ON THE NATURE OF THE CRANIOFACIAL APPARATUS OF PETROMYZON, by T. H. Huxley, *Sec. R.S.*

In the first part of the 'Vergleichende Anatomie der Myxinoiden,' published in 1835, Johannes Müller gave an exact and exhaustive account of the form and arrangement of the various parts which make up the cartilaginous skeleton of the skull and face in the Lampreys. He distinguishes a 'Hirn-capsel' or *brain case;* two 'Gehör-capseln' or *auditory capsules;* a 'Nasen-capsel' or *olfactory capsule;* and 'Gesichts-knochen' or *facial cartilages.* The latter are, in front, a 'Ringförmige knorpel-stuck' or *annular cartilage;* two 'Griffel-förmige Knochen' or *styliform cartilages,* connected by their anterior ends to the annular cartilage and by their posterior ends giving attachment to lateral muscles; a 'vordere grosse Mundschild' or *anterior dorsal cartilage;* a 'hintere Mundschild' or *posterior dorsal cartilage;* two vordere Seiten platten' or *antero-lateral cartilages;* and two 'zweite Seiten platten' or *postero-lateral cartilages.*

The *Brain case* consists of a *basilar plate,* the centre of which is traversed by the anterior end of the notochord. This is continued superiorly into the narrow *occipital arch,* which forms the only cartilaginous part of the roof of the skull; while laterally it passes into two cartilaginous bars, which bound the lower lateral regions of the skull. The brain rests upon a fibrous membrane stretched between these, which may be termed the *sub-cerebral membrane.* The inner and ventral edge of each of these *lateral bars* of the skull is continued into a solid cartilaginous floor, which lies between the naso-palatine canal and the mucous membrane of the mouth. Müller terms this the *hard palate.* It terminates behind by an excavated edge between the *auditory capsules;* while, in front, it is closely united with the hinder edge of the posterior dorsal cartilage. The olfactory capsule rests on this cartilage, and is united with the lateral bars of the skull, and the naso-palatine canal extends backwards, between the sub-cerebral membrane and the hard palate, to terminate in a cæcal dilatation behind the posterior edge of the latter.

Fig. 1.

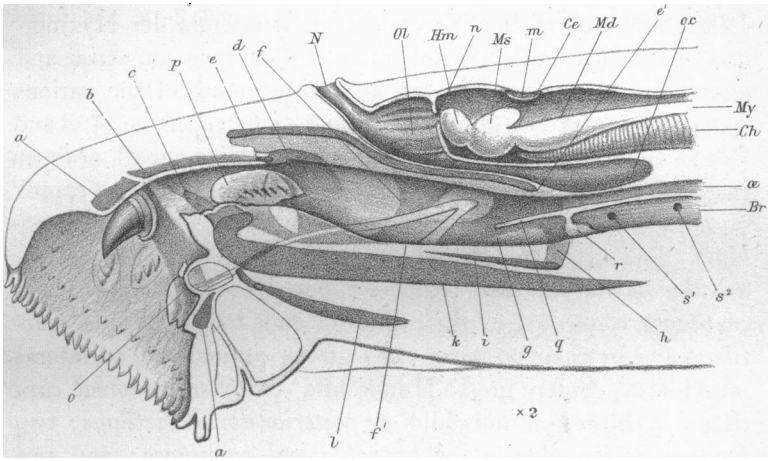
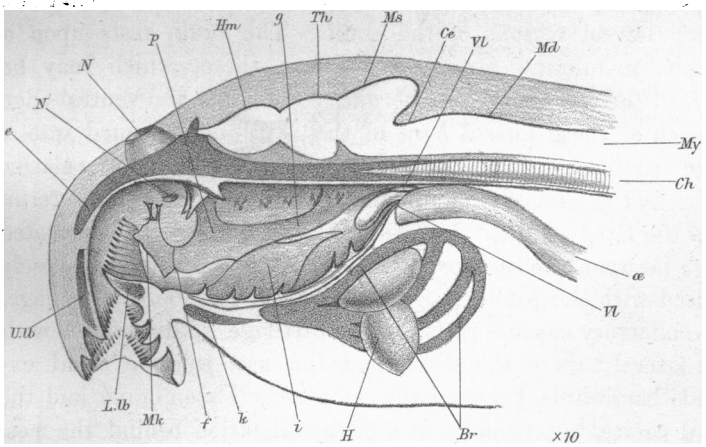


Fig. 2.



