Morphological Studies.

II.—The Development of the Peripheral Nervous System of Vertebrates.

PART I.—ELASMOBRANCHII AND AVES.

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MORPHOLOGICAL STUDIES.

INTRODUCTION.

Nearly three years ago I published (No. 6) in the pages of the 'Quart. Journ. of Micr. Sci.,' some researches on the morphology and development of the so-called "organs of the lateral line," which appeared to me then, as now, to be in reality special branchial sense organs. When those researches were first undertaken in Professor Semper's laboratory (No. 4), it was far from my intention to investigate the development of the cranial nerves and ganglia, but in the course of the work it soon became obvious that the thorough study of those sense organs could only be accomplished by including the cranial nerves and ganglia in the sphere of the observations. And, indeed, almost the first Elasmobranch embryo examined showed unmistakeably that the cranial ganglia and the sense organs of the lateral line are intimately associated in their morphology and development.

The researches then published include also attempts to homologise the sensory portion of the nose and ear with the sense organs of the lateral line. And it is partly with the wish to get more light on this question that last year I undertook the investigation of the first beginnings of the cranial and spinal ganglia. Two papers—very different in their stimulating effects—urged me all the more to a thorough study of these problems.

In a short notice Dr. van Wijhe (No. 61)—whose right to an opinion on this matter is unquestionable—considered his researches on Ray embryos entitled him to combat my previously published views of the nature of the nose. I give in the following lines van Wijhe's own words.

He says: "Die Auffassung nach welcher der Olfactorius ein segmentaler Nerv sei, ist neulich wieder von Dr. Beard vertreten. Er gründet dieselbe auf die Theilnahme der Epidermis an der Bildung des Reichnerven und seines Ganglions, wie dies auch bei den Nerven der Seitenorganen der Fall ist und glaubt die Reichgruben seien deshalb den Seitenorganen und der Olfactorius den Nerven dieser Organe homolog."
J. BEARD.


. . . . . "Dass nun die Zellen der Anlage des Riechorganes an der Bildung des Nerven und seines Ganglions theilnehmen ist, wie mir scheint, bei einer solchen Enstehungsweise a priori zu erwarten, und stimmt mit der Nervenbildung bei vielen Wirbellosen uberein."

. . . . . "Wenn Beard jetzt, seiner früheren Behauptung entgegen, den Olfactorius und die Seitennerven nebst ihren Ganglien allein aus der Epidermis entstehen lasst, so kann er dies wohl nie beweisen, weil der Stamm der Nerven sich ursprünglich aus dem Medullarrohre entwickelt."

The above statements relate to some of the most important problems in the development of the peripheral nervous system. And if the whole of them are to be maintained in van Wijhe's sense they present insuperable difficulties in the way of the acceptance of my previous interpretations. To me the most serious question then, and before then, was the nature of Marshall’s neural ridge and its supposed origin as an outgrowth of the central nervous system. If I had left it entirely untouched in my previous work, such a proceeding can be easily excused. In the first place, my material did not then appear to me sufficient to settle the matter, and the complete study of the "neural ridge," &c., required more time than I could then devote to it. Further, I could not without ample justification declare Marshall’s account and that of Balfour to be at the basis erroneous. And when Professor Gegenbaur, in his recent work (No. 21, p. 42), makes me the reproach that I
never entertained the question of the epiblastic origin, apart from the central nervous system, of the neural ridge, the accusation is unjust; for I can assure Professor Gegenbaur that such was far from being the case.

And, as it now turns out, van Wijhe’s objection that the main root of the nerve arises as an outgrowth of the central nervous system will not hold, for the origin of what he calls the main root, in the case of the cranial and spinal ganglia, is demonstrably in principle in accordance with the account of the development of the olfactory nerve and ganglion, as given by van Wijhe himself. In fact, in the main, I accept gladly and gratefully van Wijhe’s researches on the olfactory organ as supporting and confirming my view of its homology. But for a fuller discussion of this matter, I must ask the reader to wait till the ground has been cleared by the detailed account of the researches on the very first origin of the cranial ganglia in nearly all classes of Vertebrates.

And now a few words on the second work, which was the great stimulating agent in impelling the researches about to be recorded. If the reader will refer to the introduction of my work on the branchial sense organs (No. 6) he may read that “at present we are acquainted with no Invertebrate nervous system which is built on the same plan as that of Vertebrates.” This conclusion led me to take up an attitude of expectancy rather than of negation towards the Annelidan theory of the origin of Vertebrates. And while I felt compelled to doubt the homology between the “Seitenorgane” of the Capitellidae and the “Seitenorgane” of Vertebrates, so ably maintained by Eisig, I was not without hopes that further researches on Invertebrates might reveal facts on which a comparison of the peripheral nervous system of Vertebrates, with some allied stock of Invertebrates, probably Annelids, might be maintained.

