Dr. Dohrn's Inquiries into the Evolution of Organs in the Chordata.

By

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SEVEN years elapsed from the publication of the ' Ursprung der Wirbelthiere' before the appearance of the first of Dohrn's ' Studien zur Urgeschichte des Wirbelthierkörpes,' that on the mouth of Teleosteans. As he points out in a short preface to that paper the three chief peculiar articles of faith in his previous essay, in comparison with the views current at the time, were that the ancestors of Vertebrates closely resembled Annelids, that the principle of change of function was the safest guide in tracing morphological histories, and that the extent to which degeneration might proceed was unlimited.

In the attempt to reconstruct the Vertebrate ancestor, Dohrn has concentrated his attention almost exclusively on the actual structure and development of the organs of existing Vertebrates, convinced that a great deal of what was generally believed concerning the relation of the organs was inaccurate, and that no light could be thrown on the question by hasty conclusions drawn from superficial resemblances of the organs of Vertebrate and other embryos, until the organisation of the Vertebrates themselves was more thoroughly investigated.

The following is a list of the studies with the dates of publication :

1882.   I. " Der Mund der Knochenfische."
      II. "Die Entstehung und Bedeutung der Hypophysis bei den Teleostiern."
1883.   III. "Die Entstehung und Bedeutung der Hypophysis bei Petromyzon Planeri,"

Ancestral Mouth.—In the first of these studies reference is made to the question of the position of the ancestral mouth, which in the 'Ursprung der Wirbelthiere' was located between the crura cerebelli in the fourth ventricle. Professor Fritsch and Mr. Sanders argued that this was an untenable supposition, because it would be impossible to accept the consequence of it, namely, that all the cerebral nerves belonged to a supra-œsophageal ganglion. Dohrn acknowledges the justice of the objection, and provisionally abandons the quest of the ancestral mouth. He has never since resumed the inquiry. He deals with investigations of the development of the actual mouth, the results of which confirm his view that the aperture represents a united pair of gill-clefts. In embryos of Teleosteans he found that there was no stomodæum, and that the mouth arose as a pair of enteric outgrowths which at first opened to the exterior, one on each side, the apertures only subsequently meeting in the middle ventral line.

Hypophysis of Teleosteans and Petromyzon.

The hypophysis also in Teleosteans, according to the second paper of the series, does not arise from an ectodermal oral invagination or stomodæum, but from a pair of endodermal evaginations in front of those which form the mouth. The organ therefore represents a pair of præoral gill-clefts (i. e. it is derived in the Teleosteans from the endodermal parts of

such a pair) which in the actual development of Teleosteans never acquire an opening to the exterior. In a postscript to this paper Dohrn mentions Hatschek's results concerning the origin of the ciliated pit in Amphioxus. This pit is the left of a pair of anterior evaginations of the endoderm, which opens to the exterior while the other remains closed. According to Dohrn these two diverticula are homologous with the hypophysis in the Teleostean, and the opening in Amphioxus is the persistent branchial opening. The ciliated pit of the Ascidians is also homologous with that of Amphioxus. According to Bateson the proboscis cavity with its pore in Balanoglossus is homologous with the ciliated pit in Amphioxus, but whether the body cavity of the proboscis in Balanoglossus can be derived from a pair of gill-clefts is a question which seems to threaten to do away with the possibility of the diagnosis of organs according to their embryological origin.

The hypophysis in Petromyzon has a unique history in the individual, and this forms the subject of the third member of the series. The examination of the embryos of Petromyzon was undertaken by Dohrn in order to prove that the fundamental difference generally supposed to exist between the branchial cartilages of Selachians and of Petromyzon was entirely imaginary, but the discussion of this subject is postponed till the hypophysis has been considered. Scott[1] had stated that the hypophysis of the Lamprey arose as an ectodermal invagination connected with the nasal pit.

Balfour had doubted this result, but Dohrn entirely confirmed it, except that he found the hypophysial invagination to be at first separate, lying between the commencing mouth and nasal cavity, and that he pointed out that the whole long nasal duct of the adult which runs back beneath the brain is as much part of the hypophysis as the follicular organ formed from its inner extremity.[2] The nasal duct is in fact a fused pair of ectodermal

[1] 'Morph. Jahrb.,' vii.

