Huygens Institute - Royal Netherlands Academy of Arts and Sciences (KNAW)

Anatomy. — *"Short history of the head of Vertebrates."* By Dr. H.
C. Delsman. (Communicated by Prof. J. Boeke).

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In preparing a second edition of my theory on the origin of
Vertebrates I was led to indulge once more in a number of ques-
tions relating to their structure and development. Applying to these
the principles of my theory I arrived again at several new points
of view. As the completion of the more elaborate article will probably
be delayed for some time, I wish to give here a short summary
of the views arrived at concerning the structure of the head
of Chordates, though I will not add now a complete account of the
considerations which induced me to embrace certain conceptions and
to reject others. It seems to me that with the records now at hand
we have approached considerably nearer to the solution of this problem
than one would be inclined to conclude from a more superficial
acquaintance with the chaos of divergent and contradictory opinions
of older and of more recent investigators.

The history of the head of Vertebrates is closely related to that
of the animal pole of the egg and of the blastula in the animal
kingdom. Already in *Volvox* we find a contrast between two opposed
poles of the colony, expressed by the stronger development of the
red stigmata characteristic of Flagellates at the one pole and of the
plasmodesms, serving for the transport of food between the cells, at
the other. In the development, too, which begins with an egg cleavage
reminding one of the spiral type, the contrast between the two poles
becomes evident. The colony swims with the animal pole forward,
rotating round the main axis (for literature cf. Janet, 1912). The
same holds for the free-swimming blastula — "the animal Volvox"
as Huxley (1877, p. 678) called it — of different groups of marine
animals, the planula of Coelenterata and other pelagic larvae. The
animal half of the blastula as a rule develops into a sensory and
nervous centre, the so-called apical plate of larvae like the trocho-
phore, arising from the four animal cells of the eight-celled stage
(1st quartet of micromeres). The animal pole and the prae-oral lobe
or prostomium, to which the apical plate gives rise, as a rule
continue to indicate the anterior end of the body in free-moving

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animals such as Annelids, Molluscs, Arthropods, Chordates and Ente-
ropneusts, as is the case already in *Volvox* and the pelagic blastulae
and larvae.

Sessile forms such as Coelenterates, Echinoderms, Ascidians (WILLEY,
1894, p. 329), however, often attach themselves with the anterior
end. Then the prae-oral lobe loses its significance as a sensory and
nervous centre. This is equally the case in burrowing animals like
the earth-worm, *Amphioxus* and *Balanoglossus*.

In Polychaetous Annelids the whole segmented soma, ecto-, ento-
as well as mesoderm, takes its origin from the four vegetative cells
of the eight-celled stage, i.e. from the vegetative half of the blastula.
Prostomium and soma are met with again in Chordates. With
Annelids and Anthropods one or some of the anterior segments
unite with the prostomium to form the head; this is equally the
case in Vertebrates.

In *Amphioxus* [1]) we can hardly speak of anything of the kind.
The Annelidan stomodaeum has grown out in a backward direction
and has become the medullary tube (DELSMAN, 1913a, p. 649), which
even surpasses the soma in length (formation of the tail, DELSMAN,
1917b, p. 1271). The mouth, situated in Annelids ventrally just behind
the limit of prostomium and first segment (peristomium), is found
again in *Amphioxus* as the neuropore on the corresponding place
(DELSMAN, 1913b), viz. dorsally, at the boundary of prostomium and
soma, just in front of the first mesodermic segment, which is the man-
dibular segment of van WIJHE (1893, p. 157), the "collar-cavity" of
MACBRIDE (1898, p. 599). The fore-end of the notochord is originally
situated right under the neuropore and equally indicates the limit
of prostomium and soma. Sense organs and ganglia have been
lost or become indistinct in *Amphioxus*. The brain vesicle cor-
responds to the deuterencephalon (KUPFFER, 1905) of Craniotes.
The somites from the foremost up to the last develop uniform
myotomes constituting together the voluntary longitudinal trunk
musculature. The first pair sends out a "rostral prolongation"
(Kopffortsatz) into the prae-oral lobe in which also muscle fibres
develop which, however, subsequently disappear.

In the larva the gill-clefts regularly alternate with the myotomes
(WILLEY's figures, 1891, HATSCHEK, 1892. p. 145), so there is eume-
tamerism. Only secondarily, after the "critical stage" (WILLEY, 1891,
p. 202), it gets lost. The left gill-cleft between the first and the
second somite becomes the larval mouth, its antimere is the club-

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[1]) The reader is invited to compare the following descriptions with the plate.

shaped gland (van Wijhe, 1893, p. 153, cf. also His, 1887, p. 429); they represent the second pair of gill-slits. The first pair of gill-pouches, at the limit of prostomium and first segment, is represented by the bilaterally symmetrical "anterior entoderm pockets" or "head-cavities" (Hatschek, 1892, p. 144) of which only the left one still gets an opening, known as Hatschek's pit, to the exterior; the right one does not open, but gives rise to the so-called praeoral coelome.

