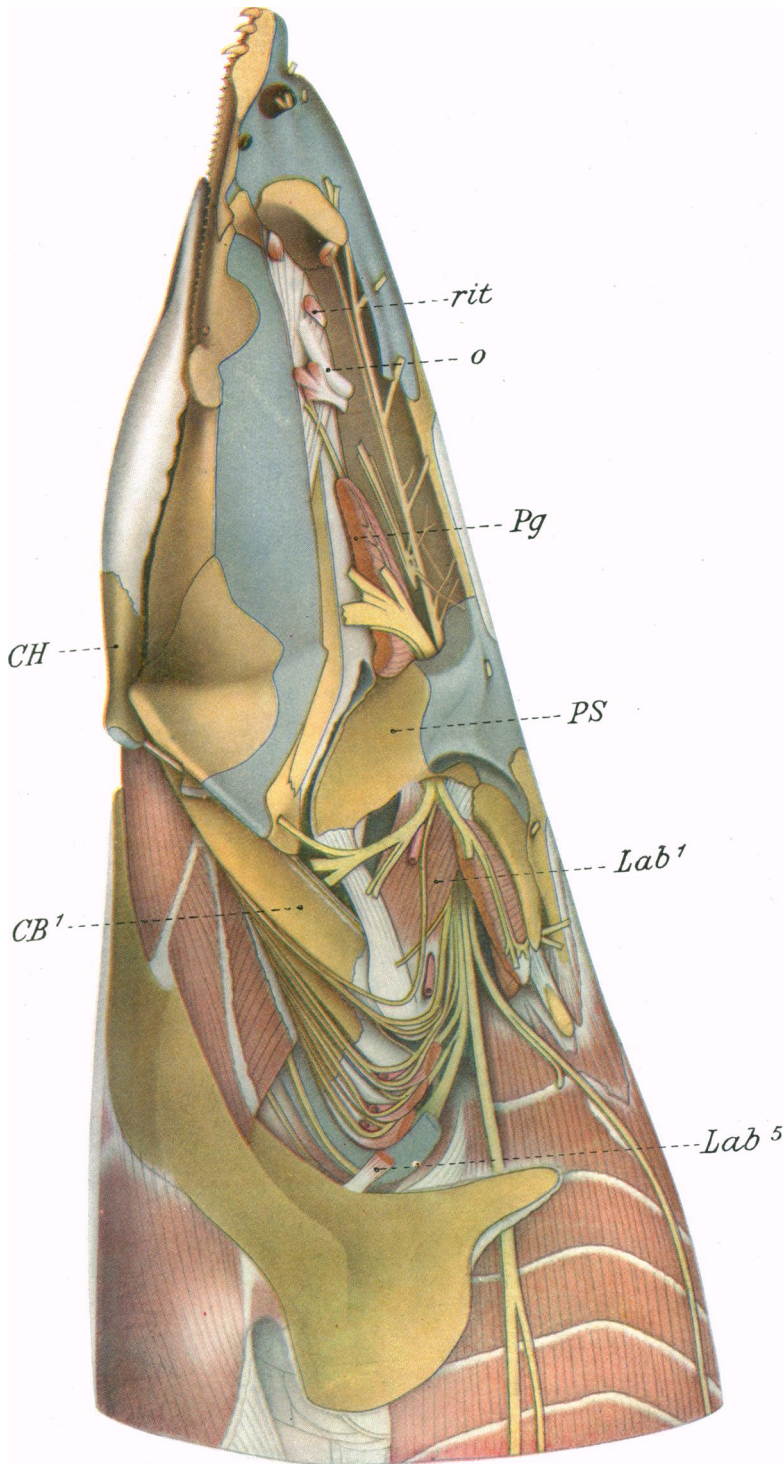


Fig. 48. A still deeper dissection of head of large *Polypterus bichir* from Abyssinia. $\times 2$.