[2] It seems extremely probable, although I am not aware that it has been suggested before, that the nasal duct which in Myxine opens into the pharynx, is homologous with the so-called nasal duct of Petromyzon. If this be so, of

pits originally belonging to the pair of gill-clefts which has been transformed into the hypophysis. The function of the nasal duct in the adult is apparently to draw in water in order that it may reach the olfactory organ and then expel it; it is probably, to use an undignified word, a sniffing organ, necessitated by the disconnection of the mouth from the function of respiration. This new function of the hypophysial gill-cleft could easily be derived from its original one.

Visceral Arches of Elasmobranchs.

In order to demonstrate the fallacy of the argument that the external branchial cartilages of Selachians were the representatives of a primitive " external" branchial skeleton retained in the existing Cyclostomata, it would have been sufficient, says the beginning of the fourth study, to describe the development of these two cartilages (two to each arch) in Selachians and compare it with the quite different history of the branchial skeleton in the Lamprey. But it seemed advisable to give a complete account of the development of the Elasmobranch gill-arch, as previous results were fragmentary.

It is to be understood that a typical arch such as the first, second, or third branchial, is under consideration, not the hyoid or the posterior, which are either modified or reduced. In a horizontal section of the arch towards its middle the cavity of the arch surrounded by its epithelial cells (head-cavity of

course the connection between the pharynx and the nasal pits in Myxine is formed by the hypophysis and not by a nostril properly so named. The hypophysial invagination in the embryo of Petromyzon comes into very close relation with the pharynx as well as with the infundibulum, and on the hypothesis which I have supported in my paper on Kupffer's vesicle, &c., that the infundibulum represents the original mouth, it is easy to understand how a separation between infundibulum and pharynx might occur in either of two ways, by leaving the hypophysis connected only with the infundibulum as in Petromyzon, or by leaving the communication between hypophysis and pharynx still open as in Myxine. In other Vertebrates again the hypophysial invagination has been absorbed into the stomodæum, and reaches from thence to the infundibulum, but has not retained a connection with the pharynx. These speculations can of course only be tested by examination of the development of Myxine.

Balfour and his school) is seen in the centre dividing the section into an anterior and posterior half. This cavity is continuous below with the pericardium. The artery of the arch is on the posterior side of the cavity, or as it is better to call it, from the destination of its walls, of the muscle tube of the arch. The branchial processes grow out first on the pos-terior side, and along their base appears a vein which opens dorsally into the artery. Similarly on the anterior side appear branchial processes with an anterior vein, also opening into the artery. The two veins become connected by two hori-zontal commissures. In the adult the posterior vein becomes disconnected from the anterior and unites with the anterior vein of the arch behind it.

The cartilaginous arch arises as a condensation of mesoderm cells posterior to the muscle-plate. Between the upper and lower venous commissures, where the muscle-tube is already diminished in thickness, condensation of mesoderm cells takes place also on the anterior side, and the two condensed masses uniting, eliminate the muscle-tube between them. This separa-tion of the muscle-tube does not take place dorsally and ven-trally, because the cartilaginous arch bends inwards in those regions. A central part of the muscle-tube is thus separated and lies on the inner side of the arch; it becomes the adductor arcus visceralis. Both Gegenbauer and Vetter believe the adductor mandibulæ to be homodynamous with the adductor arcus, but this is an error, the former is homodynamous with the whole musculature of one (or more) arch. The external middle portions of the tubes form the musculi interbranchiales; the dorsal, externally the constrictor superficialis, internally the interarcuales. Other muscles come from the ventral portions. The coracohyoid is a true body muscle, and has nothing to do with visceral arches.

The cartilage already described, the middle portion first developed, forms the two middle internodes of the adult arch. Above these dorsally is the basale, below the copulare. The cartilage separates the adductor from the interarcualis above, from the coracobranchialis below. The cartilage is internal to

the artery; and the artery is at first posterior to the muscle-tube. The branchial cartilaginous rays arise as condensations of mesoderm cells separate from the arch, and between the artery and posterior vein. The so-called external cartilages are simply the most dorsal and the most ventral of the series of rays altered somewhat in position, and therefore have no similarity with the arches in Petromyzon, which are true arches.

Branchial lamellæ are never developed on the anterior side of the hyoid arch, or of the spiracular arch. The external filaments of the embryo arise as simple elongations of the posterior lamellæ of each arch, the anterior not elongating at all. A curious suggestion is made concerning the function of these elongated filaments, namely, that they serve to absorb yolk; how the yolk gets into them could not be discovered, but yolk is present in the filaments and in their veins, in the posterior branchial vein, and the efferent arteries, never in the branchial artery or in the heart.