To each somite a dorsal nerve belongs, to the first one, however, two, situated close to each other and compared by Hatschek (1892) to the two parts of the trigeminus in Craniotes, which commonly is considered as a double nerve, by me, however, with Balfour (1878, p. 214) as a single one which sometimes may be split into two (cf. facialis and acusticus) and belonging to the first or mandibular segment (v. infra). The same holds for both the anterior spinal nerves of Amphioxus, which accordingly I designate together as no 1. No distinction can be made as yet between cranial and trunk nerves, dorsal and ventral roots remain separated along the whole body. Here already, however, the fourth nerve (Hatschek's 5th, 1892, p. 143), the future vagus, is distinguished by its strong development and it is especially this nerve which communicates with the longitudinal plexus supplying the gills (ramus branchio-intestinalis vagi of Craniotes). Thus the first four somatic segments evidently correspond to the trigeminus-, the acustico-facialis-, the glossopharyngeus- and the vagus-segment of Craniotes (v. infra).

The prostomium does not contain any mesoderm of itself, its mesoderm is derived from the first somite, as is also found very generally in Annelids (cf. e.g. Meyer, 1890, p. 299). The proper, ectodermal, so-called primary or larval, mesenchyme (Conklin, 1897, p. 151) of the prostomium of Annelids, a last remnant of the mesenchyme of the primary body-cavity of flatworms (Meyer, 1890), has evidently disappeared in Vertebrates, together with the so-called head-kidney of the trochophora, a last rest of the protonephridia of flat-worms which, however, have been preserved in certain Annelids and in Amphioxus (Goodrich, 1902).

The asymmetrical origin of the mouth of Amphioxus gives us the key to the interpretation of the larval asymmetry.

Petromyzon is distinguished from Amphioxus by the possession of a praechordal brain, the palaeocranium of Kupffer, which together with the inverted eyes has arisen from the dorsal half of the surface of the prostomium, so that the neuropore, also in the other Craniotes, is not situated any longer dorsally, and above the anterior end of the notochord, but terminally, far in

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front of the end of the notochord and close to the animal pole (DELSMAN, 1916, 1917). *Petromyzon* resembles *Amphioxus*, however, by the complete segmentation of the mesoderm (HATSCHEK, 1910) and the separate course of the dorsal and ventral roots of the spinal nerves. The series of well-developed somites continues forward as far as the prostomium. As is the case in most of the Annelids that possess them (FAUVEL, 1907, p. 110), the static vesicles are situated in the second segment of the soma, being the hyoid- or facial-acoustic-segment, but more in the hinder half of it. Thus in *Petromyzon* and in all Craniotes two pro-otic segments may conveniently be distinguished, the mandibular or trigeminus-segment and the hyoid- or acustico-facialis-segment. Behind the ear-vesicles then follow the segment of the glossopharyngeus, that of the primary vagus, that of the first spinal nerve, the ganglion of which in Gnathostomes fuses with that of the vagus ("spinalartiger Vagus-anhang", HATSCHEK, 1892, p. 156) and those of the subsequent spinal nerves. The first pair of somites again send out each a prolongation into the prostomium, the so-called praemandibular somite (HATSCHEK, 1910, p. 481), comparable to the "Kopffortsatz" in *Amphioxus*, and thus not to be considered as a proper somite. The two pro-otic somites do not contribute any more to the formation of the longitudinal trunk musculature, but together with the so-called "praemandibular somite" give rise to the eye-muscles. The post-otic somites all form regular myotomes, constituting the longitudinal trunk-musculature. This, consequently, unlike in other Craniotes, also holds for the glossopharyngeus- and the primary-vagus-somite, though in both a beginning of reduction manifests itself in the breaking up of the internal, deeper parts of these myotomes during development (KOLTZOFF, 1901, p. 329). Evidently this is caused by the strong development of the auditory capsule, which extends backward into the first and the second post-otic segment, the myocommata between the first and the second and between the second and the third myotome as a consequence attaching themselves to the auditory capsule and the first free neural arch being situated between the third and the fourth myotome (cf. e.g. GOODRICH, 1909, p. 40). Superficially, however, the first and the second myotome do not differ from the subsequent ones.

As in *Amphioxus* branchiomerism and mesomerism correspond, the eight gill-pouches, of which the first, the spiracular one, does not break through, alternate with the 1st—9th somite (NEAL, 1897, p. 447, KOLTZOFF, 1901, p. 432). In front of the first somite lies a median mouth. That the mouth of Craniotes corresponds to two fused gill-slits is a supposition (DOHRN, 1875) which, though not supported

in a convincing way by embryology, is yet rendered probable by a comparison with *Amphioxus*. The mouth of Craniotes is at any rate a different one from that of *Amphioxus* which corresponds to the left spiracle (van Wijhe, 1907 [1])), while that of Ascidian-larvae is again another one. It breaks through at the place of the neuropore so that even the anterior part of the medullary tube, the former stomodaeum, contributes towards the formation of the new entrance to the gut (Huntsman, 1913). The secondary nature of the Vertebrate mouth is thus clearly shown.

