

**THE DEVELOPMENT OF THE SKULL,
VISCERAL ARCHES, LARYNX AND
VISCERAL MUSCLES OF THE SOUTH
AFRICAN CLAWED TOAD,**

***XENOPUS LAEVIS* (DAUDIN) DURING THE PROCESS
OF METAMORPHOSIS (FROM STAGE 55 TO STAGE 66)**

(With 45 Figures in the Text)

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I. INTRODUCTION AND HISTORICAL REVIEW

It was the project of Dr. P. D. NIEUWKOOP, the director of Hubrecht Laboratory, Utrecht, Holland, to elaborate a Normal Table of the very interesting South African clawed toad, *Xenopus laevis* (Daudin) in the form of an international teamwork. The various subjects of the entire project were assigned to about twenty members. A summary of the results of their findings has been published in the "Normal Table of *Xenopus laevis* (Daudin)", edited by NIEUWKOOP and FABER (1956).

The share of the present authors involves a study of the development of the skull, visceral arches, larynx and visceral muscles of this species during the process of metamorphosis, and to find out the homology of the various parts concerned with this study, as compared with those of both aglossal and phaneroglossal salientians.

There are two main views concerning the systematic position of the tongueless salientians: one by GADOW (1909) who put them in the suborder Aglossa and separated them from the phaneroglossal species. The other by NOBLE (1931) who put them in one family the Pipidae which together with the family Discoglossidae compose the suborder Opisthocoela. Thus NOBLE included a tongued group with the tongueless species. However, it is of interest to mention that although most of the recent workers follow NOBLE's system of classification, yet the term Aglossa is still of common use (PATERSON, 1951).

The Pipidae, according to NOBLE (1931) is classified into two subfamilies, the Xenopinae including *Xenopus*, *Hymenochirus* and *Pseudhymenochirus*, and the Pipinae including *Pipa* and *Protopipa*. Later, a new genus *Hemipipa* was added to the Pipinae by RIBEIRO (1937) quoted from PATERSON (1951) and DE CARVALHO (1939).

In 1951, PATERSON noted that there is "little factual basis for the inclusion of *Xenopus* and *Hymenochirus* in the same subfamily".

In spite of the exhaustive amount of work done on the phaneroglossal salientians, little information is present on the aglossal species. Among those workers who were engaged with the cranial morphology one may refer to PARKER (1876) who studied metamorphosing stages of *Pipa pipa* (L.) and *Xenopus calcaratus* Ptrs. (S. *Dactylethra capensis*, according to DE BEER, 1937). PARKER noticed that the larva of the former species does not possess tentacles and that the palatoquadrate cartilage possesses a processus cornuquadratus medialis (prepalatine process). In the latter species, he found that during metamorphosis the annulus tympanicus separates from the palatoquadrate cartilage.

Later, HIGGINS (1920) restricted his work on the morphology of the

nasal capsules of a large collection of amphibian species, among which was *Pipa pipa*. The author noted in this species that the cornu trabeculorum extends in the floor of the nasal capsule under the cartilago obliqua. He also noticed a cartilago alaris (alinasal cartilage) supporting the capsule anteriorly.

In 1932, DE VILLIERS studied the sound conducting apparatus of the adult stages of *Xenopus laevis*, *Hymenochirus curtipes* Noble, and *Pipa americana*. He recorded that all these species lack a processus ascendens partis externae plectri and that an operculum fenestrae ovalis is only present in *Xenopus laevis*.

In the following year, KOTTHAUS worked on the development of the chondrocranium of the larva of *Xenopus laevis* and considered that the antero-lateral extensions of the ethmoid plate ("Gaumendach") represent the cartilagines labiales superiores.

Later, EDGEWORTH (1935) examined the chondrocranium of *Xenopus fraseri* Boulenger and *Pipa pipa*, and found that both species lack a separate suprarostrals system. He also compared the cranial characters possessed by *X. fraseri* with those of *X. laevis* previously described by KOTTHAUS (1933).

In 1939 a, PATERSON studied various developmental stages of *Xenopus laevis* and recorded the cranial characters of few larval, one metamorphosing and newly metamorphosed individuals. From this study, she tried to deduce the main changes which occur during metamorphosis.

In 1939 b, PATERSON reported on the olfactory organ of *Xenopus laevis* and showed that the larval tentacle has nothing to do with the development of the so called "tentacle" of the adult stage.

In 1945, she worked on the adult cranial morphology of *Hymenochirus curtipes* and came to the conclusion that there is far more resemblance between this species and *Pipa pipa* than between either of them and *Xenopus laevis*.

WEISZ (1945 a and b) studied the early larval stages of *Xenopus laevis*, but did not refer to the previous findings of KOTTHAUS and PATERSON, neither in his text nor in his bibliography. Among the important characters found by this author is the presence of a foramen prooticum (orbital foramen). He reported that this foramen serves for the passage of the n. trochlearis as well as the branches of the V, VI, and VII nerves.

In 1949, PATERSON worked on the development of the inner ear in *X. laevis* and noticed the presence of one perilymphatic foramen which she homologised with the foramen perilymphaticum inferius of the phaneroglossal species rather than with the single foramen perilymphaticum of the Caudata.

In 1951, she worked on the nasal cavities of the Pipidae with special reference to *Hemipipa carvalhoi* de Miranda-Ribeiro, and came to the conclusion that there is morphological similarity as regards the nasal cavities between *Xenopus laevis* and *Hemipipa carvalhoi*.

Recently, SMIT (1953) gave an account on the development of the occipito-atlantal joint in *X. laevis*.

Among the early workers who have tackled problems on the hyobranchial apparatus of the Aglossa, one may refer to RIDEWOOD (1897 a) who gave an account on the metamorphosis of this apparatus in *Pipa pipa* and also in *Xenopus laevis*. In the latter species, he described three early metamorphosing stages only, due to the paucity of the material. He stated that *Pipa americana* loses the ceratohyalia during metamorphosis, while *Xenopus laevis* retains them in the adult stage. RIDEWOOD (1899) also investigated the adult hyobranchial apparatus of *Hymenochirus boettgeri* (Torn.). He found that this species is unique among the salientians in having adult ossified hyalia with small cartilaginous lamellae projecting from their medial borders. He concluded that the group Aglossa is characterised by the possession of a hyoglossal foramen, a pair of large wing-shaped postero-lateral processes "alae", and a small corpus hyoideum. The author attributed the above characteristics of the Aglossa to the loss of the tongue and the reduction of the hyoglossal muscles.

A similar condition to *Hymenochirus boettgeri* was described in *Hymenochirus curtipes* by PATERSON (1945).

The study of the larynx of the Aglossa was mainly carried out by RIDEWOOD who dealt with *Xenopus laevis* and *Pipa pipa* in 1897 a and with *Hymenochirus boettgeri* in 1899. He found that the larynx of each of these species is characterised by its large size, its cartilaginous continuity with the thyroid processes of the hyobranchial apparatus and finally by the absence of the vocal cords.

Concerning the visceral muscles very little and incomplete work has so far been carried out. Actually, the first author who should be mentioned in this connection is EDGEWORTH (1930), who described the masticatory and hyoid muscles of the larvae of *Xenopus laevis*. One of his important conclusions is that both MM. quadrato-hyo-angularis and orbitohyoideus are represented by the M. levator hyoidei. He mentioned that the last-named muscle originates on the processus muscularis quadrati, passes downwards fan-shaped and is inserted both on the ceratohyale and MECKELS' cartilage.

It is of interest to point out that in 1935, EDGEWORTH noted the absence of the M. levator mandibulae externus in *X. fraseri*.

GROBBELAAR (1935) made a study on the adult muscles of *X. laevis*.

The latest account is by PATERSON (1939 a), who from few larval and a metamorphosing stage of *X. laevis* tried to find out the history of the visceral muscles during metamorphosis. She considered that the M. levator hyoidei consists of two fasciculae, an outer M. orbitohyoideus, and an inner M. quadrato-hyo-angularis. She also mentioned that the last-named muscle of the larva persists as a separate muscle in the metamorphosed individual.

II. MATERIAL AND TECHNIQUE

The material used for the present work has been collected by Mr. J. FABER of the Hubrecht Laboratory, Utrecht, Holland from the ponds of the Inland Fisheries Department in Stellenbosch, South Africa. The material was kindly sent, already fixed in Lenhossek fluid and preserved in alcohol, by Dr. N. MILLARD of Cape Town, South Africa. The specimens include twelve successive stages which comprise a typical larval stage (55), two premetamorphic stages, before the exposure of the fore-limbs (56 & 57), eight metamorphosing stages (58-65) and a newly metamorphosed individual (66). The identification of these stages, their age in days and their distinctive characters have already been published in the "Normal Table of *Xenopus laevis* (Daudin)" (NIEUWKOOP and FABER, 1956).

The fixed material was decalcified in 5 % trichloroacetic acid from 1-4 days according to the age of the specimen. Serial sections of 25 microns thick were cut and stained by MASSON's trichrome stain following FOOT (1933) in the cytoplasmic and connective tissue stains. The main steps of the staining technique are similar to those previously followed by SEDRA (1950).

Sections as well as graphical and contour reconstructions were done by the aid of a Leitz microprojection apparatus directly on the graph paper. This procedure gave very accurate and quick results.

III. DESCRIPTION OF STAGES

1. Stage 55

(A typical larval stage)

Since the jaws are greatly related with the skull, they are dealt with first and then followed by the hyobranchial apparatus, the larynx and the visceral muscles.

A. *The Skull and Jaws*

1. The occipito-auditory region: The occipital arch is confluent with the atlas vertebra (Fig. 1, vrb. 1) except dorsally. The free parts of this arch are represented by a pair of cristae occipitales laterales (cs.oc.l.) which extend obliquely forwards and upwards and meet a median dorsal

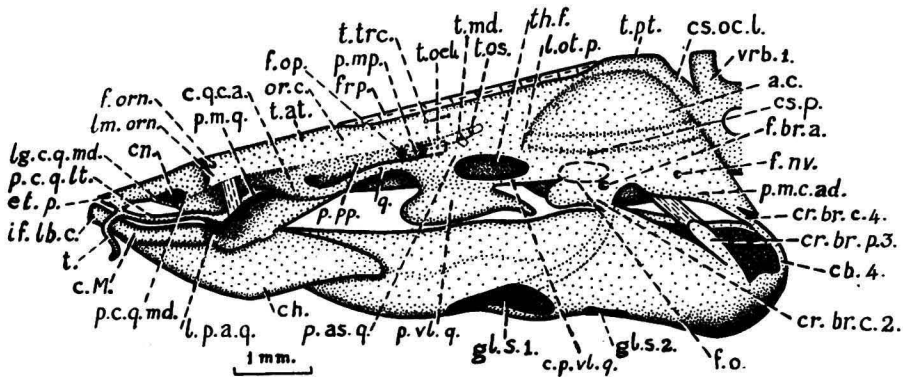


Fig. 1. Stage 55. Graphical reconstruction of a left side view of the skull, jaws, and hyobranchial apparatus. (The border of the fenestra ovalis, f.o., is represented by a broken line since it is masked by the crista parotica, cs.p.).

roof, the tectum posterius (Figs. 1, 2 & 3, t.pt.). The anterior extent of the occipital arch can be limited laterally by a pair of foramina jugularia (Figs. 2 & 4, f.j.) which are concealed by the auditory capsules (a.c.) and through which the glossopharyngeal and vagus nerves pass.

The dorso-medial edges of the auditory capsules (Figs. 2 & 3, a.c.) anterior to the region of the tectum posterius, represent the taeniae tecti marginales (t.t.mg.).

The floor of this region is composed of the planum basale (Fig. 5, pl.b.) which surrounds the notochord (n.) posteriorly, forming a hypochordal

commissure (hp.c.). More anteriorly, there is no cartilaginous floor for the notochord.

The auditory capsules are well developed, each possesses a conspicuous crista parotica (Fig. 1, cs.p.) which is prolonged, all over its length, into

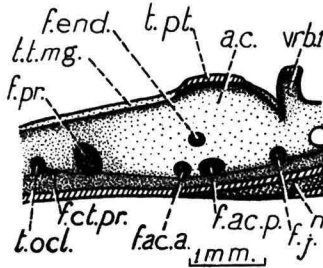


Fig. 2. Stage 55. Graphical reconstruction of the right side auditory capsule as seen from the medial surface.

a broad plate-like processus muscularis capsulae auditivae (p.m.c.ad.). This is perforated by a small foramen for a branch from the glossopharyngeal nerve (f.nv.) and by a larger one for a branchial artery (f.br.a.).

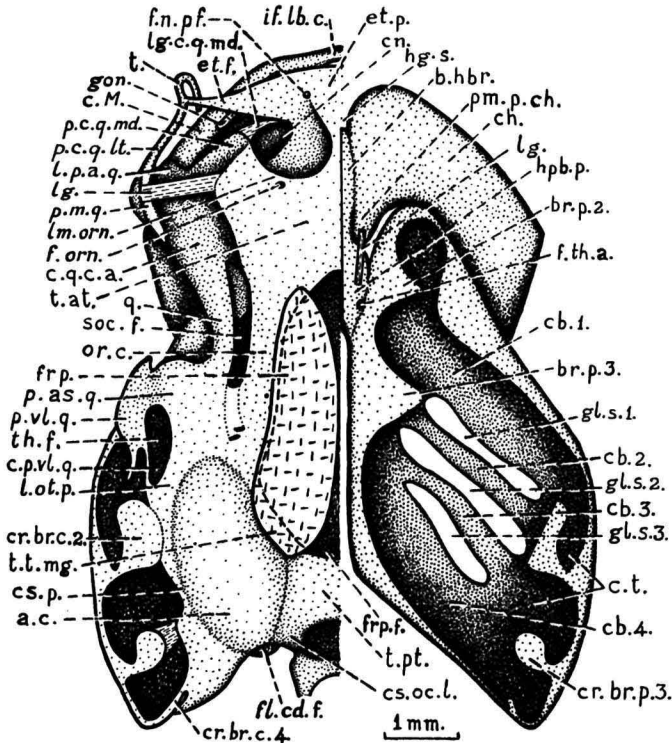


Fig. 3. Stage 55. Graphical reconstruction of the left side half of the skull, jaws and hyobranchial apparatus and of the right side half of the hyobranchial apparatus alone as seen from the dorsal surface. (The taenia tecti marginalis, t.t.mg., is labelled although it is covered by the fronto-parietal. The branchial rays are not shown).

On the side wall of each capsule lies a wide fenestra ovalis (f.o.) which is spanned with fibrous connective tissue and is masked externally by the shield-like *processus muscularis capsulae auditivae*.

The medial capsular wall (Fig. 2, a.c.) is pierced with the *foramina acustica anterius* and *posterius* (f.ac.a. & f.ac.p.) and also with the *foramen endolymphaticum* (f. end.) which lies at a higher level than and nearly between the two acoustic foramina.

The posterior region of each capsule is confluent through the *foramen perilymphaticum inferius* (Fig. 4, f.p.if.) with the *subcapsular condyloid fossa* (cd.f.). The floor of this fossa (Fig. 5, fl.cd.f.) is fused with the *occipital arch* posteriorly and is broadly confluent with the capsular floor

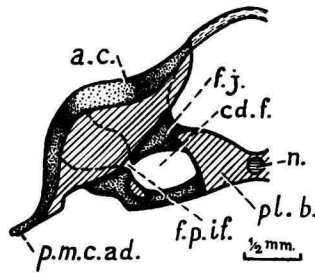


Fig. 4. Stage 55. Contour reconstruction of the auditory capsule in the region of the *foramen jugulare* as seen from the posterior surface.

(a.c.) anteriorly. The fossa itself is mostly spanned posteriorly with dense fibrous tissue leaving a small laterally directed aperture for the outlet of the *glossopharyngeal* and *vagus* nerves.

The antero-lateral wall of each capsule is confluent with the *larval processus oticus* (Figs. 1, 3 & 5, l.ot.p.) which is broadly continuous with the *processus muscularis capsulae auditivae* posteriorly, and with the so called *processus ascendens quadrati* (p.as.q.) anteriorly.

Just in front of each auditory capsule lies the *foramen prooticum* (Fig. 2, f.pr.) through which the *n. ophthalmicus superficialis VII*, *n. maxillo-madibularis V*, *n. ophthalmicus profundus V*, *n. palatinus VII*, *n. hyomandibularis VII* and the *vena capitis lateralis* pass.

2. The orbito-temporal region: The floor of this region is formed by the *basis cranii* (Fig. 5, b.c.) which represents the fused *trabeculae*. Below this lies the *cuneiform parasphenoid* (psf.), the posterior end of which underlies the *notochord*.

Dorsally, there is a wide *fronto-parietal fenestra* (Fig. 3, frp.f.) which is spanned with a darkly pigmented connective tissue membrane. The fenestra is covered with a pair of developing *fronto-parietal bones* (frp.) which are thin medially and are bound with connective tissue fibres.

Laterally, the side walls of the cranium are represented by the *orbital cartilages* (Fig. 1, or.c.) which are thick and long.

In the temporal region, the palatoquadrate cartilage (Figs. 1 & 3, q.) is suspended to the neurocranium through the broad processus ascendens quadrati (p.as.q.) which is fused with the pila antotica as well as with the orbital cartilage. Laterally, this process extends into the ventrally directed processus ventro-lateralis quadrati (Figs. 1, 3 & 5, p.vl.q.). The latter sends a thin medial commissure (c.p.vl.q.) which is fused with the

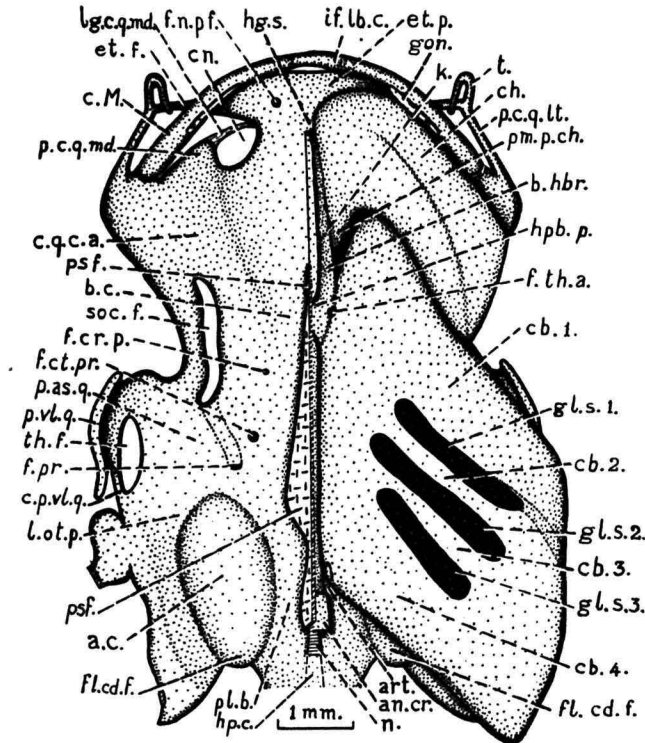


Fig. 5. Stage 55. Graphical reconstruction of a ventral view of the skull and jaws on the left side and of the skull, jaws, hyobranchial apparatus and larynx on the right side.

processus muscularis capsulae auditivae. This commissure acts as a support for the thymus foramen (th.f.) laterally.

The processus ascendens quadrati is pierced with two nerve tunnels which leave it dorsally above the foramen prooticum. The anterior tunnel is for the outlet of the n. maxillo-mandibularis V (Fig. 1, t.md.) and the posterior one serves for the passage of the n. ophthalmicus superficialis VII (t.os.). The two tunnels proceed anteriorly into a common groove.

The palatoquadrate cartilage (Fig. 1, q.) proceeds forwards and slightly downwards as a slender bar, which bounds a narrow subocular fenestra (Figs. 3 & 5, soc.f.). This fenestra is spanned by a layer of fibrous connective tissue.

Ventrally, the foramen prooticum (Fig. 5, f.pr.) proceeds into a groove which lodges the n. ophthalmicus profundus V, n. palatinus VII, n.

hyomandibularis VII and the vena capitis lateralis. This groove is supported ventrally by a connective tissue layer.

Medial to the groove of the foramen prooticum, the basis cranii is pierced with the foramen caroticum primarium (Fig. 5, f.ct.pr.) for the passage of the arteria carotis interna. More anteriorly, the orbital cartilage possesses two nerve tunnels, a narrow dorsal trochlear tunnel (Figs. 1 & 6, t.trc.) and a much wider ventral oculomotor tunnel (t.ocl.). The former

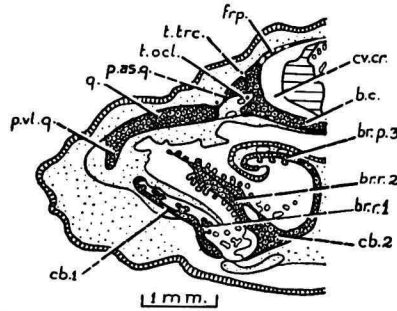


Fig. 6. Stage 55. Transverse section in the region of the external openings of the trochlear and oculomotor tunnels.

serves for the exit of the n. trochlearis and the latter for the passage of the n. oculomotorius and the arteria ophthalmica magna. The oculomotor tunnel opens externally at the anterior level of the processus ascendens quadrati (Fig. 6, t.ocl. & p.as.q.).

A short distance in front of the oculomotor tunnel lies the optic foramen (Fig. 1, f.op.) which separates a relatively short pila metoptica (p.mp.) from a much longer pila praeoptica (p.pp.). Anterior to the foramen caroticum primarium the basis cranii is pierced by a narrow foramen cranio-palatinum (Fig. 5, f.cr.p.) through which passes the palatine branch of the arteria carotis interna.

3. The ethmoid region: The floor of this region is formed by the basis cranii which extends anteriorly into a broad ethmoid plate (Figs. 5 & 7,

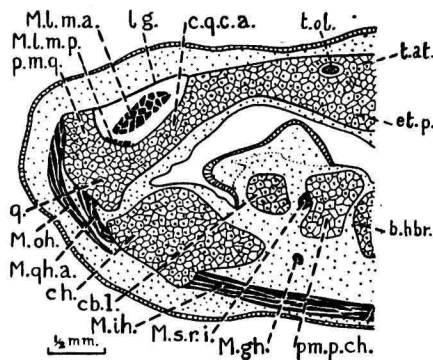


Fig. 7. Stage 55. Transverse section in the region of the processus muscularis quadrati.

et.p.). This plate is pierced with a pair of foramina for the passage of the medial nasal branches of the profundus nerve (Figs. 3 & 5, f.n.pf.). The ethmoid plate extends laterally into the ethmoid flanges (et.f.).

Posteriorly, the ethmoid region possesses a broad tectum anterius (Figs. 3 & 7, t.at.) which forms a roof for this area and connects the orbital cartilages. Both the tectum anterius and the basis cranii are confluent together through a broad vertical septum which separates two olfactory tunnels (Fig. 7, t.ol.) for the passage of the olfactory nerves. At the anterior level of the tectum anterius lies the orbitonasal foramen (Fig. 1, f.orn.) which is limited anteriorly by a thin, weakly developed, lamina orbitonasalis (lm.orn.). The tectum anterius flows anteriorly into a median crest which separates the two nasal cavities from each other.

In the ethmoid region, the palatoquadrate bar has two outgrowths, a medial commissura quadrato-cranialis anterior (Figs. 1, 3 & 7, c.q.c.a.) and a lateral processus muscularis quadrati (p.m.q.). The former is broadly confluent with the side wall of the cranium and is prolonged forwards into a triangular processus cornuquadratus medialis (quadrato-ethmoidal process of DE BEER, 1937) (Figs. 1, 3 & 5, p.c.q.md.). This is connected with the side of the ethmoid plate, anterior to the choana (cn.), through a ligamentous band, the ligamentum cornuquadratum mediale (lg.c.q.md.). The processus muscularis quadrati is short and thick. It is directed upwards in its posterior half, while anteriorly it is more or less horizontal. This process is connected with the commissura quadrato-cranialis anterior through a dense, ligamentous band (Figs. 3 & 7, lg.). Anteriorly the processus muscularis quadrati proceeds into a slender cartilaginous bar, the processus cornu quadratus lateralis (Figs. 1, 3 & 5, p.c.q.lt.) which gains fusion with the lateral edge of the ethmoid flange (et.f.). Just at this area, it gives off a tentacular cartilage (t.) to support the corresponding tentacle. This tentacular cartilage is a long and slender process. Just medial to the base of the processus cornu quadratus lateralis, the palatoquadrate cartilage gives off a small process which is the larval pars articularis quadrati (Figs. 1 & 3, l.p.a.q.) for the reception of the articular region of the lower jaw. Slightly posterior, the palatoquadrate cartilage possesses an articular facet for the ceratohyale.

The lower jaw is simple in being composed of a pair of, MECKELS' cartilages (Figs. 1, 3 & 5, c.M.) fused together through a median inferior labial cartilage (if.lb.c.) which is curved with its convexity facing downwards. An osseous element on the medial surface of MECKELS' cartilage represents the primordium of the goniale (Figs. 3 & 5, gon.).

B. *The Hyobranchial Apparatus*

1. The hyoid arch:

a. The ceratohyalia (Figs. 1, 3 & 5, ch.) are massive and well developed. They extend obliquely parallel with the lower jaw. Ventrally, each ceratohyale possesses a prominent ridge (Fig. 7) for the insertion of the

hyoid muscles. Dorsally, there is a slight protuberance for articulation with the overlying palatoquadrate cartilage. The postero-dorsal border of each ceratohyale possesses a deep concavity for lodging the anterior region of the corresponding branchial chamber (Figs. 3 & 7, ch. & cb. 1). Medially, each ceratohyale is extended into a postero-medial process (Figs. 3 & 5, pm.p.ch.).

b. The basihyale does not exist separately but is continuous with the basibranchiale into a median basihyobranchiale which will be dealt with later.