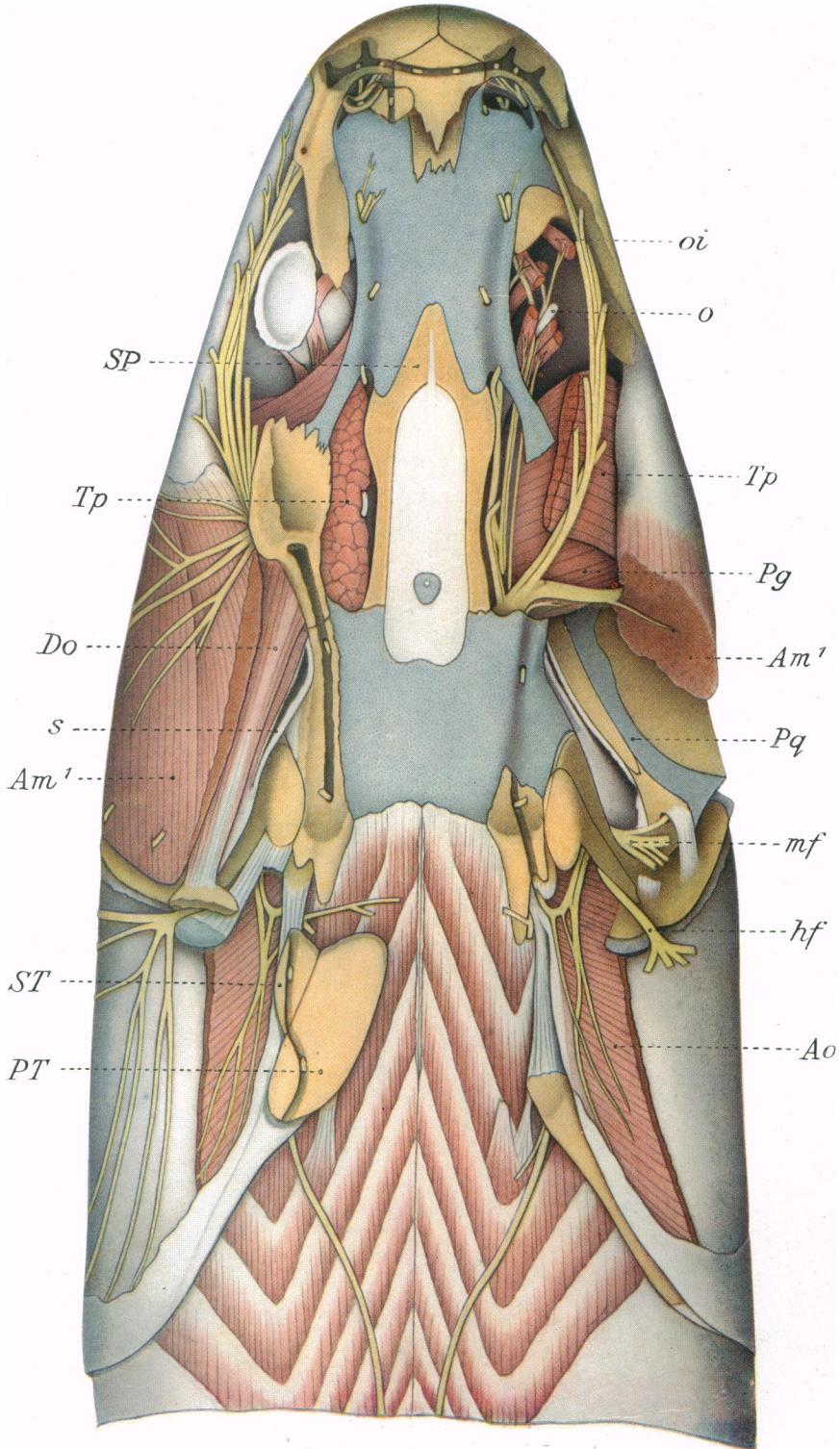


Fig. 49. Dorsal view of head of large *Polypterus bichir* from Abyssinia, with skin and dermal bones removed. $\times 2$.