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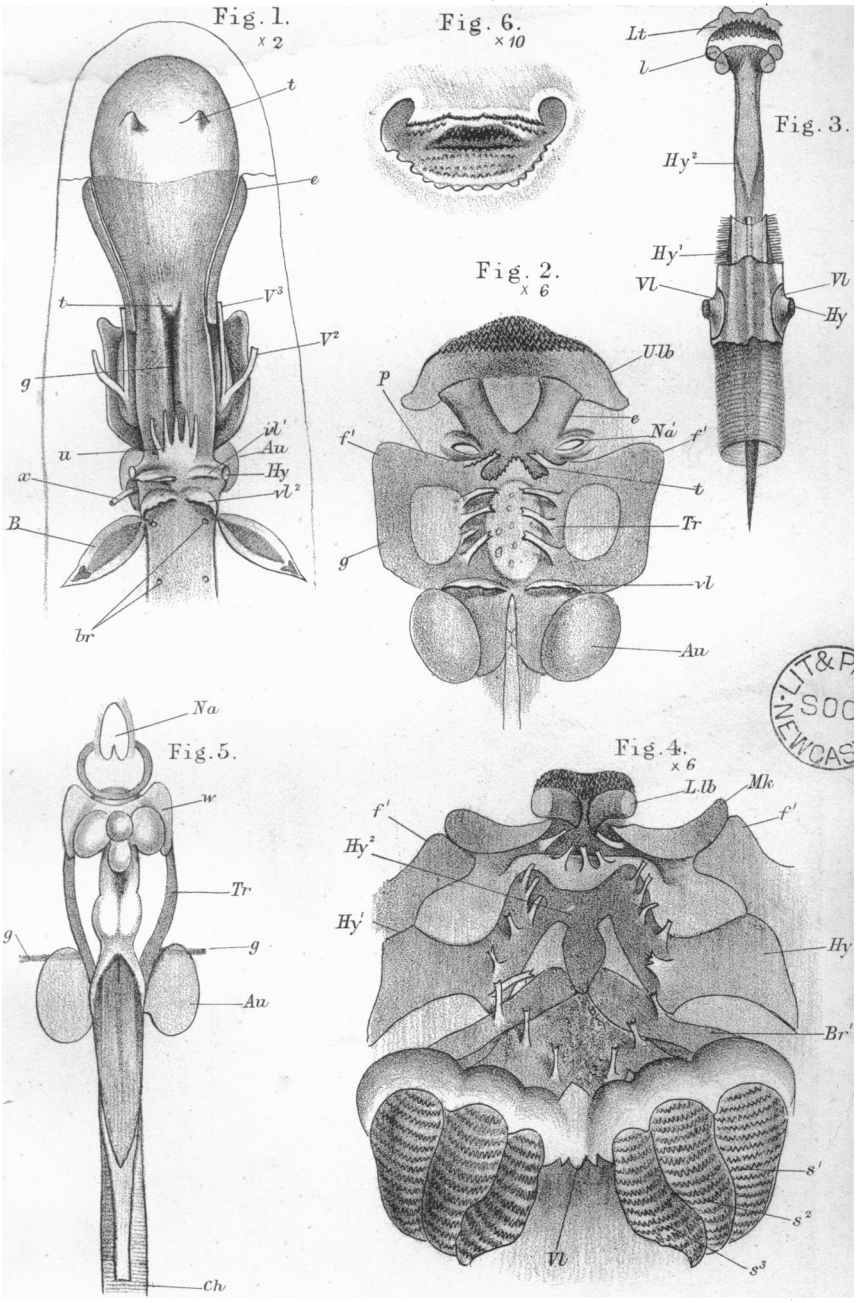

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The anterior end of the hard palate is prolonged outwards and downwards on each side into an *anterior lateral process* (Vorder-seiten Fortsatz); this meets at an acute angle with a *posterior lateral process* (Hinter-seiten Fortsatz), which at its dorsal end is closely connected with the auditory capsule. Diverging from the dorsal or attached extremity of this, at an acute angle, is the downwardly directed *styliform process* (stielförmige Fortsatz, *i*). With the ventral extremity of this, the elongated horizontally directed *cornual cartilage* ("Knorpelplatte, am Fortsatz *i* befestigt; dient zur Befestigung der Zungenmuskeln") is connected.

In the middle ventral line is the long *lingual cartilage* ("knorpeliger Stiel der Zunge"), which is pointed behind, but bifurcates in front, the two short branches supporting the lobes of the tongue.

On the ventral side of this is another, elongated, but much shorter cartilage, the *median ventral cartilage* ("Zungenbein"), the anterior end of which is transversely enlarged, and lies immediately on the ventral side and in front of the anterior end of the lingual cartilage. The extremities of the anterior end of this cartilage are connected with the antero-lateral cartilages, which again are united by ligamentous fibres with the inner surface of the anterior dorsal cartilage close to its anterior edges.

Müller considers that the annular cartilages answer to the labial cartilages of the Elasmobranchs; that the styliform process and the cornual cartilages, with the median ventral cartilage, correspond with parts of the hyoidean arch in other Vertebrata; that the lateral bars of the skull are the homologues of the palatine bones of the latter; and that the inverted subocular arch formed by the anterior and posterior lateral processes corresponds with the "temporale, tympanicum, jugale, transversum, pterygoideum (?) of Cuvier" in Osseous Fishes (l. c. p. 163). He is further of opinion that the posterior dorsal cartilage has nothing to do with the skull, and that, together with the anterior dorsal cartilage and the lateral cartilages, it forms a series of structures special to the Lampreys and not represented in other Vertebrates (l. c. p. 164).

Agassiz, in the "Recherches sur les Poissons fossiles" (Tome 1,

1835—43), availing himself of Müller's description and figures, and of the embryological investigations of Vogt, makes a most important rectification in the nomenclature of the parts.

In describing the skull of *Ammocœtes branchialis* (p. 113) he justly states that it corresponds with that of the embryo at the moment of the first appearance of cartilage. "The point of the notochord advances freely into the space comprised between the 'anses latérales' absolutely as in the embryo of Salmonidæ."

In *Petromyzon* he recognizes the "anses latérales" in the lateral cranial bars described by Müller and regarded by him as palatines. The subocular arch is the "*arc pterygoidien*," which, in the Cyclostomes, as in embryos, is not yet separated from the cranium by articular faces[1]. The styliform cartilage is considered to be the hyoid, while the other cartilages are reckoned as labial.

In 1844—6, Professor Owen[2] gave the following account of the structure of the lamprey's skull.

"In the lamprey (*Petromyzon*, fig. 26) the occipital cartilage is continued backwards in the form of two slender processes (*c*) upon the under part of the chorda dorsalis (*ch*) into the cervical region. The hypophysial space (*hy*) in front of the occipital cartilage remains permanently open, but has been converted into the posterior aperture of the naso-palatine canal. The sphenoidal arches (5) are very short and approximated towards the middle line and the presphenoid and vomerine cartilage (13) is brought back closer to the sphenoidal arches. Two cartilaginous arches (24) circumscribe elliptical spaces outside the presphenoid plate: these appear to represent the pterygoid arches, but, as in the embryo of higher fishes, are not separated from the base of the skull by distinct joints. The basal cartilages after forming the ear capsules (16) extend upwards upon the sides of the cranium (fig. 11), arch over its back part, and leave only its upper and middle part membranous, as in the human embryo, when ossification of the cranium commences. Two broad cartilages (*ib.* 20, 21) may represent upon the roof of the infundibular suctorial mouth the palatine and maxillary bones, and anterior to these there is a labial cartilage (*ib.* 22). There are likewise cartilaginous processes (*ib. r. s.*) for the support of the large dentigerous tongue and the attachment of its muscles." *l. c.* pp. 72, 3.

