

EXPLANATION OF PLATE XXXIV.

- Fig. 1. *Euryope bipartita*, p. 549.
 2. — *nigricollis*, p. 550.
 3. *Lefevrea æneicolle*, p. 527.
 4. *Rhembastus maculicollis*, p. 538.
 5. *Diboloides bicolor*, p. 553.
 6. *Neodera transversicollis*, p. 564.
 7. *Serraphula ænea*, p. 557.
 8. *Eugonotes longicornis*, p. 559.
 9, 10. *Candezea variopennis*, p. 574.
 11. *Luperus nigrosuturalis*, p. 567.
 12. *Aulamorphus hollisi*, p. 572.

4. On the Structure and Development of the Hyobranchial Skeleton of the Parsley-Frog (*Pelodytes punctatus*).
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(Plate XXXV.)

When writing recently upon the Hyobranchial Skeleton of *Xenopus* and *Pipa* I adverted to the fact (16. p. 116) that the hyoglossal foramen so characteristic of these two genera is most nearly paralleled among the phaneroglossal Anura in *Pelodytes*, and (16. p. 117) that in the hyoidean cornu of *Pelodytes* is seen the retention of a condition of dissolution which is transient in *Pipa*. The opportunity for a more exhaustive study of the hyobranchial skeleton of *Pelodytes* has since been afforded to me by Mr. G. A. Boulenger, F.R.S., of the Natural History Museum, London, who most generously placed at my disposal an extensive series of larvæ collected by himself, and in an excellent state of preservation, together with numerous adults of the same species (*P. punctatus*) both living and in spirit.

The hyobranchial skeleton of the adult *Pelodytes* is remarkable in many ways, and, except in the case of the thyrohyals and the postero-lateral processes adjoining, it is difficult at first sight to see what relation exists between the various parts and those of the more familiar hyobranchial skeleton of the Common Frog. The anterior or hyoidean cornu is divided; and the detached posterior portion, flat and broad in front (*h'*, fig. 9, Plate XXXV.), tapers backwards into a curved rod of cartilage (*h''*), which rises up to be attached to the auditory region of the skull. The study of the metamorphosis of the hyoid arch (*postea*) shows that in the adult but little is missing of its total length. The only part of the arch which is not represented in the adult skeleton is that between the anterior extremity of the cartilage marked *h'* in fig. 9 and the part of the great plate marked *h*. The relations are readily grasped by referring to the hyoid of the recently metamorphosed animal (fig. 8), where the lateral foramen (*fl*, fig. 9) has not yet been

enclosed. The lateral foramen of the adult skeleton is thus not due to a secondary fenestration in a continuous plate of cartilage as might be supposed, but owes its origin to the closure of a deep notch or sinus. By a similar process of overgrowth of marginal cartilage the hyoglossal sinus (*hgs.*, fig. 9), constant in all tongued Anura, is, in *Pelodytes*, very nearly converted into a foramen such as occurs in the Aglossa. The enclosing cartilages (*pa.*) are secondary additions to the most anterior parts of the hyoidean cornua (see figs. 8, 7, and 6), and in some specimens actually overlap one another. The posterior and anterior thirds of the hyoglossal space are closed by membrane, while the middle third transmits the large hyoglossal muscles.

If we disregard for the moment the detached parts of the hyoidean cornua, the outline of the hyobranchial skeleton is definitely elliptical in shape, the continuity of the ellipse being broken in six places. There is nothing remarkable about the thyrohyals (*t.*, fig. 9); they are broadest behind and are narrowest at two thirds of their length from the posterior end. The cartilaginous processes (*ppl.*, fig. 9) running parallel to the thyrohyals on their external side are more strongly developed than is usual in Phaneroglossa, and their swollen extremities touch the circumscribing ellipse. The deep notches in front of and behind this process are closed by imperforate membrane.

On the ventral surface of the basal plate or body of the hyoid is a curious splint-bone (*v.*, fig. 9), consisting of a short central transverse bar, from the extremities of which project a pair of long antero-lateral processes and a pair of short tapering postero-lateral horns. The extremities of the latter extend along the ventral surface of the anterior ends of the thyrohyals. The ossification is partly buried in the hyoglossus muscle, some of the fibres of which pass between the bone and the basal plate. The bone is attached to the rest of the hyobranchial skeleton only by its extremities and is readily dissected off. It is not an ossification of the cartilage of the basal plate like the paired and frequently unsymmetrical ossification of *Bombinator*, but rather corresponds with the V-shaped ventral bone of *Alytes* and the paired ossification of *Discoglossus*¹.

There are numerous muscles in relation with the hyobranchial skeleton of Anura, and, in making a comparative study of this portion of the skeleton in different genera, the evidence which the muscles afford towards the recognition of homologous skeletal parts is not infrequently of the greatest value. It is only in the Frog (*Rana*) that the muscles of this region of the body have been studied with any degree of precision, and, since the hyobranchial skeleton of this genus is most familiar to anatomists, I have instituted a comparison between the areas of muscle insertion in the hyobranchial skeleton of *Pelodytes* and *Rana*. The muscles of

¹ Parker (12. pl. 20. fig. 10) does not show these splint-bones; but, as he himself has since admitted (Phil. Trans. Roy. Soc. vol. 173. 1882 (1883), p. 139), the specimen there figured is one of *Rana esculenta*, and not of *Discoglossus*.

Pelodytes are so similar to those of the Frog that no difficulty besets their determination; but differences occur in the relative sizes of certain of the muscles in the two genera, and also in the extent of their surfaces of attachment. The impression of the ventral trunk of the m. sternohyoideus is large and of the same shape in both (*sh.*, figs. 10 and 11). Its anterior broader end lies to the outer side of the hyoglossal notch. Since it lies to the inner side of the lateral foramen in *Pelodytes*, and is just internal to the deep depression in the edge of the hyoid plate of the Frog bounded anteriorly by the curving hyoidean cornu, these latter spaces would appear to be homologous; and the assumption is supported by the fact that they are covered in by a membrane which is perforated in both cases by the glossopharyngeal nerve and the lingual branch of the carotid artery (*ix.*, figs. 10 and 11). The antero-lateral process of the Frog (*pal.*, fig. 11), therefore, is represented in *Pelodytes* by the cartilage (*pal.*, fig. 9) which bounds the lateral foramen posteriorly. The chief difficulty in the way of the interpretation of the hyobranchial skeleton of *Pelodytes* is now practically overcome. The cartilage bounding the lateral foramen externally is in part the hyoidean cornu and in part a forward growth of the processus antero-lateralis—a conclusion which is supported by a study of the development (see fig. 8); while the internal boundary represents the first or proximal portion of the hyoidean cornu of the Frog—the part which Gaupp (5) calls the “manubrium” and which Parker (12) in some of his figures of *Anura* marks “hypohyal.”