2. The branchial apparatus:

a. The branchial arches (Figs. 3 & 5, cb. 1-4), on either side, are completely confluent with each other forming a branchial chamber which is cup-shaped with a wide concavity directed dorsally. Each chamber is perforated ventrally by three gill slits (gl.s. 1-3) separating the four ceratobranchialia from each other for some distance only. The second and third ceratobranchialia are comparatively narrower than the first and fourth ones. The dorsal rim of the whole chamber (Fig. 3) is curved internally into a ledge.

The area of the branchial chamber lateral to the gill slits represents the commissura terminalis (Fig. 3, c.t.). This is synchondrotically attached to the processus muscularis capsulae auditivae in two regions; one opposite to the second ceratobranchiale (the second cranio-branchial commissure) (Figs. 1 & 3, cr.br.c. 2) and the other opposite the dorso-medial edge of the fourth ceratobranchiale (the fourth cranio-branchial commissure) (cr.br.c. 4). Opposite to the third branchial arch, there is the third cranio-branchial process (cr.br.p. 3), which is syndesmotically connected with the processus muscularis capsulae auditivae (p.m.c.ad.).

The ledge projecting from the medial region of the branchial chamber is broad and extends as a horizontal shelf. This shelf is more developed opposite the second and third ceratobranchialia forming the second and third branchial processes (Figs. 3 & 6, br.p. 2, 3).

The outer surface of the whole branchial chamber is smooth. However, its inner surface is ragged with a very large number of branchial rays (Fig. 6, br.r. 1-3). The rays present on the first and fourth ceratobranchialia are much shorter than those on the second and third ones. Each of the latter arches, possesses one long ramified arboreal ray (br.r. 2) which is continuous with the second and third branchial processes respectively.

b. The hypobranchial plate (Figs. 3 & 5, hpb.p.) is a small piece which is confluent with the bases of the first pair of ceratobranchialia. It is pierced with a pair of foramina for the passage of the thyreopharyngeal arteries (f.th.a.).

c. The basihyobranchiale (Figs. 3 & 5, b.hbr.) is a well developed structure with a broad, deep ventral keel (Fig. 5, k.). It is confluent posteriorly with the hypobranchial plate as well as with the anterior

region of the bases of the first pair of ceratobranchialia. It extends anteriorly to the base of the larval hyoglossal sinus (hg.s.). Loose cartilage cells join the medial sides of the ceratohyalia with the basihyobranchiale (Fig. 7, ch. & b.hbr.). The postero-medial processes of the ceratohyalia (Fig. 3, pm.p.ch.) form a peg-socket articulation with the dorsal surface of the basihyobranchiale (b.hbr.). This articulation is strengthened by a ligament (lg.) binding both structures.

C. *The Larynx*

The only structures developed are the primordia of the arytenoids (Fig. 5, art.) which are oval and formed of juvenile cartilage cells. The annulus cricoideus (an.cr.) is only feebly developed dorsally and is composed of a median cartilaginous piece fringed with dense mesenchyme cells.

D. *The Visceral Muscles*

The visceral muscles include the mandibular, hyoid, branchial, hypobranchial spinal, and the laryngeal muscles.

1. *The mandibular muscles* are represented by the following three masticatory and one intermandibularis muscles:

a. *M. levator mandibulae anterior* (Figs. 7-9, M.l.m.a.). This is the largest and most dorsal of all three masticatory muscles, and, from a dorsal view, it mostly conceals the other two. It originates from the palatoquadrate cartilage (q.) near the level of the orbit. Its fibres extend forwards, and at the level of the anterior border of the processus muscularis quadrati it splits into three main parts:

i. *Pars medialis* (Fig. 9, M.l.m.a.p.md.) inserted by a long tendon onto the dorso-medial border of MECKELS' cartilage (c.M.).

ii. *Pars intermedius* (Figs. 8 & 9, M.l.m.a.p.im.) is broadly inserted onto the dorsal surface of MECKELS' cartilage, just in front of the insertion of the *M. levator mandibulae posterior*, which will be mentioned later.

iii. *Pars lateralis* (M.l.m.a.p.lt.) extends forwards and is inserted onto the ventral surface of the tentacular cartilage (Fig. 8, t.).

Contraction of the M.l.m. anterior elevates the lower jaw and retracts the tentacle.

b. *M. levator mandibulae posterior* (Figs. 7-9, M.l.m.p.) arises from the palatoquadrate cartilage at the level of the processus muscularis quadrati. Its fibres extend obliquely forwards and downwards and are inserted onto the dorsal surface of MECKELS' cartilage just behind the insertion of the *pars intermedius* of the M.l.m. anterior. Contraction of this muscle helps in the elevation of the lower jaw.

c. *M. levator mandibulae externus* (Figs. 8 & 9, M.l.m.e.) arises from the anterior edge of the processus muscularis quadrati. It is poorly developed, and is inserted onto the outer border of MECKELS' cartilage. Its contraction helps in the elevation of the lower jaw.

d. *M. intermandibularis posterior* (Figs. 7, 8 & 10, *M.im.p.*). This is in the form of a thin, flat sheet extending transversely across the floor of the buccal cavity. Fibres from the ventral surface of MECKELS' cartilage spread medialwards and meet those of the other side in a median raphé. Contraction of this muscle elevates the floor of the mouth.

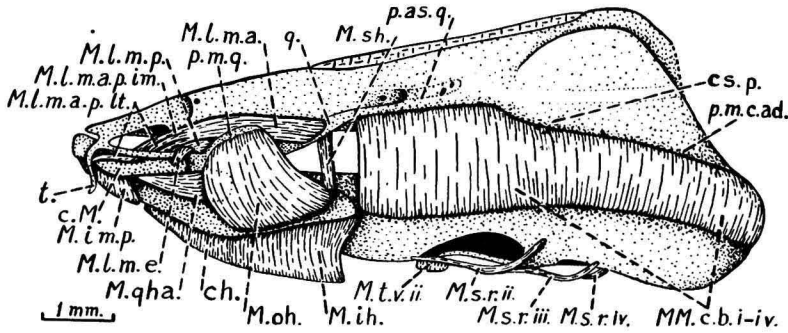


Fig. 8. Stage 55. Graphical reconstruction of a left side view of the visceral muscles.

2. *The hyoid muscles* are represented by the following three levator hyoidei and one interhyoideus.

a. *M. orbitohyoideus* (Figs. 7, 8 & 10, *M.oh.*). This is a large muscle, which originates from the uppermost edge of the processus muscularis quadrati. Its fibres extend ventrally and are inserted onto the ventro-lateral surface of the ceratohyale. Contraction pulls the ceratohyale upwards.

b. *M. suspensoriohyoideus* (Fig. 8, *M.sh.*). This is a very weak muscle, which originates from the ventro-lateral edge of the palatoquadrate cartilage. Its fibres extend ventrally and are inserted onto the dorsal edge of the ceratohyale just behind the insertion of the *M. orbitohyoideus*. Contraction of this muscle pulls the posterior portion of the ceratohyale upwards. This together with the contraction of the *M. orbitohyoideus*

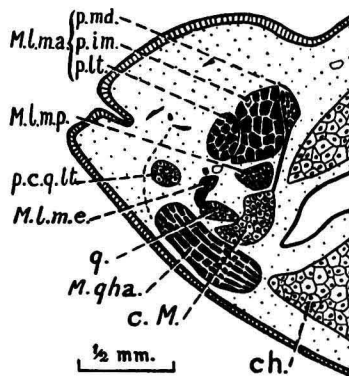


Fig. 9. Stage 55. Transverse section in the region of division of the *M.l.m.* anterior into three fasciculae.

results in the increase of the width of the buccal cavity, i.e. reverse action of *M. intermandibularis posterior*.

c. *M. quadratohyoangularis* (Figs. 7–10, *M.qha.*). This muscle represents the *MM. suspensorio-*, *quadrato-*, and *hyo-angularis* present in other salientians and can thus be given this complex name. It originates from the articular surface between the palatoquadrate cartilage and the ceratohyale, medial to the *M. orbitohyoideus* (Fig. 7). Its fibres extend forwards and are inserted by a narrow tendon on the ventro-lateral surface

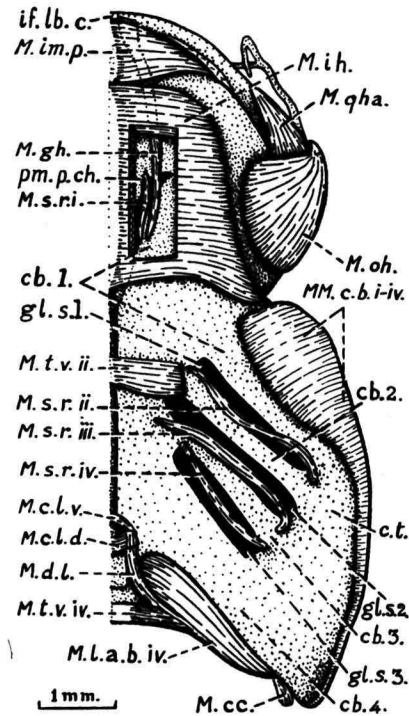


Fig. 10. Stage 55. Graphical reconstruction of a ventral view of the visceral muscles. A window-cut is made in the *M. interhyoideus* to expose the *MM. geniohyoideus* and *subarcualis rectus i.*

of *MECKELS'* cartilage. Contraction of this muscle pulls the lower jaw downwards and outwards, i.e. helps in opening the mouth.

d. *M. interhyoideus* (Figs. 7, 8 & 10, *M.i.h.*). This is a very broad and thin muscle, which extends horizontally across the floor of the buccal cavity, behind the *M. intermandibularis posterior*. The fibres, on either side, are attached to a ridge present on the ventral surface of the ceratohyale. They pass towards the middle line where they meet in a median raphé. Contraction helps in the elevation of the floor of the mouth.

3. *The branchial muscles* are represented by four continuous constrictores branchiales muscles, four separate subarcuales recti muscles, and two separate transversi ventrales muscles.

a. MM. constrictores branchiales i-iv (Figs. 8 & 10, MM.c.b. i-iv.). These represent four muscles, which have become more or less completely continuous with each other. They form a thin, broad sheet of muscle fibres, which cover the dorso-lateral surface of the whole branchial chamber. The muscle fibres which belong to the first constrictor branchialis arise from the processus ascendens quadrati (Fig. 8, p.as.q.) and the region just behind it. The rest of the muscle sheet, which represents the second, third, and fourth constrictores branchiales, arises from the crista parotica processus muscularis capsulae auditivae. All fibres extend outwards and downwards in a semicircular fashion and are inserted onto the lateral border of the branchial chamber, which is represented by the commissura terminalis. Contraction of these muscles elevates the whole branchial chamber upwards and outwards resulting in a decrease in its volume.

b. M. subarcualis rectus i (Figs. 7 & 10, M.s.r.i.) is a very thin strip of muscle, which originates on the first arcus branchialis and inserts onto the postero-medial process of the ceratohyale. Contraction brings these two structures closer to each other.

c. M. subarcualis rectus ii (Figs. 8 & 10, M.s.r.ii.) is a thin, long muscle band, which originates from the base of the second arcus branchialis just medial to the first gill slit and is inserted on the lateral wall of the same arch posterior to the level of the same gill slit.

d. M. subarcualis rectus iii (Figs. 8 & 10, M.s.r.iii.). This runs more or less parallel to the above mentioned muscle. It arises from the third arcus branchialis and is inserted onto the same arch just posterior to the level of the second gill slit.

e. M. subarcualis rectus iv (Figs. 8 & 10, M.s.r.iv.). This runs more or less parallel to the last two mentioned muscles. Its origin and insertion is on the third arcus branchialis.

Contraction of the MM. subarcuales recti ii, iii & iv results in the widening of the branchial chamber as a whole.

f. M. transversus ventralis ii (Figs. 8 & 10, M.t.v.ii.) is a fairly well developed muscle, the fibres of which pass from the base of the second ceratobranchiale medialwards and meet those of the other side in a median raphé.

g. M. transversus ventralis iv (Fig. 10, M.t.v.iv.). This together with M. levator arcuum branchialium iv (M.l.a.b.iv.) and M. dilatator laryngis (M.d.l.) take their origin from the postero-medial wall of the fourth ceratobranchiale and the ventral surface of the processus muscularis capsulae auditivae. The fibres of this muscle extend medialwards above the M. dilatator laryngis and meet those of the other side in a very broad and thin median raphé.

Contraction of the MM. transversi ventrales ii & iv brings the ventral walls of the branchial chambers closer to each other. This results in the widening of these chambers. In other words, these muscles together with

the MM. subarcuales recti ii, iii, and iv have reverse action to the MM. constrictores branchiales i-iv.

h. M. levator arcuum branchialium iv (Fig. 10, M.l.a.b.iv.) originates from the processus muscularis capsulae auditivae and is inserted onto the postero-medial surface of the fourth ceratobranchiale. Contraction helps in elevating the branchial chambers upwards.

i. M. cucullaris (Fig. 10, M.cc.) originates from the anterior edge of the scapula and inserts onto the fourth arcus branchialis just ventral to the attachment of M. levator arcuum branchialium iv. Contraction brings the branchial chamber closer to the scapula.

4. *The hypobranchial spinal muscles* are represented by:

M. geniohyoideus (Fig. 10, M.gh.). This is a long, thin strand which originates from the medial border of the first ceratobranchiale close to the M. subarcualis rectus i. The fibres of this muscle extend forwards and are inserted onto the ventral surface of the inferior labial cartilage. Contraction pulls the medial part of the lower jaw backwards and thus opens the mouth.

5. *The laryngeal muscles* comprise the dilatator and constrictor muscles of the larynx:

a. M. dilatator laryngis (Fig. 10, M.d.l.). Its fibres after separation from the M. levator arcuum branchialium iv and M. transversus ventralis iv extend forwards and are inserted onto the lateral wall of the arytenoid. Contraction dilates the larynx.

b. M. constrictor laryngis. This consists of two components, namely dorsalis (Fig. 10, M.c.l.d.) and ventralis (M.c.l.v.), which originate from dorsal and ventral raphé respectively, and are inserted onto the arytenoids. Contraction of these two components constricts the larynx.

2. Stage 56

The main changes which have taken place are the following:

1. The two fronto-parietal bones have extended more medially into thin sheets which are more or less confluent synostotically leaving a median parietal foramen. This thin synostosis will be more distinct in stage 60 (cf. Fig. 15, frp. & f.pt.).

2. The tunnel for the n. maxillo-mandibularis V is now longer and opens near the anterior level of the processus ascendens quadrati.

3. The M. intermandibularis anterior makes its first appearance. It is represented by very few muscle fibres which stretch horizontally between the medial walls of the inferior labial cartilage. The fibres are uninterrupted by a median raphé.

3. Stage 57

(A stage just before the exposure of the fore-limbs)

No obvious change has taken place at this stage. However, remarkable increase in the size of the different structures has occurred.

4. Stage 58

(First stage of metamorphosis)

The occipito-atlantal joint which begins to appear at this stage will not be dealt with since it has already been elaborately studied by SMIT (1953).

The important changes are:

1. In the auditory region, perichondral ossifications appear on the crista occipitalis lateralis, the inner lining of the condyloid fossa, the planum basale (cf. Fig. 16, pl.b.), and also on the medial wall of the auditory capsule (a.c.). These ossifications collectively form the so called occipito-prootic ossification (oc.pr.os.). It is accompanied with a process of enchondral destruction.

2. In the ethmoid region, there is a septum nasi (Fig. 11, s.n.) represented posteriorly by a thin vertical lamella, and spreading dorsally into a narrow tectum nasi (t.n.). Anteriorly, the septum nasi extends into a pair of chondrifying centres (Fig. 12, s.n.). Each of these centres sends a thin transverse element, the so called crista intermedia (cs.itm.). The crista intermedia is prolonged backwards in the form of procartilage cells, the lamina inferior (Fig. 11, lm.if.). Dense mesenchyme cells lie between the edge of the lamina inferior and the underlying ethmoid plate (et.p.) to form a vertical commissure (cm.) between both structures. Bounding the antero-lateral area of each nasal capsule is a broad cartilago alaris (Fig. 12, cg.al.). This possesses a horizontal shelf which separates two grooves for the reception of the two compartments of the cavum medium. The horizontal shelf of the cartilago alaris joins the crista intermedia through a vertical bridge.

Osseous tissue has accumulated lateral to the nasal region and dorsal to the ethmoid flanges (Figs. 11 & 12, et.f.) representing the primordium of the maxilla (mx.). The nasal bone (Fig. 11, ns.) is evident as a thin small osseous sheet at the anterior boundary of the tectum anterius and extends slightly over the posterior region of the tectum nasi.

3. The *M. intermandibularis anterior* (cf. Fig. 21, *M.im.a.*) becomes well differentiated and occupies the cavity of the inferior labial cartilage.

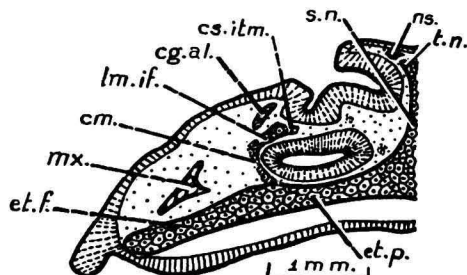


Fig. 11. Stage 58. Transverse section in the ethmoid region showing the dense mesenchyme condensation between the lamina inferior of the crista intermedia and the ethmoid plate.

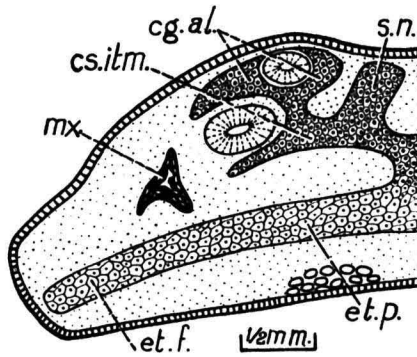


Fig. 12. Stage 58. Transverse section in the ethmoid region showing the paired nature of the septum nasi anteriorly.

5. Stage 59

(An early stage of metamorphosis)

The important changes which have occurred at this stage are:

1. In the auditory region, the membrane spanning the fenestra ovalis (Fig. 13, *f.o.*) develops a chondrifying centre which gives rise to the pars interna plectri (*p.i.pl.*). An operculum fenestrae ovalis (*op.*) appears as an outgrowth from the posterior border of the fenestra itself.

2. In the nasal region, the lamina inferior and the commissure, referred to in the previous stage, have transformed into proper cartilage.

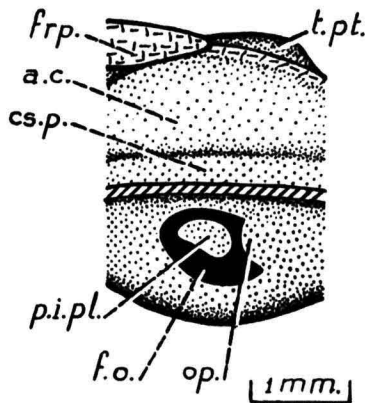


Fig. 13. Stage 59. Graphical reconstruction of a portion of the left side auditory capsule with the crista parotica removed to show the region of the fenestra ovalis.

6. Stage 60

(A metamorphosing stage)

In this stage growth in size has reached its maximum. The main changes are:

1. In the auditory region, the occipito-prootic ossification (Figs. 14, 15 & 16, *oc.pr.os.*) has extended more on the dorsal and ventral surfaces and shows itself in the form of osseous patches on the outer surface.

2. The tunnel for the n. maxillo-mandibularis V (Figs. 14 & 15, t.md.) opens on the processus ascendens quadrati (p.as.q.) slightly anterior to that of the n. ophthalmicus superficialis VII (t.os.). This backward shift of the outlet of the n. maxillo-mandibularis V is due to cartilage decay in the major part of the roof of the tunnel. The tunnel for the n. ophthalmicus superficialis VII is now wide and somewhat vertical.

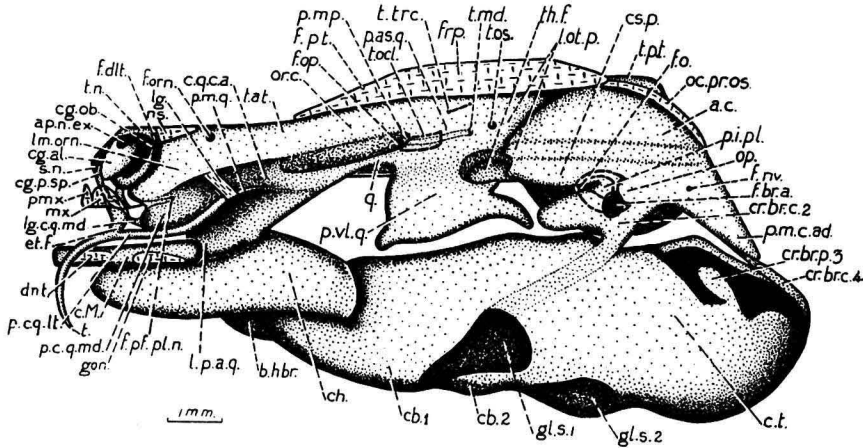


Fig. 14. Stage 60. Graphical reconstruction of a left side view of the skull, jaws and hyobranchial apparatus. (The septomaxilla is not shown).

3. The cartilaginous bar connecting the processus ventro-lateralis quadrati (Fig. 14, p.v.l.q.) with the crista parotica (cs.p.) has largely broken down and is now represented by two little protrusions.

4. In the nasal region, the lamina orbitonasalis (Figs. 14, 15 & 16, lm.orn.) has become more developed and is connected with the processus cornu quadratus medialis (p.c.q.md.) through a band of procartilaginous tissue marked posteriorly by the foramen for the ramus communicans between n. ophthalmicus profundus V and n. palatinus VII (f.pf.pl.n.).

The ethmoid plate (Fig. 16, et.p.) as well as the ethmoid flanges (et.f.) are eroding rostro-caudally, to a level just anterior to that of the foramina for the medial nasal branches of the profundus nerve (f.n.pf.).

The skeletal elements of the nasal region are more developed. The anterior two components of the septum nasi (cf. Fig. 12, s.n.) have met dorsally and enclosed a median nasal fossa occupied with connective tissue. The tectum nasi (Fig. 17, t.n.) is somewhat broader over the anterior half of the nasal region and is now attached to a new chondrifying centre, the cartilago obliqua (cg.ob.) which separates an anterior apertura nasalis externa (Figs. 14 & 15, ap.n.ex.) from a posterior fenestra dorso-lateralis (f.dlt.). The cartilago obliqua extends outwards and downwards and becomes fused with the lamina inferior (Fig. 17, lm.if.) through a planum terminale (pl.t.) which itself is extended into a ventrally directed processus lingularis (p.lng.). Between the crista intermedia and the

lamina inferior projects a thin horizontal and backwardly directed process (hz.p.).

There is new cartilage addition over the eroding ethmoid plate (Fig. 17, et.p.), representing the solum nasi (so.n.) which is continuous with the commissure (cm.) connecting the lamina inferior with the ethmoid plate. Medially, the solum nasi is connected with the cartilago alaris (cg.al.) through a new chondrifying centre the cartilago praenasalis superior (cg.p.sp.). Thus, a new permanent floor for the nasal capsule, represented now by the solum nasi, is developing and will gradually replace the decaying larval ethmoid plate.

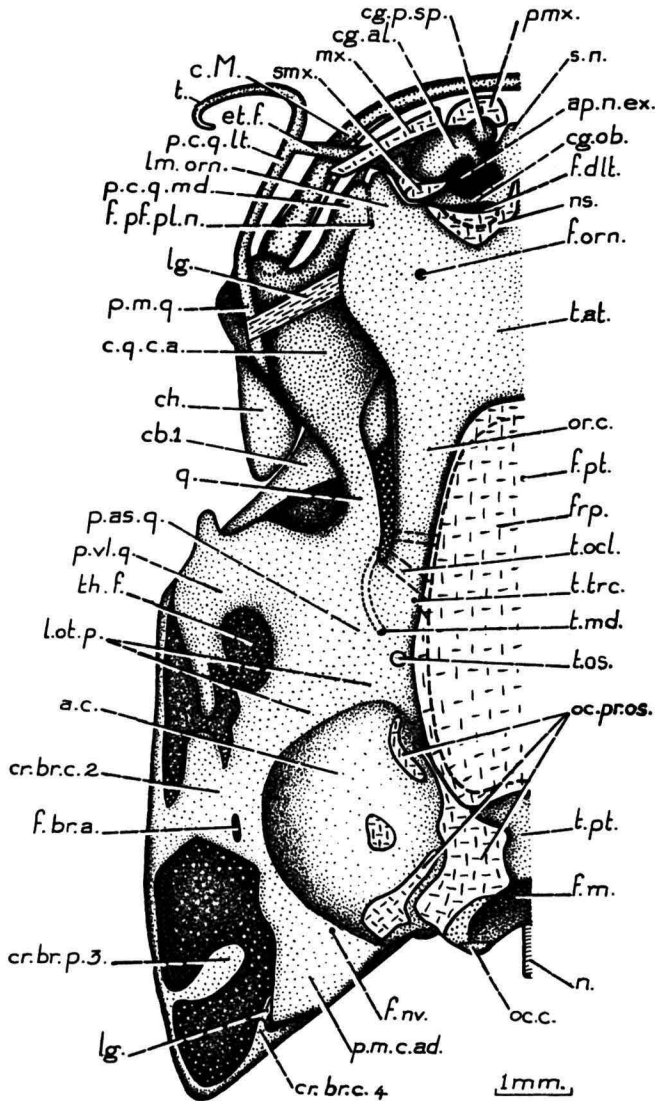


Fig. 15. Stage 60. Graphical reconstruction of the left side half of the skull, jaws and hyobranchial apparatus as seen from the dorsal surface.