It appears from the context (p. 71) that by "sphenoidal arches" Professor Owen means the *trabeculæ cranii* of Rathke,

[1] l. c. p. 114. At p. 132, what is here termed "*arc pterygoidien*," is named "*arc palatin*."

[2] Lectures on the Comparative Anatomy and Physiology of the Vertebrate Animals, 1846.

as he applies the term to the *anses latérales* described by Vogt in *Coregonus*, which are nothing but these *trabeculæ*, and the homology of which with the lateral bars of the cranium in the lampreys, had already been pointed out by Agassiz.

In 1858 I stated that "the skull of the lamprey is readily reducible to the same plan of structure as that which is exhibited by the tadpole, while its gills are still external and its blood colourless[1]," having been led to that conviction by a careful study of the early stages of development of the frog's skull.

In 1863[2] I expressed this view more fully, and compared the margin of the oval space upon the base of the skull to the divergent *trabeculæ cranii*, as Agassiz had originally done, and the posterior dorsal plate to the ethmo-vomerine cartilage. I expressed the opinion that the inverted cartilaginous arch which gives attachment to the hyoidean and mandibular apparatuses of a tadpole is "strictly comparable" to the subocular arch of the lamprey; but I added a doubt "whether the accessory buccal cartilages can be strictly compared to anything in other fishes, though some of them are doubtless, as Müller has suggested, the analogues of labial cartilages." I gave a figure (Fig. 75) shewing the true relation of the skeleton to the enclosed soft parts in *Petromyzon marinus*.

In his masterly monograph upon the cephalic skeleton of the Selachians[3], Gegenbaur explains that he has taken the skull in the Selachians and not that of the more lowly organized Cyclostome for the starting-point of his investigations, because the latter are in many respects abnormal and so much less directly affiliated with the other Vertebrata, that it is not wise to attempt to begin with them. He approves of the sharp line of demarcation which Haeckel has drawn between the Lampreys and Hags, as *Monorrhina*, on the one hand, and all the higher Vertebrata, as *Amphirrhina*, on the other; and though he admits the possible correctness of the interpretation of some of the parts which I have given, he doubts whether it really tends to bridge over the hiatus.

[1] Croonian Lecture, *Proceedings of the Royal Society*, 1858.

[2] Lectures on the Elements of Comparative Anatomy, on the Classification of Animals, and on the Vertebrate Skull, 1864, p. 194.

[3] *Das Kopfskelet der Selachier*, 1872.

"Da mir das Knorpelcranium der Selachier zum Ausgangspunkt so wichtig erschien, weil es einen tiefer stehenden Zustand repräsentirt, bedarf es noch der Rechtfertigung wegen des Ausschlusses der Cyclostomen, die gleichfalls mit einem Knorpelskelete versehen und zudem noch in der ganzen übrigen Organisation eine tiefere Stufe einnehmend, jenen Anförderungen noch besser hätten entsprechen müssen. Darauf kann erwiedert werden, dass sowohl in dem Cranium wie in vielen Punkten ihrer übrigen Organisation die Cyclostomen bedeutend abweichende Verhältnisse darbieten und keinen so directen Anschluss an die übrigen Wirbelthiere bieten. Sie würden daher von Haeckel mit allem Recht als Monorrhina den Amphirrhinen gegenüber gestellt. Die darin ausgesprochene Auffassung kann kaum schärfer präcisirt werden. Von so abweichenden keine stricten Vergleichungen zulassenden Formen auszugehen, wäre kein glücklicher Gedanke. Wenn auch die Deutungen, welche Huxley einzelnen Theilen des Craniums gab, dasselbe dem Cranium der Amphirrhina näher gerückt scheint, so besteht darüber doch keineswegs Sicherheit. Die gewiss vorhandene Verbindung mit den Amphirrhinen mag noch zu weisen sein, aber die Entfernung, welche zwischen diesen und den Cyclostomen liegt, wird dadurch nicht vermindert."[1]

In describing the skull of *Menobranchus lateralis*[2], I have remarked that

"No known Elasmobranch, Ganoid, or Teleostean fish presents so incompletely developed a chondrocranium as that of *Menobranchus*. On the other hand, the latter is much like that of a Lamprey if we leave the ossification of the *Menobranchus* skull and the accessory cartilages of the *Petromyzon* out of consideration. And this fact, taken together with the curious resemblance in development between the Lampreys and the Amphibia (which are much closer than those between any of the higher Fishes and the Amphibia[3]) suggest to my mind the supposition that, in the series of modifications by which the Marsipobranch type has been converted into that of the higher fishes, the most important terms must have been forms intermediate in character between the *Dipnoi* and the Marsipobranchii." (*l. c.* pp. 197, 8[4]).

Finally, in a 'Preliminary Note upon the Brain and Skull of *Amphioxus lanceolatus*,' read before the Royal Society last year,

[1] Gegenbaur, *Das Kopfskelet der Selachier*, Einleitung, p. 9, 1872.
[2] *Proceedings of the Zoological Society of London*, 1874.
[3] Unfortuately we know nothing of the development of the *Dipnoi*.
[4] I have not yet had time to study Goette's large and elaborate work on the development of Bombinator igneus ("Entwickelungsgeschichte der Unke"), published this year, with the attention it deserves, but I notice at p. 692, the remark, that "der vollendete Zustand des Kopfes, wenigstens der Neunaugen ganz entschieden auf die Anuren-larven hinweist." I am further glad to find that Dr Goette takes the same view as I have done respecting the relations of the *Anura* with the Cyclostomes (p. 744).