While in *Amphioxus* the endostyle arises as a ventral bulging out of the gut just in front of the mouth, in the first somatic segment, in *Ammocoetes* it originates, like the rudiment of the thyroid gland in Craniates, in the same segment but consequently just behind the mouth (Van Wijhe, 1907, p. 75).

From the anterior post-branchial myotomes (Neal, 1897, p. 444, Koltzoff, 1902, p. 304) ventral buds grow out, similar to those which in Gnathostomes produce the musculature of the paired limbs. Growing down behind the last gill-slit and then forward they give rise to the hypobranchial musculature which is supplied by the ventral roots of the same post-branchial myotomes (7th—12th post-otic somite after Neal) that have produced the muscles, as holds equally for the musculature of the limbs. The original eumetamerism of gill-slits and somites afterwards, as in other Craniates, gets lost, by a backward extension of the branchial sac, by which the gill-slits are caused to disperse and the originally post-branchial myotomes 7—12 now come to lie epibranchially. The ventral roots of these somites continue to pass behind the last gill-slit on 'their way to the hypobranchial muscles and during the elongation of the branchial basket they unite one by one to a common horizontal stem, which springs from six roots and bends downward behind the last gill-slit. This stem we can call the hypoglossus or plexus cervicalis (fig. 1). (See following page).

The primarily epibranchial somites give rise to the epibranchial musculature, supplied by the corresponding ventral roots in front of the hypoglossus.

The 5th, 7th, 9th and 10th cranial nerves of Craniotes innervate the primordial branchial musculature (Musculi constrictores) which, though striated, must be counted with the visceral musculature

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[1]) Regarding the mouth of *Amphioxus* we now come to a conclusion somewhat different from that reached formerly (1913, *b*). An interpretation of the praemandibular cavity of Craniotes diverging from that of van Wijhe (1882) leads us to a confirmation of van Wijhe's conclusions on another subject.

(Van Wijhe, 1882, p. 41), since it originates from the lateral plate.

The vagus is considered by Hatschek (1892, p. 152) to be a primarily single nerve belonging to the second post-otic somite but which has collected in its ramus lateralis the lateral dorsal branches of all the spinal nerves behind it and in the same way in its ramus
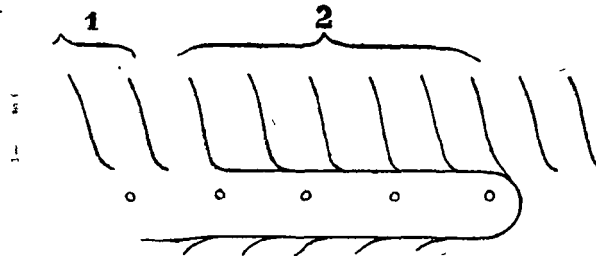

Fig. 1. The Hypoglossus of *Petromyzon*, after Neal (1897)
1 primarily epibranchial ventral roots.
2 secondarily   „   „   „   (hypoglossus).

branchio-intestinalis (with the rami post- and praetrematici), the corresponding ventral branches of as many subsequent nerves as it supplies more than one gill-slit ("partial polymerism" of the vagus). The ramus branchio-intestinalis, which may be compared to the epibranchial plexus of *Amphioxus*, no doubt, like the latter also owes its origin to the process of dispersion of the gill-slits.

For the first time we meet in *Petromyzon* the beginning of a cartilaginous skull, comparable to the head cartilage in Cephalopods and arising, like the latter, round the central part of the nervous system and the main sense-organs. It contains, besides the prostomium (which Hatschek does not distinguish from the first segment, designating it together with the latter as the acromerite, 1910), only two segments (Hatschek, 1892, p. 159), as the skull ends with the auditory capsule. The roof remains for the greater part membranous and membranous walls reach from the auditory capsules to the first neural arch, situated between the third and the fourth post-otic myotome. Through this membranous wall the glossopharyngeus and the vagus pass.

Attention must be drawn to the fact that the hypoglossus lies far behind the skull and also far behind the vagus. It does not appear from any publications on the subject that the spinal ganglia following behind the vagus are, under the influence of the latter, less developed than those situated more backwards, as may be noted regularly in Gnathostomes.

In many respects the Amphibians more closely resemble the Cyclostomes than the Selachians which, though exhibiting several

primitive features, yet in other respects remind one more of the Amniotes. This holds e.g. for the earliest stages of development of the egg, which are nearly identical in *Petromyzon* and Urodelans, and also for the origin of the hypophysis in front of the mouth involution (in Selachians and Amniotes from the roof of the latter), for the structure of the brain which still lacks a developed metencephalon in *Petromyzon* and Amphibians, for the presence of horny teeth round the mouth (in Amphibians at least in the larval stage) and for the development of the cranial muscles (EDGEWORTH, 1911, p. 292). It holds equally for the backward extension of the skull.