Returning to the muscles, the area of attachment of the sternohyoideus ventralis extends relatively farther forward in *Pelodytes* than in *Rana*, but that is all. The petrohyoideus primus is in *Pelodytes* a smaller muscle than in *Rana*. Its insertion is purely marginal in the latter genus, but in *Pelodytes* the muscle spreads on to the flat surface of the cartilage (*p*¹, figs. 10 and 11). In both cases the muscle lies between the processus antero-lateralis and the processus postero-lateralis. The petrohyoideus secundus and petrohyoideus tertius are attached to the dorso-external surface of the thyrohyal bone in both genera (*p*² and *p*³, figs. 10 and 11), but in *Pelodytes* the petrohyoideus tertius is inserted more posteriorly than in *Rana*. The fourth division of the petrohyoideus of the Frog (*p*⁴, fig. 11), attached to the posterior extremity of the thyrohyal, is absent in *Pelodytes*. In both genera the geniohyoideus externus is inserted into the proximal end of the processus postero-lateralis, the area of attachment of the omohyoideus (*oh.*) lying between those of the sternohyoideus ventralis and the geniohyoideus externus. The space between the thyrohyal and the processus postero-lateralis is closed by a tough membrane, to the middle of which, in the Frog, the dorsal constituent of the sternohyoideus (*sh.*′, fig. 11) and a part of the geniohyoideus externus are attached. In *Pelodytes*, however, the sternohyoideus dorsalis is a smaller muscle (*sh.*′, fig. 10), and it is attached to the cartilage at the bottom of the sinus, close to the insertion

of the omohyoideus. The hyoglossus in *Pelodytes* (*hg.*, fig. 10) is attached to nearly the whole of the ventral surface of the thyrohyal and to the posterior part of the basal plate or body of the hyoid. As already remarked, the greater part of the ventral splint-bone lies buried in the muscle. In the Frog the area of insertion of the hyoglossal muscle (*hg.*, fig. 11) is more restricted, and hardly extends on to the basal plate. The posterior end of the geniohyoideus internus is, in the Frog, inserted mainly into the ventral fascia of the hyoglossus, only a few stray fibres extending round this muscle to be inserted into the thyrohyal in the position marked *ghi.* in fig. 11. In *Pelodytes* the geniohyoideus internus is less bound to the hyoglossus, and its insertion into the thyrohyal (*ghi.*, fig. 10) extends to the posterior extremity of this bone.

Only two original figures of the hyoid apparatus of *Pelodytes* have been published. In the first, by Dugès (4. pl. 3. fig. 21), the lateral foramina are shown correctly, and their presence is rightly accounted for (4. p. 56) by the union of the hyoid cornua with the antero-lateral processes; but the dismembered parts of the hyoid arch are wanting. The ventral ossification is represented as of the form of a pair of triradiate bones. The hyoglossal sinus is not sufficiently enclosed in front, nor is the postero-lateral process of the hyoid shown of sufficient length. The second figure, by Parker (12. pl. 23. fig. 3), shows the lateral foramina, but the external enclosing cartilages are represented as in contact, and not confluent with one another. The dismembered parts of the hyoidean cornua are introduced into the figure, but they are too rod-like in shape and fail to exhibit the lamellar expansion. The hyoglossal sinus is more enclosed than in Dugès's figure, and is consequently more true to nature. The ventral splint-bone, however, is triradiate and unsymmetrical, like one of those figured by Dugès. The figure given by Cope (2. pl. 76. fig. 6) is admitted to be based on those of Dugès and Parker, and thus calls for no special criticism.

In the tendency for the processus anteriores to narrow the opening of the hyoglossal sinus, in the presence of lateral foramina, and in the dismemberment of the hyoidean cornua, the hyobranchial skeleton of *Pelobates* very closely resembles that of *Pelodytes*. My attention was directed towards this genus by Mr. Boulenger, who kindly supplied me with specimens of *Pelobates fuscus*, and at the same time expressed his conviction that the hyoidean cornua were disjointed in all those genera which he includes in the family Pelobatidæ (1. p. 432), and that Parker's figure of the hyobranchial skeleton of *Pelobates* (12. pl. 25. fig. 9) showing the hyoidean cornua continuous was incorrect. I am happy to be in a position to confirm his suspicions with regard to Parker's figure, and, as the matter is so important, I trust I may be pardoned for a slight digression here from the genus which forms the subject of this contribution. In the hyobranchial skeleton of *Pelobates* (fig. 12) the anterior processes are directed inwards and slightly backwards, exactly as in *Pelodytes*, but they do not reach the median line. The lateral foramina are smaller and more pear-shaped, and in

half-grown specimens the cartilage bounding the foramen postero-externally is very thin and readily tears away, giving the impression that there exists here an unenclosed sinus such as is shown by Dugès (4. pl. 3. fig. 18) and Parker (12. pl. 25. fig. 9). Both Dugès and Parker fail to depict the hyoid arch correctly. The liberated part of the cornu (*h'*, *h''*, fig. 12) resembles very closely in size and shape that of *Pelodytes*. It is lamellar in front, and ends behind in a hooked process attached to the skull. Parker errs by representing it as rod-like and not separated from the rest of the arch, while Dugès fails to notice it at all in pl. 3. fig. 18, but shows it as a rod-like cartilage in pl. 13. fig. 79. Parker (12. p. 261) says that there are two small centres of ossification on each side in the anterior cornua of *Pelobates*, but this statement I cannot confirm. Cope's figure (2. pl. 76. fig. 5) of the hyoid of *Pelobates* is not original, but is admitted to be based on the figures of Dugès and Parker. The thyrohyals of *Pelobates* are massive, more especially in old specimens; and the epiphysis is produced laterally beyond the outer edge of the shaft, giving to the thyrohyal a hooked appearance.

