

Citation:

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Anatomy. — “*On the metamerological signification of the cranio-vertebral interval.*” By Dr. J. A. J. BARGE. (Communicated by Prof. L. BOLK).

(Communicated in the meeting of May 29, 1915).

In the so exceedingly extensive literature concerning the history of the development of vertebral column and cranium two problems chiefly draw continually the attention: the so-called resegmentation of the vertebral column (*Neugliederung der Wirbelsäule*) and the metamery of the cranium.

Both problems have been studied circumstantially, and the bibliography of both can boast of classical essays from the best days of morphology. The more remarkable it must be called, that the two fundamental views, that served as a guide to the numerous investigators in this department, and, which, at present at least, in principle, are pretty well generally admitted, have constantly been studied separately, and never yet in their mutual relation.

It is especially to this fact that I wish to fix the attention in this communication, in order to show in this way at the same time, how for this reason the signification of important carefully stated facts has remained unobserved.

Since GOETHE and OKEN expressed in the “Vertebral theory of the cranium” for the first time the idea, that the bones of the cranium, at least those of mammals, could be grouped into a number of segments, which show some similarity with vertebrae, the doctrine concerning the metamery of the cranium has passed through a long period of development. It is superfluous to describe here this historical development already for this reason that most of the manuals give a summary of this idea more detailed than seems desirable in the short compass of this communication.

It may suffice to point out, that the question that was put when this problem was investigated, has constantly varied, and that the phases of development of this idea can probably be best characterized by the following formulations of the problem.

1. Are there evidences that prove, that the cranium has been constructed of a number of segments corresponding to vertebrae?

2. Is the cranium, or at least part of it, formed in its embryonal development in a similar way and of equivalent material as the vertebral column?

3. Are there indications, that make it probable, that at least part

of the cranium was segmented in a previous period of the phylogenetical development?

In this last form the problem is at the present moment still being discussed, though the arguments that are now brought forward to enable us to come to an affirmative answer of this question, are of a character quite different from those which GEGENBAUR, who was the first to formulate it in this way, developed for it. At present the state of the problem is indeed so, that a positive answer of the question is no longer contested by any of the investigators, and they only do not agree in stating how great the part of the cranium is, over which the mentioned segmentation extends.

In connection with the much earlier ontogenetical investigations of RATHKE, GEGENBAUR distinguished in the cranium 2 parts, a frontal not segmented part and a posterior segmented part. The two parts are designated as the vertebral part and the praevertebral one.

According to GEGENBAUR, who formed his theory from the phenomena of the Selachier-cranium, the vertebral part would form by far the greater part of the cranium; only the region in which the N. opticus and the N. olfactorius pierce through the skull, would belong to the praevertebral region. The vertebral part constructed by fusion of about 9 cranial vertebrae would be primary, and it is only after conrescence of these elements, that the praevertebral part would have been developed by excrescence in a frontal direction of the cartilageous part formed in the above mentioned manner, under adaptation to the olfactory groove and the optical organ.

We do not find with GEGENBAUR a primitive part of the cranium, — principally to be distinguished from the other segmented part of the cranium —, which ought to be maintained as real primordial cranium contrary to the vertebral column. The body of vertebrates consisted of a number of equivalent segments. The frontal part of these has fused for the formation of the cranium, the posterior part forms the vertebral column. Secondarily, by excrescence, an unsegmented part has still been added to the segmented part of the cranium.

STÖHR added to this the opinion that the number of segments used for the construction of the cranium is not constant, and continually increases in the series of vertebrates. The craniovertebral interval shifts consequently more and more in a caudal direction. Other investigators could confirm the correctness of this view. SAGEMEHL succeeded in showing, that the cranium of higher developed pisces and of amniotes has increased in a caudal direction with 3 vertebrae. This cranium would consequently be the Selachiercranium

augmented with 3 vertebrae. With regard to the formation of the Selachiercranium SAGEMEHL is of the same opinion as GEGENBAUER. It would namely have taken existence from metameres. It is however of great importance to remark here, that, according to SAGEMEHL, these metameres had not yet the character of vertebrae, and that consequently the fusion-progress of these metameres in order to form the Selachier-cranium is not equivalent to the addition of the 3 vertebrae to the Selachier-cranium, which we observe with higher pisces and amniotes.