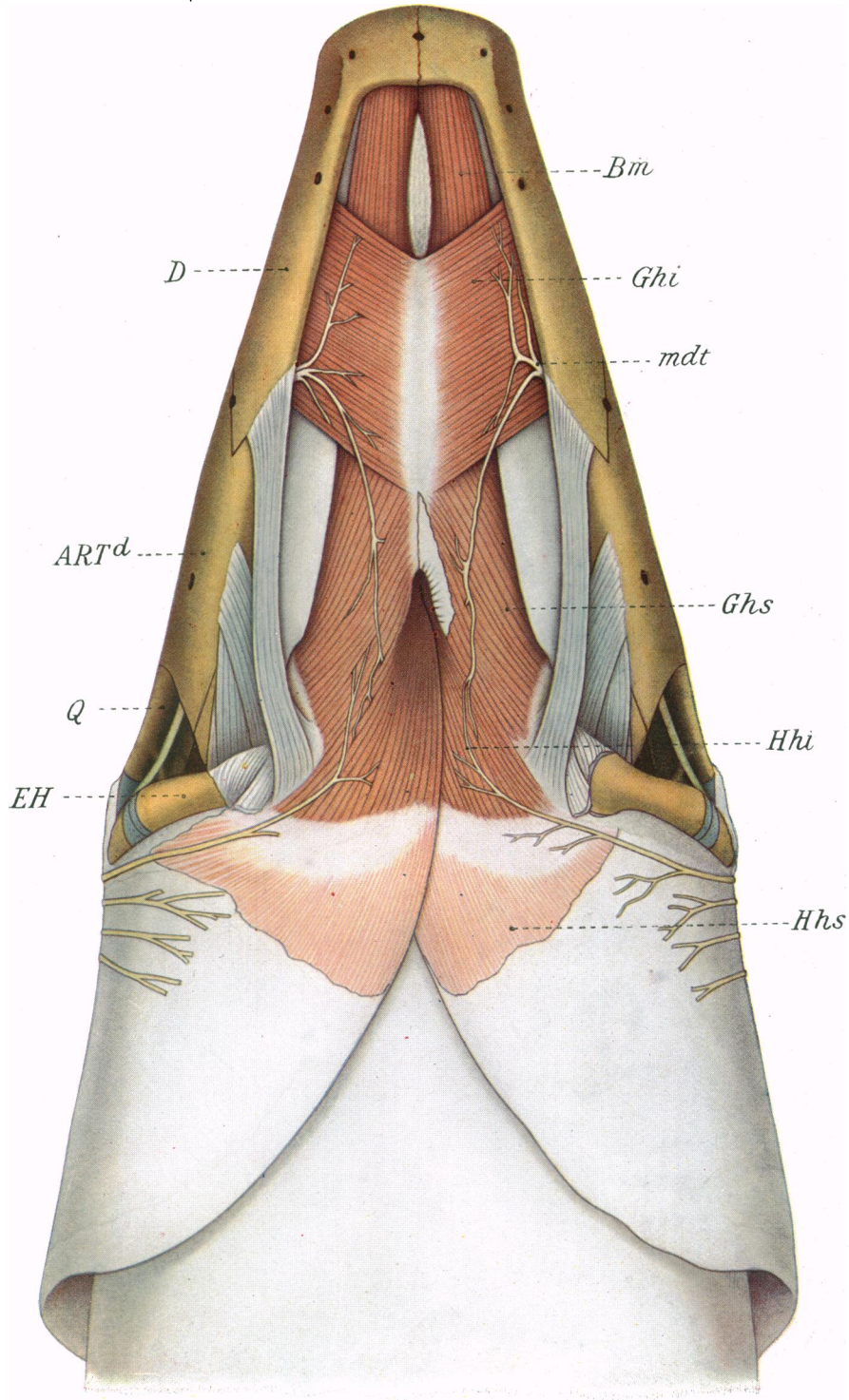


Fig. 50. Ventral view of a second head of large *Polypterus bichir*, with skin removed. $\times 2$.