I compared the skull of the Lamprey in its *Ammocœtes* stage with that of *Amphioxus*, with the view of shewing (1) that numerous anterior proto-vertebræ, answering to those which in the higher Vertebrata give rise to vertebræ (among other products of their metamorphosis), but which neither in the head, nor in any other part of the body of *Amphioxus* develope vertebræ, correspond with the region in which the chondrocranium is developed in the Ammocœte, and (2) that neither in the Ammocœte do these proto-vertebræ give rise to vertebræ, but that the brain-case, as in *Menobranchus*, is formed partly by the parachordal cartilages (which are chondrifications of the investing mass of the notochord, comparable to that which precedes the development of the vertebræ in the spinal column of the Frog); and partly by the trabeculæ which, in my view, are homologous with branchial arches[1]. In the Croonian Lecture to which I have already referred, the following passage occurs :—

"The cranium never becomes segmented into somatomes: distinct centra and intercentra like those of the spinal column are never developed in it. Much of the basis cranii lies beyond the notochord. In the process of ossification there is a certain analogy between the spinal column and the cranium, but that analogy becomes weaker and weaker as we proceed towards the anterior end of the skull.

Thus it may be right to say that there is a primitive identity of structure between the spinal or vertebral column and the skull; but it is no more true that the adult skull is a modified vertebral column,

[1] Goette has put forward a very different view of the nature of the trabeculae (l. c. p. 629). "The original foundation of the whole skull consists firstly, of the posterior basis cranii, a cartilaginous plate, which incloses the notochord, in which I distinguish, as in the trunk, an axial part, the notochord with its external sheath, and lateral plates homologous with the arches of the vertebræ." (This answers to what I have named the parachordal portion of the skull.) "To this are added the two pair of arches, which, as continuations of these lateral plates, at their anterior and posterior ends, embrace laterally, and eventually arch over the anatomical base of the fore-brain and a part of the hind-brain. This anterior pair of arches belongs therefore to the first segment of the body under discussion; it forms the first vertebral arch, which in agreement with the general position of this segment is horizontal. But it has no corresponding centrum—inasmuch as the axial structure by which the latter should be produced, the notochord, was drawn back from the fore-head (Vorderkopf) to the anterior margin of the hind-head." According to this interpretation, which is worthy of serious consideration, though I entertain grave doubts whether it can be sustained, the trabeculæ represent not the most anterior pair of visceral arches, as I have supposed, but the most anterior pair of neural arches. How this view is to be reconciled with the relations of the trabeculæ to the trigeminal nerve and to the organs of the higher senses, is not clear to me.

than it would be to affirm that the vertebral column is a modified skull."

The immense extension of our knowledge of the minute details of the structure and development of the vertebrate skull in the seventeen years that have elapsed since those words were written, and which is largely due to the investigations of Mr Parker, whose elaborate and numerous contributions to this difficult branch of anatomy seem hardly to be as well known as they ought to be abroad[1], has, so far as I know, revealed no fact inconsistent with their fullest signification.

The segments of the *Amphioxus* head are not vertebræ, and in the Lamprey, as in every known vertebrate animal, the cranial region takes on the characters of a skull without passing through any stage of vertebration[2].

At the end of my brief paper I stated that I proposed at some future time to shew "in what manner the skull of the Marsipobranch is related to that of the higher vertebrata, and more especially to the skull of the frog in its young tadpole state."

For this purpose it was needful to go over the structure of the lamprey's skull afresh, and unfortunately my supply of these fish was small, and I have been unable to procure fresh ones until recently. I have examined them by the ordinary way of dissection, and by making transverse sections which form admirable Canada-balsam preparations.

The dorsal wall of the circular lip which surrounds the mouth of the lamprey (Pl. XVII. Fig. 1) is longer than the ventral wall, and hence has the form of a hemispherical bell, set obliquely on to the body. On the ventral side, the lip is separated by a deep transverse constriction from the rest of the head, but this constriction dies away laterally, and hardly any trace of it remains on the dorsal aspect. The inner surface

[1] For example, I do not find Mr Parker's name in the long 'Autoren Verzeichniss' appended to Goette's work, though the memoir *On the Structure and Development of the Skull of the Common Frog*, the best piece of work of its kind which has appeared since Dugès' *Recherches*, was published in 1871.

[2] It is to be hoped that this statement will prevent persons of even the largest powers of misunderstanding from imagining that the demonstration of the multi-segmentation of the head of *Amphioxus*, is a relapse on my part into archetypal fancies such as those of which I endeavoured to shew the futility a score of years ago.

of the lip is beset with the well-known horny teeth, and its margins are provided with numerous short lamellar papillæ, of which those on the ventral side are the longest and largest.

The opening into the buccal chamber, in the posterior and dorsal region of the bell-shaped cavity of the lip, is small. Immediately below it is a projection (Pl. XVII. Fig. 1, *o*) convex forwards, flat or concave on its dorsal aspect, and having a horny envelope, the edge of which is produced into a number of denticulations, the longest of which is median. I shall term this the *mandibular tooth*. On the ventral side of it is a transverse fold which bears two papillary eminences. The *annular cartilage* (*a*) is lodged in the posterior part of the lip, and its ventral part lies just below this fold.