SAGEMEHL calls the Selachier cranium protometamere, the cranium enlarged by the addition of 3 vertebrae auximetamere.

VAN WIJHE showed that with Selachiers 9 segments (primordial vertebrae, somites) can be distinguished at the dorsal head mesoderm, which correspond entirely with and are equivalent to those of the trunkregion. GEGENBAUER'S view, that the head would be nothing else but a transformed part of the trunk, was certainly supported by this discovery. VAN WIJHE'S discoveries were however not of such great signification for the skeleton, as he could show, it is true, that sclerotomes originated from the primordial vertebrae, but it appeared likewise from his investigations, that this segmentation of the primitive formation of the skeleton was immediately again suppressed.

The investigations of FRORIEP are of great importance for the problem of the cranium metamery.

FRORIEP likewise distinguishes 2 parts of the cranium, one formerly segmented part and one unsegmented part. In this respect he consequently agrees with GEGENBAUR. Not so however with regard to the place of the boundary-line between the two regions. According to GEGENBAUR this boundary-line would be situated far frontally, and the unsegmented part would be restricted to the part of the cranium, formed secondarily in the neighbourhood of the olfactory groove and the optical organ. FRORIEP however admits as boundary-line between the two regions the spot, where the N. Vagus pierces through the base of the skull. The earlier segmented part is thus, according to FRORIEP, but very small and confines itself only to the occipital region. FRORIEP showed now that with cow and hen this occipital part behaves ontogenetically as the frontal part of the vertebral column, and consequently shows likewise the design of primordial vertebrae, vertebral arches and nerves, whilst in the region lying before the vagus nothing is perceptible that could be compared to the segmentation in the spinal trunk-region. In accordance herewith FRORIEP distinguishes in the cranium a spinal and a praespinal part.

What FRORIEP could show with regard to the N. hypoglossus is likewise of importance. He found namely in the course of this cerebral nerve, always conceived as purely motorical, spinal ganglions, and so it was obvious that this nerve would be nothing else than the complex of the nerves belonging to the spinal cranium-region.

This view of FRORIEP's concerning the spinal character of the occipital region of the cranium finds in reality no longer contradiction. From all sides confirmations of his discoveries have come also with other species of animals. Everywhere it has been possible to indicate that embryonally the occipital part of the cranium shows great similarity with the vertebral column. The part of the problem regarding the metamery of the cranium has ceased to be a problem. At best there is only question of the number of metameres, that can be distinguished in the spinal part. The question after the origin and the eventual segmentation of the part in front of the N. vagus still remains. On this point the views are still divided. For us it has for this moment no interest.

What is interesting for us, is the fact, that the most caudal part of the cranium, i. e. the occipital part, shows distinct proofs of a previous segmentation which corresponds entirely with that of the region of the vertebral column. It is of importance to emphasize here already that the above mentioned segmentation is a segmentation of metameres or primordial vertebrae with myotome and sclerotome, not a segmentation in vertebrae.

The second problem mentioned in the beginning is the so-called re-segmentation of the vertebral column (*Neugliederung der Wirbelsäule*). The quintessence of this problem is the question, whether the intervertebral joints with a full-grown individual are the same as the intervals found embryonally between the primordial vertebrae. In other terms, whether the intersegmental and the intervertebral intervals are the same, and the cartilagenous and the osseous vertebrae originate from the sclerotome of one primordial vertebra (metamere.)