A septomaxilla (Figs. 15 & 17, smx.) has now developed. This is a horse-shoe-shaped membrane bone resting on the outer surface of the planum terminale.

The praemaxilla (Figs. 14, 15 & 16, pmx.) is now evident as a thin dorso-ventrally directed element in front of the nasal region. Teeth

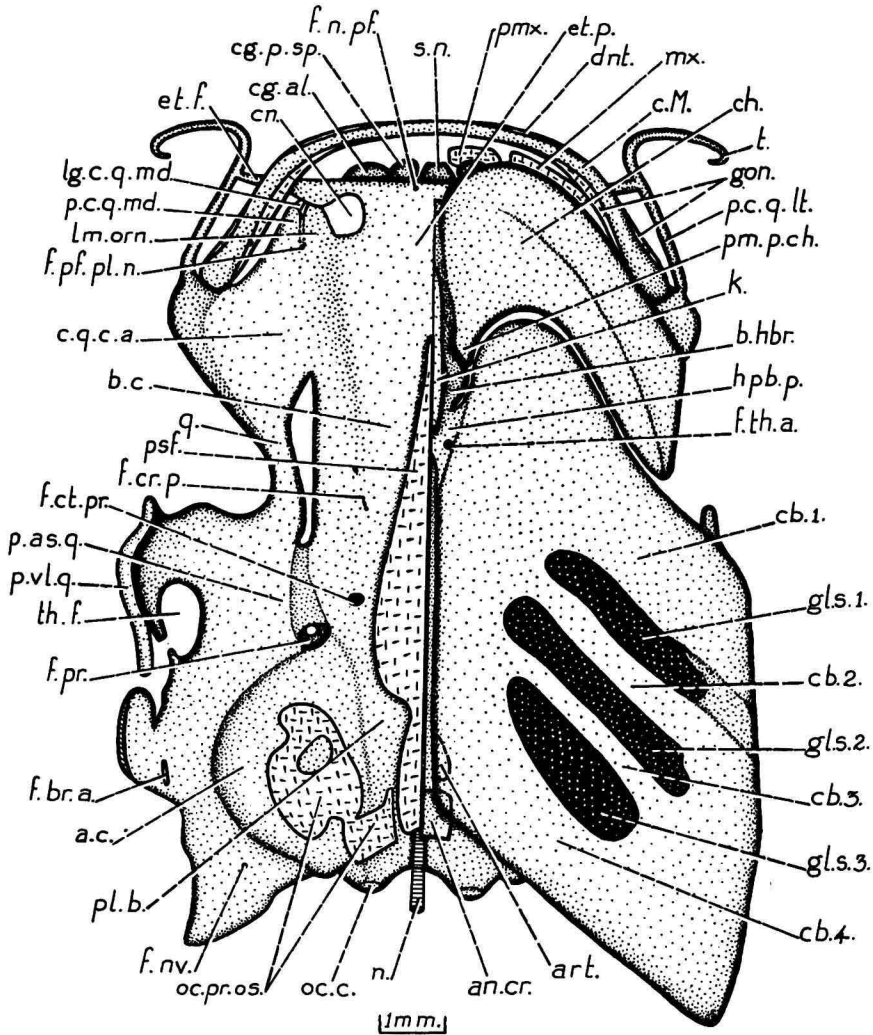


Fig. 16. Stage 60. Graphical reconstruction of a ventral view of the skull and jaws on the left side and of the skull, jaws, hyobranchial apparatus and larynx on the right side.

begin to show their appearance in the epithelium underneath the praemaxilla and maxilla (mx.).

5. In the lower jaw, the goniale (Figs. 14 & 16, gon.) possesses an outer ossifying centre which is thin and feebly developed as compared with the medial one. The dentary (dnt.) has developed as a thin osseous sheet on the outer anterior half of MECKELS' cartilage (c.M.).

6. In the hyobranchial apparatus, the ligament connecting the third cranio-branchial process (Fig. 15, cr.br.p.3) with the processus muscularis capsulae auditivae (p.m.c.ad.) has disappeared, while the fourth cranio-branchial commissure (cr.br.c.4) is now represented by a ligament (lg.).

7. The *M. geniohyoideus* becomes divided longitudinally into two fasciculae, namely, the partes medialis and lateralis. The separation begins some distance behind the anterior end, and proceeds gradually backwards.

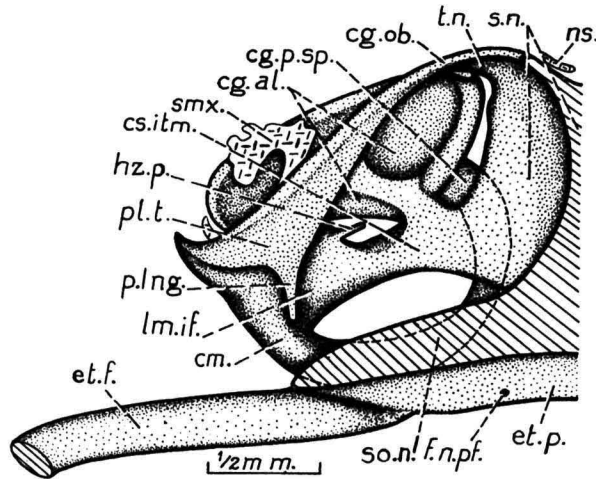


Fig. 17. Stage 60. Contour reconstruction of the nasal capsule as seen from the posterior surface. (Broken lines represent the boundaries of the solum nasi, so.n., and cartilago praenasalis superior, cg.p.sp.).

7. Stage 61

(A progressive metamorphosing stage)

The changes which have occurred are:

1. In the auditory region, the occipito-prootic ossification (Figs. 18–20, oc.pr.os.) is more pronounced especially on the ventral surface. The cartilaginous layer below the notochord (Fig. 20, n.) has decayed and is replaced by a ligamentous band.

The periphery of the processus muscularis capsulae auditivae (Fig. 18, p.m.c.ad.) as well as that of the crista parotica (cs.p.) is undergoing destruction.

The pars interna plectri (Figs. 18 & 20, p.i.pl.) has extended forwards into the developing pars media plectri (p.m.pl.).

2. The basis cranii (Fig. 20, b.c.) as well as the orbital cartilages (or.c.) are eroding enchondrally. The ventral region of the foramen prooticum (f.pr.) is now wider due to the destruction of its boundary. This foramen is divided by a connective tissue strand into two foramina, an anterior larger foramen for the exit of the n. palatinus VII and n. ophthalmicus profundus V and a posterior narrow foramen for the

passage of the n. hyomandibularis VII and the vena capitis lateralis.

3. In the nasal region, the procartilaginous band connecting the lamina orbitonasalis (Figs. 18–20, *lm.orn.*) with the processus cornu quadratus medialis, referred to in the previous stage, has transformed into proper cartilage. The lamina orbitonasalis is now prolonged into the so called processus maxillaris anterior (*p.mx.a.*). The lateral border of the lamina orbitonasalis is fringed with juvenile cartilage cells.

As a result of the continued erosion of the ethmoid plate (Fig. 20, *et.p.*) the foramina for the medial nasal branches of the profundus nerve, now take exit through the connective tissue which stretches between the narrow solum nasi (*so.n.*) and the septum nasi (*s.n.*). The ethmoid flanges have completely eroded.

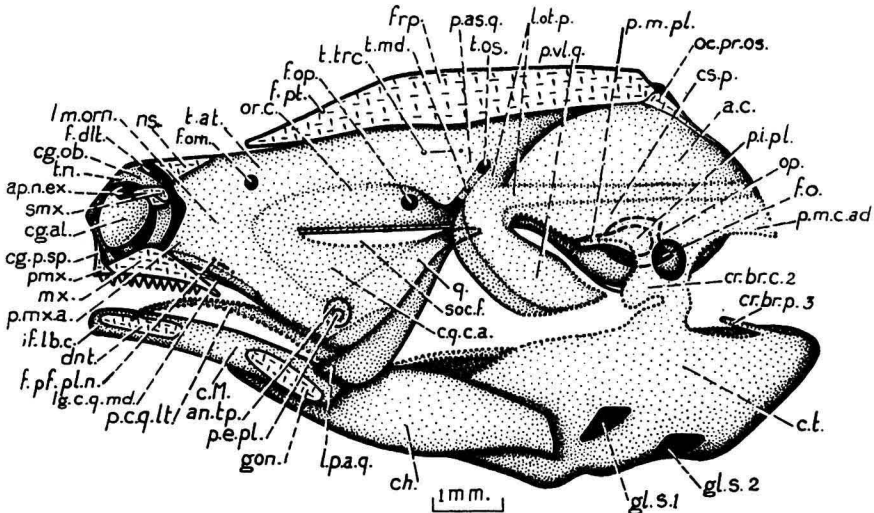


Fig. 18. Stage 61. Graphical reconstruction of a left side view of the skull, jaws and hyobranchial apparatus. (The dotted borders represent resorbing cartilage).

The cartilago obliqua (Figs. 18 & 19, *cg.ob.*) is now broader and runs obliquely forwards and upwards into the wide tectum nasi (*t.n.*).

A very small anterior protrusion from the septomaxilla (Fig. 19, *smx.*) extends outside the apertura nasalis externa (*ap.n.ex.*). The praemaxilla (Figs. 18 & 20, *pmx.*) and the maxilla (*mx.*) are now dentulous. The developing teeth are completely fused with the jaw bones, thus they are of the acrodont type. The praemaxilla has well developed pars frontalis supporting the cartilago praenasalis superior (*cg.p.sp.*) and a broad pars palatina with a short pars dentalis. The maxilla shares in acting as a skeletal support for the floor of the corresponding nasal capsule and possesses a well developed pars frontalis in the region of the cartilago alaris (*cg.al.*), a broad pars palatina and a small pars dentalis.

4. In the upper jaw, the palatoquadrate cartilage (Fig. 18, *q.*) has tilted downwards and backwards forming an anterior angle of about 50°

with the floor of the cranium. The posterior end of the palatoquadrate cartilage, which is well chondrified, is suspended to the cranium through the larval processus oticus (l.ot.p.). The processus ascendens quadrati (p.as.q.), the larval processus oticus and the processus ventro-lateralis quadrati (p.vl.q.) are decaying and are composed of loose cartilage cells.

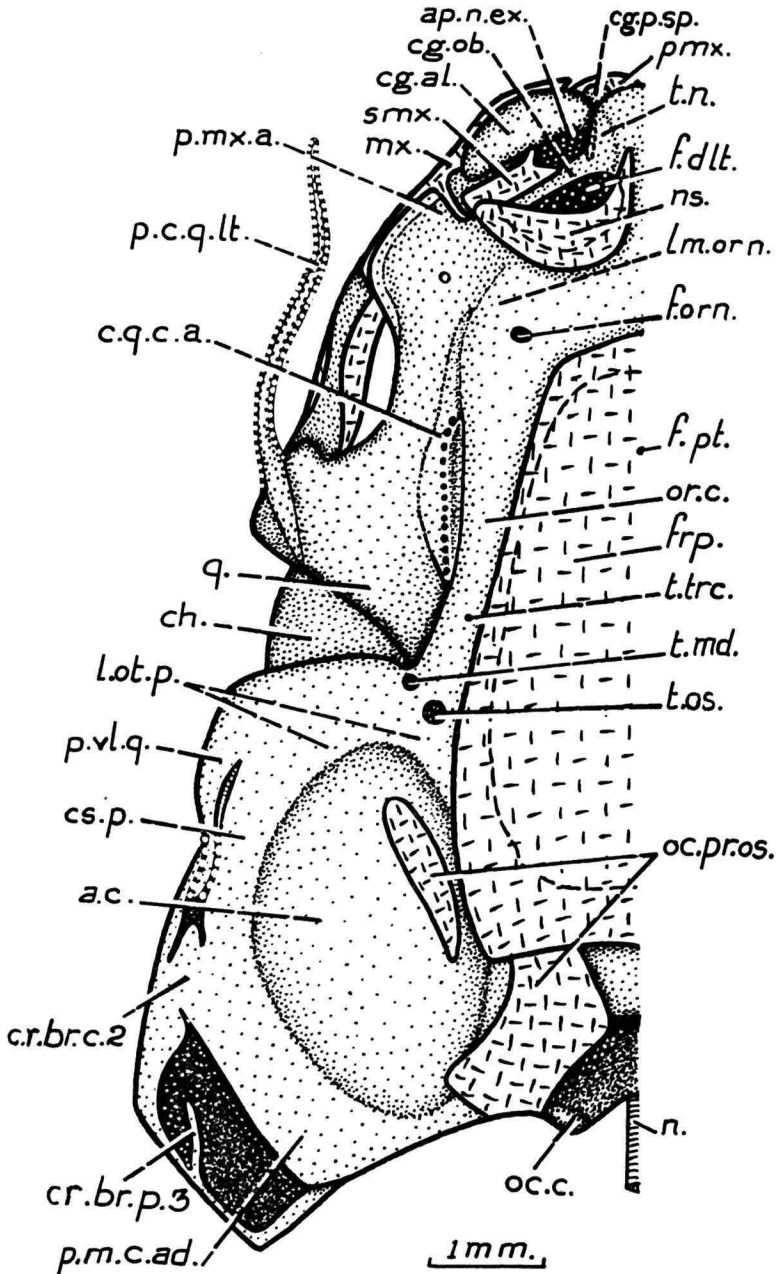


Fig. 19. Stage 61. Graphical reconstruction of the left side half of the skull, jaws and hyobranchial apparatus as seen from the dorsal surface.

The processus muscularis quadrati has largely eroded and the ligament connecting it with the commissura quadrato-cranialis anterior (Fig. 18, c.q.c.a.) has disappeared. Just above the level of the processus muscularis quadrati, there are two new centres of chondrification, an outer centre representing the pars externa plectri (p.e.pl.) and an inner larger one representing the annulus tympanicus (an.tp.).

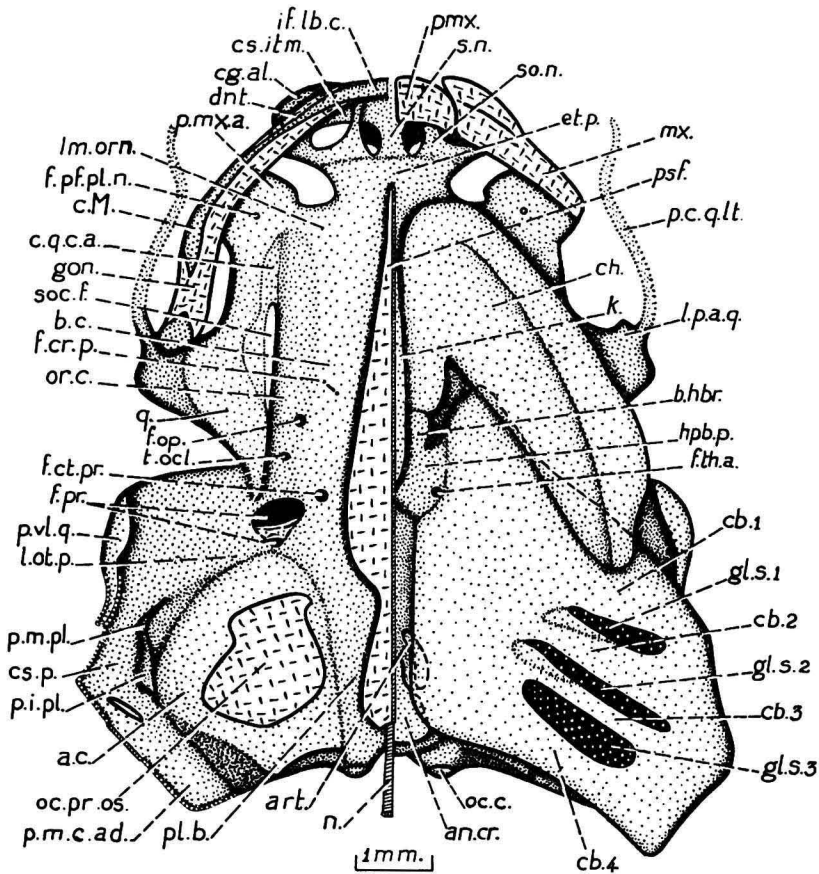


Fig. 20. Stage 61. Graphical reconstruction of a ventral view of the skull and jaws on the left side and of the skull, jaws, hyobranchial apparatus and larynx on the right side.

The commissura quadrato-cranialis anterior is decaying medio-laterally leaving a well chondrified lateral region which has increased in length.

The processus cornu quadratus lateralis (Figs. 18–20, p.c.q.lt.) is eroded rostro-caudally with the result that the tentacular cartilage has largely disappeared.

The ligamentum cornu quadratum mediale (Fig. 18, lg.c.q.md.) is on the way to disappear.

5. The lower jaw has increased in length and the two lobes of the goniale (Fig. 20, gon.) have fused ventrally.

6. In the hyobranchial apparatus, the posterior end of each ceratohyale (Fig. 20, ch.) has shifted towards the middle line. Resorption of each branchial chamber (cb. 1-4) takes place in its periphery, thus gradually diminishing its size. This reduction is more pronounced in the antero-posterior direction.

The fourth cranio-branchial commissure has completely decayed. Remains of the third cranio-branchial process (Fig. 18, cr.br.p.3) are still present, while the second cranio-branchial commissure (cr.br.c.2) is eroding.

The hypobranchial plate (Fig. 20, hpb.p.) is broader. The anterior region of the basihyobranchiale (b.hbr.) as well as its keel (k.) are decaying.

7. In the larynx, the roof of the annulus cricoideus (Fig. 20, an.cr.) is growing in size. It now develops a median triangular floor with an anteriorly directed apex.

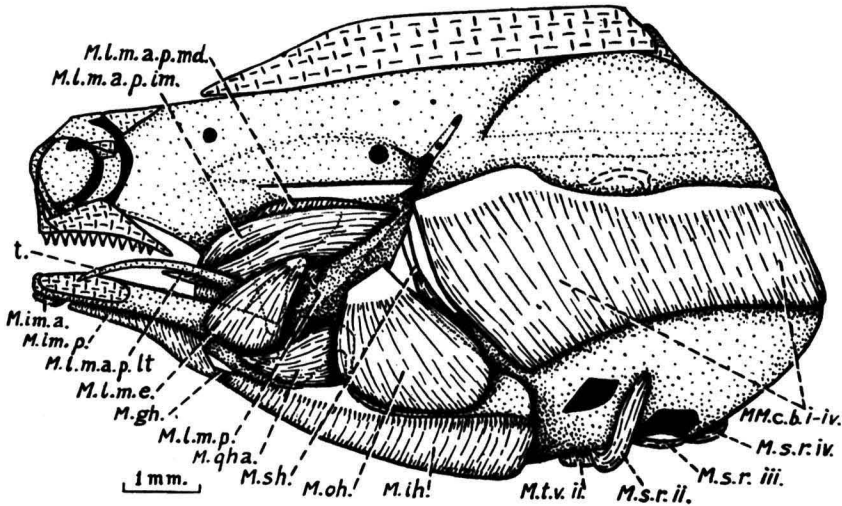


Fig. 21. Stage 61. Graphical reconstruction of a left side view of the visceral muscles.

8. The M.l.m. anterior pars lateralis (Fig. 21, M.l.m.a.p.lt.) has retracted following the destruction of the tentacular cartilage (t.). The proximal half of this muscle becomes closely opposed to the M.l.m. anterior pars intermedium (M.l.m.a.p.im.).

9. The M.l.m. posterior (M.l.m.p.) becomes inserted on the medial edge of the goniale, which extends on the ventro-medial border of the lower jaw.

10. The M.l.m. externus (M.l.m.e.) is now much more developed and is inserted onto the whole lateral surface of the goniale, thus concealing the latter in a side view.

11. The M. intermandibularis posterior (M.im.p.) is now partly attached to the medial surface of the goniale, in addition to its connection with MECKELS' cartilage.

12. The *M. quadratohyoangularis* (*M.qha.*) is inserted onto the ventral surface of the goniale. Its surface of origin becomes closely applied to an upgrowing connective tissue tendon from the *M. interhyoideus* (*M.ih.*). The latter begins to acquire a new attachment on the palatoquadrate cartilage.

13. The *M. orbitohyoideus* (*M.oh.*) originates by loose connective tissue fibres just posterior to the decaying edge of the processus muscularis quadrati. It is inserted onto the side of the ceratohyale close to the tendon of the *M. interhyoideus*.

14. The anterior fibres of the *M. suspensoriohyoideus* (*M.sh.*) become more or less continuous with the postero-medial fibres of the *M. orbitohyoideus*.

8. Stage 62

(A progressive stage of metamorphosis)

The main changes which have taken place are:

1. In the auditory region, the occipito-prootic ossification (Figs. 22–24, *oc.pr.os.*) is more developed.

The processus muscularis capsulae auditivae (Figs. 22 & 24, *p.m.c.ad.*) and the crista parotica (*cs.p.*) are highly eroded and are now reduced in size. This reduction in size has resulted in the exposure of the plectral apparatus in a side view (Fig. 22). The pars media plectri (*p.m.pl.*) has now extended forwards.

2. The eroded basis cranii (Fig. 24, *b.c.*) is now in the form of connective tissue supported ventrally by the parasphenoid (*psf.*). The latter is now longer and is curved anteriorly below the septum nasi (*s.n.*).

The orbital cartilages (Fig. 24, *or.c.*) like the basis cranii, are represented

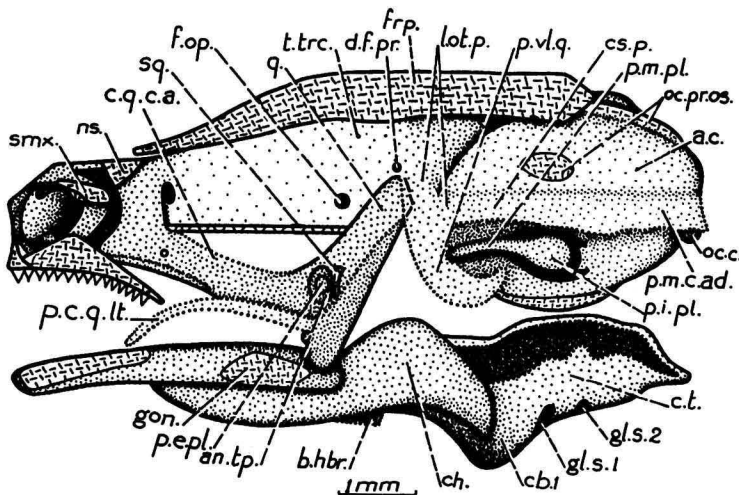


Fig. 22. Stage 62. Graphical reconstruction of a left side view of the skull, jaws and hyobranchial apparatus.

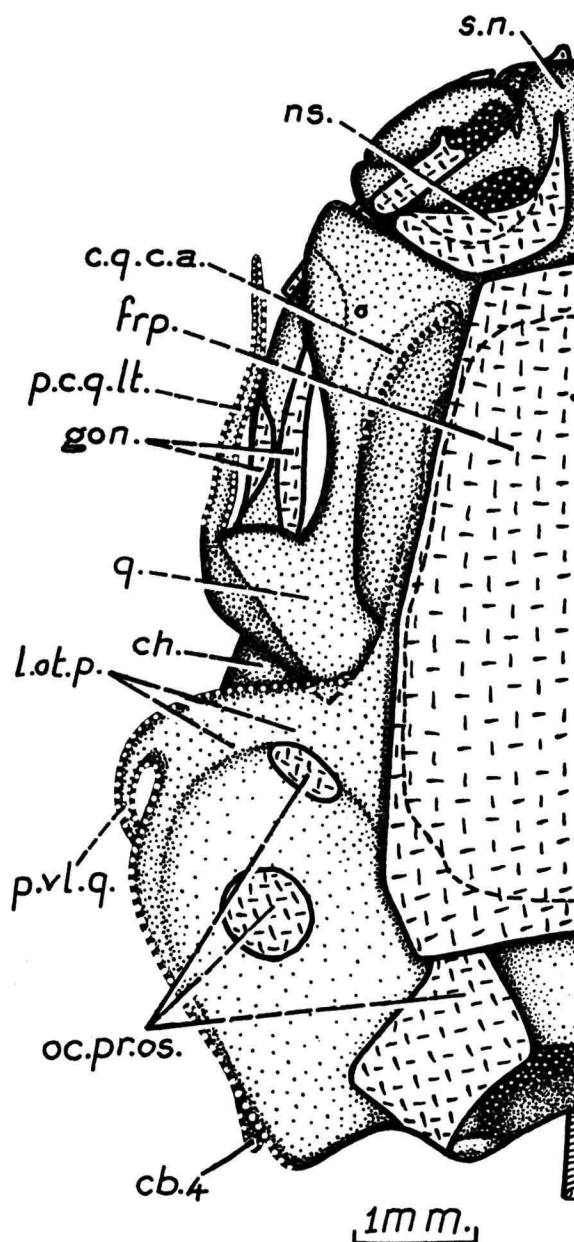


Fig. 23. Stage 62. Graphical reconstruction of the left side half of the skull, jaws and hyobranchial apparatus as seen from the dorsal surface.

by connective tissue. The outlet for the oculomotor tunnel (t.oel.) has shifted backwards in the surrounding connective tissue and comes to lie antero-lateral to the foramen caroticum primarium (f.ct.pr.).