Into the last the first three post-otic somites have now been incorporated, together with the first free neural arch of *Petromyzon* which in ontogeny appears as the so-called occipital arch, bounding behind the foramen vagi (STÖHR, 1879, 1881). The occipital region of Amphibians accordingly contains only one vertebral rudiment (SEWERTZOFF, 1897, p. 262). Between the occipital arch and the auditory capsule in early ontogeny three somites can be recognized (MISS PLATT, 1897, p. 448, for *Necturus*, SEWERTZOEF 1897, p. 260, for *Pelobates*, possibly also for *Siredon*, cf PLATT, 1898, p. 450) the last of which lies over the space between the 4th and the 5th gill-slit (MISS PLATT, 1897, MARCUS for Gymnophiones, 1910). These three are the somites of the glossopharyngeus, of the primary vagus, and of the first spinal ganglion which fuses with the latter ("spinalartiger Vagusanhang", HATSCHEK, 1892, p. 158). Of this fusion indications were observed in ontogeny by MISS PLATT, (1897, p. 448) and MARCUS, (1910, p. 378). To the last head-segment in young stages a ventral root, a so-called occipital nerve (FÜRBRINGER, 1897, p. 353), was observed in a few cases (FÜRBRINGER, 1897, p. 486, PETER, 1898, p. 42, DRÜNER, 1901, 1904, OSAWA, 1902, MARCUS, 1910, p. 376) which, however, during further development disappears. Of the three post-otic somites only the posteriormost in Urodelans and Gymnophiones still produces a regular myotome, which gives rise to the anterior segment of the longitudinal trunk musculature and, like the 3d post-otic myotome of *Petromyzon*, is inserted at the auditory capsule. Both the anterior post-otic myotomes, the deeper parts of which already in *Petromyzon* showed reduction, have been suppressed, evidently by the extension of the auditory capsule; only the second may still produce a few muscle fibres (MISS PLATT, 1897, p. 447, MARCUS, 1910, p. 430). In phaneroglossan Anurans, however, the 3d and the 4th post-otic myotome (SEWERTZOFF, 1895, p. 269) also disappear, together with the ventral root of the latter two, being that of the first free spinal nerve.

The gill-pouches, five in number in *Necturus*, the foremost corresponding to the spiracle, again regularly alternate with the 6 anterior somites (PLATT, 1894, 1897). Thus the five head somites are all epibranchial, the occipital arch lying right above the last gill-slit (PLATT, 1897, p. 452). By the restricted backward extension of the cranium the sphere of influence of the vagus causing the suppression of the subsequent spinal ganglia extends beyond the craniovertebral limit; in Amphibians as a consequence the first free spinal ganglion is always absent. Since in phaneroglossan Anurans also the ventral root gets lost (see above), the first spinal nerve is wholly absent here. The vagus does not supply more than three gill-slits, being that of the primary vagus, of the "spinalartiger Vagusanhang" and the first free spinal nerve which either has no dorsal root or is wholly absent.

The hypobranchial musculature is formed in Urodelans from ventral buds of the anterior two post-branchial (4th and 5th post-otic somite) and the last epibranchial myotome (3^d post-otic somite) (MISS PLATT, 1897, p. 452) and innervated by the ventral roots of both the former somites, being the first two free spinal nerves, which in Urodelans together constitute the wholly post-cranial hypoglossus. The latter now partly lies within the sphere of influence of the vagus which causes the anterior root to have no dorsal ganglion. The ventral root of the last epibranchial myotome gets lost, as was mentioned above.

Epibranchial musculature is absent.

The olfactory grooves, situated in Annelids dorsally on the prostomium just in front of the limit between prostomium and first segment, are found in Craniotes at the corresponding place, viz. ventrally on the prostomium just in front of the mouth. Only in *Petromyzon* has a secondary monorhinism been established.

In Selachians as well as in Amniotes the enormous yolk-contents of the egg has in a corresponding way influenced the course of the earliest development, in both these the metencephalon has developed and the pituitary body does not originate any longer in front, but from the roof of the mouth evolution. In both the skull has annexed a number of vertebral elements constituting the regio occipitalis. In *Acanthias* the rudiments (or at least the indication, SEWERTZOFF, 1899) of four vertebrae may be observed (HOFFMANN, 1894, p. 638), the foremost of which corresponds to the occipital arch of Amphibians (SEWERTZOFF, 1895, p. 260) and, like the latter, is separated by three somites from the auditory capsule. Thus three segments have been added to the skull; in *Scyllium* and *Pristiurus*

where the skull is one segment shorter (Hoffmann, 1894, p. 638, Sewertzoff, 1899, p. 302) than in *Acanthias*, only two. Thus in the latter forms the skull contains, besides the prostomium, seven segments (equalling the number of visceral archs [1]), of which one is post-branchial; in *Acanthias* eight, of which two are post-branchial, in *Hexanchus* and *Heptanchus* probably still a few more (v. infra). Mesomerism and branchiomerism again correspond (Van Wijhe, 1882, Ziegler, 1908, 1915). As in Amphibians the two anterior post-otic somites no longer develop myotomes, but the second somite still forms a rudimentary one. From the remaining occipital somites, however, myotomes are still developed.