The *inferior median cartilage* (Pl. XVII. Fig. 1, *l*) lies beneath the integument, and separated from it by a large subcutaneous sinus[1], amidst the ventral muscles. The anterior edge of the cross-piece in which it terminates is connected by fibrous tissue with the support of the mandibular tooth. Behind the latter, the tongue (*p*) rises from the floor of the buccal cavity and nearly closes it. It is divided by a deep longitudinal groove into two lobes, united for a short distance in front. The opposed surfaces of these lobes present minute horny denticulations arranged in a curved anteroposterior series.

The *buccal cavity* itself has the form of an elongated tube with delicate and transparent walls. Its roof is folded longitudinally so as to form a groove (Pl. XVIII. Fig. 1, *g*) which is much deeper in front than behind. A small papillose elevation (*t*) bounds the anterior end of this groove, and for a short distance from its commencement its sidewalls are obliquely folded. This buccal portion of the alimentary canal terminates behind by dividing into two tubes, one of which lies on the dorsal side of the other, both occupying the median plane. The upper tube (Pl. XVII. Fig. 1, *œ*) is the very slender *œsophagus* which traverses the whole length of the branchial region to pass into the gastro-intestinal division of the alimentary canal. The lower, much larger tube is the so-called 'respiratory bronchus,' or *branchial*

[1] This communicates with the system of cavities described as Lymphatic by Langerhans. It contained blood in the specimens I examined. See Milne-Edwards' "Leçons," III. p. 369.

canal (*Br.*). The wall of the buccal cavity between these two tubes is produced into a sort of horizontal shelf, the free edge of which is directed forwards and is divided into five tentacular processes, of which the median is the shortest (Pl. XVII. Fig. 1, *f*; Pl. XVIII. Fig. 1, *u*). These overhang the entrance of the branchial canal, and doubtless serve to prevent the entrance of solid particles into it. Two small, flat pieces of cartilage which are wide in front and narrow behind, and are similar in colour to the other cartilages, support the horizontal shelf from which the tentacles spring. They diverge outwards and backwards towards the styliform processes. The axis of each tentacle and the middle of the 'shelf' between the two cartilages just described, are occupied by a colourless cartilaginous tissue. Behind and below this tentaculated shelf the entrance of the branchial canal is further protected by two folds of the lining membrane (Pl. XVII. Fig. 1, *r*; Pl. XVIII. Fig. 1, *v l*), the free edges of which are directed backwards and towards one another. The dorsal half of each of these valves is nearly vertical; the ventral half slopes backwards until it becomes nearly horizontal. These valvular folds constitute the *pharyngeal velum*, and are, doubtless, the metamorphosed velum of the Ammocœte. They must readily allow of the passage of water into the branchial canal, but must obstruct its exit[1]. Behind these, is another smaller and much more delicate pair of valvular folds (Pl. XVIII. Fig. 1, *vl*[2]), which when they flap back, cover the first internal branchial aperture. There is a depression behind each of the pharyngeal vela, and a bristle could sometimes be passed through the wall into a small space outside it. This I conceive to be the remains of the hyoidean cleft which opens externally in the Ammocœte[2].

When the lining wall of the buccal cavity is removed, two large muscles are seen to lie between it and the lateral skeletal parts. The upper is attached by a long tendon to the middle of the hinder edge of the anterior dorsal cartilage, on each side of the papillose elevation at the anterior end of the dorsal groove already described. The lower, fleshy throughout

[1] See Stannius, *Handbuch der Zootomie*, I. p. 240, and Rathke's description of these parts in his *Bemerkungen ueber den innern Bau der Pricke*, 1825.

[2] *Proceedings of the Royal Society*, 1875, p. 128, Fig. D. 1.

its length, is inserted into the tongue. Each of these muscles arises from the styliform process, the position of which exactly corresponds with that of the outer attached edge of the velum. Immediately subjacent to the ventral wall of the buccal cavity lies the strong aponeurotic sheath of the lingual muscles with the lingual cartilage (Pl. XVII. Fig. 1, *k*), which they ensheath. The two *cornual cartilages* (*i*) are imbedded in this sheath, their long edges being close to, and nearly parallel with, one another (Pl. XVIII. fig. 3).

Thus it is obvious that the *lingual cartilage* has the same relations as the median ventral element of the hyoidean arch in the higher Vertebrata, and that the *cornual cartilages* and the *styliform processes* represent lateral elements of the same arch. Müller attached the same signification to the cornual cartilages, but not to the lingual cartilage.

In this case what is the *median ventral cartilage* which Müller regarded as the body of the hyoid? The hyoidean arch is complete without it and has no special connexion with it, the bent up anterior end of the lingual cartilage simply playing over it. I conceive it to be a median ventral element of the mandibular arch; notwithstanding that, in the higher vertebrates, such an element, though the analogy of the other arches would lead us to expect its presence, is not known to occur.

The third division of the trigeminal nerve passes over the expanded anterior end of this cartilage, traverses the ventral half of the annular cartilage, and runs along the anterior edge of the latter to its dorsal extremity[1]. Thus although its halves are united dorsally, the annular cartilage would seem to be essentially a post-oral structure. The inverted subocular arch formed by the posterior (*f*) and anterior (*f'*) lateral processes lies at the sides of the posterior part of the buccal cavity. The second and third divisions of the trigeminal nerve (Pl. XVIII. fig. 1, V^2, V^3) perforate the membrane which connects them, the third running obliquely downwards and forwards to its distribution (Pl. XVII. fig. 1); the second turning outwards and passing to the sides of the head.

[1] See Born, *Ueber den inneren Bau der Lamprete*, Heusinger's *Zeitschrift*, 1827, Tab. VI. fig. 7.

The posterior lateral process therefore answers, in all essential respects, to the suspensorial cartilage or proximal division of the mandibular arch, though possibly the dorsal end of the hyoidean arch may be united with it.