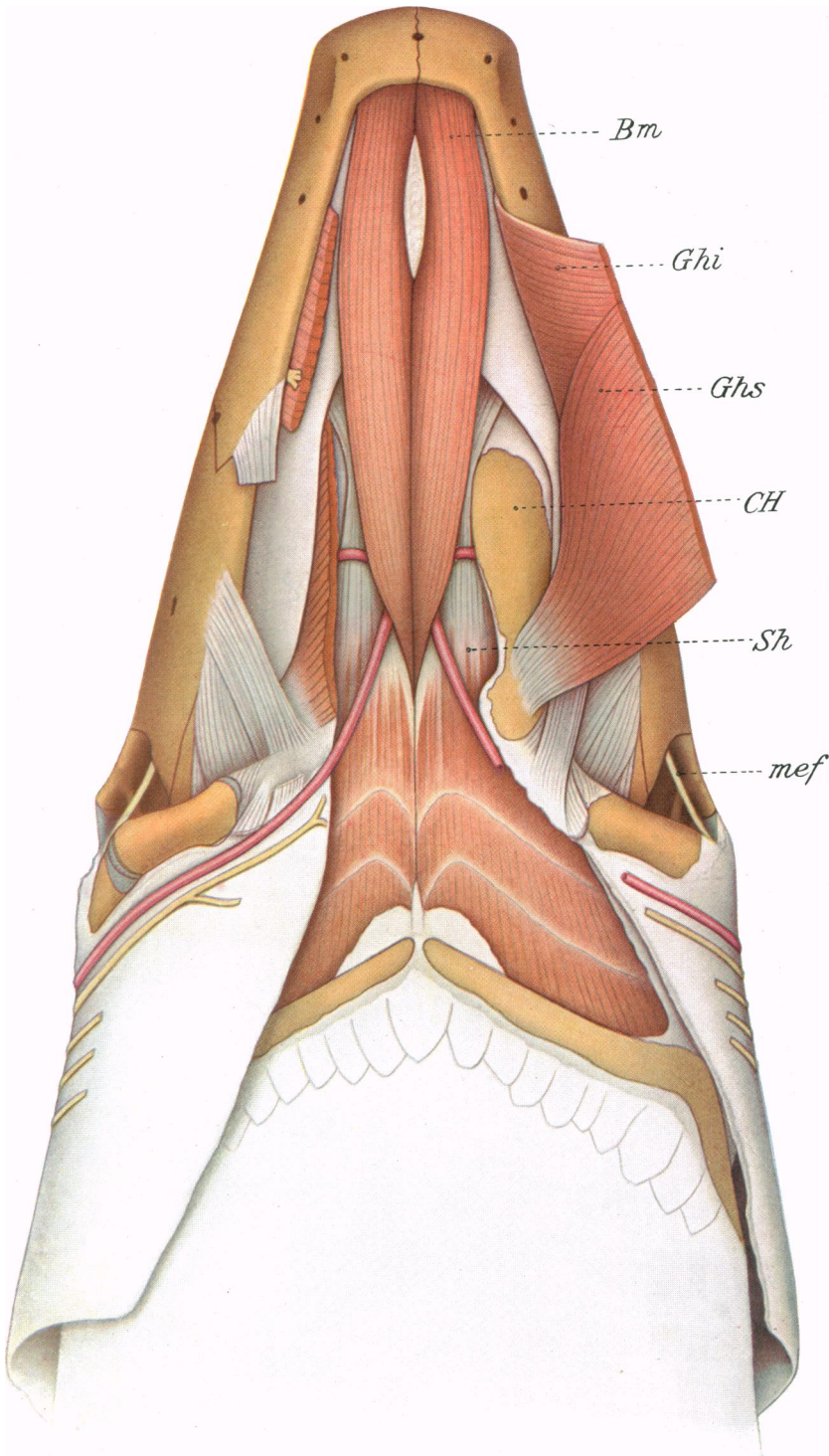


Fig. 51. A deeper dissection of a second head of large *Polypterus bichir*. $\times 2$.