From these the epibranchial musculature is formed (Dohrn, 1885, p. 446, Hoffmann, 1898, p. 265), which in all other Gnathostomes, and also in rays already, is absent. It still reaches its strongest development in the primitive *Hexanchus* and *Heptanchus* (Fürbringer, 1897, p. 416). The hypobranchial musculature (Musculi coraco-arcuales) originates from the ventral buds of the last epibranchial and the first four post-branchial myotomes, being the 4th—8th post-otic somite, according to Neal (1897, p. 450), and only of the latter four, all post-branchial, according to Hoffmann (1898, p. 263). It is supplied by the ventral roots of these latter four myotomes, which partly lie within the range of the skull, partly behind it, forming together the plexus cervicalis. The gill-slits here too dispersing afterwards in a backward direction, this plexus cervicalis again comes to run in a curve round behind the last gill-slit; by the strong elongation of
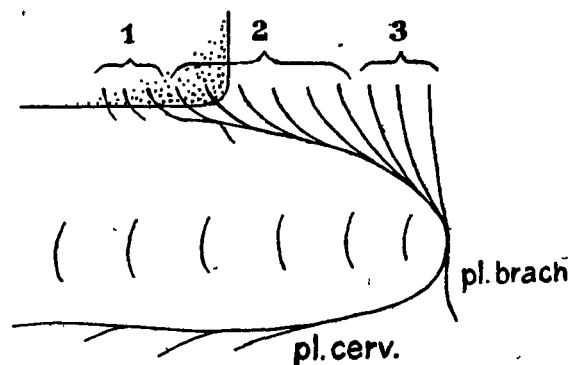

Fig. 2. Plexus cervico-brachialis of *Heptanchus*, after Fürbringer. (1897).
1. primarily epibranchial ventral roots.
2. plexus cervicalis (hypoglossus). 3. plexus brachialis.

[1] Accordingly two less than the well-known number given by van Wijhe (1882), who considered the praemandibular cavity as the first somite and counted the hyoid segment as two.

the branchial basket it is even united with the plexus brachialis into a common stem, the plexus cervico-brachialis, which only distally splits into a branch to the hypobranchial musculature and one to the pectoral fin (fig. 2). This common plexus was seen by HOFFMANN (1901, p. 39) to form during development in exactly the same way as is described by NEAL for the hypoglossus of *Petromyzon*. The skull in *Acanthias* containing 8 segments, of which 6 post-otic, we may expect that of the four roots of the hypoglossus or plexus cervicalis after HOFFMANN's statements the anterior two (5th and 6th post-otic somite) will pass through the skull. This indeed proves to be the case (FÜRBRINGER, 1897, p. 362). In no Selachian is the number of intra-cranial (occipital) hypoglossus roots, as far as has been definitely stated, more than 2 (FÜRBRINGER, l.c. p. 404), often one or none. From this the approximate number of post-branchial segments incorporated into the skull may be derived. Provisionnally we must say "approximate" since we have insufficient evidence as to the participation or non-participation of the last epibranchial somite. NEAL (1897, p. 461) supposes that a transitory crowding forward of the posterior gill-slits causing the last one to lie under and not behind the last epibranchial myotome, as observed by himself in *Acanthias* and by Miss PLATT (1897, p. 458) in *Necturus*, sometimes allows the ventral growth of a myotome, which otherwise would be prevented.

In front of the occipital hypoglossus roots (*y, z,* of FÜRBRINGER) a few ventral occipital nerves may still be found which either remain independent (*Hexanchus, Heptanchus*) or at first may join the plexus, but supplying only epibranchial musculature (*x, w, v,* of FÜRBRINGER), and therefore are comparable to the ventral roots of the first six post-otic myotomes of *Petromyzon* for which the same holds. Thus of the occipital myotomes and nerves only the anterior ones are primarily epibranchial, the one or two posterior ones are of post-branchial origin, but have become epibranchial only secondarily by the dispersion of the gill-slits.

In *Hexanchus* and *Heptanchus* where the number of gill clefts is greater, but the number of occipital hypoglossus roots not less than in pentanch sharks, the skull accordingly may be expected to comprise at least one or two segments more than in *Acanthias*. This is also confirmed by what follows. The sphere of influence of the vagus on the dorsal roots following it in *Scyllium* etc. reaches to a little behind the cranio-vertebral limit, the second free spinal ganglion only is again nearly normal, the first as a rule being absent (FÜRBRINGER, l.c. p. 392). In *Acanthias* there is formed in the last

head-segment a more or less developed spinal ganglion, which however no longer produces a dorsal root. In *Hexanchus* and *Heptanchus*, however, the last occipital nerve is provided with a well-developed dorsal root with a ganglion, so here the influence of the vagus no longer reaches quite to the end of the skull, which in these forms passes more or less gradually into the vertebral column. This holds still more for the Chondrostei, where in several species a considerable number of dorsal and ventral roots leave the skull (FÜRBRINGER, 1897, p. 450) and where even the whole brachial plexus can have been incorporated into it (ibid., p. 457). For the supposition that in *Hexanchus* and *Heptanchus* the longest skull among Selachians is found, we may also point out the well developed primarily epibranchial nerves (*v, w, x* of FÜRBRINGER). In pentanch sharks the hindmost of these roots, as a consequence of the decreasing number of gill-slits, pass into post-branchial or hypoglossus-roots. The same holds for the development of the epibranchial, musculature.

