Notes on the Development of the Chondrocranium of Polypterus Senegalus.

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With 16 Text-figures.

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INTRODUCTION

THE chondrocranium of Polypterus is far better known in the later stages than in the earlier stages. Pollard (1892) described the cranial anatomy of a half-grown specimen, Budgett (1902) described a 30-mm. larva, and Lehn (1918) gave a detailed account of the neurocranium of a 55- and a 76-mm. specimen. The skull of the adult was first described by Traquair (1871); his description was added to by Bridge (1888), and finally an exhaustive description was given by Allis (1922). The chondrocranium of younger stages is, however, far less well known. The three existing young stages were briefly described by Graham Kerr (1907), and the mandibular and hyoid bars with their associated muscles of the same specimens were described by Edgeworth (1929). De Beer (1926) drew attention to the important morphological characters in the chondrocranium of Polypterus. Thus it can be seen that existing accounts of the development of the chondrocranium of

Polypterus are mainly confined to the older stages, and the development of the young stages is only poorly known.

At the suggestion of my friend and former tutor, Dr. G. R. de Beer, I determined to re-examine Budgett's material and to give a description of the chondrocranium, which would embody all the available information. Working with so few specimens this proved to be rather disappointing, but a few new facts have come to light, which justify a fresh account of these young stages. A really comprehensive review will be impossible until more young larvae of this interesting primitive fish have been collected.

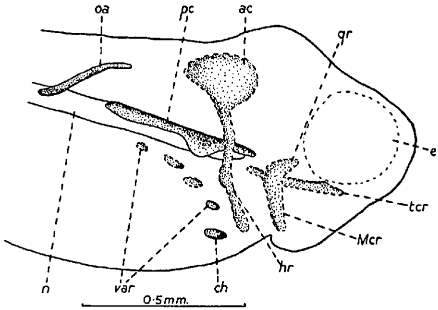
I am greatly indebted to Dr. G. R. de Beer for his criticism and encouragement without which this work would not have been undertaken. This work was carried out partly in the Department of Zoology in the University of Glasgow, where I was privileged to work during a visit. I would like to take this opportunity of thanking Professor Graham Kerr, whose generosity and hospitality alone made this work possible. The reconstructions were made later in the Zoology Department of the University of Leeds, and I desire to express my gratitude to Professor Garstang for giving me every facility during my work and for invaluable criticism. It is, however, to the late Mr. J. S. Budgett, who died from diseases contracted whilst obtaining the material, that I owe my greatest debt.

The material consisted of those three larvae, 6·75, 8·0, and 9·3 mm., briefly described by Graham Kerr (1907), and the 30-mm. larva described by Budgett (1902). Reconstructions were made by the graphical, glass-plate, and blotting-paper-wax methods.

Description of Specimens

Stage 32. 6·75-mm. larva (Text-figs. 1 and 2).

This is the youngest known specimen in which the skeleton is developed. The parachordals, occipital arch cartilages, and the ceratohyals are alone formed of cartilage, the remaining skeleton is merely represented by a procartilaginous aggregation of nuclei. The parachordals are well chondrified and expand into flanges laterally underlying the auditory sacs. They lie

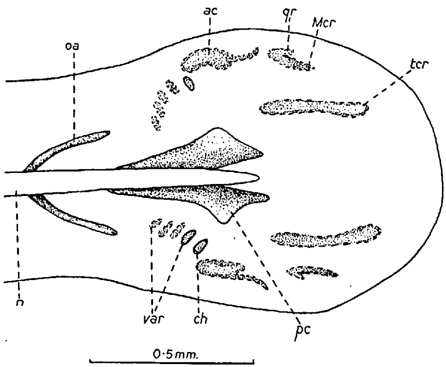


TEXT-FIG. 1.

Polypterus senegalus. Reconstruction of a lateral view of a 6·75-mm. larva. Procartilage with broken outline.