The fused fronto-parietal bones (Fig. 23, frp.) extend forwards and reach the posterior limit of the nasal bones (ns.).

3. In the nasal region, the area of the olfactory tunnels is now deeper due to the softening of its cartilaginous tissue.

The larval ethmoid plate (Fig. 24, et.p.) is more destroyed.

The medial region of the nasal bone (Fig. 23, ns.) is extended forwards.

4. In the upper jaw, the palatoquadrate cartilage (Fig. 22, q.) is pressed through the larval processus oticus (l.ot.p.) on the anterior wall of the auditory capsule (a.c.). The larval processus oticus is composed

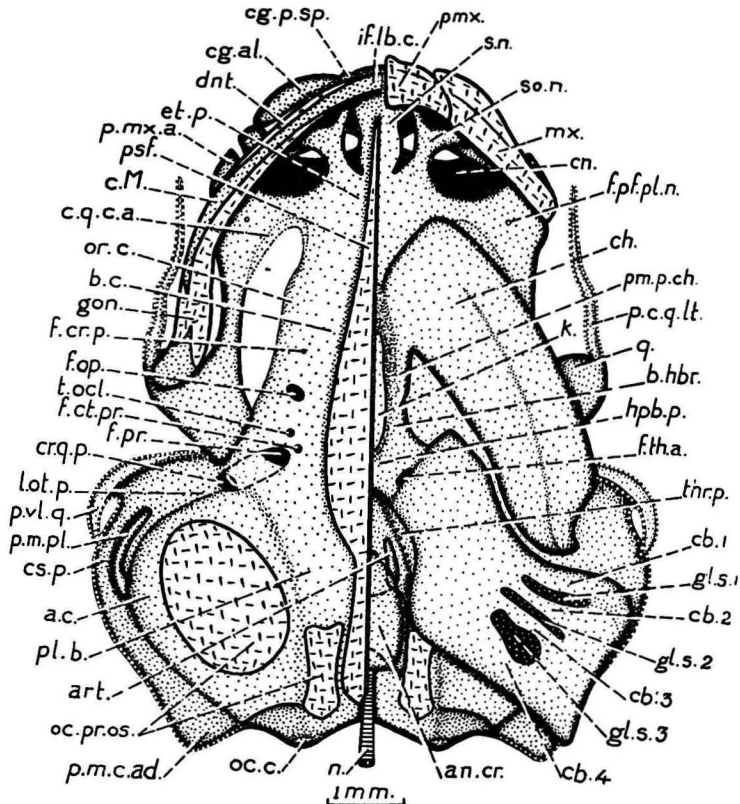


Fig. 24. Stage 62. Graphical reconstruction of a ventral view of the skull and jaws on the left side and of the skull, jaws, hyobranchial apparatus and larynx on the right side.

of decayed cartilage cells which merge backwards into the crista parotica (cs.p.) and outwards into the breaking down processus ventro-lateralis quadrati (p.v.l.q.).

The palatoquadrate cartilage has shifted slightly upwards and backwards making an anterior angle of 65° with the floor of the cranium. This backward shift is followed by the elongation of the lateral part of the commissura quadrato-cranialis anterior (c.q.c.a.).

The processus ascendens quadrati as well as the pila antotica are completely eroded. Due to this cartilage destruction, the two tunnels for the n. maxillo-mandibularis V and the n. ophthalmicus superficialis VII

take a common exit which represents the dorsal outlet for the foramen prooticum (Fig. 22, d.f.pr.). The connective tissue strand separating the two ventral components of the original foramen prooticum (Fig. 24, f.pr.) is now wider. The postero-lateral component of this foramen represents the future cranio-quadrato passage (cr.q.p.).

The medial portion of the commissura quadrato-cranialis anterior as well as the processus muscularis quadrati are nearly completely eroded. Some osteoblasts invade the debris of the processus muscularis quadrati forming the primordium of the squamosum (Fig. 22, sq.).

The processus cornu quadratus lateralis (p.c.q.lt.) is now merely composed of decayed cartilage debris.

The tentacular cartilage as well as the ligamentum cornu quadratum mediale have completely disappeared.

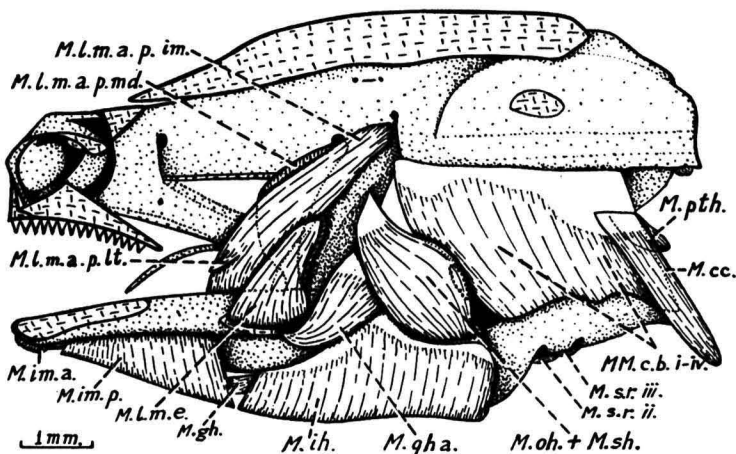


Fig. 25. Stage 62. Graphical reconstruction of a left side view of the visceral muscles.

5. In the hyobranchial apparatus, the postero-medial process of each ceratohyale (Fig. 24, pm.p.ch.) is now continuous with the basihyobranchiale (b.hbr.). The ligamentous band which connects both structures dorsally has disappeared.

Each branchial chamber (Fig. 24, cb. 1-4) has diminished in size as a result of the progressive resorption of its periphery especially in its antero-posterior extent. The branchial rays and processes are also eroding.

The third cranio-branchial process and the second cranio-branchial commissure have completely disappeared (Fig. 22). Thus, at this stage the branchial system has lost continuity with the skull.

From the posterior region of the hypobranchial plate (Fig. 24, hpb.p.) and just medial to the eroding branchial chambers (cb. 1-4), there are two new chondrifying processes which represent the primordia of the thyroid processes (thr.p.).

6. The annulus cricoideus (Fig. 24, an.cr.) is more developed. Its

roof is concave posteriorly and is confluent with the floor in this region through procartilage cells. The area of this continuity is short in the antero-posterior extent, so that the main side wall of the larynx is composed of connective tissue.

7. The *M. suspensoriohyoideus* comes into close contact with the postero-medial wall of the *M. orbitohyoideus* (Fig. 25, *M.oh.* + *M.sh.*). The latter originates by loose connective tissue fibres on the decaying

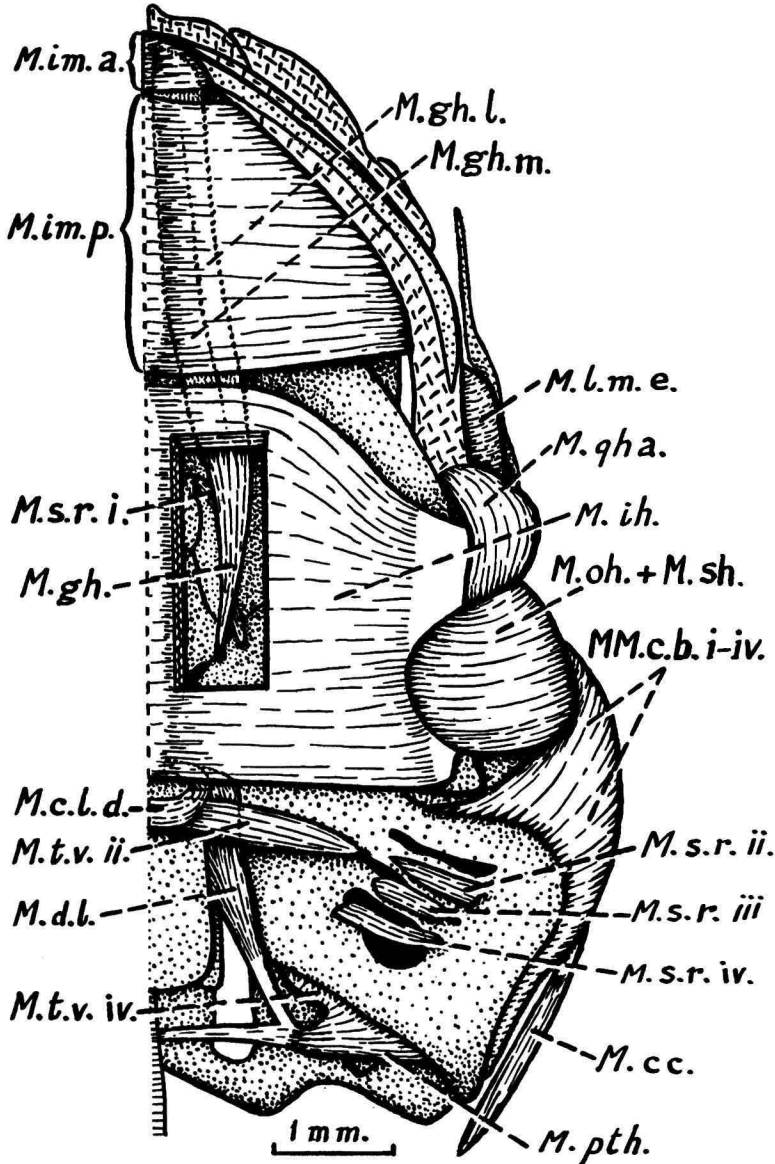


Fig. 26. Stage 62. Graphical reconstruction of a ventral view of the visceral muscles.

part of the processus muscularis quadrati, indicating a transitory stage, just after which the surface of origin of this muscle becomes changed. The fibres still pass downwards and backwards; the backward path is even more pronounced here than in earlier stages, apparently due to the backward shift of the surface of insertion. The anterior fibres of the M. orbitohyoideus are inserted onto the tendon of the M. interhyoideus, the posterior fibres on the ceratohyale.

8. The MM. constrictores branchiales i-iv (Figs. 25 & 26, MM. c.b. i-iv.) are in a process of reduction in compactness and in importance following the process of resorption of the whole branchial chamber. The individual fibres become loosely attached to each other, and are in a process of dissolution. This is more noticeable in the posterior third of the whole muscle, where extensive development of tendinous attachments with the skull takes place.

9. The MM. subarcuales recti ii-iv (M.s.r.ii-iv.) have become relatively shorter and thicker than in previous stages; but, they have definitely decreased in volume.

10. Appearance of the M. petrohyoideus (M.pth.) apparently on the expense of the M. transversus ventralis iv and M. levator arcuum branchialis iv. This muscle arises from the crista parotica in close connection with the connective tissue fibres of the MM. constrictores branchiales. The M. petrohyoideus extends downwards and medialwards towards the laryngeal region, where the muscles of both sides meet in a broad and thin ventral raphé representing that of the M. transversus ventralis iv of the larva.

9. Stage 63

(An advanced stage of metamorphosis)

The important changes are:

1. In the auditory region, the processus muscularis capsulae auditivae has completely disappeared. The crista parotica (Fig. 27, cs.p.) has largely decayed and is now represented by a ledge of loose cartilage cells.

The pars interna plectri (Fig. 27, p.i.pl.) is now closely opposed to the operculum fenestrae ovalis (op.).

2. The connective tissue surrounding the original foramen prooticum (Fig. 28, v.f.pr.) has largely disappeared resulting in the great widening of this foramen. A new chondrifying centre, the post-palatine commissure (p.p.cm.) develops from the planum basale (pl.b.). This commissure divides the original foramen prooticum into a medial ventral outlet for the foramen prooticum (v.f.pr.) and a lateral cranio-quadrate passage (Fig. 27, cr.q.p.) which is now vertical.

The progressive backward shift of the oculomotor tunnel results in its continuity with the foramen caroticum primarium (Fig. 28, f.oc.+ct.pr.). The foramen cranio-palatinum is now occluded by connective tissue.

The annulus tympanicus (Fig. 27, an.tp.) is now more or less crescent-shaped. The pars externa plectri (p.e.pl.) is growing in size.

3. In the upper jaw, the larval processus oticus (Fig. 27, l.ot.p.) is in the connective tissue stage, and is pressed on the auditory capsule (a.c.) as well as on the anterior eroded area of the crista parotica (cs.p.). The processus ventro-lateralis quadrati has completely disappeared.

The palatoquadrate cartilage (Fig. 27, q.) is progressively shifting upwards and backwards making an anterior angle of about 85° with the floor of the cranium. Its medial region is brought closer to the post-palatine commissure (Fig. 28, q. & p.p.cm.) while its ventral corner grows backwards into a posterior spur (Fig. 27, p.s.q.). Ossification on

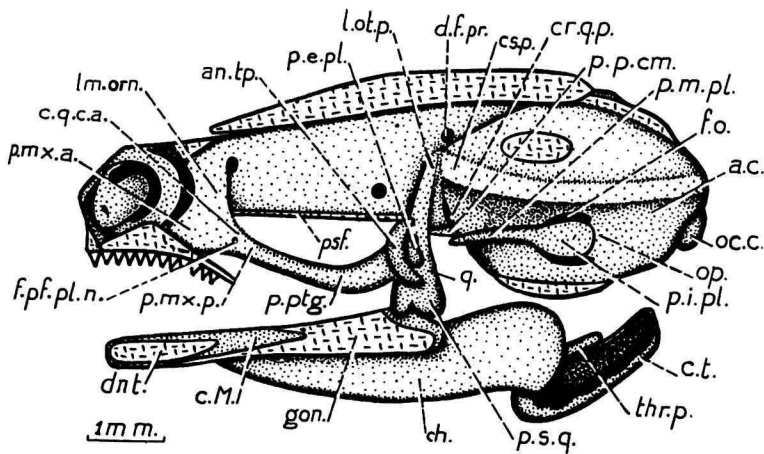


Fig. 27. Stage 63. Contour reconstruction of a left side view of the skull, jaws and hyobranchial apparatus. (The septomaxilla, squamosum and pterygoideus are not shown).

the ventral surface of the palatoquadrate cartilage medial to the pars articularis quadrati, forms a triangular pterygoideus bone (Fig. 28, ptg.).

Remnants of the eroded commissura quadrato-cranialis anterior (Fig. 27, c.q.c.a.) are still evident medial to the foramen for the ramus communicans between n. ophthalmicus profundus V and n. palatinus VII (f.pf.pl.n.). The well chondrified lateral region of the commissura quadrato-cranialis anterior is now in the form of a long, slender subocular bar joining the lamina orbitonasalis (lm.orn.) anteriorly with the palatoquadrate cartilage posteriorly. This subocular bar can be differentiated into two regions, a posterior region overlying the pterygoideus and is the primordium of the processus pterygoideus (Figs. 27 & 28, p.ptg.) and an anterior portion which is the primordium of the processus maxillaris posterior (Fig. 27, p.mx.p.).

The processus cornu quadratus lateralis has completely disappeared.

4. In the hyobranchial apparatus, the medial borders of the ceratohyalia (Fig. 29, ch.) are eroding. The anterior region of the basi-

branchiale (b.hbr.) as well as the keel have decayed, thus the hyoglossal sinus (hg.s.) becomes deeper.

Each branchial chamber (Fig. 29, cb. 1-4) is represented by a sheet of decayed cartilage debris and is ready to disintegrate completely. It is irregular dorsally (Fig. 27) due to the breaking down branchial rays. The region of the commissurae terminales (Figs. 27 & 29, c.t.) is now narrower.

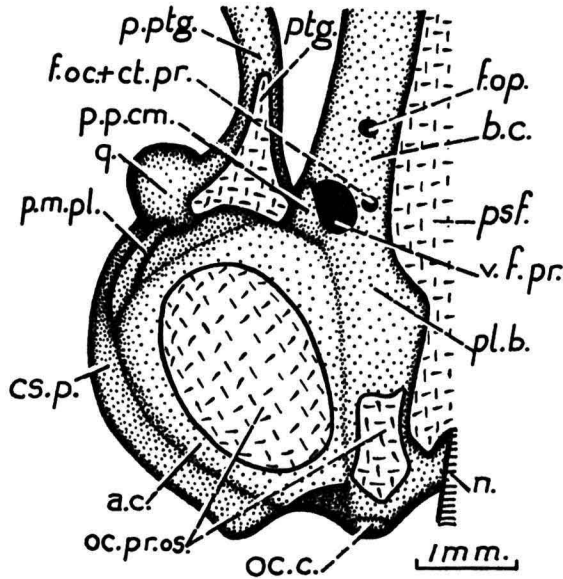


Fig. 28. Stage 63. Graphical reconstruction of the posterior left side half of the skull as seen from the ventral surface.

From the basihyobranchiale as well as from the hypobranchial plate (Fig. 29, hpb.p.) a new chondrifying centre grows laterally forming the primordium of the so called ala (al.). This structure lies in front of and slightly dorsal to the corresponding branchial chamber and is completely separate from it.

The thyroid processes (Fig. 29, thr.p.) are now well developed and have no histological relationship with the decaying branchial chambers.

The foramen for the thyreopharyngeal artery (Fig. 29, f.th.a.) is now wider and lodges the corresponding thyroid gland.

5. The pars lateralis of the M.l.m. anterior loses its individuality and becomes continuous with the pars intermedius of the same muscle.

6. The MM. orbito- and suspensoriohyoideus fuse completely and begin to acquire a new surface of origin on the auditory capsule.

7. The MM. constrictores branchiales i-iv, subarcuales recti i-iv, and transversus ventralis ii are represented by dissolving muscle fibres.

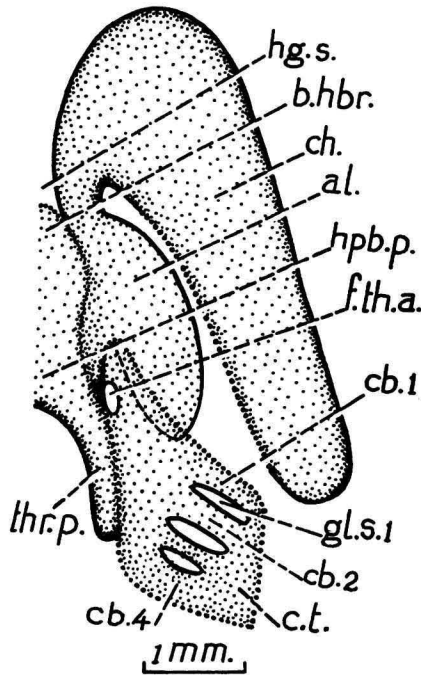


Fig. 29. Stage 63. Graphical reconstruction of the right side half of the hyobranchial apparatus as seen from the ventral surface.

10. Stage 64

(A late stage of metamorphosis)

The main changes are:

1. In the auditory region, the cartilaginous tissue present on the lateral wall of the auditory capsule (Fig. 30, a.c.) is thick especially in front of the level of the fenestra ovalis (f.o.), while that present on the dorsal, ventral and medial walls (Figs. 31 & 32, a.c.) is highly eroded and is largely replaced by the occipito-prootic ossification (oc.pr.os.).

The pars media plectri (Figs. 30 & 31, p.m.pl.) has now gained fusion with the pars externa plectri (p.e.pl.), thus the whole plectral apparatus is now a complete unit. The annulus tympanicus (Fig. 30, an.tp.) is growing in size and shows a more backwardly directed ventral rim.

2. The common outlet for the previous oculomotor tunnel and the corresponding foramen caroticum primarium (Fig. 32, f.oc.+ct.pr.) is separated from the ventral outlet of the foramen prooticum (v.f.pr.) by means of a thin strand of connective tissue fibres.

3. In the nasal region, the fused fronto-parietal bones (Fig. 30, frp.) are extended anteriorly into a supraethmoid region which partially covers the nasal bones (ns.).

The parasphenoid (Fig. 32, psf.) has grown further anteriorly under the septum nasi (s.n.) to which it is bound through dense connective tissue fibres.

The previous tectum anterius as well as the vertical septum joining it with the floor of the cranium are decaying. Thus, the cavum cranii has now extended forwards and comes to lie over the posterior region of the septum nasi. At the same time the olfactory tunnels are shorter and pass ventro-laterally to the nasal capsules.

The ventral surface of the processus maxillaris anterior is broad and flat and acts as a support for the underlying maxilla (Fig. 32, mx.).

The antero-medial protrusion of the nasal bone (Fig. 31, ns.) is now long and narrow.

4. In the upper jaw, the larval processus oticus has completely disappeared and instead the dorsal region of the palatoquadrate cartilage (Fig. 30, q.) grows and forms the adult processus oticus (a.ot.p.) which

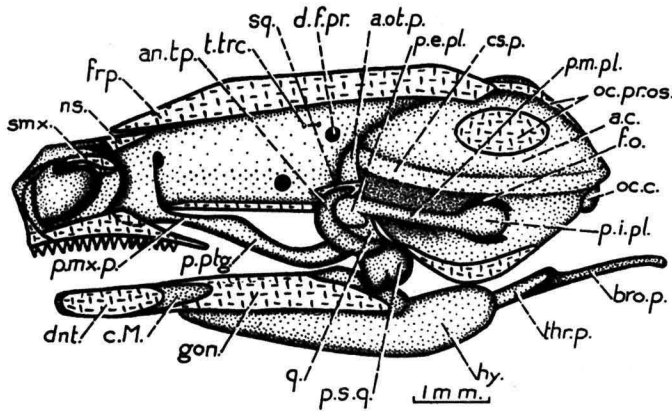


Fig. 30. Stage 64. Graphical reconstruction of a left side view of the skull, jaws, hyobranchial apparatus and larynx. (The pterygoid is not shown).

is bound to the auditory capsule (a.c.) through a thin layer of connective tissue fibres.

The palatoquadrate cartilage (Fig. 30, q.) has shifted further backwards and the anterior angle which it makes with the floor of the cranium is wider and now measures about 105° . The medial border of the palatoquadrate is now in close contact with the post-palatine commissure (Fig. 32, p.p.cm.) which bulges below the level of the floor of the cranium. A narrow connective tissue layer intervenes between both structures. The palatoquadrate spur (Fig. 30, p.s.q.) is more developed.

The squamosum (Fig. 30, sq.) is now T-shaped. It lies medial to the annulus tympanicus (an.tp.) and is bound to the lateral surface of the palatoquadrate cartilage through dense connective tissue fibres.

The pterygoid (Fig. 32, ptg.) is broad posteriorly and narrow anteriorly. Its posterior region underlies a portion of the post-palatine commissure (p.p.cm.), and its anterior part slightly overlaps the processus pterygoideus (p.ptg.). The processus pterygoideus itself is slightly thicker than the processus maxillaris posterior (Fig. 30, p.mx.p.).

Owing to the complete disintegration of the medial region of the commissura quadrato-cranialis anterior, the foramen for the ramus communicans between n. ophthalmicus profundus V and n. palatinus VII no longer penetrates the cartilage but the connective tissue medial to the processus maxillaris posterior.

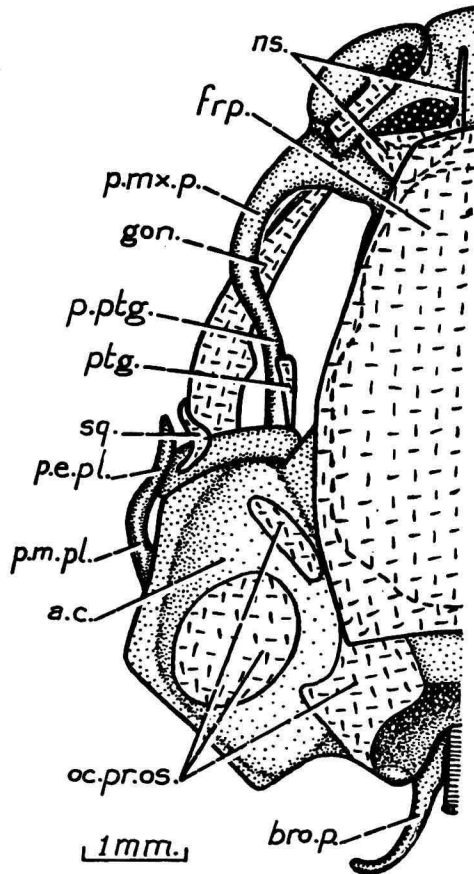


Fig. 31. Stage 64. Graphical reconstruction of the left side half of the skull, jaws, hyobranchial apparatus and larynx as seen from the dorsal surface.

5. The lower jaw is longer with the posterior region of the goniale (Figs. 30 & 32, gon.) completely investing the major portion of MECKELS' cartilage.

6. In the hyobranchial apparatus, the ceratohyalia are comparatively slender and may be given now the name hyalia (Figs. 30 & 32, hy.). Their distal ends are flexed dorsally towards the floor of the auditory capsules. The medial border of each hyale is eroding.

The hyoglossal sinus (Fig. 32, hg.s.) is now deeper due to the progressive erosion of the basihyobranchiale. The latter is completely confluent with the hypobranchial plate forming the so called corpus hyoideum (c.hy.).

The branchial chambers have completely disappeared and the thyroid foramina no longer acquire a posterior boundary.

The alae (Fig. 32, al.) as well as the thyroid processes (thr.p.) are growing in size. The former possess thin lamellae of juvenile cartilage cells on their lateral borders.