There is no ventral ossification such as occurs in *Pelodytes*. But whether this fact points to a closer alliance between *Pelodytes* and *Alytes* than between *Pelodytes* and *Pelobates* is, I take it, very doubtful. The bones, in the first place, are not ossifications of the hyobranchial skeleton, but ossifications applied to the surface of it at a late stage of development. If we compare the adult hyoids of *Pelobates*, *Pelodytes*, and *Alytes* we find that the two former resemble one another and differ from the third in the disjoining of the hyoidean cornua, the presence of lateral foramina, and the partial enclosure of the hyoglossal sinus; while the two latter resemble one another and differ from the first only in the presence of the ventral splint-bone. Also, if we compare the larval hyobranchial skeleton of the three, we find that in *Alytes* the basihyal extends so far back as to completely separate the hypobranchial plates from one another, whereas in both *Pelodytes* and *Pelobates* the two hypobranchial plates are in contact in the median line for some distance behind the basihyal. And in *Alytes* there is a well-marked median plate of cartilage (the "erste Copula" of Gaupp, 5. p. 412) situated in front of the opaque fibrous band connecting the ceratohyals; but I find no trace of this in larvæ of *Pelobates* and *Pelodytes*. And these latter are fundamental differences appearing early, and of an importance which it would be difficult to exaggerate.

Development of the Hyobranchial Skeleton of Pelodytes punctatus.

The method employed in the investigation of the larval hyobranchial skeleton was of the simplest character. The tadpoles were dissected under spirit, the mandible and hyoid arch disarticulated from the palatoquadrate cartilage, and the branchial skeleton

carefully freed from the skull. The œsophagus was then cut in front of the liver, and the whole of the floor of the pharynx thus liberated. The heart and larynx were then dissected away, the gills, muscles, and mucous membrane removed, and only sufficient connective tissue left to keep the skeletal parts in their natural relations. No staining reagents were employed, and the whole of the dissection was performed under a simple microscope of a magnification of ten diameters, in powerful reflected light. The series of larvæ examined was very extensive, but it will suffice to select eight stages only of these for description. The important changes in the hyobranchial skeleton do not begin until the tail is reduced to about one-third of its maximum length, but they then proceed with considerable rapidity. In fact, two larvæ exactly similar in external appearance and having the merest stump of the tail remaining may show considerable differences in the structure of the hyobranchial skeleton. In such cases it is necessary to make the dissections first and to arrange the specimens in series afterwards. The youngest tadpole I have been able to examine is one with the hind limbs just appearing as buds on the surface of the body, but from this onwards, as far as the adult condition, the series is as complete as could be wished. It should be noted that the hyobranchial skeleton of the first seven stages is drawn from the dorsal side, in order to show the spicula and the articular ends of the hyoidean cornua. Figs. 8 and 9, however, exhibit the ventral surface, because the spicula have by this time disappeared, the hyoidean cornu has no longer an articular surface, but is firmly adherent to the auditory capsule, and because the interesting ventral ossification is only to be seen in this view. In order to facilitate comparison the figures are not drawn to the same scale, but as nearly as possible of the same absolute size. The approximate magnification is given in each case. The introduction of the mandible into the figures serves to show not only the gradually increasing size of the gape, but also illustrates the interesting manner in which the distal extremities of the hyoidean cornua get pushed farther and farther back as the mandibular rami elongate posteriorly. Throughout this contribution, although ostensibly devoted to a consideration of the hyobranchial skeleton, I have purposely avoided all reference to the columella auris and stapedial cartilages.

STAGE 1. *Distance from snout to root of tail, 13 mm. Length of tail, 16 mm. Length of hind limbs, 1 mm.* (Plate XXXV. fig. 1.)

There is nothing very remarkable about the hyobranchial skeleton of *Pelodytes* in its early stages, since it conforms tolerably well with what might be considered the normal for tadpoles in general. There is but a single unpaired median constituent, and not two, as, for instance, in *Alytes*. Although Parker (12) speaks of this skeletal part of the Anuran larva as the "basibranchial" and Stannius (19. p. 64), Hoffmann (7. p. 45), and Gaupp (5) apply to it the non-committal name "copula," the general

consensus of opinion (Dugès (4), Götte (6), Schulze (18), and others) is that it represents the "basihyal." Not wishing to enter upon an exhaustive and possibly futile discussion of the morphological value of this part, I accept the latter determination and call the median plate of cartilage (*bh.*, fig. 1) the basihyal. This median cartilage is connected with two pairs of large lateral cartilages, the so-called "ceratohyals"¹ in front and the branchial plates behind. The ceratohyals (*ch.*, fig. 1) stand out nearly at right-angles to the long axis of the body, and slope but slightly backwards. Their distal ends articulate by an obliquely elongated convex surface (*ha.*, fig. 1) with the under surface of the palatoquadrate cartilage. The internal or mesial extremities are broad and flat, with a delicately curved inner edge, and are united together in front of the basihyal by a broad band of fibrous tissue (the "queres, fibröses Band" of Rathke, 14. p. 132, *Pseudis paradoxa*; and the "pars reuniens" of Gaupp, 5, *Rana fusca*). In front of this is the hyoglossal notch, at present V-shaped, but later semicircular.

The branchial skeleton consists of two branchial plates, right and left, attached to the posterior part of the basihyal, and in contact with one another for a short distance in the median line behind it. Each is connected, at about one-fourth of its width from the median line, with the backwardly projecting cusp of the flattened part of the ceratohyal. The small triangular space (*s*, fig. 1) thus enclosed between the basihyal and the ceratohyal and branchial plate of each side is filled with a loose connective tissue, which only undergoes chondrification in Stage 4. The antero-internal part of each branchial plate is on the same level as the basihyal and ceratohyal, but the remaining grid-like portion of the plate is deeply concave above. The four curved bars, the so-called "ceratobranchials," are directed outwards and backwards and are connected together at their distal end by an irregular marginal band of cartilage ("commissura terminalis" of Gaupp, 5; "epibranchiale" of Schulze, 18) and at their proximal ends by the common hypobranchial plate (*hbr.*, fig. 1). The distal halves of the ceratobranchials bear on their anterior and posterior surfaces a series of four or five irregular, short, blunt outgrowths of