EXPLANATION OF LETTERING OF TEXT-FIGS. 1–16.

abc, anterior basicapsular commissure; *ac*, auditory capsule; *an*, abducens nerve; *aoc*, aortic canal; *ar*, anterior rectus; *bb*, basibranchial; *bcf*, basicapsular fenestra; *bf*, basicranial fenestra; *can*, canal for ophthalmic nerve and superior oblique; *cb 1–4*, ceratobranchials 1–4; *ch*, ceratohyal; *da*, dorsal aorta; *ds*, dorsum sellae; *e*, eye; *eb*, epibranchial portion of ceratobranchial; *ec*, epiphysial cartilage; *ect*, ectethmoid cartilage; *ep*, ethmoid plate; *er*, external rectus muscle; *ff*, foramen for facial nerve; *fpo*, foramen of profundus and oculomotor nerves; *fso*, foramen of superficial ophthalmic nerve; *fta*, foramen for trigeminus and abducens nerve; *fv*, vein foramen; *gf*, glossopharyngeal nerve; *hb 1–4*, hypobranchials 1–4; *hf*, hypophysial fenestra; *hh*, hypohyal; *hn*, hypoglossal nerve; *hr*, rudiment of hyosymplectic; *hs*, hyosymplectic; *h7*, hyoid branch of facial; *ins*, internasal septum; *iob*, inferior oblique; *ir*, inferior rectus; *lao*, lateral aorta; *lbc*, labial cartilage; *lc*, lateral commissure; *llf*, lateral line foramen; *lon*, lamina orbitonasalis; *Mc*, Meckel's cartilage; *Mcr*, procartilaginous rudiment of Meckel's cartilage; *m7*, mandibular branch of facial; *n*, notochord; *o*, occipital bone; *oa*, occipital arch; *oat*, orbital artery; *oc*, oculomotor nerve; *op*, otic process of palatoquadrate; *ops*, opisthotic bone; *pbc*, posterior basicapsular commissure; *pc*, parachordal cartilage; *pf*, palatine branch of facial nerve; *pfc*, prefacial commissure; *pn*, pathetic nerve; *ppp*, post-palatine process; *pq*, palatoquadrate; *pr*, posterior rectus; *prp*, pro-otic process; *pt*, profundus nerve; *pv*, pituitary vein; *pvf*, pituitary vein foramen; *qr*, procartilaginous rudiment of quadrate; *r*, rostrum; *sh*, stylohyal; *sob*, superior oblique; *soc*, supra-orbital closely on either side of the notochord but their anterior ends diverge, leaving the anterior end of the notochord free. There are no separate polar cartilages. The trabeculae are widely separated procartilaginous tracts of nuclei, and lie freely below



TEXT-FIG. 2.

Polypterus senegalus. Reconstruction of dorsal view of 6·75-mm. larva.

the brain. The occipital arches are well chondrified; their bases are in contact with the notochord, and they bend forwards and outwards, their anterior ends being unconnected. The auditory capsule and hyoid bar are represented by continuous procartilaginous structures. The mandibular bar is an L-shaped aggregation of nuclei, the dorsal part, according to Edgeworth, representing the quadrate portion, and the ventral, Meckel's cartilage. The ceratohyals are small ventral cartilages lying

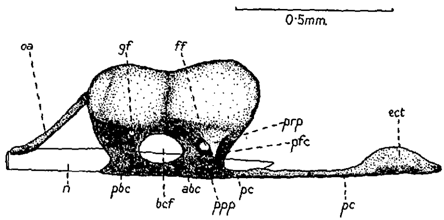
Explanation of Lettering of Text-figs. 1–16 (*cont.*)

cartilage; *sop*, superficial ophthalmic nerve; *sph*, sphenoid bone; *spt*, sphenotic bone; *sr*, superior rectus; *tc*, trabecula cranii; *tcom*, trabecula communis; *tm*, taenia marginalis; *tr*, trigeminus nerve; *ts*, tectum synoticum; *var*, visceral arch rudiments; *vcl*, vena capitis lateralis; *vf*, foramen for vagus nerve; *vn*, vagus nerve.

directly posterior to the lower ends of the hyoid rudiments. Above and behind the ceratohyals lie the rudiments of the more posterior visceral arches consisting of a small chondrification and small tracts of procartilage. At this early stage it is not possible to determine the individual fates of these structures with certainty.