REMAK already answered this in the negative. VAN BAER admitted still that the embryonal primordial vertebrae correspond with the permanent later vertebrae. REMAK showed that in the primordial vertebrae the intervertebral musculature originated, and at the same time the blastema, from which the permanent vertebrae take their origin. According to him the permanent vertebra is formed in this way: The primitive vertebral bodies (sclerotomes they are called at present) originating in the primordial vertebrae (metameres) fuse together, and, at the same time, new intervals come into existence for the secondary

(permanent) vertebrae in the middle between the original intervals. A secondary (permanent) vertebra consists consequently of the caudal and cranial halves of two adjoining primitive vertebrae fused together. According to REMAK there was in the development of the vertebral column one moment, in which the blastema, from which the vertebrae will originate, is entirely unsegmented. For a considerable time REMAK'S theory about the "re-segmentation of the vertebral column" has not been recognised by many anatomists. Recent investigations however have done justice to him. Especially the investigations of v. EBNER have turned the scale here, and in the first place the discovery of the so-called intervertebral-fissure.

On the frontal section through an embryo (cf. fig. 1) one sees on either side of the chorda the bodies of the primordial vertebrae.

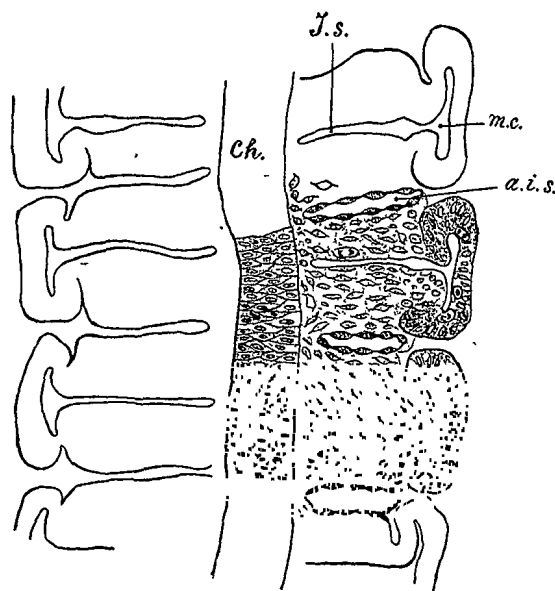


Fig. 1.

Frontal section through an embryo of *Tropidonotus natrix* (after v. EBNER).

ch. = chorda dorsalis; *I.s.* = intervertebral fissure;
a.i.s. = arteria interprotovertebralis; *m.c.* = myocoel.

At a certain stage of the development one sees occur in it the differentiation that causes the formation of the products that are derived from it.

The primordial vertebra, in which the primordial vertebral cavity is situated, shows a medial and a lateral lamella. The lateral lamella is the cutis lamella, from which the derm with adnexa takes its origin; the medial one is the muscle lamella from which the musculature develops itself. Moreover originates from this medial lamella of the primordial segment the blastema (mesenchym) from which

the skeleton will form itself, and with Amniotes a rather considerable part of it is used. This mesenchym accumulates between the chorda and the medial lamella of the primordial vertebra, so that the primordial vertebrae are pushed in a lateral direction from the chorda. The intervals between the different primordial segments are distinctly indicated by the transversal course of the intersegmental- or interprotovertebral vessels.

What is now v. EBNER's discovery?

This that from the lumen of the primordial vertebra a narrow fissure runs in a medial direction to quite near the chorda. This fissure, called by v. EBNER intervertebral-fissure divides each segment into a clearly defined anterior and a posterior (cranial and caudal) half. With *Tropidonotus natrix* (upon which v. EBNER made his first investigations) this fissure is most distinct in the neighbourhood of the spinal ganglions. More dorsally it disappears; ventrally it can easily be followed as far as the region of the chorda. As was said this fissure was first observed by v. EBNER in *Tropidonotus natrix* and afterwards it was shown by the same investigator in hens, mice and bats. This discovery was soon confirmed by other investigators with other animals and also with man. The existence of the fissure is no longer contested. VAN EBNER could also already show that the intervertebral fissures agreed completely with the joints of the later permanent vertebrae. According to him they disappear in the end in the dense mass of tissue, in which afterwards the articular cavities between the vertebrae occur.