¹ I fail to see the practical utility of the introduction by Gaupp (5) of new non-committal terms, such as *hyale*, *branchialia*, and *planum branchiale*. It is doubtful, most anatomists will admit, whether the structures so designated correspond exactly to the ceratohyal, ceratobranchials, and hypobranchials of the fish, and it would have been desirable if, in the first instance, less definitive terms had been employed until the true homologies of the parts had been determined. But now that the names have been in use for so long and are so familiar, it is only confusing matters to attempt to replace them by names more vague in their significance. When the implied homology has been definitely disproved, when the so-called ceratohyal of the tadpole has been shown to be something quite different from the ceratohyal of the fish, and so on, then will be the time for a radical change in our nomenclature. We are, however, still in the dark with regard to the morphological significance of the Anuran hypobranchial skeleton, and the onus of the proof of the false homology implied by the terms at present in use lies with the objectors.

cartilage. On the external edge of the first ceratobranchial these processes are of considerable length and form a series of five or six. Similar, but more irregular, cartilaginous processes stand out from the postero-internal border of the fourth ceratobranchial and from the external border of the commissural cartilage. If, now, these irregular finger-shaped processes of the first ceratobranchial were confluent laterally so as to form a continuous curved wall, and if the same coalescence occurred with regard to the processes of the commissural cartilage and fourth ceratobranchial, the whole branchial skeleton would assume the form of two approximately hemispherical cartilaginous basins perforated at the bottom by three oblique slits—a form of branchial skeleton which is peculiar to *Xenopus* (16). Which of the two forms is the more primitive, that with the irregular palisade, or that with the continuous marginal wall, it is difficult to say; but I am inclined to regard the branchial skeleton of the early *Xenopus* larva as more primitive than that of any other Anuran larva yet described¹. The fourth branchial cleft (the last of the three perforations in the branchial cartilage) is shorter than the two preceding. The distal end of the third ceratobranchial is exceptionally broad, and is characterized by the constant presence of either a deep notch or a foramen.

The proximal end of the first ceratobranchial is broad, and merges indistinguishably into the cartilage of the hypobranchial plate. It bears a backwardly directed spicule of cartilage (*sp*¹, fig. 1). The second ceratobranchial (*cbr*², fig. 1) is bound by connective tissue to the posterior surface of the first ceratobranchial, to the median side of this spicule. The proximal part then curves upwards and backwards, and giving off a backwardly directed spicule of its own, diminishes in thickness and becomes continuous with the cartilage of the proximal end of the third ceratobranchial, just where the latter unites with the hypobranchial plate². The third ceratobranchial curves over in a similar manner, and has its own spicule (*sp*³, fig. 1). The fourth ceratobranchial is broader and far more irregular in shape than the other three. It curves up, is confluent with the hypobranchial plate, and sends backwards a curved cartilaginous process, which may possibly represent the spicule of this arch. It should be noted that the whole of the cartilage of the branchial plate is continuous throughout. This continuity is obvious at the distal ends of the arches, but, on account of the sharp curvature of the

¹ Schulze (18. p. 11) and Naue (9. p. 14) seem to regard the front wall belonging to the first ceratobranchial as a thin, continuous, concave plate of cartilage in the forms of Anura which they respectively studied. The plates are probably subject to a great amount of individual variation, but in none of the numerous larvæ which I have examined (*Rana*, *Bufo*, *Alytes*, *Pelobates*, *Pelodytes*, *Hyla*) have I found the wall nearly so continuous and entire as in *Xenopus*.

² I fail to see the force of Gaupp's argument (5. p. 403) for considering the parts of the first two branchial bars lying internal to their spicules as belonging to the hypobranchial plate rather than to the ceratobranchials (branchialia) themselves.

proximal ends and the consequent angle which they make with the plane of the hypobranchial plate, it requires very careful observation to demonstrate the fact in this region. The only fibrous connection is that between the first and second ceratobranchials just anterior to the second spicule. The spicular cartilages are definitely continuous with the cartilage of the ceratobranchials, and do not give one the impression of their having arisen independently. These spicules (I have adopted Gaupp's name for these processes) of the Anuran larva have been the subject of a good deal of controversy by reason of the interpretation which Parker put upon them in his third contribution to our knowledge of the skull of *Batrachia* (12). I have already in an earlier communication (16. p. 113) expressed my views on the subject and do not propose to discuss the matter farther. My observations on the specimens which form the subject of this paper tend to confirm the view of Gaupp (5. p. 408), that the spicules have no morphological value, but that they are merely processes of cartilage developed from the proximal ends of the ceratobranchials to support the horizontal fold or velum which covers over the anterior half of the branchial cavity, and which undergoes reduction at the same rate as the spicules.

The mandible is quite diminutive, and consists of four subequal cartilages. The median pair of these (*m*, fig. 1) carry the lower horny beak, the lateral pair (*m'*) are articulated with the palatoquadrate cartilage.

STAGE 2. *Distance from snout to root of tail, 20 mm. Tail at its maximum development, 28 mm. in length. Length of hind limb, extended, 21 mm. Fore limb not yet extended. Horny beaks still present.* (Plate XXXV. fig. 2.)

But few differences are to be noted between this and the preceding stage. The whole skeleton is considerably larger, the hyoglossal notch is more rounded than before, and the four constituent cartilages of the mandible are beginning to straighten out. Except for these features the description already given of the hyobranchial skeleton in the first stage would apply equally well in this Stage 2. In fact, my chief object in introducing this into the series was to show that the hyobranchial skeleton attains its maximum larval dimensions without any appreciable change in shape.

STAGE 3. *Distance from snout to root of tail, 16 mm. Length of tail, 20 mm. Length of hind limb, extended, 19 mm. Length of fore limb, extended, 8 mm. Horny beaks no longer present.* (Plate XXXV. fig. 3.)¹

The metamorphosis of the hyobranchial skeleton is now

¹ I have here given the measurements of the specimen the hyobranchial skeleton of which is shown in fig. 3. It will be observed that the specimen is smaller than the average; but if all the above measurements be multiplied by $\frac{5}{4}$ the figures will be seen to be intermediate between those of the specimens chosen to represent Stages 2 and 4.