7. The larynx is shifting forwards by progressive cartilage addition

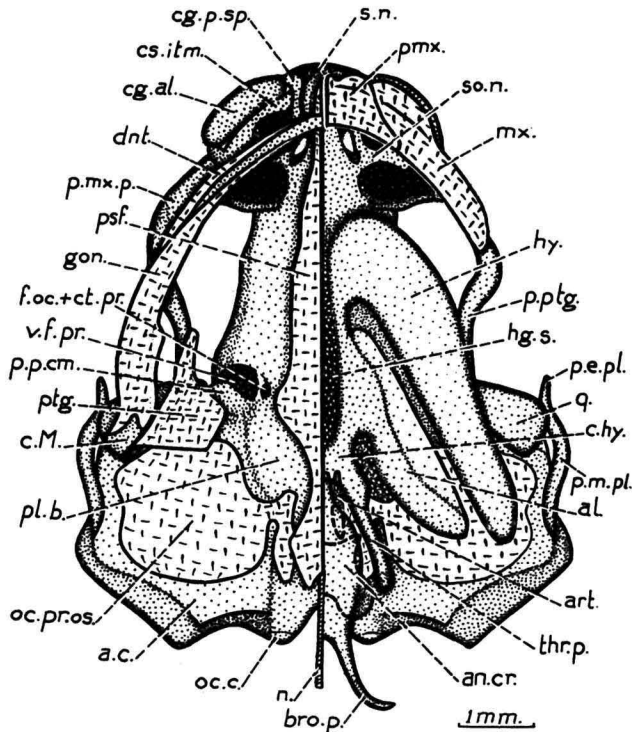


Fig. 32. Stage 64. Graphical reconstruction of a ventral view of the skull and jaws on the left side of the skull, jaws, hyobranchial apparatus and larynx on the right side.

in the antero-posterior direction. It comes to lie between the thyroid processes. The anterior regions of the arytenoids (Fig. 32, art.) now lie dorsal to the corpus hyoideum (c.hy.). The floor of the annulus cricoideus (an.cr.) lies in close contact with the corpus hyoideum; the perichondrium between both elements is distinct. The roof of the annulus cricoideus has well chondrified, ventrally flexed rims which support the posterior ends of the arytenoids. The bronchial processes (bro.p.) which are smooth and long are procartilaginous and have grown backwards from the floor of the annulus cricoideus.

8. The compound pars intermedius and pars lateralis of the M.l.m. anterior becomes completely fused with the M.l.m. posterior. These give rise to the so called M.l.m. posterior (Fig. 33, M.l.m.p.) of the meta-

morphosed animal. The M.l.m. anterior pars medialis is, therefore the adult M.l.m. anterior (M.l.m.a.).

9. The M. intermandibularis posterior (Fig. 34, M.im.p.) is now wholly attached to the medio-dorsal surface of the goniale.

10. The compound M. orbito-suspensoriohyoideus (Figs. 33 & 34, M.osh.) possesses a broad surface of origin onto the crista parotica. The fibres extend downwards and become closely attached to the tendon of the M. interhyoideus.

11. The M. quadratohyoangularis (M.qha.) has moved backwards and is now coming in close connection with the M. orbitosuspensoriohyoideus. Its fibres now extend more or less vertically downwards and is inserted onto the postero-ventral surface of the lower jaw.

12. The M. interhyoideus (M.ih.). The fibres of this muscle converge into a very strong tendon, which passes vertically upwards through the groove between the hyale and the lower jaw and becomes attached to the palatoquadrate cartilage. Medially, this tendon retains its connection to the hyale, while laterally it is attached to the MM. quadratohyoangularis and orbitosuspensoriohyoideus.

13. The M. dilatator laryngis (Fig. 34, M.d.l.) loses its connection with the M. petrohyoideus (M.pth.). The former gains a new surface of origin on the annulus cricoideus (an.cr.). The latter retains its original connection with the corresponding one on the other side through a very thin ventral raphé, which lies below the annulus cricoideus.

14. The M. cucullaris (M.cc.) is now more thick and compact. It still retains its original attachments, originating from the crista parotica, and inserted onto the medial border of the pectoral girdle close to the glenoid cavity.

11. Stage 65

(A stage just prior to the end of metamorphosis)

The most conspicuous changes are:

1. In the auditory region, each auditory capsule (Figs. 35 & 36, a.c.) is largely formed by the occipito-prootic ossification (oc.pr.os.). In addition to this bony lining, the lateral wall possesses a thick layer of cartilage which is grooved in front of the fenestra ovalis (Fig. 35, f.o.). Along this groove extends the pars media plectri (p.m.pl.) which is now perichondrally ossified. The pars externa plectri (p.e.pl.) is kidney-shaped. Both the annulus tympanicus (an.tp.) and the squamosum (sq.) are growing in size.

2. Complete continuity takes place between the ventral outlet of the foramen prooticum and the previous common exit for the oculomotor tunnel and the foramen caroticum primarium (Fig. 36, v.f.pr'.) by the destruction of the connective tissue strand between both foramina.

The ventro-lateral wall of the skull just lateral to the parasphenoid (Figs. 35 & 36, psf.) has ossified forming the orbitosphenoid (ors.).

3. In the upper jaw, the adult processus oticus (Fig. 35, a.ot.p.) is

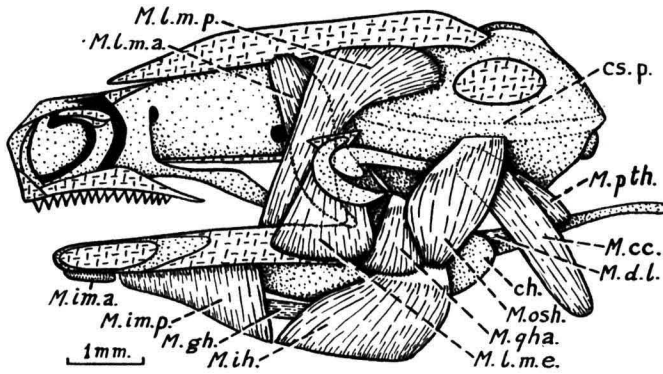


Fig. 33. Stage 64. Graphical reconstruction of a left side view of the visceral muscles.

now composed of juvenile cartilage cells and is synchondrotically confluent with the auditory capsule (a.c.) and the crista parotica (cs.p.).

The backward shift of the palatoquadrate cartilage (Fig. 35, q.) has

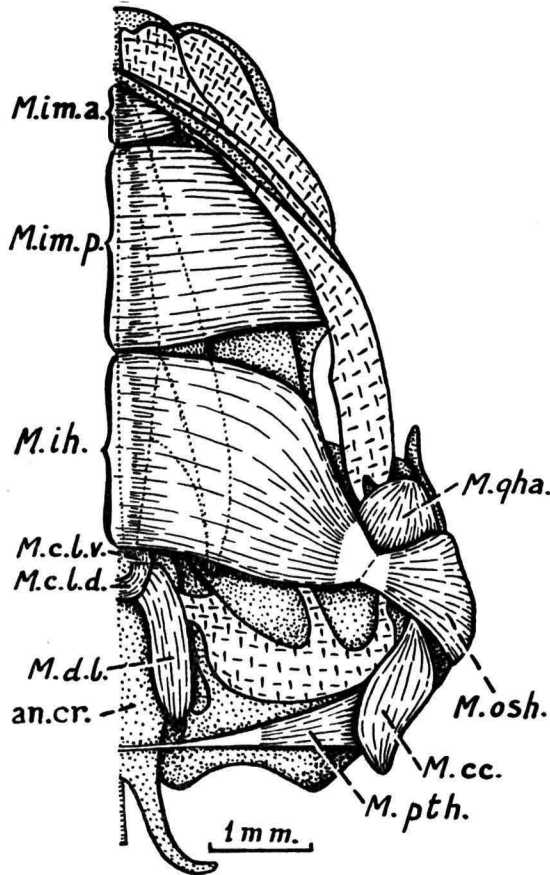


Fig. 34. Stage 64. Graphical reconstruction of a ventral view of the visceral muscles.

increased and now makes a wider anterior angle with the floor of the cranium. This angle measures about 110° .

The processus maxillaris posterior (Fig. 35, p.mx.p.) is now longer. The pterygoid (Fig. 36, ptg.) is larger in size and overlies the processus pterygoideus (p.ptg.) anteriorly.

4. In the hyobranchial apparatus, the antero-medial regions of the hyalia (Fig. 36, hy.) are now bound together with procartilage cells, thus transforming the previous hyoglossal sinus into a hyoglossal foramen (hg.f.).

Each ala (Fig. 36, al.) which is now larger, possesses a small anterior process (al.p.) representing the antero-lateral process of other salientians.

Each thyroid process (Fig. 36, thr.p.) has extended backwards reaching the posterior limit of the skull.

5. The *M. quadratohyoangularis* comes to lie in close connection with the antero-medial border of the *M. orbitosuspensoriohyoideus*. The last named muscle is now inserted onto the posterior end of the lower jaw.

12. Stage 66

(A newly metamorphosed toadlet)

A. The Skull and Jaws

1. *The occipito-auditory region*: The auditory capsules (Figs. 37–40, a.c.) are largely formed by the occipito-prootic ossification (oc.pr.os.). The posterior end of each auditory capsule is confluent with the corresponding condyloid fossa which remains mostly spanned from behind with dense fibrous connective tissue. The fossa is continuous laterally with the labyrinth cavity through the foramen perilymphaticum inferius and medially with the cavum cranii through the foramen jugulare (cf. Fig. 4 of stage 55). The cavum cranii opens posteriorly by the foramen magnum (Fig. 38, f.m.), which is bounded dorsally by the tectum posterius

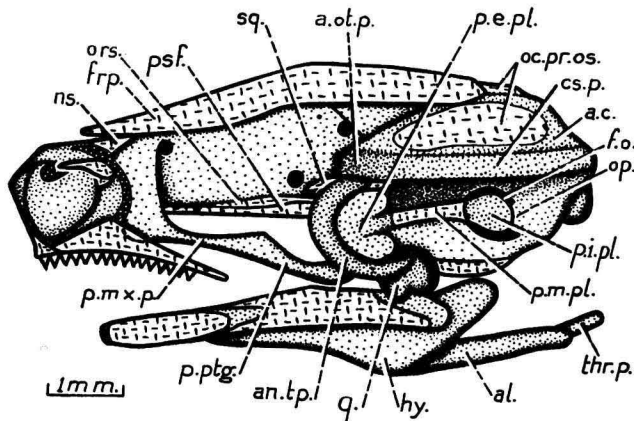


Fig. 35. Stage 65. Graphical reconstruction of a left side view of the skull, jaws and hyobranchial apparatus. (The pterygoid is not shown).

(t.pt.). The medial part of the tectum posterius is still cartilaginous while its lateral parts are ossified and are continuous with the occipitoprotic ossification. The occipital condyles (oc.c.) are cartilaginous.

The medial capsular wall which is now represented by a thin shield-like osseous structure still possesses the foramen acusticum posterius, foramen acusticum anterius and the foramen endolymphaticum as was previously described in stage 55 (cf. Fig. 2).

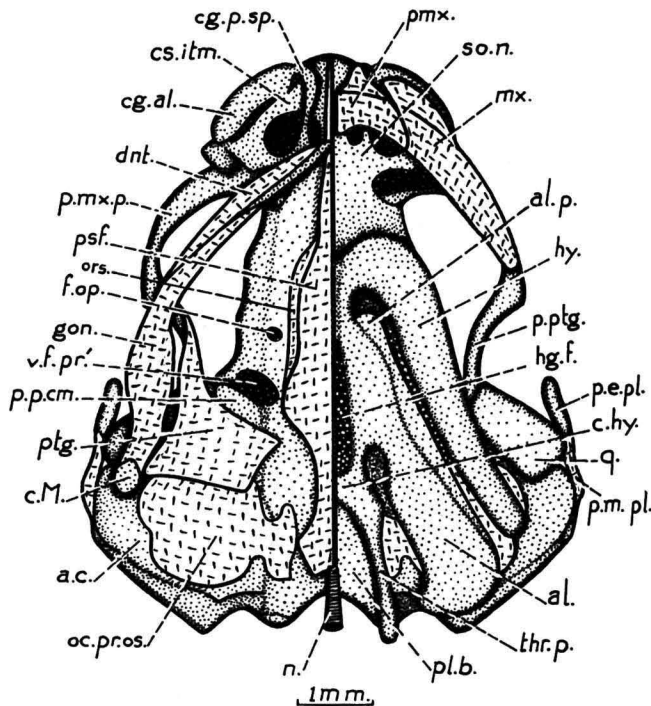


Fig. 36. Stage 65. Graphical reconstruction of a ventral view of the skull and jaws on the left side and of the skull, jaws and hyobranchial apparatus on the right side.

On the side wall of each auditory capsule, there is a deep groove limited dorsally by the crista parotica (Fig. 40, cs.p.) and ventrally by a thickened cartilaginous band. This groove extends forwards and leads into the cavum cranii through the cranio-quadrata passage, which serves as an exit for the n. hyomandibularis VII and the vena capitis lateralis.

The middle ear system consists of the operculum fenestrae ovalis and the partes interna, media and externa plectri. The operculum (Fig. 37, op.) is a feebly developed outgrowth from the posterior border of the fenestra ovalis. The rest of the fenestra ovalis is plugged with the cartilaginous pars interna plectri (p.i.pl.), which shows a slight dorsal synchondrotic attachment with the wall of the auditory capsule. The ventral rim of the pars interna plectri possesses a slit-like opening (sl.) which is spanned

medially with connective tissue. The pars media plectri (p.m.pl.) is a rod-like structure extending outwards and forwards. It is perichondrally ossified with a central core of cartilage cells. Its middle region is closely opposed to the thickened band of the auditory capsule by a very thin layer of fibrous connective tissue. The pars externa plectri (p.e.pl.) is a kidney-shaped cartilaginous structure. It is thick at the centre and thinner at the margins.

The annulus tympanicus (Fig. 37, an.tp.) is sickle-shaped and is discontinuous posteriorly. Medial to the annulus tympanicus, lies the tri-radiate squamosum (Fig. 41, sq.), which possesses an anterior well pronounced processus zygomaticus and a posteriorly curved ventral limb. This bone is bound with the adult processus oticus (a.ot.p.), the crista parotica (cs.p.) and the palatoquadrate cartilage (q.) through fibrocartilage.

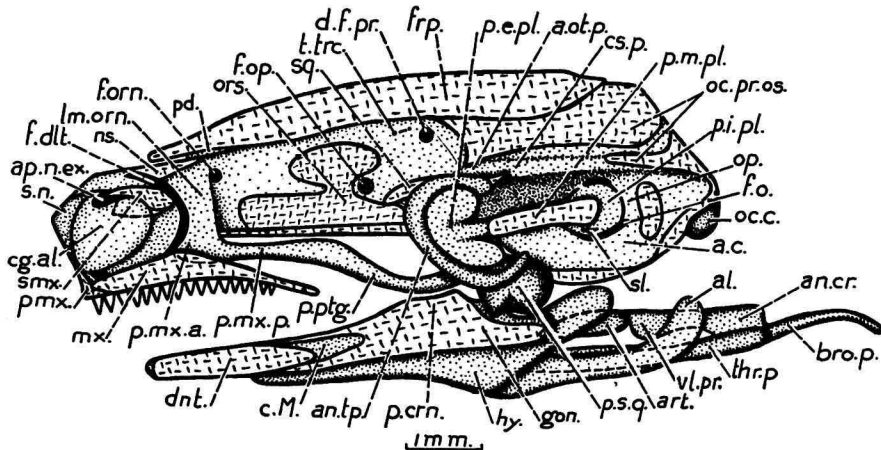


Fig. 37. Stage 66. Graphical reconstruction of a left side view of the skull, jaws, hyobranchial apparatus and larynx.

The floor of this region is formed by the planum basale (Figs. 39 & 40, pl.b.) which is enchondrally destroyed. The posterior region of the planum basale possesses a ventral groove for lodging the notochord (Fig. 39, n.) which is mostly floored with dense connective tissue. The anterior tip of the notochord as well as the anterior region of the planum basale are supported by the parasphenoid (psf.).

The palatoquadrate cartilage (Fig. 41, q.) extends obliquely downwards and backwards forming an anterior angle of about 115° with the floor of the skull. The pars articularis quadrati possesses a well developed posterior spur (p.s.q.). Just in front of the auditory capsule, the palatoquadrate cartilage extends dorsally into the adult processus oticus (a.ot.p.) which consists of juvenile cartilage cells. Medially, it is closely opposed to the post-palatine commissure (Fig. 39, p.p.cm.) which is a short, ventral cartilaginous bulge from the planum basale. Close to the

inner border of this commissure, lies the common ventral outlet of the foramen prooticum (v.f.pr'). This foramen acts as an entrance to the arteria carotis interna and as an exit for the n. oculomotorius, n. ophthalmicus profundus V, and n. palatinus VII.

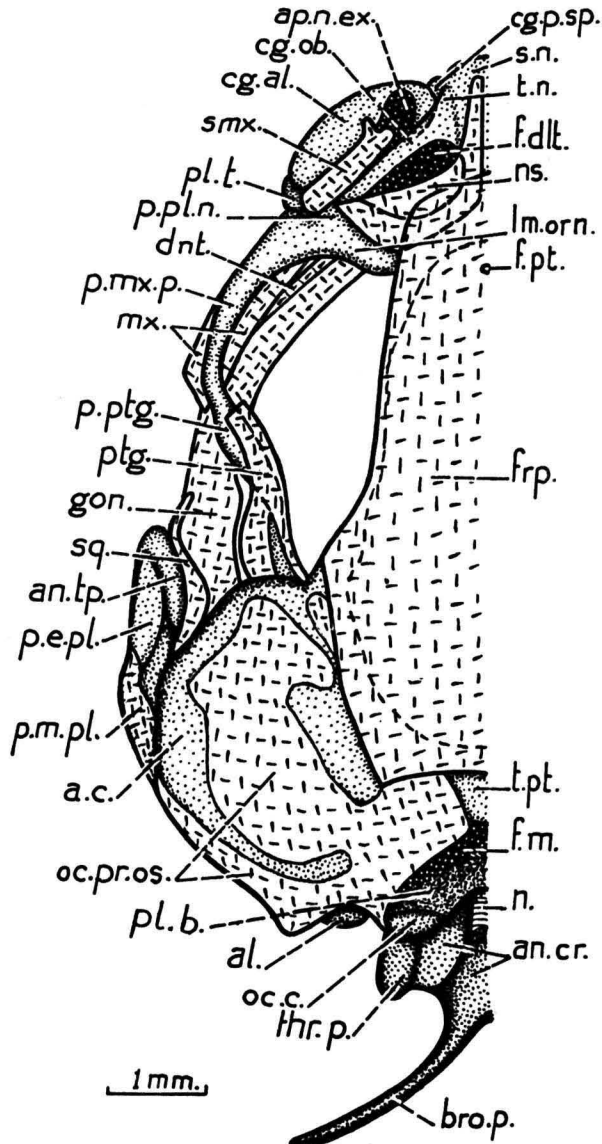


Fig. 38. Stage 66. Graphical reconstruction of the left side half of the skull jaws, hyobranchial apparatus and larynx as seen from the dorsal surface.

2. *The orbito-temporal region:* The roof possesses a wide fronto-parietal fenestra which together with the anterior half of the tectum posterius are covered by the fused fronto-parietal bones (Fig. 38, frp.). This compound bone is convex dorsally, possesses a median crest on its

inner surface and a parietal foramen (f.pt.) at its anterior sixth. It also extends forwards into a supraethmoid portion which covers part of the nasal bones (ns.).

Each side wall is mainly ossified in front of the optic foramen (Fig. 37, f.op.). This ossification represents the orbitosphenoid (Figs. 37 & 39, ors.). The rest of the side wall is membraneous and is perforated by the dorsal

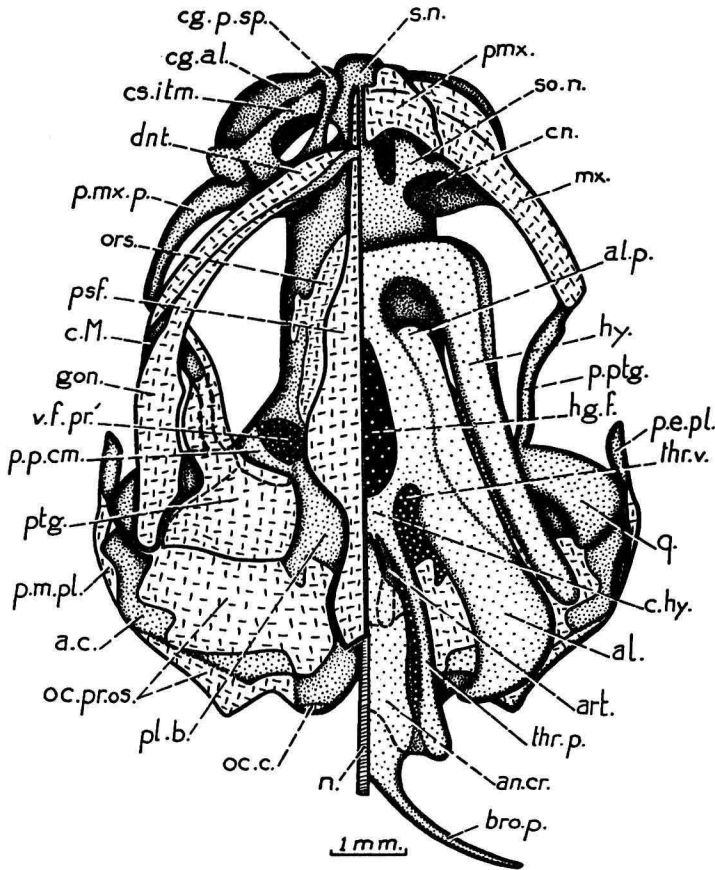


Fig. 39. Stage 66. Graphical reconstruction of a ventral view of the skull and jaws on the left side and of the skull, jaws, hyobranchial apparatus and larynx on the right side.

outlet of the foramen prooticum (Fig. 37, d.f.pr.) for the exit of the n. maxillo-mandibularis V and the n. ophthalmicus superficialis VII. It is also perforated by the trochlear tunnel (t.trc.) for the n. trochlearis.

The floor of this region is formed by the parasphenoid (Fig. 39, psf.) which, in many regions, is synostotically connected with the orbitosphenoids laterally.

The palatoquadrate cartilage extends forwards into the processus pterygoideus (Figs. 37-39, p.ptg.), which is in the form of a slender cartilaginous structure curving upwards and outwards and is continuous

anteriorly with the processus maxillaris posterior (p.mx.p.). The pterygoid bone (Figs. 38 & 39, ptg.) consists of a broad, flattened posterior part which underlies the region of the Eustachian tube and the region of contact between the post-palatine commissure and the palatoquadrate

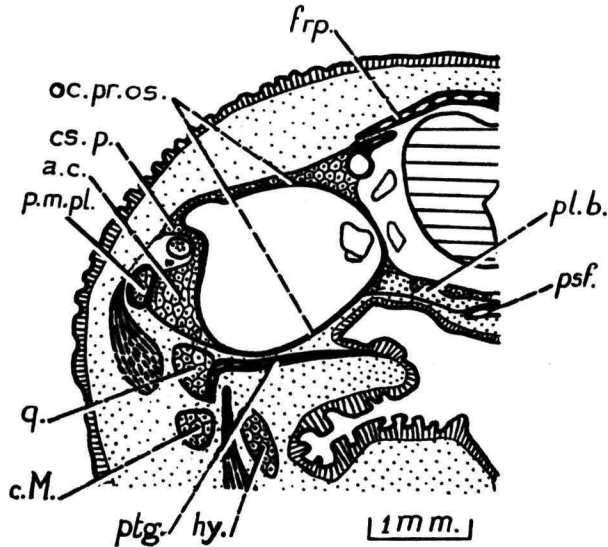


Fig. 40. Stage 66. Transverse section in the auditory region showing the well developed cartilaginous band of the auditory capsule on which the pars media plectri rests.

cartilage. It extends forwards enveloping the processus pterygoideus from the ventral and lateral sides. The two side walls meet dorsally and soon extend forwards into a slender outgrowth overlying the processus pterygoideus itself.

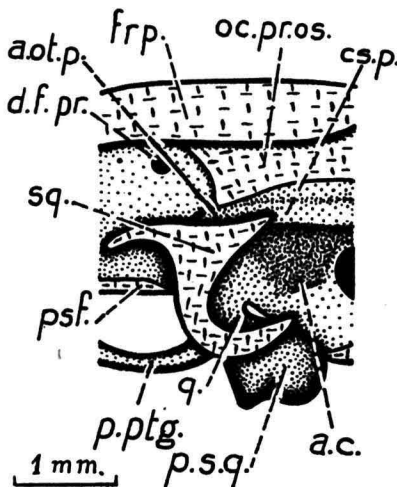


Fig. 41. Stage 66. Graphical reconstruction of the left side view of the suspensorial region of the skull. (The lower jaw and the plectral apparatus are not shown).