On the other hand in rays the cranium appears to be shorter, the number of occipital hypoglossus-roots is mostly 0, never more than 1 (FÜRBRINGER, 1897, p. 404), and the influence of the vagus reaches part of the way behind the cranio-vertebral limit, both the anterior spinal ganglia being absent (FÜRBRINGER, p. 392). There is no epibranchial musculature or occipital nerves supplying it. All this points much more to a phylogenetic decrease than to an increase of the length of the skull in the Selachians.

So in Elasmobranchs we have on the whole a partly intracranial, partly post-cranial hypoglossus the anterior roots of which as a rule are lying within the sphere of influence of the vagus and hence lose their dorsal glanglia. GEGENBAUR (1871, p. 521) called the occipital nerves "ventral vagus roots", which is right, if we consider the vagus as a partially polymeric nerve and moreover bear in mind that in Selachians we could better speak of a vago-accessorius. With the already bivalent vagus-ganglion the rudimentary ganglion of the 6th segment still fuses (NEAL, 1898, p. 238), so that the vagus ganglion is now trivalent, fused from one normal and two rudimentary ganglia.

In Amniotes the number of occipital myotomes observed during ontogeny nearly corresponds to that of Selachians. The number of intracranial (occipital) hypoglossus roots is very generally stated to be 3, thus one more than in *Acanthias*, but the number of gill-slits (5) being one less than in *Acanthias*, we must conclude that the cranio-vertebral limit almost corresponds to that of the latter form and that the skull here too contains some eight segments. Both in Selachians and

Amniotes the first pronephric tubule is found as a rule in the third somite behind the skull (FRORIEP, 1905, p. 119). The relation between myotomes and gill-slits in this case is not so evident as in lower Chordates. If, however, we take as an example the instructive figure given by VAN BEMMELEN (1889, p. 254) for the head of *Lacerta*, I think we may deduce from it as the most probable conception that the anteriormost occipital myotome figured corresponds to the first somite following behind that of the primary vagus, being accordingly the third post-otic (just as in Amphibians and Selachians), and the last epibranchial one.

This is the first of the five myotomes, which after VAN BEMMELEN give rise to the hypobranchial or tongue-musculature, while CORNING (1895, p. 165) denies the participation of this first one, only the four anterior post-branchial myotomes according to his statements contributing to it. Of these, three belong to the head, while the fourth corresponds to the atlas. Indeed, the tongue musculature is supplied by a hypoglossus with three occipital roots uniting with the first free ventral root (FURBRINGER, 1897, p. 506) to a plexus cervicalis which, however, in this case does not fuse with the plexus brachialis, which in Amniotes often shoves backwards pretty far from the head.

Thus the hypobranchial resp. tongue-musculature of Vertebrates in its origin and innervation wholly agrees with that of the paired limbs. To the hypobranchial musculature also the rule formulated by FÜRBRINGER (1879; p. 389) for that of the extremities is applicable, that the structure and innervation is not bound to distinctly numbered segments but that the place and number of the latter depends upon the situation and extension of the "segmental level" from which the organ takes its origin. Displacement in forward and backward direction, extension and reduction is possible without the myotomes themselves moving, dividing or fusing, or new myotomes being intercalated or others falling out. The anterior limit of the hypoglossus region is always determined by the situation of the last gill-slit and so by the number of gill-slits. Possibly also the hindmost epibranchial myotome can participate, though among the observations cited above there is only one concerning this point (Miss PLATT, 1897) which has not met opposition, nor does the non-participation of the corresponding ventral root exclude every possibility of doubt.

It also depends on the number of gill-slits whether the anterior hypoglossus roots come to lie within the sphere of influence of the vagus, and, together with the primarily epibranchial nerves, may be considered with some right as ventral roots of the partially polymeric

vagus (vago-accessorius) or not (GEGENBAUR). In *Petromyzon* e.g. this is not the case.

On the number of gill-slits and on the backward extension of the skull depends whether the anterior hypoglossus-roots are incorporated into the skull as occipital nerves. In *Petromyzon* the skull is short and the number of gill-slits great: the hypoglossus accordingly lies far behind the skull. Directly behind the skull we find the hypoglossus roots in Amphibians and most rays; partly in the skull and partly behind it in sharks; for the greater part in the skull in Amniotes, wholly in the skull in Chondrostei, where moreover the plexus brachialis may have been incorporated into it, as is the case in *Acipenser* (FÜRBRINGER, 1827, p. 457).