Thymus of Elasmobranchs.

At the time when the external filaments have attained to about half their length, but when the branchial rays are not differentiated, a proliferation of epithelium takes place in the upper angle of the first gill-cleft, forming a kind of bud. Similar buds are formed in the four posterior gill-clefts, but the fifth bud disappears again entirely in the Sharks, but persists in the Rays. These buds form the thymus of the adult. The cause of the separation of these portions of the branchial epithelium is the shortening of the clefts. The upper portion of the original clefts is obliterated by a coales-cence of the arches, accompanied by processes of growth which alter the original position of the terminal rays of each series, and so produce the extra-branchial cartilages. The epithelial nodules of the thymus after they have sunk into the mesoderm become associated with mesodermic cells, a process which ought not to excite surprise, since the epithelium in question originally no doubt formed branchial laminæ into which meso-derm extended. The bending of the arches above described is

connected with the formation of the united portions of the musculus constrictor superficialis, but the original cause of the whole process is to be explained only after further investigations have been described.   Ecker first definitely described the thymus of fishes in his article " Blood-vessel Glands," in Wagner's 'Dictionary of Physiology,' Bd. iv, but could find no such organ in the Sturgeon, in Cyclostomata, or in Teleosteans. In a foot-note Dohrn points out that the thymus of Teleosteans exists in the position already accurately defined by Leydig in his 'Anat. histol. Untersuchungen über Fische und Reptilien.' In this note also emphatic contradiction is made of Gegenbaur's generally accepted view that the pseudobranchia of Teleosteans is the reduced gill of the hyoid arch, and therefore not homologous with the pseudobranchia or spiracular gill of Elasmobranchs.   Dohrn maintains that Johann Müller was quite right in asserting that the pseudobranchia of Teleosteans was homologous with the spiracular gill of Elasmobranchs, and that Balfour, who has been followed by Hoffmann, was mistaken in supposing that in the Teleosteans the choroid gland represents the spiracular gill.   Stieda found that the thymus of mammals arose from only one gill-cleft, the last, or last but one ; Dohrn states that the carotid gland may possibly represent a rudimentary thymus derived from another cleft.

Branchial Skeleton and Arches of Petromyzon.

After showing that the extra-branchial cartilages of Elasmobranchs are really displaced gill rays, the next point in arguing that the branchial skeleton of Petromyzon is composed of true branchial arches, is to demonstrate the development of this skeleton, and this is the object of the fifth paper.   It is known from the researches of Scott and Balfour that the first trace of the visceral arches appears in the form of head-cavities, rounded cell-tubes between the diverticula of the gut, which afterwards form the gill-clefts.   The question of correspondence between the head-cavities and the dorsal myotomes is left for a future period.   There is a difference between the embryonic gill arches of Petromyzon and those

of Elasmobranchs in the position of the original vessel of the arch. This vessel in the latter forms lies near the outer border of the arch; in Petromyzon it lies as near as possible to the inner surface. The arch elongates and becomes flattened antero-posteriorly; the muscle-tube undergoes a corresponding compression. The cartilaginous arch arises anterior to the muscle-tube, but soon divides this tube in the middle of the arch completely, separating an adductor on the inner side from a constrictor on the outer, as in Selachians. The cells of the anterior wall of the muscle-tube have a remarkable peculiarity. They persist, in embryonic form, as long tubes, which run the whole length of the arch, and show a transverse striation only on the exterior. All the muscles run the whole length of the arch and unite, dorsally as well as ventrally, with those of the other side; the important point about this is that if the cartilaginous rods were to disappear the condition would be the same as that which actually exists in Myxine. The chief difference between the gill laminæ of the adult Petromyzon and those of Selachians is that the former are directed towards the exterior, the latter towards the interior, and this difference appears at their first origin in the embryo. It is probable that the adductors serve as inspiratory muscles by lifting up the ventral side of the branchial region, and so expanding the branchial cavities, while the constrictors are expiratory, their contraction driving the water out.