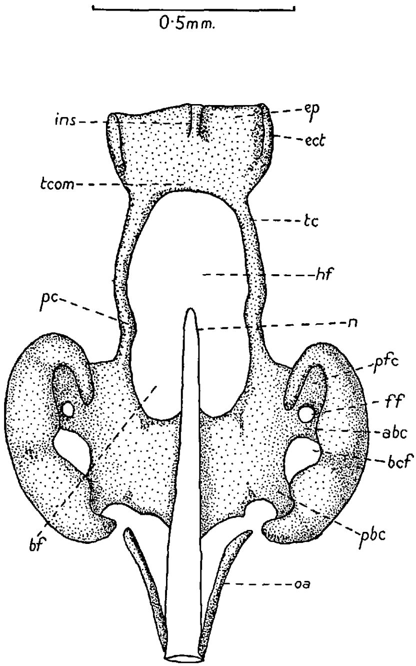
Stage 33. 8·0-mm. larva (Text-figs. 3, 4, 5, 6).

There is unfortunately a very marked gap between the preceding stage and this one. This stage has been damaged on the



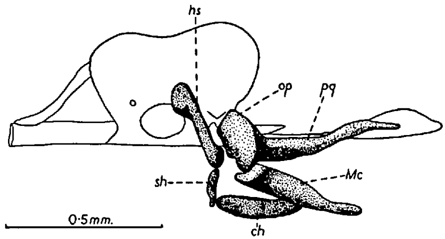
TEXT-FIG. 3.
Polypterus senegalus. Reconstruction of lateral view of neurocranium of 8-mm. larva.

left side of the head, and the reconstructions of that side have been largely reproduced from the right side. The 8·0-mm. specimen is far more fully developed than the 6·75 mm. The auditory capsule has become fused to the parachordal by the anterior and posterior basicapsular commissures. The foramen for the glossopharyngeal nerve has become separated from the basicapsular fenestra, which is still a fairly wide vacuity. The foramen for the facial nerve is bounded posteriorly by the anterior basicapsular commissure, and anteriorly by the prefacial commissure, which is fully formed at this stage. Laterally to this commissure is a well-marked down-growth, the pro-otic process, which lies outside the vena capitis lateralis. This process, together with the post-palatine process, represented in this stage by a very small lateral knob-like up-growth from the parachordal, will form the lateral commissure. The post-palatine process is median and dorsal to the lateral aorta, and



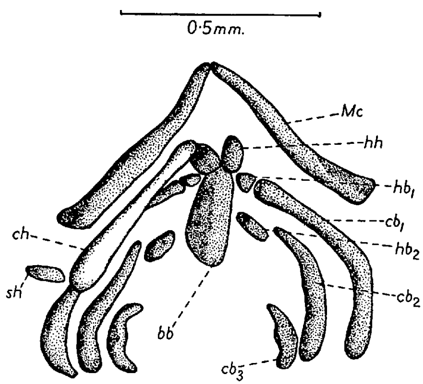
TEXT-FIG. 4.
Polypterus senegalus. Reconstruction of dorsal view of 8-mm. larva.

separates it from the head vein, to which the post-palatine commissure is lateral and ventral. The auditory capsules are roofed dorsally by only a very small quantity of cartilage, and there is no chondrification between the semicircular canals and



TEXT-FIG. 5.

Polypterus senegalus. Reconstruction of lateral view of splanchnocranium of 8-mm. larva.



TEXT-FIG. 6.

Polypterus senegalus. Reconstruction of ventral view of splanchnocranium of 8-mm. larva.