beginning. The hyoidean constituents are slightly larger than before, and the branchial are smaller. There is still a triangular space on either side of the basihyal: the spicula of the ceratobranchials are shortening up. The most interesting feature to be noted in this stage is the fenestration of the hypobranchial plate in those regions situated immediately over the thyroid bodies. The cartilage in the area marked *tf.* in fig. 3 is extremely thin, and becomes converted into a distinct perforation in Stage 4. The postero-internal margin (*t*) of the incipient foramen soon becomes rod-like. It enlarges rapidly, and when, later, the absorption of the external boundary causes the thyroid foramen to open laterally, it becomes recognizable as the thyrohyal (*t*, figs. 4-7). When recounting recently the mode of development of the hyobranchial skeleton of *Pipa*, it was with considerable hesitation that I described (16. p. 106 *et seq.*) the thyrohyals as persistent parts of the hypobranchial cartilage left by the perforation of the plate and the subsequent conversion of the foramina into deep sinuses. This view of the mode of development was so opposed to all preconceived notions that it seemed little short of heresy to give expression to it, and it was only after repeated examinations of the specimens that I could bring myself to publish the observation. The present discovery of a similar origin of the thyrohyals in a less aberrant type of Batrachian not only confirms my former view, but opens up the broader question whether, after all, this may not be their normal mode of development in Anura. A glance at figs. 3, 4, and 5 shows that the thyrohyals are terminated by those processes which, following Gaupp, I interpret as the spicula of the fourth branchial arch. These might easily be mistaken for the free ends of newly outgrowing thyrohyals, although, as a matter of fact, they are absorbed with the ceratobranchial cartilages, leaving the extremities of the true thyrohyals freely exposed. And thus become reconciled the apparently conflicting views of Saint-Ange (17. pp. 410 and 417), who considers the thyrohyals as the persistent spicules of the fourth branchial arch, and Cuvier (3. p. 397), Rathke (14. p. 39), Dugès (4. pp. 99, 101, 102), Stannius (19. p. 65), Götte (6. p. 332), Parker (11. pp. 164, 170, 171, 185, and 12. p. 259), and Gaupp (5. pp. 422 and 433), who regard them as outgrowths of the hypobranchial plate situated behind and to the mesial side of the fourth branchial arch. The alternative view that the thyrohyals of Anura are persistent ceratobranchials has been supported by Reichert (15. pp. 59 and 258), by Owen (10. p. 90), by Parker, who in his textbook (13. p. 173) unfortunately departs from the views expressed in his memoirs (*l. c.*) and states that the thyrohyals are the fourth ceratobranchials, and by Walter (21) and Cope (2. p. 234), who accept Parker's determination without reserve. Stöhr (20. p. 84), also, ventures upon a positive statement in favour of the thyrohyal being the ventral or proximal end of the fourth branchial arch; and that he does not mean by this the hypobranchial constituent of the arch is evident from his

criticism of Parker's paper contained in the footnote which he appends. The mode of development of the thyrohyals of *Pelodytes* by the formation of thyroid foramina and their subsequent disruption is calculated to shake one's faith in the recognition in the thyrohyals of Anura of late and rapidly developing fifth ceratobranchials as suggested by Meckel (8. p. 240) and Cuvier (3. p. 397); and, although the arguments which I have previously adduced in favour of this view (16. p. 112) still hold good, I must confess to entertaining a suspicion that, after all, these bones belong to the hypobranchial rather than to the ceratobranchial part of the visceral skeleton.

The mandible no longer exhibits the sharp angulation of its earlier stages. It is considerably longer than before, but the four constituents can still be clearly recognized. The membrane on the internal or mesial surface of the ramus is much thickened, and it is this which, when ossified, becomes the angulosplenial bone. There is as yet no trace of a dentary.

STAGE 4. *Distance from snout to root of tail, 20 mm. Length of tail, 23 mm. Length of hind limb, extended, 28 mm. Length of fore limb, extended, 12 mm.* (Plate XXXV. fig. 4.)

The whole aspect of the hyobranchial skeleton is beginning to change. The ceratohyals are now massive cartilages at their maximum of development, and they slope more posteriorly than before. The hyoglossal notch is both broader and deeper than in Stage 3. The triangular space on either side of the basihyal has now become filled up, not by encroachment of the surrounding cartilages, but by the differentiation of new cartilage: the outlines of the three cartilages bounding the former space are still very clearly marked. There are unmistakable signs that the branchial skeleton is past its prime. The arches exhibit a condition of incipient collapse, but are not very much smaller than in the preceding stage. The spicula have almost disappeared. There is a stump remaining of that of the second ceratobranchial, and the developing thyrohyal is still tipped with a remnant of that cartilage which probably represents the fourth spicule, but the first and third spicules have been completely absorbed. The thyroid foramen (*tf.*, fig. 4) is now a distinct perforation of the cartilage, and the thyrohyal is beginning to assume shape.

Lying at the bottom of the laryngeal sinus, between the two thyrohyals, is a tract of soft cartilage of crescentic form which only in this stage acquires a definite outline. The sinus in which it lies has been increasing in size from the very first stage, and, as will be seen by referring to the figures 5-8, continues on the increase. In the first three stages the loose cartilage occupies a larger proportion of the space, but the tissue is of such an ill-defined character that it is a matter of personal opinion whether to regard it as cartilage at all; and, on account of its undifferentiated nature, it is impossible to recognize its posterior limit. It is therefore omitted in the first three figures. The cartilage is in

the later stages gradually absorbed from behind, and disappears altogether at about Stage 8.

The mandible has elongated considerably, and the articular ends have lost the sharp bend which they possessed during the first three stages. The four segments of the mandible are still just recognizable. The angulosplenic and dentary ossifications of the perichondrium (*as.* and *d.*, fig. 4) are both present, but they are very fibrous and perfectly flexible.

STAGE 5. *Distance from snout to root of tail, 20 mm. Length of tail, 8 mm. Length of hind limb, extended, 30 mm. Length of fore limb, extended, 12 mm. (Plate XXXV. fig. 5.)*

The branchial skeleton is in an advanced stage of reduction, and its maximum width is considerably smaller than the width across the hyoidean cornua, which has not been the case previously. The specimens of this stage which I have examined confirm my previous observation with regard to the branchial skeleton of *Pipa* (16. p. 105) that there is a marked shrinkage of the cartilage, and consequently of the clefts, before the latter are broken open by the absorption of the cartilage. The three clefts in the branchial plate are, in this stage, still enclosed by the cartilage, but they are not more than one-half of the length of the clefts in Stage 4. There are marked indications that, as in *Pipa* (16. p. 106), the first commissural cartilage to yield is that joining the first and second ceratobranchials. The thyrohyals have enlarged considerably, and are composed of a firm hyaline cartilage in sharp contrast with the softer, whiter, and more opaque cartilage of the parts of the branchial skeleton undergoing absorption. The thyroid foramen is also larger than before, and there now remains but a thin neck of cartilage between it and the first branchial cleft; so that the second and third ceratobranchials appear to be connected with the hypobranchial parts of the skeleton by a common isthmus, while the first and fourth ceratobranchials are attached more directly. These facts were to be observed in Stage 4, but are more obvious here in consequence of the branchial skeleton being flatter.