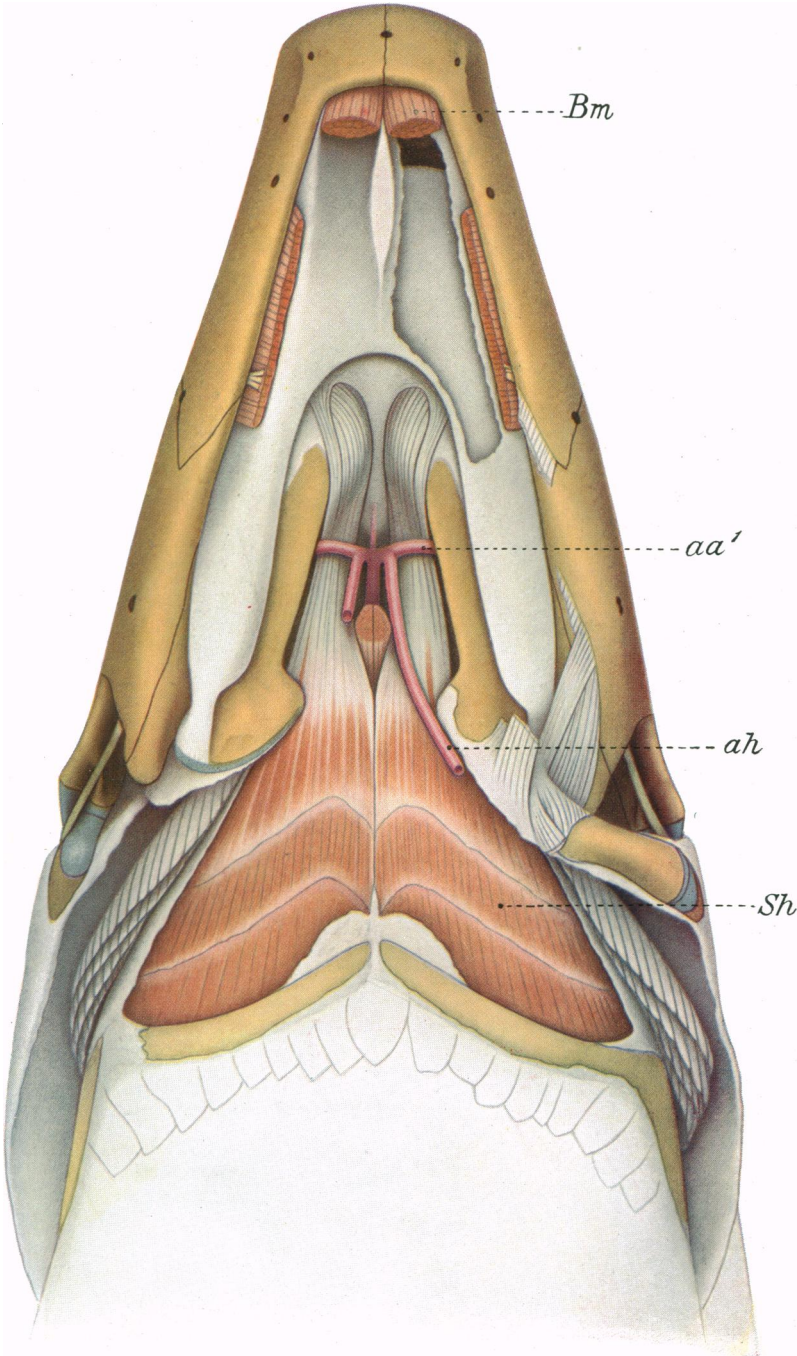


Fig. 52. A still deeper dissection of a second head of large *Polypterus bichir*. $\times 2$.