Thus it is shown that the branchial skeleton of Petromyzon is composed of true cartilaginous branchial arches. It is true that these arches in the Cyclostomata are not segmented, nor are they in the Teleostean; and this shows that Petromyzon is derived from a form more premature than the Selachian, in which the segmentation had not yet occurred. The same truth is indicated by the homology of the hypophysis with the nasal duct, an homology which, as Dohrn frankly acknowledges, was first asserted by Goette in his 'Entwicklung der Unke.' Petromyzon must have branched off from a condition in which the hypophysis was still an independent præoral pair of gill-clefts. That the gills of Petromyzon are homologous with

those of Selachians has been suggested by Huxley and P. Fürbringer, and is by Dohrn's results fully established. Myxine is a further modification of Petromyzon, and shows a remnant of the branchial skeleton in the cartilage of its ductus œsophageo-cutaneus. The internal position of the branchial artery in the embryo Petromyzon is simply explicable as a consequence of the displacement of the branchial lamellæ towards the interior, and this change of position has been brought about by the necessity of protecting the gills which arose when the present habits of the animal (either burrowing in mud or attaching itself to other animals) were acquired.[1]

Thus the theory that the branchial cartilages of Petromyzon represent an archaic system not elsewhere present except in the extra branchial cartilages of Selachians falls to the ground, and with it disappear the consequences which Gegenbaur formerly deduced from it. The Cyclostomata had no jaws it was said because their ancestors had no true gill arches from which jaws might be derived, whereas the truth is probably they have lost the jaws through the conversion of the biting

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[1] In my paper on Myxine, in the previous number of this Journal, I have described the habits of Myxine from actual observation. There can be no doubt that during far the greater portion of its time the animal lies motionless, buried in mud, with only the extremity of its snout protruding. In this condition the method of respiration, unique among fishes, namely, the constant passage of a current of water through the nostril to the gill-pouches, is the only method possible. Doubtless this method is also the most convenient when the animal is boring into the body of a fish, or when its whole body has penetrated into the flesh of its prey; and it is difficult to say which of its habits, burrowing or boring into its prey, was the prior cause in producing the existing condition of the respiratory organs. I have not yet ascertained whether the respiratory current is maintained by ciliary action, or by internal muscular action, or by both combined. No muscular respiratory movements are visible externally. Ammocœtes, it is true, burrows, although it has a branchial skeleton; and I do not know how the Ammocœtes, when buried, can carry on the method of respiration which is seen in Petromyzon. Petromyzon never burrows, it conceals itself beneath stones and in crevices, but it could not take in water by all its branchial apertures as it does unless it were surrounded by water free from sediment. The comparison of the habits of Petromyzon and Myxine illustrates the diversity of functions performed by

into a sucking mouth.   It was said that they had no limbs
because the skeleton of a limb was derived from an arch of
the branchial skeleton, and no true branchial arches were
present; the truth is that the limbs are not derived from
branchial arches, as is now generally acknowledged, and there
is a rudiment of the pelvic fin in Petromyzon, to be after-
wards described.

The Origin of the Fins of Fishes.

The true history of the origin of the limbs of fishes, paired
and unpaired fins, as Dohrn reads it, is set forth in the sixth
Study.   In the original ancestral condition the Vertebrate body
was similar in most respects to that of an Annelid.   The medul-
lary tube was an open plate, the intestine extended through
the whole length of the body to a terminal anus, and on each
segment were two pairs of appendages, processes of the body
wall provided with processes of the body musculature, in fact,
dorsal and ventral parapodia.   The nerve plate was, of course,
ventral, when the animal was reversed in position and the plate
folded into a tube, the two series of ventral parapodia were
brought together in the median dorsal line and coalesced both
laterally and longitudinally, forming the dorsal fin, which was
originally continuous along the whole length of the body.
Another change which took place was that a new anus was
formed out of the fusion of two gill-slits, and in consequence

one organ, and the contrast between the functions of homologous organs in
two forms.   An important function of the sucker-mouth of Petromyzon is to
adhere to stones in the bed of a river, and without this power the animal
would immediately lose control of its own movements, and be carried away at
the mercy of the currents in which it habitually lives.   This function is
entirely wanting in Myxine, whose mouth is not truly a sucker at all, but a
boring apparatus.   I have never seen a Myxine use its mouth to attach itself,
while Petromyzon never leaves its mouth attachment at one place, except to
immediately secure it again at another.   Yet the mouth of Myxine can take
in food without boring, as is demonstrated every day in the North Sea when
the fisherman finds on his lines numbers of Myxine which have taken the
baited hook far down into the intestine without using their teeth upon the
bait at all.