3. *The ethmoid region*: This can be subdivided into two regions, a posterior sphenethmoid and an anterior nasal region.

a. *The sphenethmoid region*: is cartilaginous and is limited from the orbito-temporal region by the orbitonasal foramen (Fig. 37, f.orn.) laterally, and by the fronto-parietal fenestra dorsally. Its ventro-lateral wall is fused with the lamina orbitonasalis (lm.orn.), which extends backwards into a long processus maxillaris posterior (p.mx.p.), and forwards into a short processus maxillaris anterior (p.mx.a.). The dorsal edge of each lamina orbitonasalis is confluent with the septum nasi, through the pars plana nasi (Fig. 38, p.pl.n.). In this region, there is a

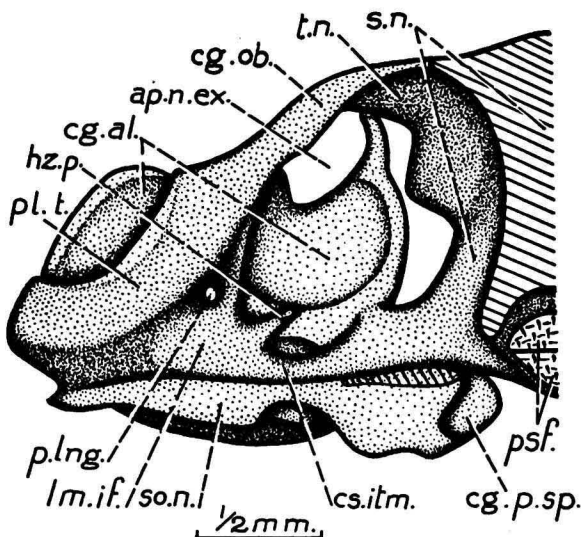


Fig. 42. Stage 66. Contour reconstruction of the nasal capsule as seen from the posterior surface. (The nasal and septomaxilla are not shown).

little cartilaginous pad (Fig. 37, pd.) which protrudes from the pars plana nasi and lies between the supraethmoid portion of the fronto-parietal and the nasal bones.

b. *The nasal region*: The sphenethmoid cartilage extends forwards into the median, vertical septum nasi (Fig. 42, s.n.), which attains its maximum breadth in its anterior region. The dorsal edges of this septum, represents the tectum nasi (t.n.), which forms a more conspicuous roof anteriorly than posteriorly. Laterally, the sphenethmoid cartilage extends into the floor of each nasal capsule forming the solum nasi (Figs. 39 & 42, so.n.), which is broad in front of the choana (Fig. 39, cn.) and more slender anteriorly. The solum nasi is continuous laterally with the lamina inferior (Fig. 42, lm.if.), which on its turn is attached with the base of the septum nasi through the crista intermedia (cs.itm.). The latter sends a horizontal, medially directed, short process (hz.p.). On the other hand, the lamina inferior is continuous with a postero-lateral protrusion, the planum terminale (pl.t.), which on its turn is attached with the tectum nasi

through the cartilago obliqua (cg.ob.). The planum terminale itself sends a slender posteriorly directed processus lingularis (p.lng.). The cartilago obliqua separates a posterior fenestra dorso-lateralis (Figs. 37 & 38, f.dlt.) from an anterior apertura nasalis externa (ap.n.ex.).

The nasal region is supported antero-laterally by the highly developed cartilago alaris (Figs. 37, 38 & 42, cg.al.), the dorsal edge of which is curved medial to the apertura nasalis externa. The cartilago alaris is continuous with the solum nasi through an anterior vertical process, the cartilago praenasalis superior (Fig. 39, cg.p.sp.). It is also synchondrotically connected with the crista intermedia (cs.itm.).

The parasphenoid (Fig. 39, psf.) which is a long cuneiform bone, extends forwards under the septum nasi into an attenuating rod. This bone is bound with the septum nasi through dense connective tissue fibres.

The septomaxilla (Figs. 37 & 38, smx.) is a long and curved bone with dorsal and medial limbs. Its dorsal limb acts as a roof for a portion of the nasal cavities and extends anteriorly into a short protrusion lateral to the apertura nasalis externa. Its medial limb rests on the lateral border of the planum terminale and the cartilago obliqua.

The nasal bone (Fig. 38, ns.) is broad posteriorly, where it covers a portion of the fenestra dorso-lateralis. It is much thinner anteriorly than posteriorly.

4. Both praemaxilla (Fig. 37, pmx.) and maxilla (mx.) are dentulous. The praemaxilla possesses a long upwardly directed pars frontalis which supports the cartilago praenasalis superior. There is a pars dentalis which is not well differentiated from the well developed pars palatina (Fig. 39, pmx.). Both praemaxillae are bound together medially through dense connective tissue fibres.

The maxilla (Fig. 39, mx.) extends backwards to the limit of the processus maxillaris posterior. It possesses a pars frontalis in its anterior region where it is flexed slightly upwards. The pars palatina is well developed and supports the nasal capsule ventrally.

5. The two rami of the lower jaw are synchondrotically connected through a small cartilaginous band. The major portion of each ramus is formed of MECKELS' cartilage (Figs. 37 & 39, c.M.) which is surrounded with two bones:

- a. The dentary (dnt.) covers the antero-lateral part.
- b. The goniale (gon.) covers the antero-medial part and invests the major portion of the posterior half of MECKELS' cartilage with the exception of its articular region which does not show any signs of ossification. The goniale gives a dorso-medial processus coronoideus (Fig. 37, p.crn.).

B. *The Hyobranchial Apparatus*

The hyalia (Fig. 39, hy.) are slender cartilaginous structures extending backwards under the auditory capsule to which they are bound by loose

connective tissue fibres. They are confluent with each other in front of the large oval hyoglossal foramen (hg.f.). The anterior half of the lateral edge of each hyale is in the form of a lamella composed of juvenile cartilage cells.

The corpus hyoideum (Fig. 39, c.hy.) is small in size and forms the posterior and postero-lateral boundaries of the hyoglossal foramen.

The thyroid processes (thr.p.) are long, slender pieces which are wholly cartilaginous. They spring out from the corpus hyoideum and enclose a hyolaryngeal sinus.

The ala (al.) is a thin, cartilaginous plate broadly continuous with the lateral border of the corpus hyoideum. Each ala possesses a small antero-lateral process (al.p.) and a thin lateral lamella which is flexed dorsally in its posterior half. Between each ala and the corresponding thyroid process, there is a thyroid vacuity (thr.v.) for lodging the thyroid gland.

C. *The Larynx*

The arytenoids (Fig. 39, art.) are two long, narrow structures, thicker posteriorly than anteriorly. Their anterior tips overlies the corpus hyoideum.

The annulus cricoideus (Figs. 37 & 39, an.cr.) consists of a slightly short roof and a broad, long floor. The roof gives a pair of ventro-laterally directed processes (Fig. 37, vl.pr.) which support the bases of the arytenoids. In the floor, the anterior region is narrow and is fixed to the corpus hyoideum. Just behind this area the floor is U-shaped in cross section with the concavity facing upwards. More posteriorly, it is in the form of a flat plate which is prolonged backwards into a pair of slender, smooth bronchial processes (Figs. 37-39, bro.p.).

The side walls are mainly membraneous except posteriorly where the roof and the floor of the annulus cricoideus are continuous with each other, as well as with the distal extremities of the thyroid processes.

D. *The Visceral Muscles*

1. *The mandibular muscles* are represented by the following three levator mandibulae and two intermandibularis muscles.

a. M.l.m. anterior (Fig. 43, M.l.m.a.) represents the pars medialis of the larval muscle. It arises from the dorso-lateral surface of the fronto-parietal bone (frp.). The fibres extend obliquely downwards and backwards medial to the M.l.m. posterior (M.l.m.p.), and are inserted by a very long and strong tendon onto the dorso-medial side of the goniale (gon.). Contraction of this muscle helps in closing the mouth.

b. M.l.m. posterior (M.l.m.p.). This represents the larval partes intermedius and lateralis of the M.l.m. anterior together with the larval M.l.m. posterior. It is the largest levator muscle and is characterised by its very broad surfaces of origin and insertion. The major part arises from the auditory capsule (a.c.). The fibres extend obliquely forwards

and downwards and are inserted onto the goniale. Contraction helps in closing the mouth.

c. *M.l.m. externus* (Figs. 43 & 44, *M.l.m.e.*). This is a more or less triangular, thick muscle with wide surfaces of origin and insertion. It arises mainly from the medial surface of the squamosum (*sq.*) and annulus tympanicus (*an.tp.*) and partly from the ventral border of the palatoquadrate cartilage. Its fibres extend ventrally, fan-shaped and are inserted onto the outer surface of the goniale. Contraction helps in closing the mouth.

d. *M. intermandibularis anterior* (*M.im.a.*). The fibres are attached to the ventro-medial edges of MECKEL'S cartilage. They extend from side to side uninterrupted by tendinous fibres. Contraction of this muscle draws

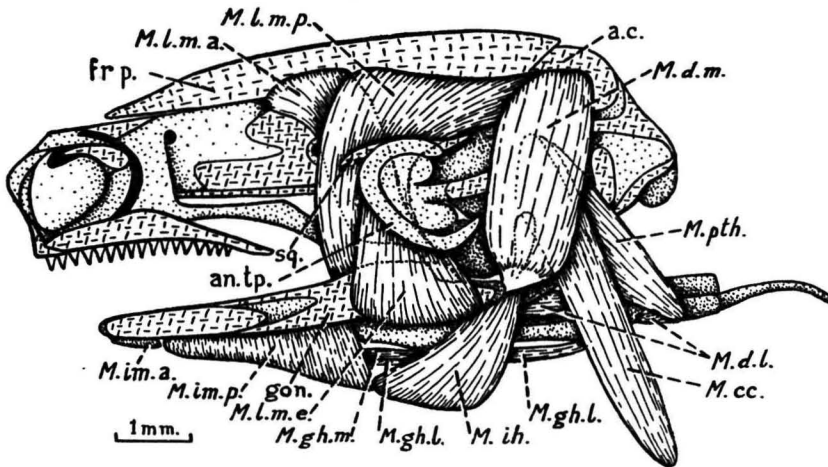


Fig. 43. Stage 66. Graphical reconstruction of a left side view of the visceral muscles.

the two anterior parts of the lower jaw closer to each other, and helps in raising the floor of the mouth.

e. *M. intermandibularis posterior* (*M.im.p.*). The fibres are attached to the dorso-medial border of the goniale. They extend downwards and medialwards to meet those of the other side in a median raphé. Contraction helps in raising the floor of the mouth, and also rotates the two halves of the lower jaw in such a way that it is loosened from the upper jaw. Consequently, the contraction of this muscle helps in opening the mouth.

2. *The hyoid muscles* are represented by the following two muscles:

a. *M. depressor mandibulae* (*M.d.m.*). This represents the fused MM. orbitohyoideus, suspensoriohyoideus, and quadratohyoangularis of the tadpole. It arises from the dorso-lateral surface of the auditory capsule. The fibres extend vertically downwards, and as they approach the lower jaw they converge into a short and strong tendon, which is

inserted onto the posterior end of the lower jaw. Contraction of this muscle opens the mouth.

b. *M. interhyoideus* (*M.ih.*). The muscle fibres meet in a median raphé. On either side they converge into a strong tendon which runs

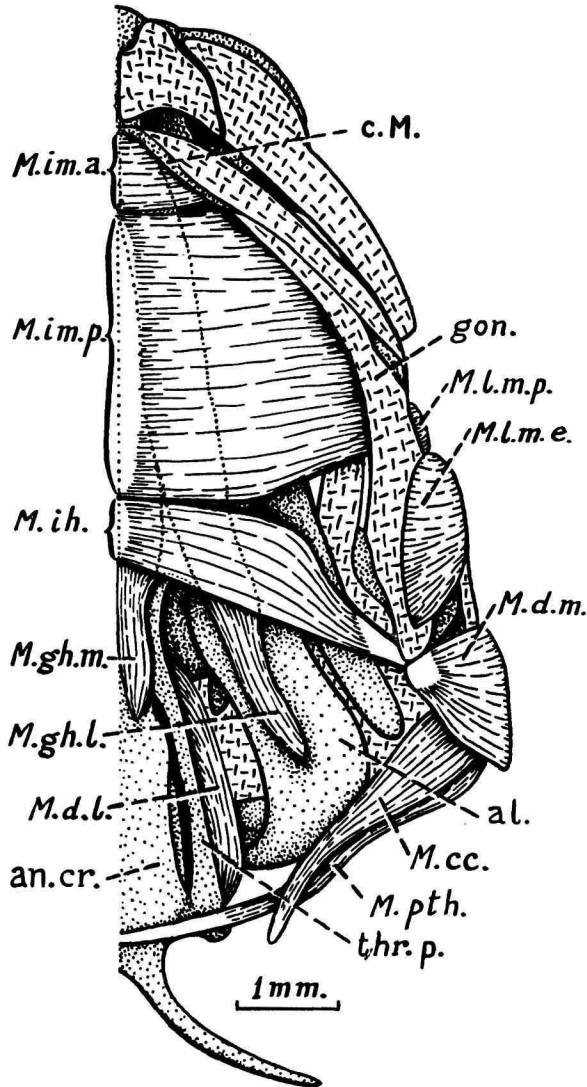


Fig. 44. Stage 66. Graphical reconstruction of a ventral view of the visceral muscles.

vertically and is attached to the palatoquadrate. Contraction helps in raising the floor of the mouth.

3. *The branchial muscles* are represented by the following two muscles:

a. *M. petrohyoideus* (*M.pth.*). This arises from the auditory capsule. Its fibres extend medialwards ventral to the annulus cricoideus and meet

those of the other side in a very long and thin median raphé. Contraction elevates the larynx.

b. *M. cucullaris* (*M.cc.*) arises from the auditory capsule and is inserted onto the corresponding scapula of the pectoral girdle.

4. *The hypobranchial spinal muscles* are represented by: the *M. geniohyoideus*, which consists of two parts, *medialis* (*M.gh.m.*), originating from the annulus cricoideus and *lateralis* (*M.gh.l.*) originating from the mid-ventral surface of the ala (*al.*). The fibres of the two parts extend forwards, approach each other, and at the level of separation between the *MM. interhyoideus* and *intermandibularis posterior*, the two parts extend

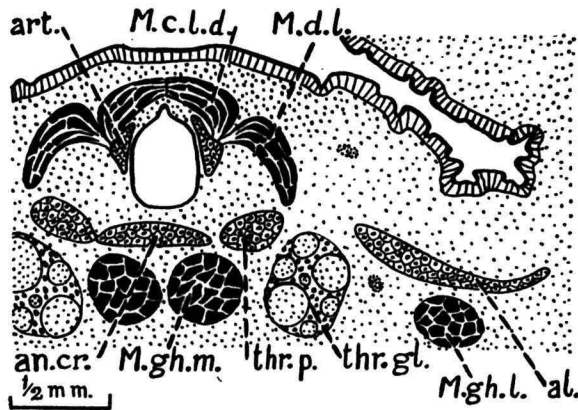


Fig. 45. Stage 66. Transverse section in the laryngeal region.

close to each other, and are inserted onto the antero-ventral surface of MECKELS' cartilage. Contraction pulls this part of the lower jaw backwards, and thus helps in opening the mouth.

5. *The laryngeal muscles* are represented by:

a. *M. dilatator laryngis* (*M.d.l.*) originating from the region of connection between the annulus cricoideus and the thyroid process and inserted onto the arytenoid (Fig. 45, art.) close to the insertion of the *M. constrictor laryngis dorsalis* (*M.c.l.d.*). Contraction increases the size of the laryngeal chamber.

b. *M. constrictor laryngis* consists of dorsal (Fig. 45, *M.c.l.d.*) and ventral components. Both components arise from median dorsal and ventral raphé respectively, and are inserted onto the arytenoids. Contraction constricts the larynx.

IV. DISCUSSION AND CONCLUSIONS

The metamorphosis of the skull, visceral arches, larynx and visceral muscles in *Xenopus laevis* (Daudin), shows a number of interesting features, some of which are specific for the known aglossal species, while others are shared with certain phaneroglossal salientians. Thus, a comparison of those significant features with their homologues in other salientians is necessary. These features will be dealt with under the following headings: Skull, jaws, hyobranchial apparatus, larynx and visceral muscles.

A. *The Skull*

1. It has been shown above that the larval crista parotica together with the processus muscularis capsulae auditivae form a broad shield-like structure which is in synchondrotic continuity with the distal region of the corresponding branchial chamber opposite the second and fourth ceratobranchialia. These characters, which are unique for *Xenopus laevis*, were first described by KOTTHAUS (1933) who only missed the continuity with the fourth ceratobranchiale. Such cartilaginous connections seem to give additional support to the massive branchial chambers which carry an important rôle in the peculiar mode of feeding. They are therefore considered as adaptations rather than structures of phylogenetic importance.

2. Another important character, which is here described for the first time, is that the operculum fenestrae ovalis develops as a small outgrowth from the posterior border of the fenestra ovalis. However, PATERSON (1939 a) regarded it to be "more obviously fused with the upper part of the auditory capsule" in the newly metamorphosed specimens; thus she missed the original continuity of the two structures. A similar condition to that of *Xenopus laevis* occurs in *Heleophryne* (RAMASWAMI, 1944) where the operculum is in cartilaginous continuity with the auditory capsule in premetamorphic and adult stages. In other known salientians, wherever an operculum fenestrae ovalis is present, this structure develops from a separate centre of chondrification in the membrane spanning the fenestra ovalis (KINGSBURY and REED, 1909). In other words, *Xenopus* and *Heleophryne* deviate from all other known salientian species.

3. It is also interesting to mention that where as the majority of the salientians possess a sphenethmoid bone, in *Xenopus laevis* there is a pair of orbitosphenoid bones, a character which was first described by PATERSON (1939 a) and is shared with *Ascaphus truei* Stejneger (DE

VILLIERS, 1934 and VAN EEDEN, 1951), *Leiopelma archeyi* Turbott and *Leiopelma hochstetteri* Fitzinger (ELSIE STEPHENSON, 1951).

4. Two membrane bones in the skull are of special interest:

a. The parasphenoid is exceptional among the majority of salientians in forming the effective floor of the orbital region of the skull, after the complete destruction of the basis cranii during metamorphosis. A similar condition is present in the adult stage of the closely related *Hymenochirus curtipes* (PATERSON, 1945). Anteriorly, the parasphenoid extends below the septum nasi (Present work, NOBLE, 1931 and PATERSON, 1939 a). A similar median extension has also been described in *Xenopus clivii* Peracca (NOBLE, 1931). An unlabelled ossification which occupies a position similar to that of *X. laevis* has also been shown in Figs. 8, 9 and 14 in *Hemipipa carvalhoi* (PATERSON, 1951). This median extension was considered by NOBLE to arise from the fusion of two ossifications (praevo-mers) in *X. laevis* and *X. clivii*. However, the present findings as well as those of PATERSON contradict NOBLE's view and clearly show that in *X. laevis*, it is a mere extension of the parasphenoid and is never of paired origin.

b. The fronto-parietals, which are paired bones in the majority of the phaneroglossal salientians, are fused together in all known aglossal species. Thus, in addition to *X. laevis* (Present work and PATERSON, 1939 a), such a fusion is exhibited by *Pipa pipa* (PARKER, 1876), *Pipa parva* Ruthven and Goige (EATON, 1942) and *Hymenochirus curtipes* (PATERSON, 1945). This fusion is also met with in some phaneroglossal species belonging to different families such as *Nectophryne misera* Mocq. (RAMASWAMI, 1937), *Philautus petersi* Boulenger (RAMASWAMI, 1939), *Rana mascareniensis* Duméril and Bibron (AL-HUSSAINI, 1941) and *Atelopus moreirae* de Miranda-Ribeiro (BADENHORST, 1945). It seems that the fusion of the fronto-parietals bears no phylogenetic significance, since this character is not constant in the closely related species.

5. The larval and early metamorphosing stages possess a pair of foramina cranio-palatina, a character which is here described for the first time. These foramina become occluded late during metamorphosis. A similar condition occurs in *Leiopelma archeyi* (N. G. STEPHENSON, 1951).

6. A further new observation is that the oculomotor foramen, which is present in the larval stages, becomes confluent with the foramen caroticum primarium as well as with the foramen prooticum during metamorphosis. Thus, the n. oculomotorius takes exit with the branches of the trigeminal and facial nerves. As a result of this, the pilae metoptica and antotica become continuous. A similar condition has been described in the adult stage of *Hymenochirus curtipes* (PATERSON, 1945).

7. It is well known that the n. trochlearis penetrates the side wall of the cranium in all known salientians including *X. laevis* (Present work and PATERSON, 1939 a) with the only exception of *Ascaphus truei* (VAN EEDEN, 1951). However, WEISZ (1945 a) who did not refer to PATERSON's

work stated that in a 35 mm larva of *X. laevis*, the n. trochlearis has no separate foramen but takes exit with the V, VI and VII nerves through a common foramen which he termed "orbital foramen". The present work agrees with PATERSON's conclusions.

8. The nasal capsule of this species was previously described by PATERSON (1939 a) and in accordance with her findings the capsule of *X. laevis* is greatly related to that of the Phaneroglossa rather than to other members of the Aglossa. However, there are certain points which need special attention:

a. It is well known that in Salientia the cartilago alaris gives an anterior protrusion, the cartilago praenasalis superior and that the solum nasi forms the floor of the nasal capsule. Here, in *X. laevis* both the cartilago praenasalis superior and the solum nasi are confluent together (Present work and PATERSON, 1939 a & b). However, PATERSON (1939 b) illustrated in Figs. 3 a, 3 b and 5 the chondrification present in the floor of the nasal capsule as "superior prenasal cartilage"; a condition which does not fit with the general terminology of this structure, which should have been labelled as solum nasi.

b. PATERSON (1939 a & b) correctly reported the complete absence of the cartilago praenasalis inferior in *X. laevis*; a character which is also shared with *Hemismus marmoratus* (Peters), (DE VILLIERS, 1931) and *Hymenochirus curtipes* (PATERSON, 1945). However, in 1951 PATERSON illustrated in Figs. 3, 6, 7 & 10 of *X. laevis*, a structure which she labelled correctly only in the first figure as cartilago praenasalis superior, while in the others it was given the name cartilago praenasalis inferior. This perhaps was due to a misprint. The present work confirms the complete absence of the cartilago praenasalis inferior in *X. laevis*.

c. PATERSON (1939 b) mentioned that the medial region of the cartilago alaris undergoes destruction in later stages of metamorphosis. However, the present study reveals that no change what so ever takes place in this region from its early development (Stage 58) until the end of metamorphosis.

B. *The Jaws*

1. *The palatoquadrate cartilage, its attachment to the larval skull and its behaviour during metamorphosis.*

It has been shown above that the palatoquadrate cartilage is firmly attached to the cranium through the larval processus oticus, processus ascendens quadrati, commissura quadrato-cranialis anterior and processus cornu quadratus lateralis. In addition to these cartilaginous connections, there is a ligamentum cornu quadratum medialis which stretches between the processus cornu quadratus medialis and the ethmoid plate. Quite a number of structures are in need of special attention:

1. One of these concerns the larval processus oticus, the morphological

relationship of which as well as its phylogenetic significance will be dealt with separately.

a. KOTTHAUS (1933) and PATERSON (1939 a) recorded that in *X. laevis* the larval processus oticus is exceptionally broad, and bounds the processus ascendens quadrati and the palatoquadrate cartilage with the anterior and lateral areas of the auditory capsule. However, PUSEY (1943), after comparing the condition of *X. laevis* with that of *Ascaphus truei* restricted the term "larval otic process" for the lateral connection with the auditory capsule only. The first view was afterwards supported by VAN EEDEN (1951). It also finds support in the present work for the following reasons:

i. The anterior as well as the lateral connections of the larval processus oticus with the auditory capsule lie outside the vena capitis lateralis and antero-lateral to the n. hyomandibularis VII, thus showing the same relations common to other salientians (DE BEER, 1937).

ii. PUSEY (1938 & 1943) considered that in the Salientia, the adult processus oticus usually develops in the area of the larval one. Since it has been shown above that the adult otic connection in *X. laevis* is related with both the anterior and lateral attachments to the auditory capsule, it follows that these two connections must represent a larval processus oticus.

iii. If the larval processus oticus in *X. laevis* is confined only to the lateral attachment with the auditory capsule, then the only connection with the palatoquadrate cartilage will be through the thin cartilaginous bar, ventral to the thymus foramen. This narrow, feeble connection, which disappears early during metamorphosis (Stage 60) is logically not the main larval otic connection with the palatoquadrate cartilage.

b. As regards the phylogenetic significance of the larval processus oticus, GAUPP (1893) considered it as a larval specialization. Later, PUSEY (1938 & 1943) recorded the absence of the larval otic connection from *Alytes obstetricans* (Laurenti), *Discoglossus pictus* (Gravenhorst) and *Bombina variegata* (Linné) and its presence in *Rana temporaria* (L.) and *Ascaphus truei* where he regarded its presence as a secondary feature. Recently, SEDRA (1950) supported PUSEY's view in considering that those salientian tadpoles which lack such a process show a primitive character. SEDRA confirmed this conclusion by stating that the Apoda (Caecilia), which are far more primitive than the Salientia, lack such a larval otic attachment. He also pointed to its absence in all members of the family Discoglossidae, which is the most primitive family after the Leiopelmatidae, as well as in *Megophrys* which is regarded as the most primitive genus in the family Pelobatidae (NOBLE, 1931).