The permanent vertebrae come now into existence each in the region that is limited between 2 intervertebral-fissures. Consequently each vertebra belongs to two segments and is constructed of the caudal half of a discretionary segment and the cranial half of the next following one. This agrees consequently entirely with REMAK's assertion cited above, with this difference however, that the intervertebral-fissures that indicate the intervals between the permanent vertebrae, can already be observed when the intervals between the segments have not yet disappeared, so that the unsegmented blastema, which, according to REMAK, should exist for some time, does in reality not occur.

After this explanation it is obvious what must be understood by re-segmentation of the vertebral column. The segmentation that is expressed by the permanent vertebrae, is different from that which is given by the primordial vertebrae; a new and another segmentation has taken place.

How do now the fused caudal and cranial segments behave in

the forming of the vertebra? This depends upon the species of animal in question. With some animals we see that the originally caudal half and the originally cranial half have an equal part in the forming of the vertebra. With most higher Amniotes and likewise with man we see however that, at least as regards the vertebral arch, the caudal segmenthalf becomes predominant, whilst the cranial one, partly because the spinal-nerve and the spinalganglion belonging to it always lie in it, gets more into the background. It is not my intention to enter into further particulars about the share that the two segmenthalves have in the forming of the vertebra. The statements of the divers investigators diverge, which must be partly attributed to the certainly very great difficulties of the investigation, partly to the fact mentioned already above, that the relations with the different species of animals are not the same in this respect. I will only emphatically point out, that in what way the segmenthalves may behave in definite cases in the forming of the vertebra, they naturally possess a complete potency, in such a measure that from each of the two halves under special circumstances a complete vertebra can be formed. A proof of this are the so called embolomere or rhachitome vertebrae, which occur frequently with Anamnia, but are likewise found with Amniotes, which was first shown by GOETHE with *Lacerta viridis*, afterwards by MÄNNER with *Anguis* and by SCHAUINSLAND with *Sphenodon*, *Castor fiber* and *Cetaceae*.

After this very short explanation of what is essential in the metamery of the cranium and the re-segmentation of the vertebral column we shall examine, to what consequence these two dogmas lead in the ontogeny of the cranio-vertebral region.

If the doctrine of the metamery of the cranium according to FROBIEP and the later investigators is correct, and for the present there is no reason to doubt of it, then we must represent to ourselves the region of the spinal part of the cranium (the praespinal part can, as falling beyond the cranio-vertebral region, remain out of consideration) and of the vertebral column in a very young stage of embryonal development, as an uninterrupted row of anatomically (not morphologically) equivalent scleromeres, as is represented schematically in Fig. 2.

Axially the chorda(*ch.*) extends through these scleromeres, the cranial and caudal boundaries of which are indicated by the arteriae intersegmentales (*a.i.s.* interprotovertebrales). Laterally from the scleromeres one sees the myotome belonging to the connected segment

with in it the myocoel (*m.c.*) which is continued in a medial direction, in the intervertebral fissure (*f.i.v.*) of VON EBNER to quite near the

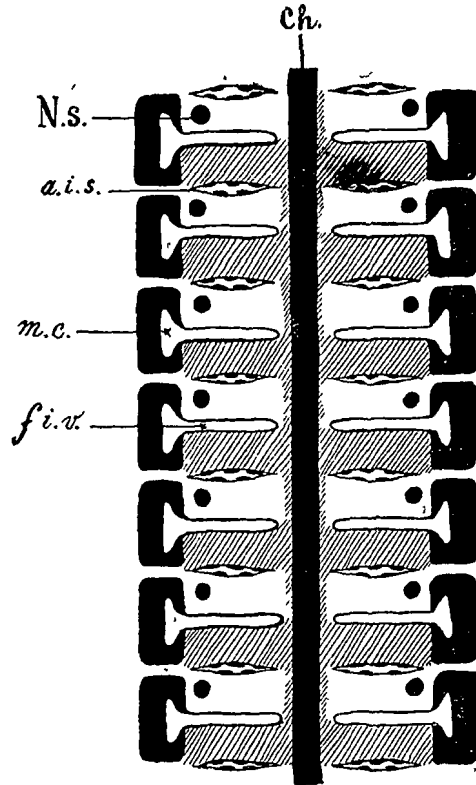


Fig. 2.