Having proceeded thus far, the further study of the cranio-facial apparatus of the Lampreys will be facilitated by comparison with that of the tadpole (of *Rana temporaria*) in the stage in which the right opercular cleft is closed, while the hind-limbs are still in the condition of mere buds (Pl. XVII. fig. 2; Pl. XVIII. figs. 2, 4 and 6).

Dugès has given an admirably clear and accurate account of the structure of the skulls of the tadpoles of *Pelobates fuscus*, *Hyla viridis*, and *Rana esculenta* in this stage; and it has subsequently been treated of by Reichert, by myself and by Mr Parker (*Phil. Trans.*, 1871). Figures of a somewhat more advanced condition of the skull of *Bombinator igneus* are given by Goette in the work already cited.

The skull of the tadpole, at this stage, consists of a cartilaginous parachordal basilar plate, the middle of which contains the anterior end of the notochord. On each side are the auditory capsules, while, in front, the basilar plate extends forwards on each side of the pituitary space to form the trabeculæ. These unite in front, but speedily diverge again to terminate abruptly, close to the upper labial cartilages (Pl. XVIII. fig., 2 *U. lb*). The nasal sacs are situated on the dorsal aspect of the head, one on each side of the origin of these ethmoidal processes of the skull (*e*), and they open directly into the anterior part of the buccal cavity. On comparing this skull with that of the young Ammocœte (Pl. XVIII. fig. 5) the justice of the comparison instituted by Agassiz, between the 'anses' of the latter (*Tr*) and the trabeculæ of vertebrate embryos in general becomes manifest. Only, in the Ammocœte, there is, as yet, nothing answering to the ethmoidal processes of the Frog's skull.

In the young Ammocœte again the median nasal sac (*Na*) is conical and its brief ventral prolongation merely overlies the commissure of the trabeculæ. If the sac could be divided into two by a median constriction it would answer to the nasal sacs

of the Frog before they communicate with the buccal cavity. The only representative of any part of the subocular arch of the adult, in the Ammocœte stage of the Lamprey, is a slender cartilaginous process (*g*) which corresponds with the dorsal end of the posterior lateral process of the adult[1].

It is obvious from the position of the lateral bars of the cranium in the Lamprey that they are, as Agassiz determined them to be, homologous with the 'anses' of the Ammocœte and therefore are modified trabeculæ—while the 'hard palate' is a chondrification of the tissue which lies between them, corresponding with that process of chondrification by which the floor of the skull in the Frog becomes completely converted into cartilage.

Nor in my judgment, can it be doubted that the posterior dorsal cartilage of the Lamprey answers to the ethmoidal processes of the tadpole's skull, the interspace between them being similarly chondrified.

Again, at the sides of the Frog's skull there is a subocular arch (Pl. XVIII. fig. 2, *p,f,g*), the posterior limb of which (*g*) is in all respects comparable to the corresponding part of the Lamprey's subocular arch; except so far as the styliform cartilage of the Lamprey may possibly represent the upper end of the hyoidean arch. For in the Frog, as I pointed out in my paper on *Menobranchus*, the hyoidean arch is simply articulated with the suspensorium and does not coalesce with it.

I have formerly assumed that the anterior pillar of the subocular arch in the tadpole (Pl. XVII. fig. 2; Pl. XVIII. fig. 2, *p*.) answers to the anterior lateral process in the Lamprey, to which it is indeed extraordinarily similar. But further consideration shews that there is a difficulty in the identification of the two. Both the second and the third divisions of the trigeminal nerve pass through the subocular membrane, and therefore on the ventral side of the arch; whereas in the Frog, as in all other Vertebrata, they run on the dorsal aspect of the palatine arcade. This is a singular anomaly (which occurs also in the Myxinoids), and it leads to the suspicion that the anterior lateral process

[1] When this passage was written I had not seen the valuable paper of Langerhans, *Untersuchungen über Petromyzon Planeri*, Freiburg, 1873. I find that he has described and figured the process here mentioned, as well as the cartilaginous olfactory capsule known to Rathke, but overlooked by Müller.

may be represented, not by the palatine process of the suspensorium of the tadpole (*p.* fig. 2), but by the orbital process, which, as is well known, arches over the jaw-muscles and nerves until it reaches the skull, with which it becomes united by fibrous tissue.

The otic process of the tadpole's suspensorium has no representative in the Lamprey, and therefore the posterior division of the seventh nerve, which takes the same course as in the Frog, does not pass through a foramen.

The oral aperture of the tadpole, in this stage, is surrounded by a deep, fringe-like, transversely-oval lip, produced on each side into a fold (Pl. XVIII. fig. 6). Dorsally, this lip, as in the Lamprey, passes evenly into the integument of the head; ventrally, it is marked off from the rest of the integument, just as in the Lamprey, by a deep transverse constriction. The inner surface of the lip is raised into ridge-like linear elevations, the free edges of which are beset with the singular spoon-shaped serrated hooks, which result from the modification of the epithelium.

There are four rows of these denticles in the lower division of the lip, and two in the upper. Behind these come the horny jaws, which are structures of a very similar nature, moulded upon the edges of two pairs of labial cartilages—an upper and a lower (*U.lb; L,lb*).

Each pair of these labial cartilages are so closely united in the middle line in this stage that it is not always easy to discern the traces of their primitive distinctness. The upper pair overlap the lower, which last form a half circle. In *Rana temporaria* the second small upper labial cartilage attached to the outer angle of each of the principal pair, which is described and figured by Dugès in *Pelobates,* appears to be absent.

The angles of the upper and lower labial cartilages are united by fibrous tissue. The outer part of the dorsal face of each lower labial cartilage articulates with the outer end of the posterior face of the short Meckelian cartilages (*Mk*). These are therefore separated by a considerable interval, occupied by the floor of the mouth (Pl. XVIII. fig. 4). Their proximal ends articulate with the ends of the suspensoria, and the long axis of each Meckelian cartilage is inclined downwards and backwards. These cartilages therefore lie at the sides of, as well as beneath the buccal cavity (Pl. XVII. fig. 2).