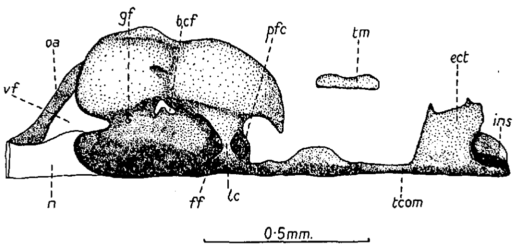
the brain except at the extreme anterior and posterior ends. The notochord still projects freely into the hypophysial fenestra, and the parachordals diverge laterally and join the trabeculae. The connexion of the trabeculae and parachordals is marked by a sinuous curve. The trabeculae are widely separated and fused with one another at the front forming a substantial plate, the ethmoid plate and trabecula communis. The sides of this plate are raised into the lamina orbitonasalis, and centrally there is a small up-growth, the internasal septum. The occipital arches are still only attached to the notochord, their anterior ends lying close but not attached to the auditory capsules.

The palatoquadrate is fully chondrified and has a well-developed otic process (termed metapterygoid process by Sewertzoff, 1926), and a downwardly directed process which articulates with Meckel's cartilage, which is well developed but not attached to its fellow of the opposite side. The posterior end of Meckel's cartilage is expanded laterally, forming a platform. The hyomandibular and symplectic are apparently represented by a single cartilage, and are no longer connected to the auditory capsule. The hyosymplectic is closely associated with the stylohyal which in its turn is associated with the ceratohyal, a well-developed rod of cartilage broad at each end but narrowing in the middle, it articulates with the basihyal through the hypohyal. The first and second hypobranchials are present, and the first, second, and third ceratobranchials; the latter, however, is only slightly developed. The median basibranchial is a broad cartilage stretching only from the posterior end of the hypohyals to the region of the second hypobranchial.

Stage 36. 9·3-mm. larva (Text-figs. 7, 8, 9, 10).

This stage shows considerably more chondrification than in stage 33. The basicapsular fenestra has become reduced to a small slit. The pro-otic process and the post-palatine process have fused to form the lateral commissure which now completely encloses the vena capitis lateralis and the palatine branch of the facial. The prefacial commissure persists. The auditory capsules are more fully roofed, although the two capsules have not yet been joined dorsally by the tectum synoticum. The occipital arches are fused to the back part of the auditory capsules enclosing a foramen for the vagus and hypoglossal nerves. The hind end of the parachordals is not connected to the bases of the occipital arches. The anterior end of the notochord projects freely for some considerable distance and has hardly been surrounded by the parachordals at all. The orbital cartilages or taeniae marginales appear as independently developed cartilages lying approximately equidistant between the auditory capsule and nasal capsule. In the olfactory capsule the lamina orbitonasalis and the internasal septum are a great deal further developed.

One of the characteristics of this specimen is the transient



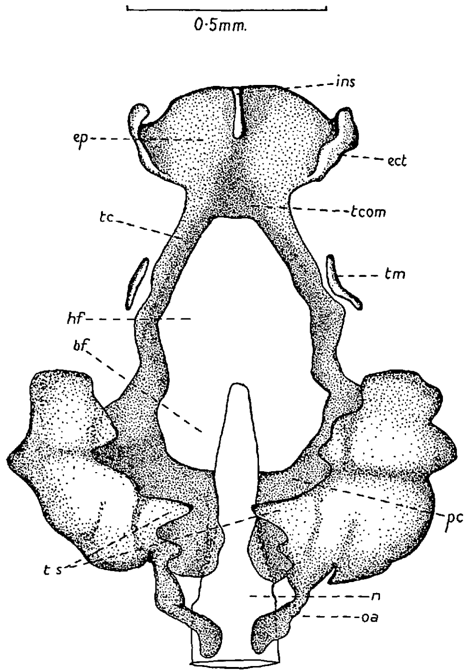
TEXT-FIG. 7.

Polypterus senegalus. Reconstruction of lateral view of neurocranium of 9·3-mm. larva.

fusion of previously distinct cartilages with one another. The hyosymplectic becomes fused to the palatoquadrate, which is itself, however, free from the trabeculae. The otic process of the palatoquadrate is very well developed. Meckel's cartilages are fused with one another anteriorly, the lateral expansions at their posterior end are more greatly developed. The stylohyal and the ceratohyal are similar to those in the 8-mm. specimen but are both more fully developed, the latter articulating with the hypohyal. All the remaining arches have the hypobranchials and ceratobranchials fused together. The basibranchial is a solid flattened median cartilage with which the hypobranchials articulate.