the postanal gut disappeared; the degeneration of the postanal gut is actually repeated in ontogeny. The contraction of the ventral part of the tail thus brought about caused the series of dorsal parapodia behind the anus to coalesce in the same manner as the ventral parapodia, and thus the median anal fin was produced. The præanal dorsal parapodia were never approximated laterally, but partly disappeared, partly coalesced longitudinally to form the existing pelvic and pectoral fins. The fins therefore have nothing to do with gills, either in the way supposed in Gegenbaur's Archipterygium theory, or in the way originally suggested by Dohrn in the 'Ursprung der Wirbelthiere.' In the theory now taught by Dohrn the metameric external gills of Annelids are left out of consideration; the ancestor, it is to be presumed, had none. The facts on which the theory is based, and which are important results of investigation however explained, are as follows:—The musculature of the pectoral fin is derived in embryos of Elasmo-branchs (Pristiurus) from a series of muscle buds separated from the ventral end of each myotome. Each bud divides into four pieces, two above and two below. The same is true of the pelvic fin. That these fins cannot be serially homologous with any parts of the gill arches is proved by the fact that the musculature of the gill arches is derived from the head cavities, and these are ventral to the myotomes. So also the gill cartilages are not homodynamous (serially homologous) with the ribs, for the ribs are between the myotomes, the series of which is continued anteriorly above the gill arches. A large number of myotomes contribute to form each fin. Behind the anus on each side muscle buds are given off from the ventral ends of the myotomes; these are serially homologous with those already described, and in all probability, although the transformation was not traced, they form the musculature of the anal fin. The musculature of the dorsal fins arises from buds given off dorsally exactly as those belonging to the paired fins are given off ventrally. The fin rays in the dorsal fins arise as median cartilaginous rays, at first quite unconnected with any other part of the skeleton. One would have expected

to find, if the theory be true, that these rays were originally double; but Dohrn says nothing of this difficulty, attaching the greatest importance to the musculature. It has been objected to Dohrn's theory by myself and Professor Carl Vogt that in Teleostean embryos there is a præanal median fin in addition to the præ-anal paired fins; to which Dohrn has replied that it has not been proved that this fin has any musculature, and therefore it is probably a new development peculiar to the class in which it occurs.

Morphology of the Mandibular and Hyoid Arches of Selachians.

We come next to a discussion of one of the most complicated chapters in Vertebrate morphology, the question of the mandibular and hyoid arches in Selachians. We will take a rapid survey of the facts as they exist according to Dohrn's investigations, and then consider the deductions he draws from them. In embryos of Pristiurus, Scyllium, Mustelus, Centrina, Torpedo, and Raja the conus arteriosus at its terminal bifurcation forms the hyoid arteries, the arteries of the hyoid arch. From each of these arteries near its origin arises another artery which runs parallel to and anterior to the hyoid artery. Between the bases of these two lies the thyroid gland, and the arteries are to be called the thyroid arteries. The hyoid artery supplies only one series of branchial laminæ, the posterior. There is also but one branchial hyoid vein, the posterior. There is only one venous commissure from the hyoid vein instead of two as in the posterior arches, and this commissure opens into the thyroid artery. The art. thyroidea has hitherto been called the art. mandibularis. The thyroid artery, after receiving the venous commissure, is continued into the spiracular artery. The hyoid vein divides dorsally into two branches, one of which runs back and joins the dorsal aorta system, the other runs forward as the carotis posterior, joins for a short distance behind the hypophysis with the same vein of the other side, then separates running one each side of the hypophysis, the vein of each side receiving a large vein from the spiracular gill.

The musculature of the hyoid arch is peculiar in this respect, that no internal portion of the muscle-tube is segmented off by the cartilage, and accordingly no adductor is formed. The musculi interarcuales are also absent, and there is a complicated system of ligaments fastening the hyomandibular cartilage. The ventral muscles, on the other hand, are similar to those of the posterior arches.

With regard to the cartilage of the hyoid arch, development shows that in the Sharks the upper middle internode, dorsal to the venous commissure forms the hyomandibular, no separate basale or dorsal internode is formed; but, as the hyomandibular carries a number of branchial cartilage rays, and also a dorsal ray, which is homodynamous with the upper extra-branchial (so-called) cartilage of the gill arches, it follows that the hyomandibular contains the basale (dorsal internode) of the hyoid arch.