There is still recognizable on the anterior edge of the second ceratobranchial the cartilaginous promontory which was in the earlier stages bound to the first ceratobranchial by fibrous tissue. The ceratohyals are directed more backwardly than in Stage 4, the outlines of their inner edges are becoming obscured, and, curiously enough, more removed from one another—a fact which is emphasized still more in Stage 6. The basihyal is still recognizable, but its contour is becoming fainter. The hyoglossal notch or sinus is now at its maximum size.

The mandible is of large size and is distinctly U-shaped. There are now only two segments to the mandible, the more median parts (the lower labial cartilages of Parker) having fused with the more lateral parts. The angulosplenic and dentary ossifications are much larger than before.

STAGE 6. *Distance from snout to root of tail, 19 mm. Length of tail, 2.5 mm. Length of hind limb, extended, 27 mm. Length of fore limb, extended, 11 mm. (Plate XXXV. fig. 6.)*¹

At this stage the branchial arches are on the verge of dissolution, and it requires the very greatest care in dissection to avoid losing the relations of the dismembered parts. The whole aspect of the hyobranchial skeleton has changed. In the middle is a faint Y-shaped mark representing the lines of junction of the two hypo-branchial plates and the basihyal. The mesial edges of the ceratohyals can still be identified, but they are wider apart than before. The hyoglossal notch is reduced in size by the addition of cartilage (*pa.*, fig. 6) to the front half of the antero-internal free edges of the ceratohyals. Although this new cartilage is confluent with that of the ceratohyal, what was previously the edge of the latter is still well-marked, thus showing that the new process is not due to an outgrowth of the original hyoidean cartilage. These new cartilages represent the anterior processes of the hyoid apparatus of the Frog (*pa.*, fig. 11) which develop late and about this stage. In fact, the figure which Gaupp gives of the hyoid of the metamorphosing tadpole of *Rana fusca* with tail reduced to 5 mm. (5. Taf. 19. fig. 8) agrees tolerably well with fig. 6 of *Pelodytes*. Gaupp applies the name "processus anterior" indifferently to the most anterior point of the original ceratohyal ("hyale") and to the later developed cartilage which constitutes the foremost part of the adult hyobranchial skeleton; but, seeing that the latter has a morphological significance different from the former, and is, moreover, absent in such genera as *Alytes*, *Discoglossus*, and *Bombinator* possessing the former, I have elected to restrict the application of the term to the latter. Parker's terminology does not help matters, but rather tends to confusion, for he marks these anterior processes of the adult hyoid as parts of the ceratohyals (12. pl. 13. fig. 10), as hypohyals (pl. 5. fig. 4), as epihyals (pl. 15. fig. 14), and as extrahyals (pl. 43. fig. 6), without offering any explanation of the want of uniformity.

The backward slope of the ceratohyals is now very strongly marked and the posterior parts are becoming reduced in width. The terminal articular surface is quite small compared with its previous extent, and the articulation will shortly give place to a rigid connection with the auditory cartilage. The thyrohyals continue to grow, but their posterior extremities are still capped with unabsorbed ceratobranchial cartilage. The outlines of the branchial arches are very indistinct, the softness of the cartilage making it difficult to distinguish them from the surrounding connective tissue and pharyngeal mucous membrane. The tri-radiate cartilage at the proximal end of the second and third branchial arches appears to be constant in its occurrence, and is

¹ These measurements are those of the figured specimen, which is slightly smaller than the average; but if the above figures be multiplied by $\frac{1}{10}$ the measurements will be seen to be intermediate between those of the specimens representing Stages 5 and 7.

evidently to be regarded as the remnant of the external boundary of the thyroid foramen.

Probably the most important fact from a morphological point of view to be learned from this stage is the mode of formation of the postero-lateral processes of the hyobranchial skeleton of the adult (*ppl.*, fig. 9). The proximal portion of the first ceratobranchial does not share in the general absorption of ceratobranchial and commissural cartilage, but is continued as a tapering central core into the middle of the distal part of the arch, which is disintegrating. This central core is of firm cartilage similar to that of the hypobranchial plate and has a sharp contour. The postero-lateral process of the adult is formed by the subsequent enlargement of this persistent proximal portion of the first ceratobranchial, and the sinus which in the later stages exists between the postero-lateral process and the thyrohyal lies morphologically between the cartilage bounding the second branchial cleft antero-externally and the cartilage which forms the postero-internal border of the thyroid foramen. Saint-Ange (17. p. 418, *Rana*), Dugès (4. pp. 98-99, pl. 13. figs. 76-79, *Pelobates*), and Götte (6. figs. 332-334, *Bombinator*) are all agreed that the process in question is either the persistent basal portion of the first branchial arch or else an outgrowth of that part of the hypobranchial plate with which the first branchial arch was formerly united¹.

On the under surface of the hyobranchial skeleton the ventral splint-bone has appeared, but it is not yet adherent to the cartilage. It is a single bone from the first, and is not formed by the coalescence of a pair. The mandible is now shaped as in the adult, and except in size and the extent of ossification does not differ materially from that of the latter.