30-mm. specimen (Text-figs. 11, 12, 13, 14, 15).

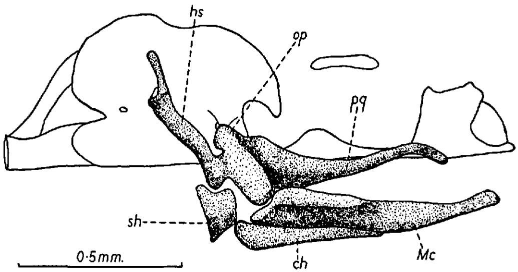
Again there is an unfortunate hiatus between this and the preceding specimen. This specimen is very nearly completely chondrified and differs but little from the 55 mm. and larger



TEXT-FIG. 8.

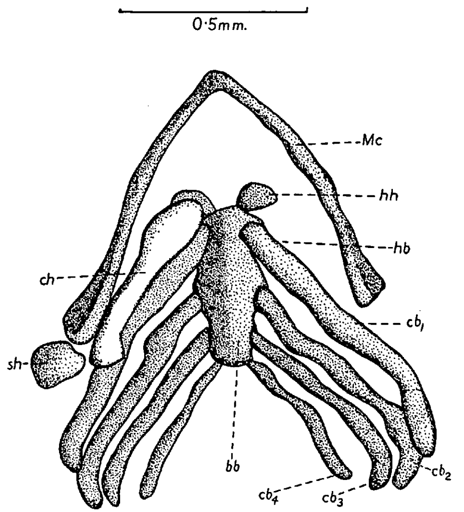
Polypterus senegalus. Reconstruction of dorsal view of 9·3-mm. larva.

specimens of Lehn (1918). Chondrification is, however, not completed in the region of the hypophysis. The hypophysial fenestra is not yet divided by a cartilaginous dorsum sellae



TEXT-FIG. 9.

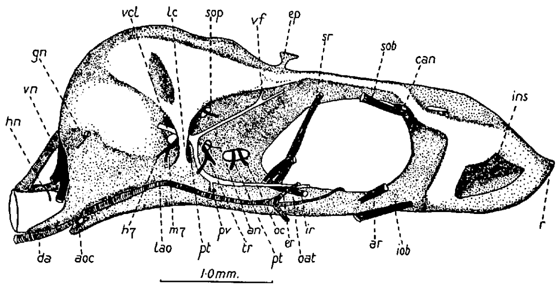
Polypterus senegalus. Reconstruction of lateral view of splanchnocranium of 9·3-mm. larva.



TEXT-FIG. 10.

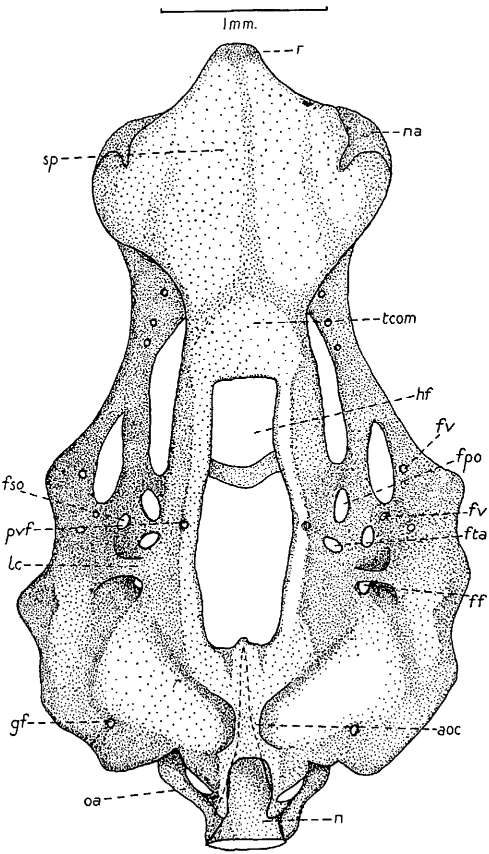
Polypterus senegalus. Reconstruction of ventral view of splanchnocranium of 9·3-mm. larva.