From the above considerations the following conclusions may be drawn :

1. FRORIEP's (1882—1887) sub-division of the head of Vertebrates into a primarily unsegmented "cerebral" part, comprising besides eye and nose also the auditory vesicles and the gill-slits, and a segmented "spinal" part (regio occipitalis) is false. GEGENBAUR's division of the skull into a prae-chordal "evertebral" and a chordal "vertebral" part is the right one, though the anterior part of the latter, as far as the occipital arch, has not formed from vertebrae, but has originated simultaneously with the latter (cf. *Petromyzon*, GEGENBAUR, 1887, p. 77, VAN WIJHE, 1889). Branchiomerism and mesomerism correspond.

A primarily unsegmented head mesoblast (FRORIEP, 1887, "Urmesoderm" of DE LANGE, 1913, p. 250), in which we could speak only of branchiomerism, does not exist; the prostomium no longer contains primordial mesoderm (cf. *Amphioxus* and the "proammion" of Amniotes).

2. FRORIEP's (1882 etc.) conception of a secondary invasion of trunk segments into the primarily unsegmented "cerebral" head and FÜRBRINGER's (1897, p. 440) opinion on a "stetiges Vorrucken" and breaking down of these myotomes with their ventral roots in the occipital region are false. FRORIEP's argument that rudimentary dorsal roots discovered by him belonging to these myotomes would indicate that they cannot belong to the vagus and must be of post-branchial origin, loses its value by the conception of the vagus as a partially polymeric nerve, which would lead us naturally to expect just such rudimentary dorsal roots. The argument of FÜRBRINGER, that the occipital nerves of the sharks unite with the anterior free spinal nerves to form the plexus cervicalis, is wholly deprived of its value by the above considerations. FRORIEP and FÜRBRINGER, not making a difference between primarily and

secondarily epibranchial myotomes, as we can do so clearly in *Petromyzon*, and taking them all for secondarily epibranchial and of post-branchial origin, arrived at erroneous conclusions. No "heiszer Kampf der Theile" (FRORIEP, 1901, p. 372): peace and rest are reigning in the occipital region.

3. FÜRBRINGER's (1897) conception of the metameric structure of the Amphibian cranium, and as a consequence also that concerning the skull of Amniotes, is false. The Amphibian skull does not, as FÜRBRINGER (l. c. p. 485) assumes a priori, contain as many segments as that of Selachians, but less (SEWERTZOFF, 1897, p. 410). The single occipital nerve which sometimes may be observed in early stages of development of Amphibians, was accounted for above. It is not to be considered as a last remnant of more occipital nerves (x, y, z) corresponding to those ·of Selachians, it is accordingly not z, but r.

The occipital hypoglossus roots of Amniotes do not owe their presence to a second annexation of free segments, but correspond to those of Selachians, not to the anterior free roots of the latter. The oldest conception (GEGENBAUR, 1871, p. 532) once more proves to be the right one here. Occipito-spinal nerves (a, b, c, etc. after FÜRBRINGER) do not exist, at least not in Amniotes. Only if with FÜRBRINGER (l. c. p. 362) one designates the last occipital nerve of *Acanthias* as a, we ought to do so equally with Amniotes. The "ganglion hypoglossi", discovered by FRORIEP (1882) in the last head segment of the sheep, evidently corresponds to the ganglion in the last head segment of *Acanthias*. The sharp distinction between proto- and auximetameric neocranium must be left out, at any rate the Amphibians have no protometameric neocranium (which is of equal length to that of Selachians), nor have the Amniotes an auximetameric neocranium (longer than that of Selachians) in FÜRBRINGER's sense. Only in Notidanidae and Chondrostei could one speak of an auximetameric neocranium and of occipito-spinal nerves.

Surely the hypoglossus has originally nothing to do with the vagus, as *Petromyzon* teaches us; that in higher Chordates it approaches the latter so closely that we may partly designate them with GEGENBAUR as ventral vagus roots, (i.e. of the partially polymeric vago-accessorius, better still of the accessorius which originates in closest connection to the anterior, rudimentary ganglia behind the vagus and in Selachians has not yet separated from the latter), is not to be accounted for by a forward movement of the myotomes and ventral roots themselves, but by a displacement of the "segmental hypoglossus level" in forward direction as a consequence of the decrease of the number of