The larger hyoidean cornu (Pl. XVIII. fig. 4, Hy^1), articulated with the posterior face of the suspensorium by a part of its anterior edge, ends dorsally in a free point; ventrally, it narrows and passes into the anterior, transversely expanded, end of a median cartilage (Hy^2), which tapers posteriorly, and is received between the coalesced ventral ends of the branchial arches. Of these there are four. The ventral part of the most anterior is still distinctly marked off from the coalesced ventral ends of the three posterior arches. The dorsal moieties of the branchial arches, when they are separated by the branchial clefts, are bent so as to be strongly convex outwards and concave inwards.

The cornu of the hyoid in the tadpole obviously answers to the *cornual cartilages* in the Lamprey. The median cartilage, the anterior expanded end of which raises the mucous membrane of the anterior part of the floor of the mouth into a rudimentary tongue, no less closely resembles the *lingual cartilage* of *Petromyzon*, while the branchial arches represent the four anterior branchial arches of the Lamprey. Not only so, but in the present stage, the branchiæ of the tadpole are, as is well known, pouches, which present no merely superficial likeness to the branchial sacs of the Lamprey. A septum extends inwards from the concave face of each branchial arch, and the septa of the two middle arches (Pl. XVIII. fig. 4) terminate in free edges in the branchial dilatation of the pharynx. Vascular branchial tufts beset the whole convex outer edge of the branchial arch, and are continued inwards in parallel transverse series of elevations, which become smaller and smaller towards the free edge of each septum, near which they cease[1].

In the young Ammocœte the septa of the branchial chambers similarly bear vascular processes, which are first developed close to the external branchial aperture, and thence extend inwards transversely[2].

The recesses at the sides of the floor of the pharynx into

[1] Dugès (*l. c.* p. 97) has carefully described the branchiæ of *Pelobates*.

[2] If these first-formed long branchial filaments of the Ammocœte projected through the small gill-clefts outwards instead of inwards, they would resemble the first-formed 'external gills' of Elasmobranchs. And this difference of direction seems to indicate the solution of the difficulty, that external gills, which are so generally developed at first in *Elasmobranchii*, *Ganoidei* and *Dipnoi*, are apparently wanting in *Marsipobranchii*.

which the interseptal clefts, or internal branchial clefts open, answer, taken together, to the branchial canal of the Lamprey, which is not shut off from the œsophagus in the Ammocœte. The anterior boundary of each of these recesses is marked by a fold of the mucous membrane, the free edge of which projects backwards and is produced into papilliform angulations so as to appear scalloped (Pl. XVIII. fig. 4). The anterior face of this fold is convex, its posterior face is concave. The inner angle of each fold passes into its fellow by a ridge, produced into one or two papillæ, which is closely adherent to the median part of the floor of the mouth. The outer angle is continued into a more delicate fold of the mucous membrane lining the roof of the mouth, the free edge of which also projects backwards. It is plain that these structures answer to the pharyngeal velum of the Lamprey[1].

Thus I think there can be no doubt that the cornua of the hyoid in the Frog, and the median cartilage which connects them, are the homologues of the cornual cartilages and the lingual cartilage of the Lamprey. Whether the styliform process of the Lamprey is really the upper end of the hyoidean arch, or whether it simply answers to the part of the mandibular arch of the tadpole which articulates with the hyoidean cornu elongated into a process, is more than I can, at present, venture to decide. The analogy of the frog and of *Chimæra* however is against the hyoidean nature of the styliform process. The lower labial cartilages in the tadpole (*l.lb*) occupy just the same position in the lip, in front of the ventral constriction, as the ventral half of the annular cartilage does in the Lamprey. Considering that the corresponding structure in *Amphioxus* is an incomplete ring open on the dorsal median line; and considering, further, the distribution of the third

[1] Some very singular tentacular structures are arranged in definite order in the roof and on the floor of the tadpole's mouth. Three or four are situated in a transverse row upon the rudimentary tongue: two over the junction of Meckel's cartilage with the lower labial cartilage: one large one immediately behind the inner or posterior nostril. Between these the roof of the mouth presents a triangular papillose elevation with its apex directed backwards—which is comparable to the papilla at the anterior end of the dorsal buccal groove in *Petromyzon*—and two parallel rows, one on each side of the roof, and one on each side of the floor of the mouth. The extremities, and sometimes the sides of these tentacula, are more or less papillose, and the central axis is in structure very similar to developing cartilage.

division of the trigeminal nerve, I incline to think that the annular cartilage of the Lamprey represents only the lower labial cartilages of the Frog. A knowledge of the development of the ring in question would decide this point, but I have not yet been able to obtain young Lampreys in which the buccal cartilages are just making their appearance. If the annular cartilage of the Lamprey answers to the lower labial cartilages of the Frog, then the upper labial cartilages will correspond in form and position to the anterior dorsal cartilage, and the small antero-lateral cartilages will perhaps have a parallel in the upper 'adrostral' cartilages in *Pelobates*.

The *posterior lateral cartilages* are directly connected with that end of the suborbital arch which answers to the articular end of the suspensorium in the frog (Pls. XVII., XVIII. figs. 1 and 2), and, in their position, exaggerate the peculiar arrangement of the tadpole's Meckelian cartilage. That they are parts of the mandibular arch I believe to be certain, but in the absence of any knowledge of their mode of development, I leave the question as to their exact homology open. Finally, the median ventral cartilage appears to have no representative in the tadpole; and, as I have already said, I take it to be an inferior median piece of the mandibular arch—not represented, so far as our present knowledge goes, in the higher vertebrata.