from the basicranial fenestra, as it is in the 55-mm. specimen of Lehn. In the 30-mm. specimen the dorsum sellae is represented by a connective-tissue membrane. Later, according to Lehn, this becomes chondrified, and finally only two very small functionless foramina remain to mark the fenestra basicranialis (Text-fig. 16). The parachordal cartilages now meet below the much-shrunken anterior end of the notochord, and the tip of



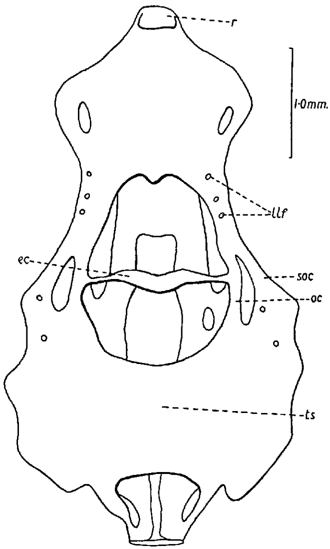
TEXT-FIG. 11.
Polypterus senegalus. Reconstruction of lateral view of 30-mm. larva.

the notochord no longer projects freely, the connexion between the parachordals being continued in front and below it. The auditory capsules are further chondrified, and the anterior and posterior semicircular canals are enclosed in cartilage much as in a Teleost, and the capsules are connected dorsally with one another by a continuous sheet of cartilage: the tectum synoticum. The lateral walls of the skull have become more chondrified, enclosing the superficial ophthalmic trigeminal, profundus, abducens, and oculomotor nerves. The profundus and oculomotor nerves pass out by the same foramen, and the pituitary vein enters the skull through its own foramen. It was particularly hoped that the early stages might throw some light on this peculiar arrangement by the development of the commissures in this region; but once again it was found that the critical stages do not exist. A true pila pro-otica cannot be



TEXT-FIG. 12.
Polypterus senegalus. Reconstruction of ventral view of 30-mm. larva.

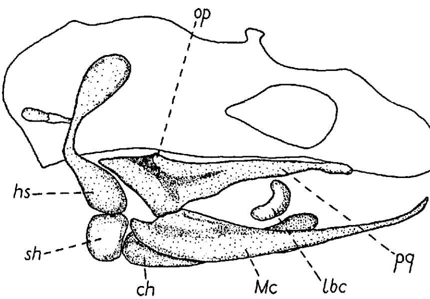
present, and the only explanation seems to be the one put forward by de Beer (1926) 'that the pila pro-otica is present separating the pituitary vein foramen from that of the tri-



TEXT-FIG. 13.
Polypterus senegalus. Reconstruction of dorsal view of 30-mm. larva.

geminal nerve, but that in the upper region it has failed to chondrify, thus allowing the profundus to slip forwards and join the oculomotor. The cartilage between the profundus-oculomotor and trigeminal foramen must be secondary.'

The bases of the occipital cartilages are now joined to the parachordals by a cartilaginous connexion. Down-growths from the parachordals in the occipital region enclose the dorsal aorta in a canal, which ends where the aorta divides. The orbital cartilages have joined both the auditory and nasal capsules and laterally to them two more cartilages, the supra-orbitals, have been formed. The anterior junction of these two cartilages are pierced three times by nerves to the lateral-line



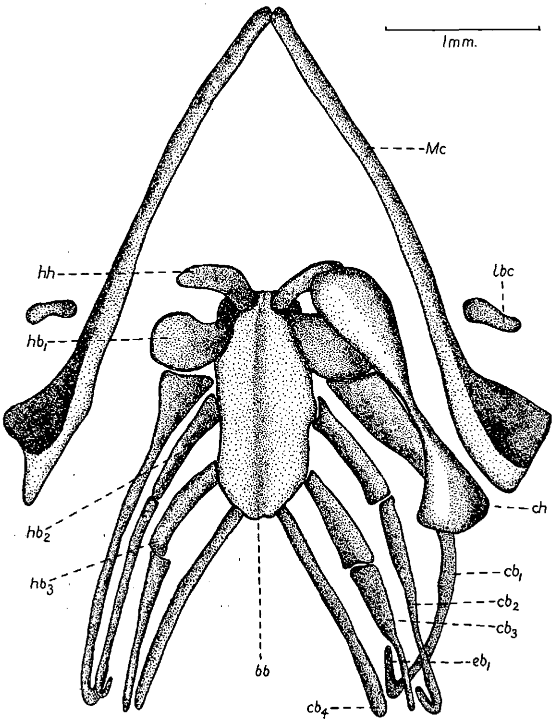
TEXT-FIG. 14.