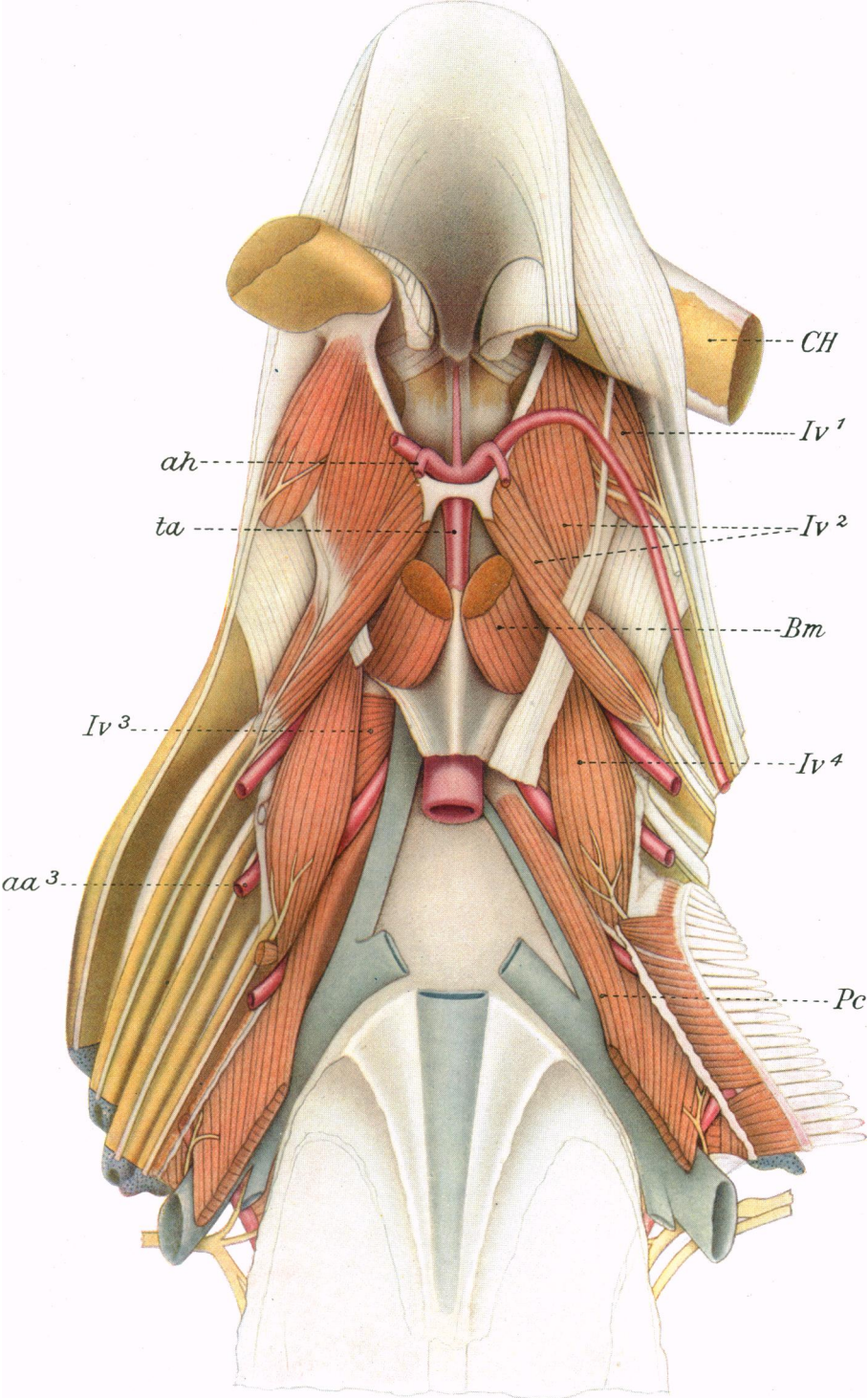


Fig. 53. Ventral view of the hyal and branchial arches of *Polypterus ornativipinnis*, with muscles attached. × 2.