Thus the craniofacial apparatus of the Lamprey can be reduced to the same type as that of the higher Vertebrata, by means of the intermediate terms afforded by the Tadpole's skull; and there appears to me to be no sufficient foundation, in the present state of knowledge, for regarding the Marsipobranch skull as one which departs in any important respect from the general vertebrate type.

To what extent all the identifications here made will stand the test of the study of the development of the Lamprey's facial cartilages remains to be seen; but the only doubt which exists in my mind is with regard to the anterior dorsal and the postero-lateral cartilages. If the annular cartilage is developed by the confluence of primitively distinct upper and lower labial cartilages, the homologues of the anterior dorsal cartilage will have to be sought in some of the anomalous palatal cartilages of the Rays; among which it might not be impossible to find

representatives of the postero-lateral cartilages. But that the parts of the face of the Lamprey present no structures, which are not to be found in one shape or another among the higher Vertebrata, appears to me to be clear.

In the Myxinoid *Marsipobranchii* there is even less difficulty in reducing the skull to the ordinary vertebrate type. Three pairs of cartilaginous rods here spring from the anterior end of the parachordal region, one pair passing forwards as the trabeculæ, and two curving backwards and to the ventral side as the mandibular and hyoidean arches respectively. The two latter have swung backwards until they take a position unlike that which they have in the Tadpole and the Lamprey, and like that which they have in the adult Frog. Not only in this respect, but in the structure of the circulatory and respiratory apparatuses the Myxinoid fishes exhibit a higher stage of organization than the Lampreys. But, at present, I can only indicate the outlines of a comparison which requires fuller discussion than can be given to it on the present occasion.

In conclusion, I will only advert to the singular resemblance in structure and mode of working between the tongue of the Marsipobranch and the odontophore of a Mollusk, as a point worthy of attention.

DESCRIPTION OF THE PLATES.

Plate XVII.

Fig. 1. Vertical and longitudinal section of the anterior part of the body of Lamprey (*P. fluviatilis*) × 3. *a.* annular cartilage; *b.* anterior dorsal cartilage; *c.* antero-lateral; *d.* postero-lateral cartilage; *e.* posterior dorsal cartilage; *e'.* hinder margin of the hard palate; *f.* anterior lateral process; *g.* posterior lateral process; *f'.* angle formed by the junction of these; *h.* styliform process; *i.* cornual cartilage; *k.* lingual cartilage; *l.* median ventral cartilage; *m.* occipital arch; *n.* posterior wall of the nasal capsule; *o.* lip-like fold with two papillæ; *p.* tongue; *q.* tentaculate branchial valve; *r.* pharyngeal velum. *N.* nasal aperture; *Ol.* olfactory sac; *Hm.* the cerebral hemispheres; *M.* midbrain; *Ce.* cerebellum; *Md.* medulla oblongata; *My.* myelon; *Ch.* notochord; *Oc.* nasal canal.

Fig. 2. Vertical and longitudinal section of the anterior part of the body of a Tadpole of *Rana temporaria* (× 10) *Ch.*, *My.*, *Md.*, *Ce.*, *Ms.*, *Hm.*, *œ.*, *N.* as before; *N'.* posterior nasal aperture; *Mk.* Meckel's cartilage; *U.lb*, *L.lb.* upper and lower labial cartilages; *e.* eth-

moidal cartilage; *f'*. angle of junction of the palatine cartilage, *p*. with the suspensorium, *g*. and the articular surface for Meckel's cartilage; *k*. median cartilage connecting the hyoid and branchial arches; *Br. Vl. Vl.* pharyngeal velum; *H*. heart.

PLATE XVIII.

Fig. 1. The anterior part of the roof of the branchial canal and of the buccal cavity of a Lamprey (×3); *b*. The two anterior branchial openings; B. The right anterior branchial sac; *x*. a bristle passed into the opening behind the right half of the *velum vl.*; *vl*^{2}. the second valvular fold in front of the first branchial aperture, more distinctly shewn than in nature; *u*. the 'shelf' with its tentacles; *g*. the median groove; *t*. its anterior termination; *e*. the anterior end of the posterior dorsal cartilage; *v*^{2}*v*^{3}. the second and third divisions of the trigeminal nerve; *Au*. the auditory capsules.

Fig. 2. The roof of the mouth of a Tadpole of *R. temporaria* (×10) *Ch., Au*. as before—*vl*. the superior vela; *t*. a median large triangular papilla, between the two which lie behind the posterior nares; *Tr*. trabeculæ; *g.f.p*. the sub-ocular arch; *e*. the ethmoidal processes; *U. lb*. the upper labial cartilage.

Fig. 3. The lingual cartilage *Hy*^{2}, the cornual cartilages *Hy'* and the styliform processes *Hy* (?) of a Lamprey magnified three times; *Lt*. the mandibular tooth; *l*. the anterior end of the median ventral cartilage, the posterior prolongation of which is supposed to be seen through the lingual cartilage; *Vl*. the lower halves of the pharyngeal vela—between which a small portion of the mucous membrane of the floor of the mouth is seen. Beneath this is the fibrous aponeurosis of the muscular sheath of the tongue and the tendon of the long retractor muscle.

Fig. 4. The floor of the mouth of the Tadpole of *Rana temporaria; Llb*. lower labial cartilage; *Mk*. Meckel's cartilage; *Hy'*. hyoidean cornu; *Hy*^{2}. median inferior piece of the hyoid; *Vl*. inferior velum; *s*. 1. 2. 3. 4. walls of the branchial sacs.

Fig. 5. The skull of a young Ammocœte, or larval Petromyzon, with the brain in situ; *Ch*. the notochord; *Au*. the auditory capsules; *g*. the lateral process; *Tr*. the trabeculæ; *w*. the lateral walls of the cranium in the region of the cerebral hemispheres; *Na*. the nasal opening embraced by the crescentic cartilage.

Fig. 6. Lips and horny upper jaw of the Tadpole (×10).