Polypterus senegalus. Reconstruction of lateral view of 30-mm. larva (simplified from Budgett).

system. Dorsally the orbital cartilages are joined by a thin cartilaginous bar, the epiphysial cartilage.

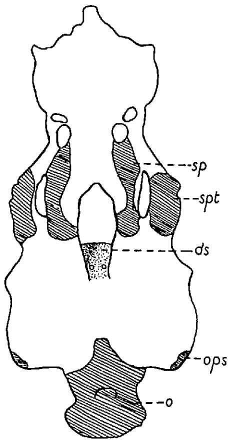
The nasal capsule is a well-chondrified box-like structure completely divided into two anteriorly by the internasal septum. At each posterior dorsal corner there is a canal through which the superficial ophthalmic nerve passes and from which the superior oblique eye-muscle arises. The olfactory capsule has relatively large external apertures and a small anterior rostrum. The trabecula communis has grown backwards, reducing the size of the hypophysial fenestra.

The palatoquadrate has become free from the hyosymplectic and the otic process greatly reduced. The rami of the lower jaw are again separate. Dorsal to Meckel's cartilage and ventral to the palatoquadrate there is a small labial cartilage. The ends of the hyosymplectic have become swollen, giving it the appear-ance of a bent dumb-bell with a small posterior process for the



TEXT-FIG. 15.
Polypterus senegalus. Reconstruction of ventral view of 30-mm. larva.

external gill cartilage. The ceratohyal has also become greatly expanded at its extremities. The first three hypobranchials and ceratobranchials are no longer fused, but the fourth is still represented by a continuous cartilage. The first hypobranchial and the anterior end of the first ceratobranchial are enormously expanded, and the posterior ends of the first and second ceratobranchials are beginning to bend dorsally forwards, forming an epibranchial portion. The completion of the epibranchials and



TEXT-FIG. 16.

Polypterus senegalus. Reconstruction of ventral view of 76-mm. larva (simplified from Lehn).

pharyngobranchials only is necessary before the adult stage is reached (Allis, 1922), the last bar being permanently unconstricted.

Text-fig. 11 represents this chondrocranium with the main nerves, blood-vessels, and eye-muscles reconstructed. Very little can be added to the excellent accounts of Pollard, Lehn, and Allis. Only the head vein and palatine branch of the facial nerve pass through the jugular canal. The former divides into a dorsal and ventral branch, the latter giving off the pituitary vein. The dorsal aorta divides into the lateral aortae which pass outwards and forwards, give off the orbital artery, and run alongside the trabeculae, and enter the cranial cavity dorsally to them near the optic nerve, as described by Allis (1908).

The posterior, superior, and inferior rectus muscles arise together, but the anterior rectus is attached farther forward to the trabecula communis. The attachment of the inferior oblique is very low down on the trabecula, and the superior oblique arises from the ophthalmic canal.

Discussion of Results.

The phylogenetic position of Polypterus has long been one of the major problems of fish classification. The older view of Huxley (1861) that Polypterus was a Crossopterygian has lost much ground in favour of the theory of Goodrich (1907, 1909, 1928) that Polypterus is an Actinopterygian, possibly a Palaeoniscid. To generalize from such fragmentary evidence as has been put forward in this paper would be impossible, nevertheless comparisons are always a temptation. The following remarks must therefore be taken only to show in what way the chondrocranium of Polypterus resemble those of other fish during its development, but not necessarily as establishing any bond of union between them. Authorities for the developments of Scyllium, Acipenser, Lepidosteus, Amia, and Teleosts are not cited in detail, but a list of the literature consulted is appended at the end.