STAGE 7. *Distance from snout to cloaca, 21 mm. No tail. Length of hind limb, extended, 30 mm. Length of fore limb, extended, 12 mm. (Plate XXXV. fig. 7.)*

Those parts of the branchial skeleton which were undergoing absorption in the preceding stage have now completely disappeared, so that the thyrohyal is separated from the postero-lateral process by a deep sinus as in the adult. The basal plate or body of the hyoid is now a continuous sheet of cartilage in which the outlines of the five constituent parts can no longer be distinguished, except that there still exists near the middle the Y-shaped mark adverted to in the description of Stage 6. Whether the hyoglossal notch deepens by absorption of the cartilage of the basal plate as, according to Gaupp (5), occurs in *Rana fusca*, I am unable definitely to say. There is no trace of the soft cartilage which is

¹ Since Gaupp (5. p. 428) has already exposed the fallacy of Parker's views on the mode of origin of the antero-lateral and postero-lateral processes of the Frog's hyobranchial skeleton, and has called attention to the confusion which Walter (21. p. 6) has introduced into the subject by calling the antero-lateral process the "hypohyale,"—the result of a mistaken reading of Parker's text-book (13. p. 173),—I refrain from further criticism of these works.

usually to be found in regions where such absorption is proceeding, but at the same time the general proportions of the basal plate suggest that it is quite possible that this process does take place. The newly added cartilages (*pa.*, fig. 7) at the inner edges of the anterior ends of the hyoid arch are now directed towards one another, having lost their forward slope; and the line of junction between them and the original hyoidean cartilage is still apparent. The greater part of the ceratohyal has become diminished in thickness so as now to have the form of a bent rod of approximately uniform diameter. About the level of the bottom of the hyoglossal sinus the ceratohyals exhibit the first indications of the absorption which later results in the dismemberment of the arch (*h.*, fig. 7). A new notch or sinus (*fl.*, fig. 7) has developed at the side of the basal plate, mainly by the absorption of the cartilage in that position. But the sinus is rendered more complete by the simultaneous outgrowth of a process (*pal.*, fig. 7) which is to be identified with the antero-lateral or alary process of the hyoid apparatus of the Frog (*pal.*, fig. 11). In consequence also of this outgrowth of cartilage the middle of the three lateral sinuses, that between the antero-lateral and the postero-lateral processes, is beginning to make its appearance.

STAGE 8. *Distance from snout to cloaca, 17 mm. Length of hind limb, extended, 25 mm. Length of fore limb, extended, 9 mm. (Plate XXXV. fig. 8.)*¹

The basal plate or body of the hyoid is now small in proportion to the size of the outstanding processes. The postero-lateral process (*ppl.*, fig. 8) is longer than before but not appreciably thicker; the sinus of which it forms the posterior boundary is much deeper than in the last stage. The antero-lateral process (*pal.*) has enlarged and is already somewhat dilated at its extremity. The first of the three lateral sinuses (*fl.*) has now the form of an ellipse, incomplete externally. One of the most noteworthy features about this stage is the separation of the distal part of the hyoidean cornu. The absorption of cartilage leading to such separation occurs antero-externally to the last-mentioned sinus, and the pointed form of the cartilage in this region shows that the dismemberment has only recently occurred. Now that the outlines of the constituents of the body of the hyoid have completely disappeared, it is very difficult to define the limits of that part of the ceratohyal which is not detached, but I should judge that a line drawn through the bottom of the hyoglossal sinus and through the middle of the lateral sinus marked *fl.* would indicate the proximal limit of the anterior or hyoidean cornu. The recently added anterior processes (*pa.*) are now indistinguishably fused with the cartilage of the ceratohyal and are directed backwardly as well as inwardly. It is curious to note how these processes first

¹ The above specimen, the hyoid of which is shown in fig. 8, happens to be slightly smaller than that representing Stage 7, but otherwise the two are perfectly indistinguishable externally.

slope inwards and forwards (fig. 6), then directly inwards (fig. 7), and afterwards inwards and backwards (fig. 8). They are nearly in contact in the middle line, and it requires but little additional growth to close the hyoglossal sinus and convert it into a foramen. The liberated part of the ceratohyal expands slightly behind its anterior pointed extremity and then diminishes again into a curved rod, the posterior end of which is attached to the back of the auditory capsule. The thyrohyals have increased in width at their posterior extremities, and, although they cannot yet be said to be ossified, the shaft is slightly more opaque than the cartilage of the epiphysis behind and the basal plate in front. The ventral ossification is disposed as in the adult, but its postero-lateral rays are very short. The anterior parts of the mandibular cartilage have not yet ossified to form the mentomeckelian bones.

STAGE 9. *Adult. Distance from snout to cloaca, 37 mm. Length of hind limb, extended, 62 mm. Length of fore limb, extended, 26 mm. (Plate XXXV. fig. 9.)*

Since the structure of the adult hyobranchial skeleton has already been described in the opening paragraphs, it will be sufficient to confine attention here to those changes which have occurred since Stage 8. The differences in appearance are due chiefly to the addition of cartilage to the periphery. This marginal addition in the case of the anterior part of the hyoid arch and the antero-lateral process has been so great as to completely enclose the first of the three lateral sinuses, forming a lateral foramen. The anterior processes of the hyoid have grown inwards in front of the hyoglossal sinus so as to touch one another, or even to overlap. It is only by analogy with the Frog that the term "processus anteriores" is applied to these enclosing cartilages; it is highly probable that the most anterior points of the hyobranchial skeleton belong to the original hyoidean cartilage and not to these processes (*cf.* figs. 7 and 8).

The postero-lateral process has developed an irregular plate of cartilage at its extremity, and, since the extremity of the antero-lateral process has grown backwards as well as forwards, the middle of the three lateral sinuses exhibits a tendency to become enclosed and converted into a foramen like that situated in front of it. The thyrohyals are now completely ossified and are more parallel than before. The postero-lateral rays of the ventral splint-bone have increased in length and underlie the anterior parts of the thyrohyals. The free parts of the hyoidean cornua are variable in shape, but the anterior end is always flat and lamellar, while the posterior has the form of a curved rod of cartilage. A comparison of this stage with the two preceding shows that the part of the hyoidean cornu missing is quite inconsiderable, and is to be estimated by the mean distance from the point marked *h* in fig. 9 to the anterior extremity of the detached part of the arch. Mentomeckelian bones are now present, and are inseparable from the dentary membrane-bones. They are not, as might be supposed,

the ossified median constituents of the larval mandible (lower labial cartilages of Parker), the outlines of which disappeared between stages 4 and 5.

SUMMARY.

The almost complete closure of the hyoglossal sinus of *Pelodytes* (*hgs.*, fig. 9) is due to the extensive development and inward slope of the processus anteriores (*pa.*, fig. 9).

The lateral foramina of *Pelodytes* (*fl.*, fig. 9) are not primary fenestrations of the basal plate, but are formed by the enclosure of the foremost lateral sinus by the confluence of the expanded end of the processus antero-lateralis with the cartilage of the hyoidean cornu.