ch. = chorda dorsalis; *n.s.* = nervus spinalis; *a.i.s.* = arteria interprotovertebralis;
m.c. = myocoel; *f.i.v.* = intervertebral fissure.

chorda. The scleromere is divided, as was described above, by this intervertebral fissure into two halves, a cranial half and a caudal half. In the cranial half we see the N. spinalis (*n.s.*), the caudal half is represented striped in conformity with the fact that it is as a rule considerably stronger tinged. Somewhere in this row of scleromeres, which encloses consequently the spinal part of the skull and the immediately adjoining part of the vertebral column at some period or other of the development the cranio-vertebral interval will manifest itself.

What is interesting for us at the occurrence of this interval is not the question, where it will present itself, in this sense, as if it were of importance for us, how many scleromeres will join the cranium. This problem remains here entirely out of consideration. What we want to know of the interval is, whether it coincides

with the interval between the scleromeres or with the intervertebral fissure of VON EBNER. Though, as far as I know, the question as such has never been put, it can however be answered with certainty from the literature. It has indeed always been found ¹⁾ (c.f. the well known investigations of FRORIEP, WEISS, GAUPP, BARDEEN and others) and my own investigations on sheep-embryones confirm this in every respect, that the craniovertebral interval coincides with a segment or scleromere interval, and that the most caudal part of the cranium is always formed by a caudal segment-half. This can be most easily ascertained by paying attention to the nerves. The nerve running in the cranial half of the scleromere, the caudal half of which forms the most caudal part of the cranium, forms with the two nerves of the two scleromeres lying in a cranial direction from it, the roots of the N. hypoglossus; the nerve in the cranial half of the next following segment in caudal direction, is the free 1st cervical-nerve running outside the cranium (c.f. Fig. 3). The caudal half of the last segment belonging to the cranium is always strongly developed and by its intensive colour distinctly to be distinguished from the weakly tinged cranial half of the in caudal direction next following segment belonging to the region of the vertebral column, in which cranial half always the first cervical-nerve is found.

If now we pay careful attention to the fact ascertained by observation, that the cranio-vertebral interval is an intersegmental one, it appears immediately that necessarily, in consequence of the process of the resegmentation of the vertebral column, one segment-half remains between the first cervical vertebra and the occipital bone. An illustration of this offers fig. 3.

We see in it as in Fig. 2 a representation of a row of segments, in which axially the chorda extends itself, and which in a lateral direction are limited by the myotomes somewhat further differentiated in comparison with Fig. 2, from which the myocoel has disappeared. Here the caudal half is likewise striped; in the cranial segment-half the spinal-nerve (*n.s.*) is indicated whilst the intersegmental vessels (*a.i.s.*) limit the segments. The line *A.B.* represents the craniovertebral interval situated intersegmentally.

In the process of the resegmentation described above, the vertebrae are formed from the segments in such a way that the caudal half of each segment fuses with the cranial half of the next following segment in a caudal direction. So e.g. the caudal half of the fourth segment (*S. IV*) will fuse with the cranial half of the fifth segment

¹⁾ These statements only regard Amniotes.

($S. V$), the caudal half of $S. III$ with the cranial half of $S. IV$, the caudal half of $S. II$ with the cranial half of $S. III$, and the caudal half of $S. I$ with the cranial half of $S. II$, and in this way