In the Sharks the first rudiment of the mandibular arch appears at the level where the hyoid vein joins the spiracular artery, but unlike the posterior rudiments it consists from the first of two cartilaginous centres: the under becomes the mandible, the upper the upper jaw, the so-called palato-quadrate. No adductor is formed in the mandibular arch. It has been generally taught that the masticatory muscle of the jaws is the homologue of the adductor, but this is not so; no homologue of the adductor is present.

There are no cartilaginous rays on the mandibular arch. The doctrine, therefore, of Gegenbauer and his followers, that the lower and upper jaw are parts of a single cartilage arch equivalent to a posterior gill arch is unfounded.

In the Rays the development of the cartilages of the hyoid arch is quite different to that described for the Sharks.

There are two cartilage-centres, one near the posterior edge of the arch, the other near the anterior side, behind the spiracular cleft; each cartilage has its own muscle system. The first cartilage is separated into a dorsal and ventral part by the venous commissure, and each part bears gill rays. The second cartilage becomes the hyomandibular, it has its own muscle

system which forms the mus. levator. The conclusion which must be drawn is that the hyomandibular in the Rays is a remnant of an arch anterior to and entirely distinct from the hyoid arch, while in the Sharks the dorsal part of the hyoid arch with its rays is fused with the hyomandibular. According to Gegenbaur the hyomandibular in the Rays represents only the mandibular process of the hyomandibular of the Sharks; if this were true there would be no rays dorsal to the venous commissure in the Rays, whereas the fact is that these dorsal rays exist, but the cartilage they belong to is separate from the hyomandibular. Dohrn finally suggests that the upper jaw is also an independent gill arch, and the mandible another, but for the present leaves the further tracing of the transformations for more profound investigations. He concludes the section on the hyoid arch in the Rays with the remark that he is satisfied to dispel the illusion that we already know what we want to ascertain.

The spiracular cartilage is next taken in hand. Dohrn has investigated its origin in Scyllium canicula and catulus, Pristiurus, Mustelus, Raja and Torpedo. He found it always a single cartilage, and states that there is no foundation for the theory that it is either an enlarged single ray, or a combination of rays. It is probably a portion of an independent arch, but what relation this arch bears to others it is at present impossible to say. The adductor mandibulæ is developed from the whole of the walls of the mandibular head cavity, no portion being separated off as an adductor; only one differentiation of a portion occurs, namely, the formation of the levator maxillæ superioris from the part lying nearest to the spiracle.

When it has been postulated that the hyoid arch is really double and contains two arches fused together, it becomes necessary to inquire what has become of the cleft originally existing between these two arches. Has the cleft disappeared without leaving a trace, or has it merely undergone a metamorphosis? Dohrn answers that the pair of clefts, i. e. the endodermal parts of them, have united in the median ventral line and formed the thyroid gland. This organ arises in the

embryo in the middle line very far forward as an outgrowth of endoderm cells close behind the mouth, and subsequently passes backwards losing its connection with the pharynx. In a note Dohrn promises in a future study to discuss the spiracular cleft of the Selachians and Ganoids, and the pseudobranch of Teleosteans, and to show that between the mandible and the hyoid in Teleostean embryos on each side a deep invagination of the ectoderm occurs, which is to be regarded as the ectodermal part of the cleft represented by the thyroid. (It is probable that this invagination is the same as that observed by other embryologists and diagnosed as the Teleostean representative of the spiracle.) In another note it is stated that evidence will at a future time be adduced to show that in the jaw and hyoid system of Teleosteans five independent visceral arches are combined : 1, upper jaw ; 2, lower jaw ; 3, spiracular cartilage ; 4, hyomandibular ; 5, hyoid.

The Thyroid of Petromyzon.