gill-slits (shortening of the branchial level), in accordance with the principle formerly put forward by FÜRBRINGER (1879) himself. This principle, together with the admirable anatomical investigations of GEGENBAUR and FÜRBRINGER, and those of others in embryological direction, now opens to us the prospect to a better understanding of the structure of the head of Chordates.
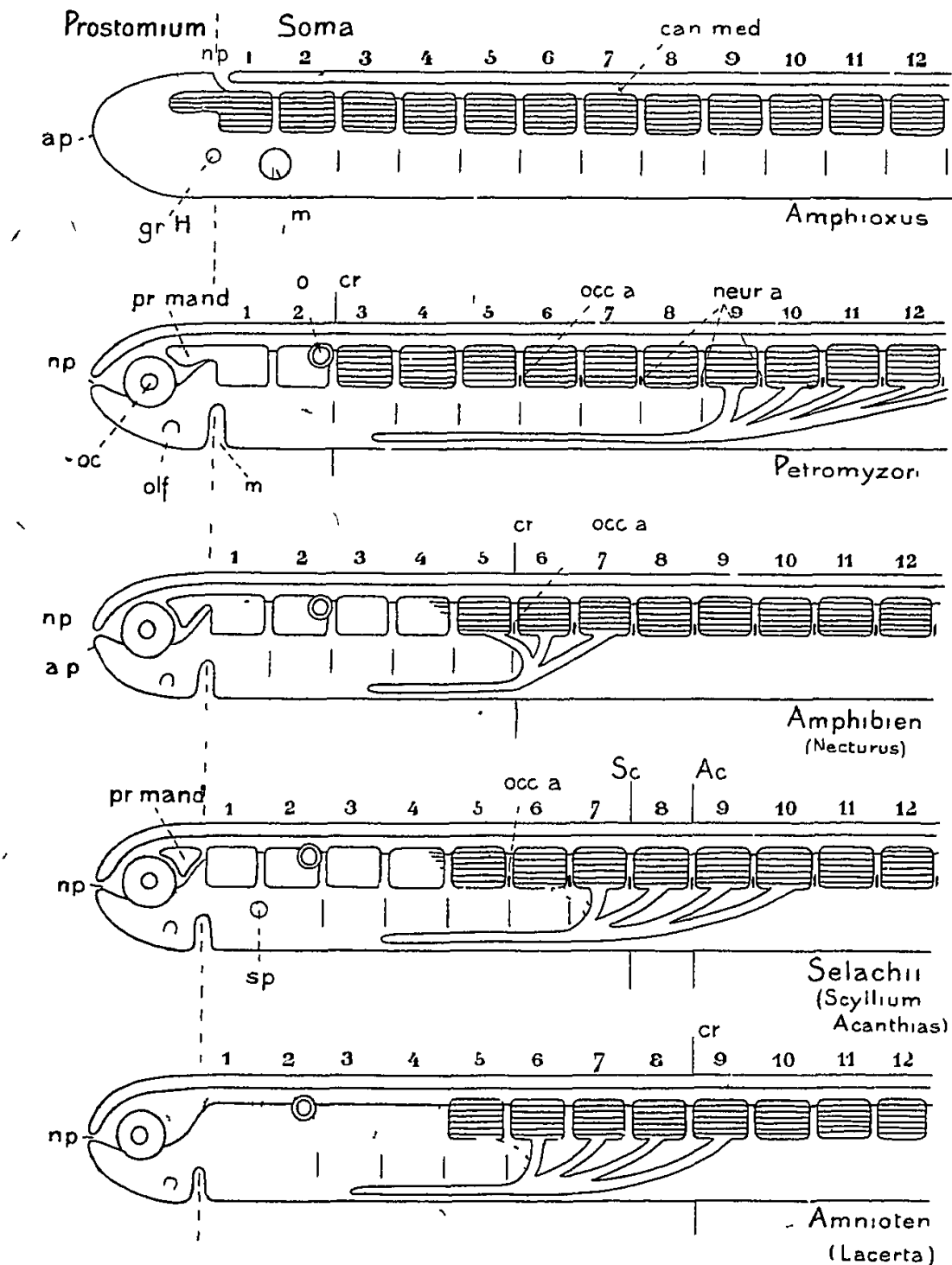
The doubt whether the structure and the history of the Vertebrate head will ever be elucidated may, I think, make place for hope. "The recent rehabilitation of *Amphioxus* as an ancestral type by DELSMAN ('13)", NEAL (1914, p. 138) wrote some years ago, "seems to justify the hope that the ancestral history of the head may yet be known and general agreement among morphologists be attained". May this expectation be realized and further investigations complete and rectify the results reached in this first attempt.

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Diagrams of the head of the main groups of Vertebrates.

Prostomium | Soma   can med

n'p 1 2 3 4 5 6 7 8 9 10 11 12

ap

gr H   m   Amphioxus

pr mand   o cr   occ a   neur a

1 2 3 4 5 6 7 8 9 10 11 12

np

oc   Petromyzon

olf   m

cr   occ a

1 2 3 4 5 6 7 8 9 10 11 12

np
ap   Amphibien
                              (Necturus)

pr mand   occ a Sc Ac

1 2 3 4 5 6 7 8 9 10 11 12

np

sp   Selachii
                           (Scyllium

                   cr   Acanthias)

1 2 3 4 5 6 7 8 9 10 11 12

np

                           Amnioten

                            (Lacerta)

The shaded squares are somites producing myotomes, the blank squares, somites not doing so. The hypoglossus roots on the whole correspond to the myotomes from which the hypobranchial musculature is formed; the root belonging to the last epibranchial somite, however, never forms part of the hypoglossus.

a. p. animal pole, can. med medullary tube, cr. cranio-vertebral limit. (Sc. in Scyllium, Ac. in Acanthias), gr. H. groove of HATSCHEK, m. mouth, neur. a. neural archs, np. neuropore, o. auditory vesicle, oc. eye, occ. a. occipital arch., olf olfactory groove, pr. mand. "praemandibular somite", sp. spiracle.