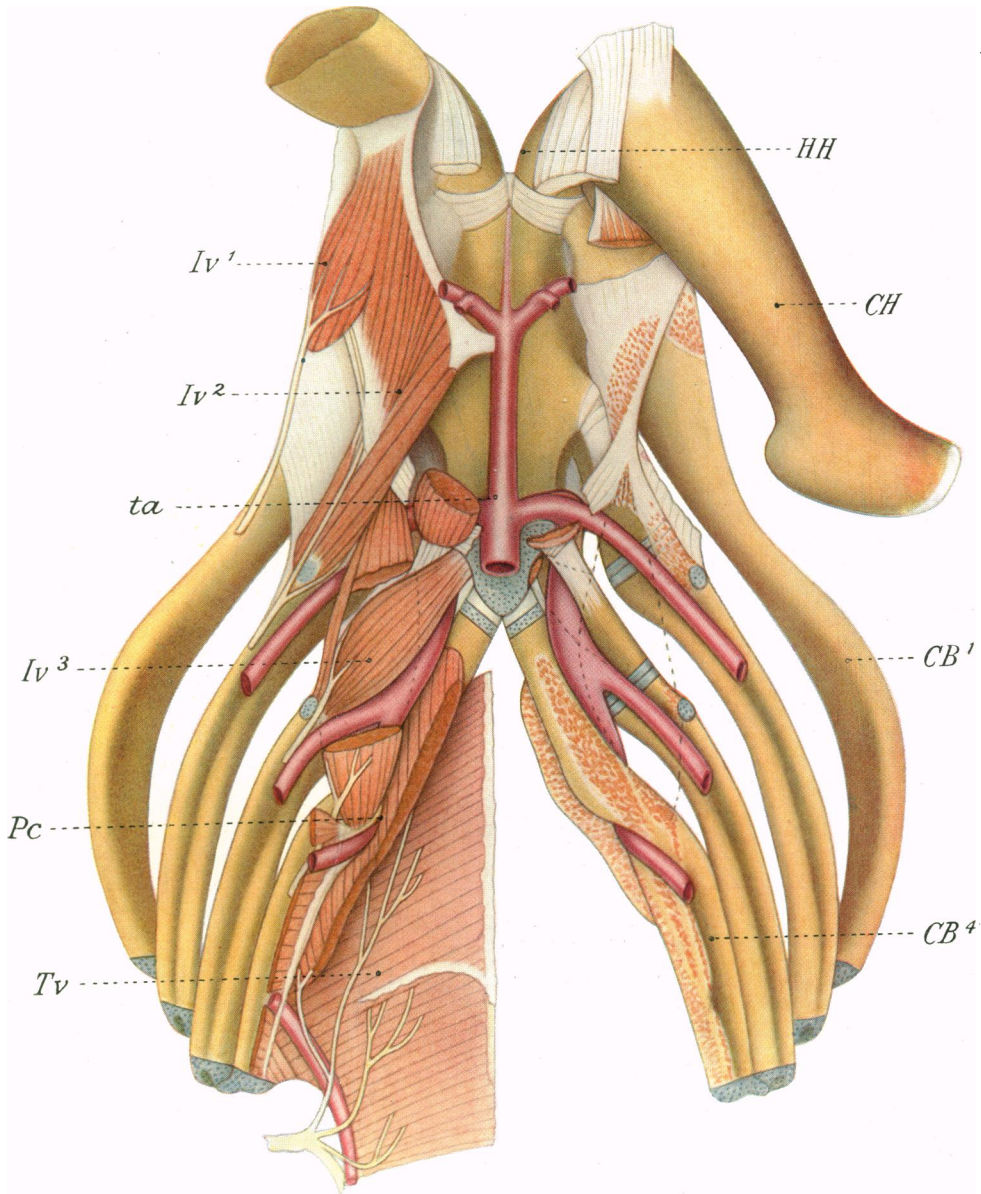


Fig. 54. A deeper dissection of the hyal and branchial arches of *Polypterus ornatipinnis*. x 2