However, VAN EEDEN (1951) discussed the larval processus oticus on different phylogenetic grounds and came to the conclusion that its presence is a primitive character, as is indicated by its presence in all Dipnoi, some members of the Caudata and in *Pipa pipa*. Moreover, he homologized it with a portion of the so called epipterygoid bone of *Capitosaurus*.

i. Concerning the relationship with the Dipnoi, it has been found recently by JARVIK (1942) that the Salientia has originated from a Crossopterygian stock, the *Osteolepiformes*; and consequently they have nothing to do with the Dipnoi as regards their origin. Thus, the Dipnoi are not a true guide in elucidating the phylogenetic significance of this process.

ii. As regards the relationship with the Caudata it has also been shown by JARVIK (1942) that the Amphibia is a diphyletic group and that the Caudata arose from another Crossopterygian stock, the *Porolepiformes*. Moreover, the processus oticus of the Caudata was homologized with the adult processus oticus of the Salientia (GAUPP, 1893) and not with the larval one.

iii. The presence of the larval processus oticus in *Pipa pipa* does not indicate the primitive nature of this process, since it also occurs in a large number of salientian tadpoles belonging to different families.

iv. Concerning the last reason raised by VAN EEDEN, it is difficult to accept the homology of the larval processus oticus in Salientia with a portion of the epipterygoid bone of a fossil "Labyrinthodont" as *Capitosaurus*; a view which was previously given by WATSON (1919) and SUSHKIN (1927), since it is known that this cartilage bone develops in the region of the processus ascendens quadrati (DE BEER, 1937).

Thus, it may be concluded that the presence of a larval processus oticus is a tadpole specialization and is not a primitive character as VAN EEDEN regarded.

2. Another important cartilaginous connection with the chondrocranium is the processus ascendens quadrati which is confluent with the pila antotica and the orbital cartilage dorsal to it (Present work, KOTTHAUS, 1933 and PATERSON, 1939 a). This high level connection has also been recorded in *Pelobates* (SCHULZE, 1892), *Megalophrys* (KRUIJTZER, 1931), *Polypedates* (OKUTOMI, 1937), *Rana hexadactyla* Lesson, *R. tigrina* Daudin and *R. curtipes* Jerdon (RAMASWAMI, 1940), all known members of the Discoglossidae (PUSEY, 1943), *Ascaphus truei* (PUSEY, 1943 and VAN EEDEN, 1951) and also in *Leiopelma archeyi* (N. G. STEPHENSON, 1951). Both PUSEY and VAN EEDEN regarded the presence of a high level attachment of the processus ascendens quadrati as a primitive character, a conclusion which includes *X. laevis* as well.

In the region of the processus ascendens quadrati the palatoquadrate cartilage extends outwards into a processus ventro-lateralis quadrati (Present work, KOTTHAUS, 1933 and PATERSON, 1939 a). Such a process is present in the closely related *X. fraseri* and *Pipa pipa* (EDGEWORTH, 1935). In the genus *Xenopus*, it is far more developed than in *Pipa*. As far as it is known, this process is not met with in any other salientian tadpole. Thus, it is regarded as a specialized feature developed apparently to help in the attachments of the branchial muscles.

3. A third cartilaginous connection between the palatoquadrate

cartilage and the cranium is the relatively broad commissura quadrato-cranialis anterior, a character which was first observed by KOTTHAUS (1933) and PATERSON (1939 a). Such a broad commissure is met with in *Pelobates* (SCHULZE, 1892), *Megophrys montana* Kuhl (KRUIJTZER, 1931), *X. fraseri* (EDGEWORTH, 1935), *Uperodon systoma* Schneider, *Microhyla ornata* (Duméril and Bibron), *Rana tigrina* (RAMASWAMI, 1940), *R. afghana* Günther (RAMASWAMI, 1943) and *Heleophryne* (RAMASWAMI, 1944).

Greatly related with this commissure is the processus cornu quadratus medialis which is syndesmotically connected with the ethmoid plate through the ligamentum cornu quadratum mediale bounding the choana anteriorly. Both process and ligament are here described for the first time and thus reveal that *X. laevis* is normal in this character with most salientian tadpoles.

At the level of the commissura quadrato-cranialis anterior there is a relatively low processus muscularis quadrati, first described by KOTTHAUS (1933) and PATERSON (1939 a). A similar low process is met with in the closely related *X. fraseri* (EDGEWORTH, 1935) as well as in *Alytes obstetricans* (VAN SETERS, 1922), *Microhyla ornata*, *Uperodon systoma* (RAMASWAMI, 1940), *Ascaphus truei* (PUSEY, 1943 and VAN EEDEN, 1951) and *Heleophryne* (RAMASWAMI, 1944).

It is noteworthy that the processus muscularis quadrati is connected through a fibrous ligament with the commissura quadrato-cranialis anterior forming the roof of the tunnel through which pass the mandibular muscles, blood vessels and nerves; a character which is also met with in *Rana temporaria* (PUSEY, 1938) and *Bufo lentiginosus* (Show) (SEDRA, 1951).

4. The anterior area of the palatoquadrate cartilage is indirectly attached to the cranium through the processus cornu quadratus lateralis. This process was previously referred to as "quadrato-ethmoidal cartilage" by EDGEWORTH (1935) and PATERSON (1939 a). Later, RAMASWAMI (1944) did not accept this terminology and introduced the term "pars articulo-trabecular commissure" since this element connects the pars articularis quadrati with the trabeculae. However, in 1945 a WEISZ, who worked on *X. laevis* did not refer to the above mentioned workers and gave the same structure the term "palato-rostral cartilage".

As this cartilaginous process is homologous with the ligamentum cornu quadratum laterale usually met with in other salientian tadpoles (SEDRA, 1950 and VAN EEDEN, 1951), the term "processus cornu quadratus lateralis" has been used here. The presence of such a chondrified connection instead of the ligamentous one in the majority of the salientians, is shared with *X. fraseri* (EDGEWORTH, 1935) and also to some extent with *Pipa pipa* (EDGEWORTH, 1935) where the process fails to gain connection with the palatoquadrate cartilage.

The processus cornu quadratus lateralis is extended anteriorly into the cartilago tentaculi which has not so far been recorded in any salientian

tadpole other than *X. laevis* (Present work, KOTTHAUS, 1933, PATERSON, 1939 a and WEISZ, 1945 a & b), *X. calcaratus* (GADOW, 1909) and *X. fraseri* (EDGEWORTH, 1935).

The suprarostrals system in *X. laevis* was regarded by KOTTHAUS (1933) to be represented by the antero-lateral extensions of the ethmoid plate (ethmoid flanges), while PATERSON (1939 a) considered it to be homologous with the antero-medial area. Later, PUSEY (1943) suggested that the cartilago tentaculi represent the lateral wings of the suprarostrals system. Actually, KOTTHAUS's and PATERSON's views do not contradict each other. Both views can be taken to explain the homology of the anterior area of the ethmoid plate with the medial region of the suprarostrals system of other salientians, while the cartilago tentaculi represent its lateral wings.

During metamorphosis, all the larval connections of the palatoquadrate cartilage to the cranium (viz. larval processus oticus, processus ascendens quadrati, commissura quadrato-cranialis anterior and processus cornu quadratus lateralis) break down and either partly or completely disappear. The destruction of these larval connections is accompanied with remarkable changes during which the palatoquadrate cartilage is remodelled and the new adult attachments are established. The most significant changes are:

1. It is the general rule in salientians with a well developed processus muscularis quadrati, that buckling and folding of the palatoquadrate cartilage posterior to this process take place (e.g. *Rana temporaria* (PUSEY, 1938) and *Bufo regularis* Reuss (SEBRA, 1950)). It is from this folded region as well as from the decaying cartilage that the adult processus oticus is formed. In *X. laevis* it has been shown above that neither bucklings nor undulations take place. This seems to be due to the broad nature of this region; a fact which is also exhibited by *Ascaphus truei* (VAN EEDEN, 1951); only breaking down of cartilage takes place in *Xenopus* and *Ascaphus*. Thus, it is evident from the previous studies as well as from the present findings that in Salientia in general the adult processus oticus is morphologically represented in the larva by the region of the palatoquadrate cartilage lying at the base of the processus muscularis quadrati and posterior to it; the processus muscularis quadrati itself does not take any part in the formation of the adult processus oticus.

2. There is no doubt about the origin of the processus pterygoideus from the commissura quadrato-cranialis anterior; a character which is exhibited by all other salientian species. However, the origin of the processus maxillaris posterior needs some explanation:

The foramen for the ramus communicans between n. ophthalmicus profundus V and n. palatinus VII is of great importance since in the larval and early metamorphosing stages this foramen lies between the lamina orbitonasalis and the commissura quadrato-cranialis anterior. Later on, this foramen lies between the same lamina and the processus

maxillaris posterior indicating that the latter has originated from the remaining part of the commissura. A similar case was found to occur in *Calyptocephala gayi* (Dum. & Bibr.) (REINBACH, 1939) and *Ascapus truei* (VAN EEDEN, 1951). The last worker considered that this is the case in all the salientians. Thus, it is evident that in *X. laevis*, the processus maxillaris posterior originates from the commissura quadrato-cranialis anterior, a fact which conforms with the findings of VAN EEDEN.

3. A third important structure related with the jaw suspension is the post-palatine commissure which was found to be of neuro-cranial origin (Present work and PATERSON, 1939 a). This structure is homologous with the pseudobasal process usually met with in the majority of the salientian species (DE BEER, 1937). However, it is exceptional from those of other salientians in being more medial in position since it lies near the ventral outlet of the foramen prooticum. This commissure is fixed to the medial region of the palatoquadrate cartilage by a thin fibrous layer. In the adult animal DE VILLIERS (1932) illustrated complete cartilaginous continuity between both structures.

4. The most important bone related to the upper jaw is the pterygoid. This is broader in the *Aglossa* (RIDEWOOD, 1897 a and PATERSON, 1939 a and 1945) than the *Phaneroglossa*. RIDEWOOD regarded the broad nature of the pterygoid as a specialization to form a ventral shelf for the medially confluent Eustachian tubes. The latter character is again specific for the *Aglossa*.

The absence of the palatine and quadratojugal in this species, is a character which is shared with some other aglossal (PATERSON, 1945) as well as some phaneroglossal species and is devoid of any phylogenetic significance.

2. *The lower jaw:*

Unlike the majority of the salientian tadpoles which possess a multi-segmented lower jaw usually composed of a pair of MECKELS' cartilages, a pair of infrarostrals and a single basimandibular (SE德拉, 1951), *X. laevis* possesses only a pair of MECKELS' cartilages fused medially with a single element (Present work; RIDEWOOD, 1897 a; VAN SETERS, 1922; KOTTHAUS, 1933; PATERSON, 1939 a; and WEISZ, 1945 a & b). This median element is the inferior labial cartilage which is homologous with the basimandibular cartilage, since it is of single origin. Even WEISZ who identified it as a "median infrarostral" mentioned also that it is of a single origin. RIDEWOOD reported that this condition exhibited by the lower jaw of *X. laevis* is a retention of a primitive character which was found to be only shared with *Leiopelma archeyi* (N. G. STEPHENSON, 1951).

C. *The Hyobranchial Apparatus*

1. Unlike the majority of the salientians where the ceratohyalia lie at right angles with the longitudinal axis of the hyobranchial apparatus,

the ceratohyalia of *X. laevis* are backwardly directed. This feature is also exhibited by *Phrynoglossus laevis* (Gthr.) (RIDEWOOD, 1898), *Ascaphus truei* (PUSEY, 1943) and *Leiopelma archeyi* (N. G. STEPHENSON, 1951) and was regarded by PUSEY as a primitive character.

As shown before, the larval ceratohyalia give rise to the adult hyalia. These are also characteristic in being broad; where as those of most other salientians are slender. The broad nature of the hyalia is also shared with *Discoglossus* and *Bombinator* (RIDEWOOD, 1897 a) and *Bombina variegata* (L.) (SLABBERT, 1945) and was considered by RIDEWOOD as a primitive character.

Xenopus laevis, therefore may be regarded as retaining primitive characters both as represented by the oblique nature of the ceratohyalia as well as the broad hyalia.

2. *X. laevis* resembles *Microhyla ornata* (RIDEWOOD, 1898) in having very highly developed branchial chambers and in possessing a single and median hypobranchial plate. Such a resemblance between these two remotely allied species, was regarded to have been arrived at independently by RIDEWOOD (1898), who added that "the similarity does not extend into the smaller structural details". The present work conforms the findings of RIDEWOOD, in regarding these two characters to be devoid of phylogenetic significance.

3. While most of the salientians possess a separate basibranchial element, in *X. laevis* (Present work; EDGEWORTH, 1935; PATERSON, 1939 a and WEISZ, 1945 a), *Pipa pipa* (EDGEWORTH, 1935) and *Leiopelma archeyi* (N. G. STEPHENSON, 1951) the basibranchiale is fused with the basihyale to form a basihyobranchiale which possesses a deep ventral keel.

4. During metamorphosis the hyobranchial apparatus is remodelled and shows three significant characters viz. the presence of a hyoglossal foramen, the presence of a reduced corpus hyoideum and the development of a pair of lateral wings, the "alae". These features which are distinctive for the members of the Aglossa (RIDEWOOD, 1897 a, 1898 & 1899) are correlated with the absence of the tongue.

a. As to the first character, two different views were put forward concerning its development. The first was given by PARKER (1876) who considered the hyoglossal foramen as a secondary fenestration in the corpus hyoideum. The second was given by RIDEWOOD (1897 a & 1899) and later confirmed by PATERSON (1939 a) who found that this foramen results from the union of the hyalia medially. The present work is in accordance with the second view. The presence of such a foramen is uncommon among the phaneroglossal species which instead possess a hyoglossal sinus. This sinus was found to be bound anteriorly by a ligamentous band in *Bombinator* and *Pelobates* (RIDEWOOD, 1897 a), *Breviceps adspersus* Peters (TREWAVAS, 1933), and by the anterior processes of the hyalia which do not fuse in *Pelodytes punctatus* (Daud.) (RIDEWOOD, 1897 b). However, fusion of the extensions of the hyalia

medially anterior to the hyoglossal sinus was only found to occur in *Hemisus guttatum* (Rapp) (BEDDARD, 1908) and *Hemisus marmoratum* (TREWAVAS, 1933) where the hyoglossal foramen is identified as a sinus. Other than the genus *Hemisus*, no indication of such a foramen is present in any other member of the Phaneroglossa.

b. The presence of the reduced corpus hyoideum accompanies the development of the hyoglossal foramen in the Aglossa and has been found to accompany the presence of a deep hyoglossal sinus in the members of the Discoglossidae and Pelobatidae (RIDEWOOD, 1897 a; TREWAVAS, 1933; MAREE, 1945; SLABBERT, 1945; and VAN ZYL, 1950).

c. Two points concerning the alae need special attention:

i. The origin of these structures was first recorded in the closely related *Pipa pipa* by RIDEWOOD (1897 a) who found that they develop from the sides of the corpus hyoideum. The same worker in the same year suggested that the alae in *X. laevis* arise in a similar manner. However, PATERSON (1939 a) who based her study on only one metamorphosing stage, contradicted RIDEWOOD's suggestion and considered that the alae in *X. laevis* originate from the remains of the reduced branchial skeleton. The present findings give support to RIDEWOOD's belief where the alae develop exclusively as extensions from the sides of the corpus hyoideum without any additions from the decaying branchial chambers.

ii. It is also of interest to find out the homology of these structures which are in the form of thin plates extending on either side of the corpus hyoideum. Comparison with the hyobranchial skeleton of the Phaneroglossa shows that the posterior broad area of the ala of *X. laevis* represents the postero-lateral process of the phaneroglossal species. This assumption is confirmed by the fact that the members of the Discoglossidae and Pelobatidae which show reduction of the tongue, all possess a fairly broad postero-lateral process (RIDEWOOD, 1897 a and TREWAVAS, 1933). The anterior region of the ala seems therefore to correspond with the antero-lateral process of the Phaneroglossa. This view agrees with that of TREWAVAS (1933) who regarded the broad lobe present in *Pseudopaludicola falcipes* (Hensel) to represent the fused alary (antero-lateral process) and postero-lateral processes of other phaneroglossans.

5. In all known members of Aglossa (RIDEWOOD, 1897 a & 1899 and PATERSON, 1939 a & 1945) there is a cartilaginous connection between the distal extremities of the thyroid processes and the annulus cricoideus. Such a hyocricoid connection was found to be exhibited by some phaneroglossal species as *Pseudopaludicola falcipes* and *Oreophrynella quelchii* Boulenger (TREWAVAS, 1933), while the majority of the other salientians possess a ligamentous attachment. This feature exhibited by *X. laevis* seems to give greater support for the highly developed larynx.

D. *The Larynx*

The larynx in the Aglossa differs from that of the Phaneroglossa in its greater development. As shown by RIDWOOD (1897 a & 1899) this organ is incorporated with the hyobranchial apparatus in the Aglossa. The annulus cricoideus in *X. laevis*, *Pipa pipa* and *Hymenochirus boettgeri* is fixed to the posterior region of the corpus hyoideum; a character which was not referred to in any known phaneroglossal species. It is exceptionally well developed in all known members of the Aglossa and fairly developed in the members of the Discoglossidae and Pelobatidae; a feature which was regarded by RIDWOOD (1897 a) to be related with the suppression of the tongue. From this annulus cricoideus a pair of simple bronchial processes protrude (Present work and PATERSON, 1939 a), while RIDWOOD (1897 a) found them to be irregular in the adult stage of this species.

A further peculiarity of the Aglossa is the absence of the vocal cords (Present work and RIDWOOD, 1897 a).

E. *The Visceral Muscles*

A summary of the history of the visceral muscles of *Xenopus laevis* during the process of metamorphosis is given in the following table:

Larval stage	Premeta- morphic stages	Metamorphosing stages					Fully metamorphosed stage
		61	62	63	64	65	
55	56-60	61	62	63	64	65	66
M.l.m. ant. { p.med.	+	+	+	+	+	+	M.l.m. anterior
M.l.m. ant. { p.intm.	+	+	+	+	+	+	M.l.m. posterior
M.l.m. ant. { p.latr.	+	+	+	+	+	+	
M.l.m. posterior	+	+	+	+	+	+	
M.l.m. externus	+	+	+	+	+	+	M.l.m. externus
M.intermand. anter.	+	+	+	+	+	+	M.intermand. ant.
M.intermand. postr.	+	+	+	+	+	+	M.intermand. postr.
M. orbitohyoideus	+	+	+	+	+	+	
M.suspensoriohyoid.	+	+	+	+	+	+	M.depress.mandib.
M.quadratohyoang.	+	+	+	+	+	+	
M.interhyoideus	+	+	+	+	+	+	M.interhyoideus
MM.const.br. i-iv.	+	+	reduced dissolve				
MM.subarc.rec. i-iv.	+	+	”	”			
M.trans.vent. ii.	+	+	”	”			
M.trans.vent. iv.	+	+	+	+	+	+	
M.l.arc.branc. iv.	+	+	+	+	+	+	M.petrohyoideus
M.eucullaris	+	+	+	+	+	+	M.eucullaris
M.geniohyoideus	+	+	+	+	+	+	M.geniohyoid.med.
	+	+	+	+	+	+	M.geniohyoid. lat.
M.dilatator laryn.	+	+	+	+	+	+	M.dilatator laryn.
MM.const.lary.dr. & vt.	+	+	+	+	+	+	MM.const.lar.dr. & vt.

From the above it may be concluded that:

1. The muscles described for the first tier are the pars intermedius

of the M.l.m. anterior, the M.l.m. externus, and the M. suspensoriohyoideus.

a. Concerning the fasciculae of the M.l.m. anterior, PATERSON (1939 a) referred to the pars lateralis of this muscle, but actually was in doubt about its correct relationship to the M.l.m. anterior itself. She mentioned that it "arises from the lateral region of the M.l.m. anterior and may be part of it". However, no reference is given to the pars intermedius.

It must be stressed here that the three fasciculae are quite distinct in the larval and early metamorphosing stages. They have a common surface of origin, but at the level of the processus muscularis quadrati they separate from each other. The pars medialis possesses a distinct long tendon inserted onto MECKELS' cartilage, the pars intermedius is broadly inserted onto the same cartilage, while the pars lateralis runs on the ventral surface of the tentacular cartilage.

b. As regards the M.l.m. externus, PATERSON (1939 a) gave the origin and insertion of a muscle which she identified as a M. quadratohyoangularis. Concerning the last-named muscle, she mentioned that "in addition to its connection with the palatoquadrate also originates on the annulus tympanicus", and that "it is inserted on the ventro-lateral margin of the mandible". These relationships exactly fit for the M.l.m. externus, which has been completely missed by previous workers.

There is no doubt here about the correct identification of the M.l.m. externus. This muscle has been found to retain its relationships and individuality throughout the whole life history of the animal and possesses the same relations to the skeletal structures as the similarly-named muscle of *Bufo regularis* (SEDRA, 1950) and all Salientia in general (EDGEWORTH, 1935).

c. The M. suspensoriohyoideus has been missed by previous workers perhaps because it is a relatively weak muscle. However, it exactly corresponds to the similarly-named muscle in other Salientia, and can be easily identified up to stage 62.

2. Among the important changes which have been observed for the first time during metamorphosis are:

a. The larval pars medialis of the M.l.m. anterior gives rise to the M.l.m. anterior of the adult. Thus, the adult muscle corresponds to the medial fasciculus only of the larval muscle.

b. The pars lateralis and pars intermedius of the M.l.m. anterior together with the larval M.l.m. posterior give rise to the M.l.m. posterior of the adult. Thus, the adult muscle is a compound one.

c. The larval MM. orbitohyoideus, suspensoriohyoideus, and quadratohyoangularis fuse and give rise to the M. depressor mandibulae of the adult, thus resembling the condition exhibited by other Salientia.

These findings contradict those of PATERSON (1939 a) where she considered that the M. levator hyoideus consists of two fasciculae, an outer M. orbitohyoideus and an inner M. quadratohyoangularis, which

in her view represent the outer and inner fasciculae of the adult *M. depressor mandibulae* respectively. However, as explained above, she was confused about the future history of the *M. quadratohyoangularis*, and at the same time she missed the *M. suspensoriohyoideus*. The muscle which she identified as the inner fasciculus of the adult *M. depressor mandibulae* is not at all a *M. quadratohyoangularis*, but it is the *M.l.m. externus*, which she also missed altogether.

Consequently, what she considered as the outer fasciculus of the *M. depressor mandibulae* actually represents the whole adult *M. depressor mandibulae* which is definitely of compound origin, being formed by the fusion of three levator hyoidei, namely the *MM. orbitohyoideus*, *quadratohyoangularis*, and *suspensoriohyoideus*.

3. There was some dispute about the origin of the *M. petrohyoideus*. PATERSON (1939 a) mentioned that "the whole course of the petrohyoideus of other Anura, and in *Xenopus* seems as though it might be a modification of a muscle such as the last levator arcuum branchialium or even in part of a transversus ventralis iv, rather than simply of the post. constrict. branchialis which is still visible during metamorphosis".

The present findings agree to a certain extent with PATERSON'S view, since it has been shown in the descriptive part that at stage 62, the *MM. transversus ventralis iv* and levator arcuum branchialium iv, become completely continuous with each other and give rise to the *M. petrohyoideus* of the fully metamorphosed individual. All four *MM. constrictores branchiales*, however, break down and disappear during the process of metamorphosis.

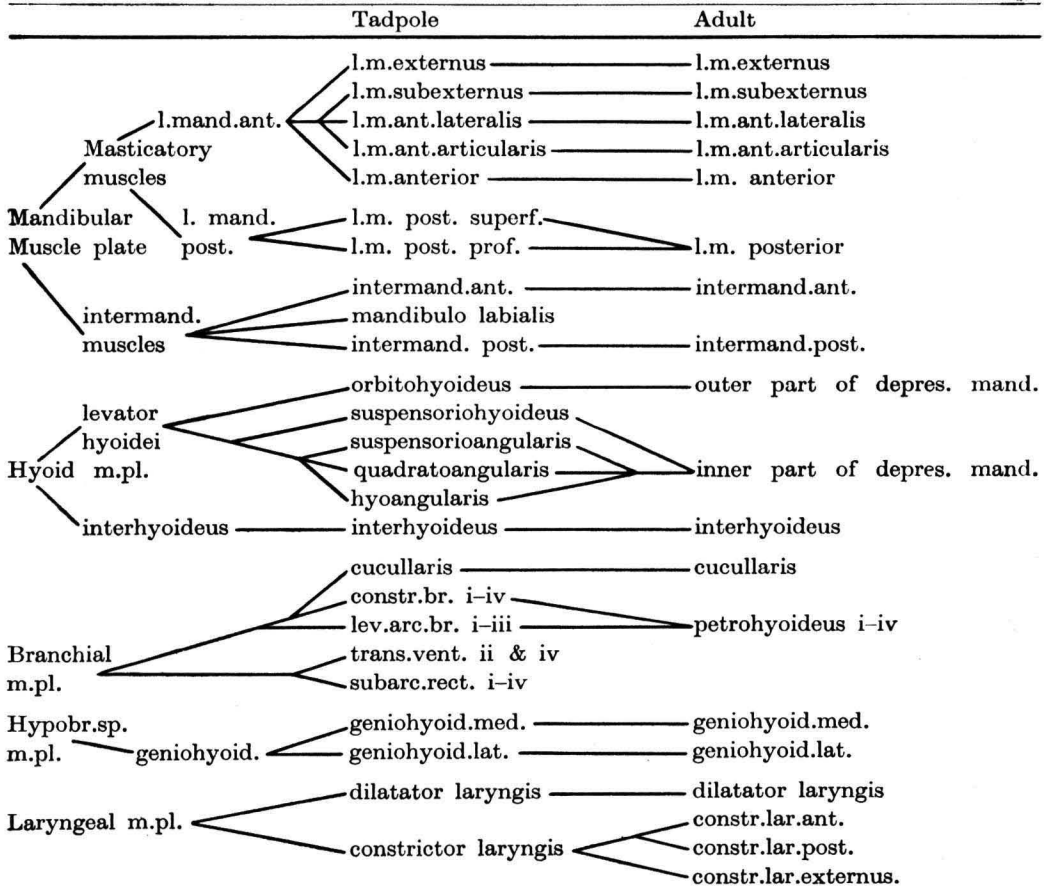
A comparison of the origin and history of the visceral, hypobranchial spinal and laryngeal muscles exhibited by the *Phaneroglossa* in general as exemplified by *Rana temporaria*, and the condition present in the *Aglossa* according to the present findings in *Xenopus laevis* may be of special interest.