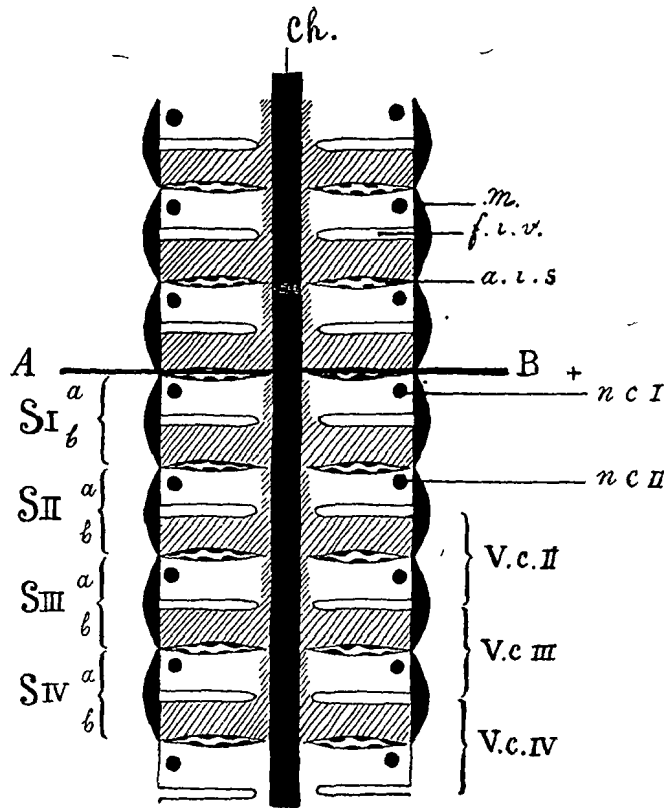


Fig 3.

ch = chorda dorsalis; $m.$ = myotome; $f.i.v.$ = intervertebral fissure; $a.i.s.$ = arteria interprotovertebralis; $A.B.$ = cranio-vertebral interval; $n.c. I$ = 1st cervical nerve; $n.c. II$ = 2nd cervical nerve.

resp. the 4th, 3rd, 2nd and 1st cervical vertebrae will be formed.

If we call the cranial half a , the caudal one b , we can say in general that the n^{th} vertebra is formed by the fusion of $S_n.b$ with $S(n+1)a$; the n^{th} vertebra has consequently for metamere formula $S_n.b + S(n+1)a$. From the first segment remains now the cranial half $S.Ia$, for it remains separated from the caudal half of the segment lying cranially from it by the cranio-vertebral interval.

The conclusion from this demonstration that has issued from no other premises than from the law of the resegmentation of the vertebral column and from the fact, that the cranio-vertebral interval is an intersegmental one, must consequently be, that between the

cranium and the vertebral column a free segmenthalf is found, that has certainly an osteogenetical, perhaps even a hemispondylogenetical potency.

It is now the question whether this potency is activated, and if so, what phenomena are the results of this activation. Though it is not the intention of this communication to give a categorical answer to the question submitted here, I will however indicate already the direction in which, according to my opinion, the answer must be looked for, and fix the attention to the fact that in the cranio-vertebral region a great many phenomena present themselves, the morphological signification of which has as yet not by far been defined in the same way by all investigators. I have here especially an eye to the variations of the atlas in the region of the sulcus arteriae vertebralis, to the different phenomena on which in fact the Pro-atlathypothesis of ALBRECHT is founded, to the concrescencia atlanto-occipitalis and the manifestation of the occipital vertebra.

I think, that all these phenomena can be brought under one point of view, namely the existence of the above mentioned segment-half *I α* .

A further investigation into this question will form the subject of a following communication.

Anatomy. — “*The genetical signification of some atlas-variations*”.

By Dr. J. A. J. BARGE. (Communicated by Prof. L. BOLK).

In the previous communication, “On the metamerological signification of the cranio-vertebral interval” I have fixed the attention to the fact, verified also by investigation, that between the atlas and the caudal boundary of the cranium, in consequence of the intersegmental position of the craniovertebral interval and of the process of the re-segmentation of the vertebral column, necessarily a free half-segment must exist, indicated for the sake of brevity as the semi-segment *I α* .

At the end of this communication the question was raised, to what phenomena the activation of the osteogenetic potency, doubtlessly existing in this semi-segment, would give rise, and the provisional answer to this question was, that, in my opinion, it would probably be possible to trace a relation between the established existence of the semi-segment and a series of phenomena in the cranio-vertebral