Although in *Pelodytes* the hyoidean cornu (*h, h', h''*, fig. 9) is broken, the portion missing is comparatively insignificant.

The spicula (*sp.*, fig. 1) are larval structures of no morphological significance. They are processes of cartilage developed from the proximal ends of the ceratobranchials to support the horizontal pharyngeal velum.

The processus postero-lateralis (*ppl.*, fig. 9) is the persistent proximal portion of the first ceratobranchial.

The processus antero-lateralis (*pal.*, figs. 8 & 9) is a secondary outgrowth of the basal plate or body of the hyoid having no relation whatever to the larval branchial bars.

The thyrohyal (*t.*, fig. 9) is the part of the hypobranchial plate of the larva which forms the inner boundary of the thyroid foramen (*tf.*, fig. 4). Its posterior end becomes free on the absorption of the ceratobranchials and the consequent conversion of the foramen into a sinus.

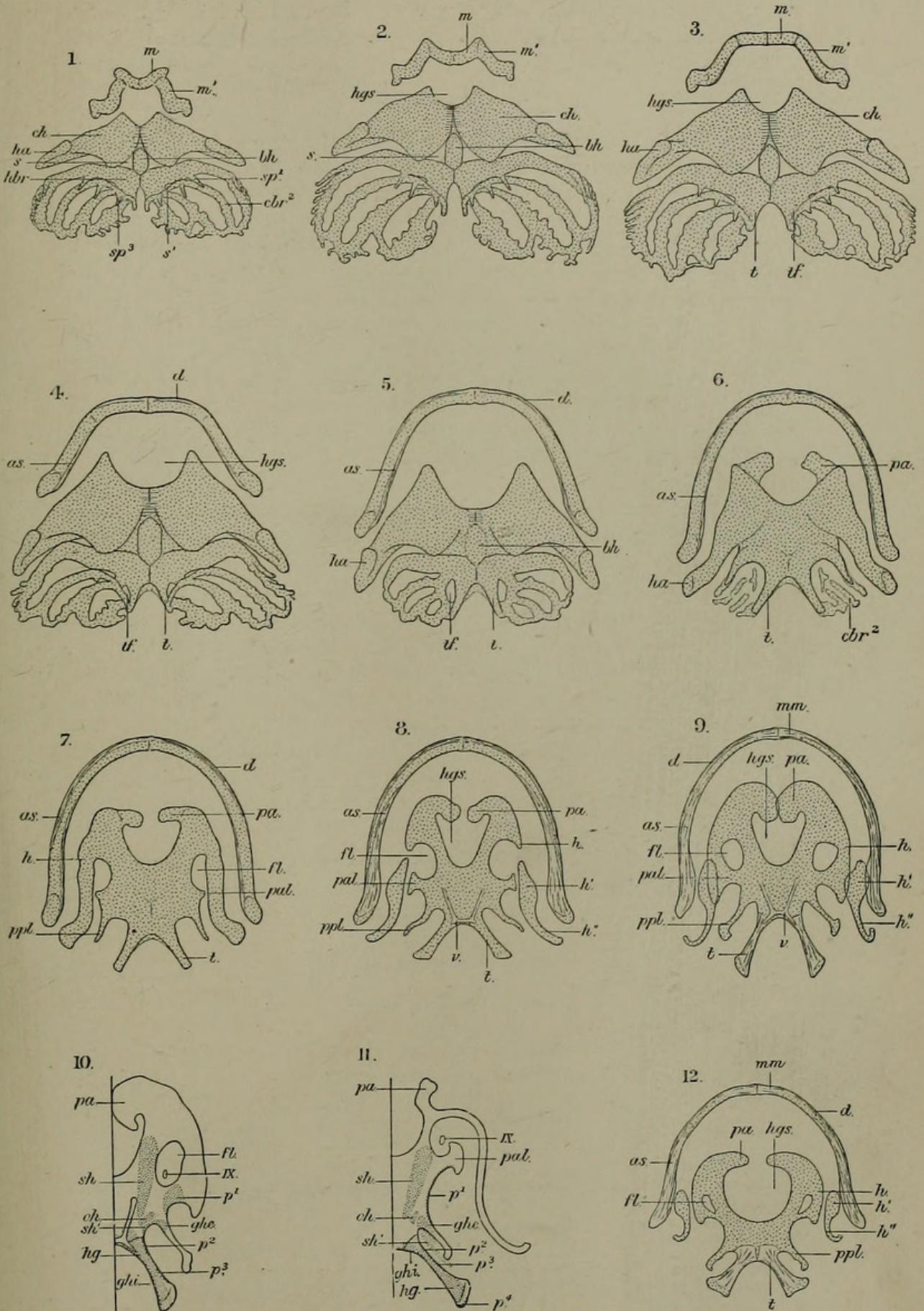
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EXPLANATION OF PLATE XXXV.

- Fig. 1. Hyobranchial skeleton and mandible of *Pelodytes punctatus*. Stage 1 (see p. 582). Dorsal view. ($\times 4$.)
2. Same. Stage 2 (see p. 585). Dorsal view. ($\times 4$.)
 3. Same. Stage 3 (see p. 585). Dorsal view. ($\times 4$.)
 4. Same. Stage 4 (see p. 587). Dorsal view. ($\times 4$.)
 5. Same. Stage 5 (see p. 588). Dorsal view. ($\times 4$.)
 6. Same. Stage 6 (see p. 589). Dorsal view. ($\times 4$.)
 7. Same. Stage 7 (see p. 590). Dorsal view. ($\times 3\frac{3}{4}$.)
 8. Same. Stage 8 (see p. 591). Ventral view. ($\times 3\frac{3}{4}$.)
 9. Same. Stage 9, adult (see p. 592). Ventral view. ($\times 2$.)
 10. Half of the hyobranchial skeleton of *Pelodytes punctatus*, adult male, showing the areas of muscle insertion. Ventral view. ($\times 2\frac{3}{4}$.)
 11. Half of the hyobranchial skeleton of *Rana temporaria*, adult male, showing the areas of muscle insertion. Ventral view. ($\times 1\frac{1}{2}$.)
 12. Hyobranchial skeleton and mandible of *Pelobates fuscus*, adult male. Ventral view. ($\times 1\frac{1}{2}$.)



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HYOID OF PELODYTES PUNCTATUS.



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