From the table below it is evident that *Xenopus laevis* exhibits many characters which are of common occurrence among other salientians; thus showing that this species together with the other tongueless ones may not be completely separated from the tongued forms. Consequently, GADOW'S view (1909) concerning the classification of the Salientia into *Aglossa* and *Phaneroglossa* is not quite suitable.

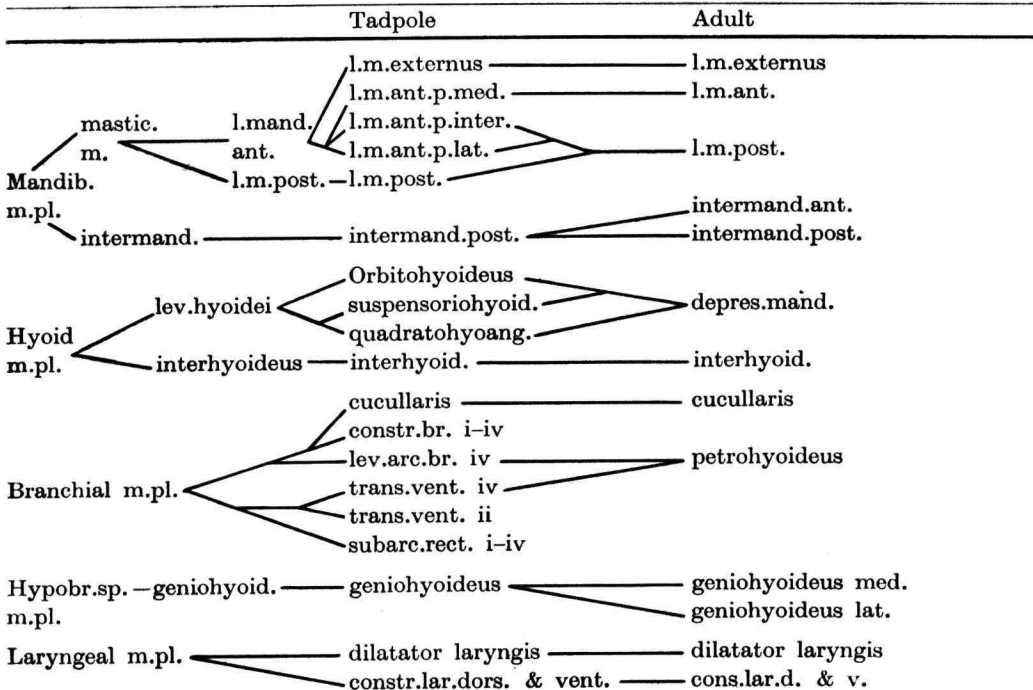
The question that now remains concerns the relationship of *Xenopus* to the other tongueless species or more particularly whether *Xenopus* and *Hymenochirus* should be included in one subfamily (the *Xenopinae* according to NOBLE, 1931) or whether it is better to separate it from the two other genera (*Hymenochirus* and *Pseudhymenochirus*) belonging to this subfamily. PATERSON (1945) noted that there is little factual basis for the inclusion of *Xenopus* and *Hymenochirus* in one subfamily.

Actually, no work has so far been done on the metamorphosis of

a) The condition in the Phaneroglossa (ex: *Rana temporaria*)



b) The condition in the Aglossa (ex: *Xenopus laevis*)



Hymenochirus. However, concerning the adult cranial morphology, one may refer to a number of important structures possessed by one while absent in the other. The following structures may be mentioned:

No.	Structures	<i>Xenopus</i>	<i>Hymenochirus</i>
1	Operculum fenestrae ovalis	reduced	absent (similar to <i>Pipa</i>)
2	Superior & inferior perilymphatic foramina	inferior only	both present
3	Orbitosphenoid bone	+	—
4	Extension of parasphenoid under septum nasi	+	absent (similar to <i>Pipa</i>)
5	Crista intermedia	+	—
6	Planum terminale	+	—
7	Solum nasi	+	absent (similar to <i>Pipa</i>)
8	Subocular bar	+	—
9	Basitrabecular process	—	+
10	Pseudobasal process	+	?
11	Teeth on praemaxilla & maxilla	+	absent (similar to <i>Pipa</i>)
12	Hyoid apparatus	single piece	divided into two portions
13	Hyalia	cartilaginous	mainly ossified

In addition to the above mentioned characters in which *Xenopus* and *Hymenochirus* differ from each other, it has been shown by PATERSON (1945) that *Hymenochirus* exhibits many characters, not exhibited by *Xenopus*, but common with the Caudata.

According to the present findings, the differences between *Xenopus* and *Hymenochirus* are so significant that they add support to PATERSON'S view (1945).

V. SUMMARY

A. The structures described for the first time in the fully developed larva (Stage 55) of *Xenopus laevis* are:

1. The foramina cranio-palatina.
2. The processus cornu quadratus medialis.
3. The ligamentum cornu quadratum mediale.
4. The fourth cranio-branchial commissure.
5. The pars intermedius of the M.l.m. anterior.
6. The M.l.m. externus.
7. The M. suspensoriohyoideus.

B. Among the new, chronologically classified observations during the process of metamorphosis are:

1. Synostosis of the two fronto-parietals at stage 56.
2. Nasal bones appear at stage 58.
3. Septomaxilla appears at stage 60.
4. Annulus tympanicus chondrifies at stage 61.
5. Processus muscularis capsulae auditivae destroyed at stage 63.
6. Post-palatine commissure develops at stage 63.
7. Foramina cranio-palatina occluded at stage 63.
8. Oculomotor tunnel and foramen caroticum primarium confluent at stage 63.
9. Partes externa and media plectri fuse at stage 64.
10. Foramen oculomotorium + caroticum primarium become confluent with the corresponding ventral outlet of the foramen prooticum at stage 65.
11. The backward shift of the palatoquadrate cartilage begins at stage 61 and is not accompanied with any undulations or bucklings.
12. Processus muscularis quadrati disappears at stage 62.
13. Ligamentum cornu quadratum mediale disappears at stage 62.
14. Processus maxillaris posterior and processus pterygoideus originate from commissura quadrato-cranialis anterior at stage 63.
15. Processus ventro-lateralis quadrati disappears at stage 63.
16. Tentacular cartilage and processus cornu quadratus lateralis destroyed at stage 63.
17. Appearance of the bones of the jaws is as follows: Maxilla at stage 58; praemaxilla and dentary at stage 60; squamosum at stage 62; and pterygoid at stage 63.

18. Second and fourth cranio-branchial commissures, and third cranio-branchial process disappear at stage 62.
19. Alae arise exclusively from the sides of the corpus hyoideum at stage 63.
20. Branchial chambers disappear at stage 64.
21. Hyoglossal foramen formed at stage 65.
22. Floor of annulus cricoideus develops at stage 61.
23. Bronchial processes appear at stage 64.
24. Larval pars medialis of M.l.m. anterior gives rise to the adult M.l.m. anterior at stage 64.
25. Larval pars lateralis and pars intermedius of M.l.m. anterior together with larval M.l.m. posterior give rise to the adult M.l.m. posterior at stage 64.
26. MM. orbito-, suspensoriohyoideus and quadrato-hyoangularis give rise to M. depressor mandibulae at stage 66.
27. M. intermandibularis anterior appears at stage 56.
28. MM. constrictores branchiales i-iv, subarcuales recti i-iv and transversus ventralis ii disappear at stage 63.
29. MM. transversus ventralis iv and levator arcuum branchialium iv give rise to M. petrohyoideus at stage 62.
30. M. geniohyoideus divides into partes medialis and lateralis at stage 60.

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VII. BIBLIOGRAPHY

- AL-HUSSAINI, A. H. (1941) The Osteology of *Rana mascareniensis* Dum. et Bibr. Bull. Fac. Sci. Fouad I Univ. 24, 75.
- BADENHORST, C. E. (1945) Die Skedelmorfologie van die Neotropiese Anure *Atelopus moreirae* de Miranda-Ribeiro, Ann. Univ. Stell. 23 A, 1.
- BEDDARD, F. E. (1908) Some notes on the muscular and visceral anatomy of the batrachien genus *Hemisis*, with notes on the lymph hearts of this and other genera. Proc. Zool. Soc. Lond. 1908 (2), 894.
- DE BEER, G. R. (1937) "The Development of the Vertebrate Skull". London.
- DE CARVALHO, A. L. (1939) Notas sôbre *Hemipipa carvalhoi* Mir.-Rib. (Batrachia, Anura: Pipidae). Bol. Biol. (N.S.) 4, (3), 394.
- DE VILLIERS, C. G. S. (1931) Some features of the Cranial anatomy of *Hemisis marmoratus*. Anat. Anz. 71, 305.
- DE VILLIERS, C. G. S. (1932) Über das Gehörskellett der Aglossen Anuren. Ibid. 74, 33.
- DE VILLIERS, C. G. S. (1934) Studies on the cranial anatomy of *Ascapus truei* Stejneger, the American "Liopelmid". Bull. Mus. comp. Zool. Harv., 77, 7.
- EATON, T. H. (1942) Are "fronto-parietal" bones in Frogs actually frontals? J. Wash. Acad. 32, 151.
- EDGEWORTH, F. H. (1930) On the masticatory and hyoid muscles of larvae of *Xenopus laevis*. J. Anat. Lond., 64, 184.
- EDGEWORTH, F. H. (1935) "The Cranial Muscles of Vertebrates" Cambridge.
- FOOT, N. C. (1933) The Masson trichrome staining methods in routine laboratory use; Stain Technology, 8, 101.
- GADOW, H. (1909) "Amphibia and Reptiles". Macmillan, London.
- GAUPP, E. (1893) Beiträge zur Morphologie des Schädels. I: Primordial-Cranium und Kieferbogen von *Rana fusca*. Morph. Arb. 2, 275.
- GROBBELAAR, C. S. (1935) The musculature of the Pipid genus *Xenopus*. South Afr. J. Sci., 32, 395.
- HIGGINS, G. M. (1920) The Nasal Organ in Amphibia. Illinois biol. Monogr., 6, 1.
- JARVIK, E. (1942) On the structure of the snout of crossopterygians and lower gnathostomes in general. Zool. Bidr. Uppsala, 21, 235.
- KINGSBURY, B. F. & REED, H. D., (1909) The Columella auris in Amphibia. Second Contribution. J. Morph. 20, 549.
- KOTTHAUS, A. (1933) Die Entwicklung des Primordial-craniums von *Xenopus laevis* bis zur Metamorphose. Z. Wiss. Zool. 144, 510.
- KRUIJTZER, E. M. (1931) De Ontwikkeling van het Chondrocranium en enkele Kopzenuwen van *Megalophrys montana*. Proefschrift, Leiden.
- MAREE, W. A. (1945) Contributions to the Cranial Morphology of the European Anuran *Alytes obstetricans* (Laurenti). Ann. Univ. Stell. 23, A., 43.
- NIEUWKOOP, P. D. and J. FABER (editors) (1956) "Normal Table of *Xenopus laevis* (Daudin)". North-Holland Publishing Co., Amsterdam.
- NOBLE, G. K. (1931) "The Biology of the Amphibia". New York.
- OKUTOMI, K. (1937) Die Entwicklung des Chondrocraniums von *Polypedates buergeri* Schlegelii. Z. Anat. Entw. gesch. 107, 28.
- PARKEE, W. K. (1876) On the structure and development of the skull in the Batrachia. Part II. Philos. Trans. 166, 601.
- PATERSON, N. F. (1939 a) The head of *Xenopus laevis*. Quart. J. micr. Sci. 81, 161.

- PATERSON, N. F. (1939 b) The Olfactory Organ and Tentacles of *Xenopus laevis*. South Afr. J. Sci., **36**, 390.
- PATERSON, N. F. (1945) The Skull of *Hymenochirus curtipes*. Proc. Zool. Soc. Lond., **115**, 327.
- PATERSON, N. F. (1949) The Development of the Inner Ear of *Xenopus laevis*. Ibid. **119** (II), 269.
- PATERSON, N. F. (1951) The Nasal Cavities of the Toad *Hemipipa carvalhoi* Mir.-Rib. and other Pipidae. Ibid. **121** (II), 381.
- PUSEY, H. K. (1938) Structural changes in the Anuran mandibular arch during metamorphosis, with reference to *Rana temporaria*. Quart. J. micr. Sci., **80**, 479.
- PUSEY, H. K. (1943) On the Head of the Liopelmid Frog, *Ascaphus truei*. 1. The chondrocranium, jaws, arches, and muscles of a partly-grown larva. Ibid., **84**, 105.
- RAMASWAMI, L. S. (1937) The morphology of the Bufonid Head. Proc. Zool. Soc. Lond. **1936**, 1157.
- RAMASWAMI, L. S. (1939) Some Aspects of the Anatomy of Anura (Amphibia) — a Review. Proc. Ind. Acad. Sci. **10** (1), 41.
- RAMASWAMI, L. S. (1940) Some Aspects of the Chondrocranium in the Tadpoles of South Indian Frogs. Half Year J. Mysore Univ. N.S. I B, 15.
- RAMASWAMI, L. S. (1943) An account of the Chondrocranium of *Rana afghana* and *Megophrys*, with a description of the masticatory musculature of some Tadpoles. Proc. Nat. Inst. Sci. India, **9** (1), 43.
- RAMASWAMI, L. S. (1944) The chondrocranium of two torrent-dwelling Anuran Tadpoles. J. Morph., **74**, 347.
- REINBACH, W. (1939) Untersuchungen über die Entwicklung des Kopfskeletts von *Calyptocephalus gayi* (mit einem Anhang über das os supra-rostrale der anuren Amphibien). Jena. Z. Naturw. **72**, 211.
- RIDEWOOD, W. G. (1897 a) On the structure and development of the Hyobranchial skeleton and Larynx in *Xenopus* and *Pipa*; with remarks on the Affinities of the Aglossa. J. linn. Soc. Lond. Zool., **26**, 53.
- RIDEWOOD, W. G. (1897 b) On the structure and development of the hyobranchial skeleton of the Parsley-Frog (*Pelodytes punctatus*). Proc. Zool. Soc. Lond. **1897**, 577.
- RIDEWOOD, W. G. (1898) On the larval Hyobranchial Skeleton of the Anurous Batrachians, with special reference to the Axial parts. J. linn. Soc. Lond. Zool., **26**, 474.
- RIDEWOOD, W. G. (1899) On the hyobranchial skeleton and larynx of the new Aglossal Toad *Hymenochirus boettgeri*. Ibid., **27**, 454.
- SCHULZE, F. E. (1892) Ueber die inneren Kiemen der Batrachier-larven II. Mitteilung, skelett, Muskulatur, Blutgefasse, Filterapparat, respiratorische Anhänge und Atmungs-bewegungen erwachsener Larven von *Pelobates fuscus*. Abh. d. k. preuss. Akad. d. Wiss. Berlin, Sitzber. **13**, 205.
- SEDRA, S. N. (1950) The metamorphosis of the jaws and their muscles in the Toad, *Bufo regularis* Reuss, correlated with the changes in the animal's feeding habits. Proc. Zool. Soc. Lond., **120**, 405.
- SEDRA, S. N. (1951) On the Morphology of the Suprarostrals System and the Mandibular Arch of *Bufo lentiginosus*. Proc. Egypt. Acad. Sci. **7**, 128.
- SLABBERT, G. K. (1945) Contributions to the Cranial morphology of the European Anuran *Bombina variegata* (Linné). Ann. Univ. Stell., **23**, A., 67.
- SMIT, A. L. (1953) The ontogenesis of the vertebral column of *Xenopus laevis* (Daudin), with special reference to the segmentation of the metotic region of the skull. Ibid. **29** A, 79.
- STEPHENSON, ELSIE M. (1951) The Anatomy of the Head of the New Zealand Frog, *Leiopelma*. Trans. Zool. Soc. Lond., **27** pt. 2, 255.

- STEPHENSON, N. G. (1951) On the Development of the Chondrocranium and Visceral Arches of *Leiopelma archeyi*. *Ibid.*, 27 pt. 2, 203.
- SUSHKIN, P. P. (1927) On the modifications of the mandibular and hyoid arches and their relations to the Brain case in the early Tetrapoda. *Palaeont. Z. Berlin*, 8, 263.
- TREWAVAS, E. (1933) The Hyoid and Larynx of the Anura. *Phil. Tr. Roy. Soc. Lond. B.* 222, 401.
- VAN EEDEN, J. A. (1951) The Development of the Chondrocranium of *Ascaphus truei* Stejneger with special reference to the relations of the palatoquadrate to the neurocranium. *Acta Zoologica Bd.* 32, 42.
- VAN SETERS, W. H. (1922) Le développement du chondrocrâne d'*Alytes obstetricans* avant la métamorphose. *Arch. Biol. Paris*, 32, 373.
- VAN ZYL, J. H. M. (1950) Die Beskrywends en Vergelykende Anatomie van die Skedel van *Discoglossus pictus* (Gravenhorst). *Ann. Univ. Stell.*, 26 A, 5.
- WATSON, D. M. S. (1919) The Structure, Evolution and Origin of the Amphibia. The "Orders" Rachitomi and Stereospondyli. *Philos. Trans.* 209, 1.
- WEISZ, PAUL B. (1945 a) The development and morphology of the larva of the South African clawed toad, *Xenopus laevis*. I. The third form tadpole. *J. Morph.* 77, 163.
- WEISZ, PAUL B. (1945 b) The development and morphology of the larva of the South African clawed toad, *Xenopus laevis*. II. The hatching and the first- and second-form tadpoles. *Ibid.*, 77, 193.

VIII. ABBREVIATIONS USED IN THE ILLUSTRATIONS

a.c.	auditory capsule.
al.	ala.
al.p.	anterior process of the ala.
an.cr.	annulus cricoideus.
an.tp.	annulus tympanicus.
a.ot.p.	adult processus oticus.
ap.n.ex.	apertura nasalis externa.
art.	arytenoid.
b.c.	basis cranii.
b.hbr.	basihyobranchiale.
bro.p.	bronchial process.
br.p. 2-3	branchial process 2-3.
br.r. 1-3	branchial rays on ceratobranchialia 1-3.
cb. 1-4	ceratobranchialia 1-4.
cd.f.	condyloid fossa.
eg.al.	cartilago alaris.
eg.ob.	cartilago obliqua.
eg.p.sp.	cartilago praenasalis superior.
ch.	ceratohyale.
c.hy.	corpus hyoideum.
c.M.	MECKELS' cartilage.
cm.	commissure between lamina inferior and ethmoid plate.
cn.	choana.
c.p.vl.q.	cartilaginous bar connecting the processus ventro-lateralis quadrati with the crista parotica.
c.q.c.a.	commissura quadrato-cranialis anterior.
cr.br.c. 2 & 4	cranio-branchial commissures 2 & 4.
cr.br.p. 3	cranio-branchial process 3.
cr.q.p.	cranio-quadrante passage.
cs.itm.	crista intermedia.
cs.oc.l.	crista occipitalis lateralis.
cs.p.	crista parotica.
c.t.	commissurae terminales.
cv.cr.	cavum cranii.
d.f.pr.	dorsal outlet of the foramen prooticum.
dnt.	dentary bone.
et.f.	ethmoid flange.
et.p.	ethmoid plate.
f.ac.a.	foramen acusticum anterius.
f.ac.p.	foramen acusticum posterius.
f.br.a.	foramen for a branchial artery.
f.cr.p.	foramen cranio-palatinum.
f.ct.pr.	foramen caroticum primarium.
f.dlt.	fenestra dorso-lateralis.

f.end.	foramen endolymphaticum.
f.j.	foramen jugulare.
fl.cd.f.	floor of condyloid fossa.
f.m.	foramen magnum.
f.n.pf.	foramen for the medial nasal branch of profundus nerve.
f.nv.	foramen for a nerve twig.
f.o.	fenestra ovalis.
f.oc.+ct.pr.	common foramen oculomotorium + caroticum primum.
f.op.	optic foramen.
f.orn.	orbitonasal foramen.
f.pf.pl.n.	foramen for ramus communicans between n. ophthalmicus profundus V and n. palatinus VII.
f.p.if.	foramen perilymphaticum inferius.
f.pr.	foramen prooticum.
frp.	fronto-parietal bone.
frp.f.	fronto-parietal fenestra.
f.th.a.	foramen for thyreopharyngeal artery.
f.pt.	parietal foramen.
gl.s. 1-3	gill slits 1-3.
gon.	goniale.
hg.f.	hyoglossal foramen.
hg.s.	hyoglossal sinus.
hpb.p.	hypobranchial plate.
hp.c.	hypochochordal commissure.
hy.	hyale.
hz.p.	horizontal process of crista intermedia.
if.lb.c.	inferior labial cartilage.
k.	keel of basihyobranchiale.
lg.	ligamentous tissue.
lg.c.q.md.	ligamentum cornu quadratum mediale.
lm.if.	lamina inferior of crista intermedia.
lm.orn.	lamina orbitonasalis.
lot.p.	larval processus oticus.
l.p.a.q.	larval pars articularis quadrati.
MM.c.b. i-iv	MM. constrictores branchiales i-iv.
M.c.l.d.	M. constrictoris laryngis dorsalis.
M.c.l.v.	M. constrictoris laryngis ventralis.
M.cc.	M. cucullaris.
M.d.l.	M. dilatator laryngis.
M.d.m.	M. depressor mandibulae.
M.gh.	M. geniohyoideus.
M.gh.l.	M. geniohyoideus lateralis.
M.gh.m.	M. geniohyoideus medialis.
M.ih.	M. interhyoideus.
M.im.a.	M. intermandibularis anterior.
M.im.p.	M. intermandibularis posterior.
M.l.a.b. iv	M. levator arcuum branchialium iv.
M.l.m.a.	M. levator mandibulae anterior.
M.l.m.a.p.im.	M. levator mandibulae anterior pars intermedius.
M.l.m.a.p.lt.	M. levator mandibulae anterior pars lateralis.
M.l.m.a.p.md.	M. levator mandibulae anterior pars medialis.
M.l.m.e.	M. levator mandibulae externus.
M.l.m.p.	M. levator mandibulae posterior.
M.oh.	M. orbitohyoideus.

M.osh.	M. orbitosuspensoriohyoideus.
M.pth.	M. petrohyoideus.
M.qha.	M. quadratohyoangularis.
M.sh.	M. suspensoriohyoideus.
M.s.r. i-iv	M. subarcuales recti i-iv.
M.t.v. ii, iv	M. transversus ventralis ii, iv.
mx.	maxilla bone.
n.	notochord.
ns.	nasal bone.
oc.c.	occipital condyle.
oc.pr.os.	occipito-prootic ossification.
or.c.	orbital cartilage.
ors.	orbitosphenoid bone.
op.	operculum fenestrae ovalis.
p.as.q.	processus ascendens quadrati.
p.at.	pila antotica.
p.c.q.lt.	processus cornu quadratus lateralis.
p.c.q.md.	processus cornu quadratus medialis.
p.crn.	processus coronoideus of goniale.
pd.	pad of cartilage between fronto-parietal and nasal bones.
p.e.pl.	pars externa plectri.
p.i.pl.	pars interna plectri.
pl.b.	planum basale.
p.lng.	processus lingularis.
pl.t.	planum terminale.
p.m.c.ad.	processus muscularis capsulae auditivae.
p.mp.	pila metoptica.
pm.p.ch.	postero-medial process of ceratohyale.
p.m.pl.	pars media plectri.
p.m.q.	processus muscularis quadrati.
pmx.	praemaxilla bone.
p.mx.a.	processus maxillaris anterior.
p.mx.p.	processus maxillaris posterior.
p.p.cm.	post-palatine commissure.
p.pl.n.	pars plana nasi.
p.pp.	pila preoptica.
p.ptg.	processus pterygoideus.
psf.	parasphenoid bone.
p.s.q.	posterior spur of palatoquadrate cartilage.
ptg.	pterygoid bone.
p.vl.q.	processus ventro-lateralis quadrati.
q.	palatoquadrate cartilage.
sl.	slit in pars interna plectri.
smx.	septomaxilla bone.
s.n.	septum nasi.
soc.f.	subocular fenestra.
so.n.	solum nasi.
sq.	squamosum.
t.	tentacular cartilage.
t.at.	tectum anterius.
th.f.	thymus foramen.
thr.p.	thyroid process.
thr.v.	thyroid vacuity.
t.md.	tunnel for n.maxillo-mandibularis V.

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t.n.	tectum nasi.
t.ocl.	tunnel for n.oculomotorius.
t.ol.	olfactory tunnel.
t.pt.	tectum posterius.
t.os.	tunnel for n.opthalmicus superficialis VII.
t.t.mg.	taenia tecti marginalis.
t.tre.	tunnel for n.trochlearis.
v.f.pr.	ventral outlet of foramen prooticum.
v.f.pr'.	common ventral outlet of foramen prooticum and foramen oculo- motorium + caroticum primarium.
vl.pr.	ventro-lateral process of annulus cricoideus.
vrbl.	vertebra I.