The chondrocranium of Polypterus is platybasic, and consequently during development it shows a strong resemblance with other platybasic skulls in the general arrangement of the cartilages, particularly in the wide divergence of the parachordals from the notochord. The parachordals of Acipenser, however, do not show this divergence, and connexion between them in front of the notochord is established early. The parachordals are formed before the trabeculae and there are no separately developed polar cartilages, as in Lepidosteus and Elasmobranchs. The trabeculae fuse anteriorly to form the floor of the skull, the trabecula communis, and from the centre of the ethmoid plate a high internasal septum is formed as in Amia and Lepidosteus. In possessing both a prefacial and a lateral commissure, Polypterus is unique among living fishes, the condition is found, however, in the Palaeoniscoids. The formation of the lateral commissure from the pro-otic and post-palatine processes without a basitrabecular process is also unique. The head vein and palatine nerve only pass through the jugular canal, the orbital artery being given off by the lateral aorta considerably farther forward. The pro-otic process forms before the post-palatine process as in Amia, thus differing from Acipenser, Lepidosteus, and Salmo. The peculiar arrangement of the oculomotor and profundus nerves and the absence or partial absence of the pila pro-otica have already been discussed.

The occipital arch remains independent till comparatively late in development, and in so doing bears a very strong resemblance to Amia, whereas in other forms it grows up from the posterior end of the parachordals. The formation of the pro-otic bridge late in development is also a characteristic of Amia and Lepidosteus.

The early appearance of the quadrate portion of the palatoquadrate is only known elsewhere in the Teleosts. The large otic process of the palatoquadrate found in the young larvae, but gradually diminishing in the later stages, has a small homologue in Amia. The hyoid and symplectic remain fused as in Amia and Selachians. The temporary fusion of hyosymplectic and palatoquadrate is reported to occur also in Clupea and Syngnathus. During development, therefore, it is with Amia particularly, and Lepidosteus, among living fishes, that the chondrocranium of Polypterus shows most resemblances. These marked Actinopterygian similarities form additional evidence in support of Goodrich's theory.

It is unfortunate that the study of the development of the chondrocranium does not throw any direct light on the problem of the absence of the myodome in Polypterus. As Watson and others have shown, a myodome was present in the Palaeoniscoids, and some of their descendants (Amia and most Teleosts) have retained it, while others (Acipenseroids, Lepidosteus, and some Teleosts) must have lost it. Polypterus possesses a subpituitary space not unlike that found in Acipenser or Lepidosteus, and therefore, if the latter have lost the myodome, its loss by Polypterus presents no insuperable difficulty. Indeed, what evidence there is goes to show that this is the most reasonable interpretation. The presence of a myodome is associated with the possession of a large and active eye. But the eye of Polypterus is small and embedded in a closely fitting and bony orbit. Indeed, the modest nature of the muscular requirements of the eye in Polypterus, is shown by the fact that the origin of the anterior rectus muscle is shifted forwards, along the side of the skull. The muscle is consequently shorter than it would be if it originated from the same point as the other recti muscles. Yet in fishes with a fully developed myodome, it is this anterior rectus muscle which (together with the posterior rectus) elongates so considerably that the myodomic space is required in order to accommodate it. The reduction in size of this muscle in Polypterus, therefore, suggests that the myodome has disappeared because it is no longer required.

Summary.

The chondrocranium of the existing specimens of the larval Polypterus have been redescribed, and the earlier specimens figured for the first time. The development of the following structures have not been described previously in Polypterus:

1. The lateral commissure which forms first from the prootic and then the post-palatine process.
2. The taenia marginales, which arise as distinct cartilages.
3. The development of the visceral arches and the temporary fusion of the first and second hypobranchials and ceratobranchials.

This development is then briefly compared with those of Scyllium, Amia, Lepidosteus, Acipenser, and Teleosts; a strong likeness being shown between it and that of Amia. The view of Goodrich is thus afforded additional support.

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