The subject discussed in Study VIII is the thyroid in Petromyzon and its homologue in Amphioxus and the Tunicata. In the larval Ammocœtes the first trace of the thyroid appears at the time when the most anterior branchial diverticula of the endoderm grow out. Its first rudiment is a diverticulum directed downwards and somewhat forwards, close beneath the median part of the first pair of branchial diverticula, which is homologous with the spiracular clefts of Selachians and the pseudobranchiæ of Teleosteans. Between the stomodæum and enteron on each side runs the most anterior branchial artery, homologous with the spiracular artery of the Selachians ; it opens into the cephalic aorta of its own side, Petromyzon possessing two cephalic aorta one on each side of the notochord. The growth backwards of the mesoderm of the velum causes the opening of the thyroid diverticulum to be pushed farther back, so that it soon comes to lie at the level of the second pair of branchial sacs, and later between the second and third. A sagittal ingrowth of mesoderm now divides the thyroid anteriorly into two halves. On each side another

pushing in forms the glandular lamella, the uninvaginated part
forming the cover-lamella.   In the glandular lamella a differ-
entiation takes places into conical masses of gland-cells, the
apex of the cone turned to the cavity of the gland, and
ordinary ciliated cells.   In the advanced larva of Ammocœtes
two ciliated grooves run transversely in the wall of the
pharynx, in front of the gill-sacs, and converge on the median
ventral line to meet in the opening of the thyroid.   These
grooves Dohrn has ascertained to be derived from the endo-
dermal sacs which represent the spiracular clefts, and which in
Ammocœtes never acquire an opening to the exterior.

Now the endostyle or hypobranchial groove of Ascidians,
e. g. Cione intestinalis or Salpa, is closely similar in histo-
logical structure to the thyroid of Ammocœtes.   There is the
same differentiation into bulbous agglomerations of gland-
cells, and a more even layer of ciliated cells.   Moreover, in the
Ascidian there is a pair of ciliated grooves immediately behind
the mouth, which ventrally converge to the hypobranchial
groove, dorsally to the ciliated pit (hypophysis).   These
grooves of the Ascidian must be homologous with those of
Ammocœtes, and must therefore represent in the Ascidian the
spiracular clefts.   And it follows that Tunicates must be
derived from fishes, not vice versâ.   The reason suggested
for the transformation is that the thyroid and spiracular clefts
have been converted into mucous-secreting organs to aid in
the conveyance of nourishment to the œsophagus.

In Amphioxus there is not a hypobranchial groove, but a
hypobranchial ridge, but this ridge has the same histological
character as the thyroid in Ammocœtes and the hypobranchial
groove in Ascidians.   A homologue of the peripharyngeal
ciliated grooves is not mentioned as occurring in Amphioxus,
and the development of the hypobranchial ridge has not been
studied.

The conclusion drawn from all this is that both Tunicates
and Amphioxus are degenerate fishes derived from ancestors
more or less similar to the Cyclostomata.   A difficulty which
arises in considering Dohrn's arguments is that no reason is

given why the spiracular endoderm sac should open into the thyroid endoderm sac, since these were presumably originally separate; the spiracle being anterior to the hyomandibular, the thyroid between hyomandibular and hyoid. Dohrn does not mention this question, being satisfied so far to show that the condition of the ciliated grooves in Tunicates is directly derivable from the condition in Ammocœtes. The derivation of the arrangement in the latter from that in Selachians is not discussed.

Rudiments of Paired Fins in Petromyzon.

In the ninth Study Dohrn returns again to the question of the fins. How, he demands, could an animal of the size and complication of the Cyclostomata obtain for itself organs of such fundamental effect on the whole organisation as pectoral and pelvic fins ? The question is perhaps not so convincing as he thinks; for, on his own hypothesis, the neural and ventral parapodia must at one time have arisen, and the theory of the evolution of organs is not at present in such a state as to make it any more easy to understand how these organs arose than how limbs could arise in the Cyclostome, unless, indeed, it were postulated that the segmented vertebrate ancestor, with its dorsal and ventral parapodia, was a creation into whose previous origin it were impious to inquire. But what is more to the point is that, although Gegenbaur believed no rudiment of fins could be discovered in the Cyclostomata, Dohrn has discovered in Ammocœtes rudiments of muscle-buds similar to those which in other fishes form the muscles of the unpaired fins. These buds, however, remain as indifferent cells during the Ammocœtes stage, and are only differentiated into the fin muscles when the metamorphosis into Petromyzon takes place. The buds are given off ventrally as well as dorsally, and as the dorsal series forms the muscles of the dorsal fin, the præanal ventral ones must at one time have formed muscles of then existing paired fins. Moreover, there is, according to Dohrn, a rudiment of the pelvic fins in Petromyzon, namely, the longitudinal folds bordering the anus. Below

these folds are a pair of muscles, called by Schneider, in his
' Beiträge zur vergl. Anatomie der Wirbelthiere,' the anal fin
muscles. According to Dohrn, these muscles serve to pro-
trude the so-called penis of the male Lamprey. Dohrn raises
the question of the possibility of copulation in the Lamprey, a
possibility which does not really exist, for in the female there
is a protrusible tube at the abdominal pore, which is shorter
but otherwise exactly similar to that of the male. Dohrn
suggests that the anal fin muscles of Schneider are homologous
with the muscles of the pelvic fin in other fishes (Selachians
especially).

Origin of the Vertebrate Paired Eyes.

The most recent study deals with the embryology and phy-
logeny of the Vertebrate eye. It was obvious to previous
embryologists that the nervous part of the eye was originally
in the wall of the brain. Lankester suggested that the an-
cestor was at this time transparent, while Balfour believed that
though the tissues may have been transparent, the original
cause of the outgrowth of the optic vesicle was the covering of
the original superficial eye by the formation of the medullary
tube. But the starting-point of Dohrn's inquiry is the deve-
lopment of the eye-muscles. Balfour indicated briefly the
origin of these muscles from the most anterior head-cavity.
Marshall (this Journal, vol. xxi) ascertained that only the
rectus internus superior, inferior, and obliquus inferior arose
from the præ-mandibular cavity, while the obliquus superior
arose from the mandibular, the rectus externus from the
hyoid. But Marshall believed that the dorsal parts of the
head cavities from which the eye-muscles were formed were
homologous with myotomes, and not with the ventral cœlom
in the trunk. Dohrn does not agree with this, and holds that
the dorsal parts, like the ventral, are not homologous with the
myotomes in the trunk, but only with the ventral walls of the
body cavity. As a consequence of this it follows that the eye-
muscles are true muscles of visceral arches, and must have
been originally branchial muscles. The reason why branchial

muscles came into relation with the eye is that the light reached the latter, when the medullary tube began to close, through the ectodermal pit of a præoral gill-cleft. This ecto-dermal branchial pit is now the lens of the eye, whose peculiar mode of formation is thus explained. The vascular part of the same gill arch is retained in the choroid gland of Teleosteans, which receives its blood supply from the pseudobranchial vein, and the arteria centralis retinæ, which is the efferent artery of the lens branchia. This hypothesis explains the vessels of the campanula Halleri, of the pecten of Reptiles and Birds, the em-bryonic lens vessels of Mammals, as remnants of the blood-vessels of the branchia represented by the lens. Leaving the eye, Dohrn next goes on to support his view that almost the whole of the head except the brain represents visceral or ven-tral structures, just as the tail contains only dorsal structures, and asserts his belief that attempts to estimate the number of myotomes in the head are all in vain. In his opinion the cerebral nerves have lost those branches which innervated myotomes and their derivatives, and have, in consequence of the extraordinary enlargement and complication of the ventral region, increased to a corresponding degree their visceral branches, at the same time having undergone great alterations in distribution on account of the changes of relative position among the gill arches. Thus, the attempts of Van Wighe and others to diagnose dorsal branches of the cranial nerves are founded in mistaken views. A ramus dorsalis of a spinal nerve never innervates a mucous tube, any more than the ramus dorsalis, so called, of a cranial nerve innervates myotomes and muscles of a dorsal fin. Again, Dohrn points out how necessary it is to understand more accurately the anatomy and develop-ment of the vertebrate organs before constructing complete and simple schemes which reduce the head to a number of myotomes as formerly to a certain number of vertebræ. A great anatomist once said that if he wished to read romances he knew better specimens than histories of creation where-with to amuse himself, à propos of which Dohrn points out that if phylogenies are to be compared with romances it is as

well to remember that the most sensational are not always the
best works of art.

We have thus given a summary of Dohrn's results and indi-
cated the point of view from which he regards the problem of
vertebrate phylogeny.   The speculations formulated in the
'Ursprung der Wirbelthiere' have been in some cases sup-
ported in others overthrown by his later researches, but he
still holds strongly to the fundamental thesis that the original
ancestor was a segmented animal more or less similar to an
Annelid, and that the organisation of Cyclostomata, Amphioxus,
and Tunicata can only be explained by profound degeneration.
Whatever the fate of his various theories may be in the future
of morphology, it is certain that his studies form a massive
contribution to the really scientific study of organogeny, and
that his independent attitude and stimulating suggestiveness
of thought are worthy of his favorite motto, "Was fruchtbar
ist allein ist wahr."