In October, 1886, appeared Kleinenberg’s epoch-making researches on the development of Lopadorhynchus (No. 41). I shall find plenty of opportunity in this and some of the fol-
lowing studies for reference to this remarkable paper, and will here only quote one passage, which may serve as a text for the researches I am about to record.


"Das bleibende Rückenmark würde dann vielleicht nur den vorderen Abschnitt der ursprünglichen Anlage enthalten. Der
Weg den die parallelen seitlichen Stränge des Bauchmarks durchlaufen haben müssen, um zum medianen Rückenmarksrohre zu werden, scheint mir durch die mitgetheilten Thatsachen aus der Entwicklungsgeschichte der Anneliden selbst hinreichend klar vorgezeichnet. 1 Noch mehr. Auch die Spinalganglien dürften ihre Homologie bei den Anneliden finden, und zwar in den Parapodialganglien. Dreht man die fig. 47, Taf. xi, 2 um, so wird die Uebereinstimmung nicht entgehen. Der Unterschied liegt nur darin, dass die Spinalganglien bei ihrem Auftreten dicht am Rückenmarksrohr liegen oder in dasselbe eingezogen sind. Die hintere Wurzel—das am besten gekannte Beispiel der Entstehung eines Nerven bei den Wirbeltieren—bildet sich gerade so wie der mediane Parapodial Nerv, und die vordere Wurzel dürfte dem Muskelnerven, der sich mit jenem zu einem Stamm verbindet, gleich zu setzen sein."

So much for the present from Professor Kleinenberg. In general terms the result of my researches is a confirmation of his views and comparisons.

If any further excuse were needed for a reopening of the question of the origin of the ganglia in Vertebrates, one would not have to seek far for ample reasons for such a course. Just as I was completing the first part of this work, three publications appeared, all of which showed the state of uncertainty and vagueness in which these questions at present exist. Professor Gegenbaur (No. 21) has undertaken no investigations on the matter, but feels himself entitled to quote as final the observations of one or other of his pupils, those of Sagemehl (No. 56) more especially appear to him to be far away above suspicion. I shall later on have occasion to point out how

1 In a subsequent paper I intend to demonstrate that the central nervous system is a paired structure which arises as two lateral plates of neuro-epithelium separated by a median ciliated groove, just as in Annelida.

2 I have reproduced this figure in Plate XIX, fig. 64. In my copy the figure has been turned through an angle of 180°, to bring it in the "Vertebrate position."
little claim Sagemehl's researches on the spinal ganglia really have to pose as a solution of the prize problem they were undertaken to solve, and will here content myself with the assertion that Sagemehl never saw any of the very earliest stages of development. Professor His (No. 34) in a paper, which in spite of a vast number of differences of opinion as to both facts and hypotheses, I cannot regard otherwise than as a valuable contribution to the morphology of the cranial nerves, has, among other things, endeavoured to establish without further observation his celebrated "Zwischenrinne" or "Zwischenstrang" theory, and he believes that all that is necessary for its final triumph is its rebaptism under the name of Ganglienerinne or strang. As this work also will occupy our attention for some time at a later stage of the work, I will only express my strong dissonance with the following extract (p. 380) with which Professor His opens his campaign against "die jüngeren vergleichendmorphologischen Schulen." It reads thus: "Bei genauerem Zusehen findet man eben dass die Differenzen nicht in dem liegen, was der eine oder der andere Beobachtungskreis an thatsächlichen Befunden ergiebt, sondern in demjenigen was die Vertreter der einen und der andern Schule zwischen den Zeilen zu lesen sich bemühen."

It will be time enough to consider the lecture which Professor His reads to us younger morphologists, when the facts of development which form the very basis of the question are placed beyond the reason of dispute. The principle of the origin of the ganglia from the epiblast, apart from the central nervous system, is one on which I can agree with Professor His. Not so with the way in which this takes place; for, paradoxical though it may sound, right as Professor His was in principle, he is till now further from recognising the true facts than any embryologist who has worked on the origin of the peripheral nervous system. Sad to relate the Zwischenstrang, &c., has as little direct connection with the origin of the ganglia as it has with the urinogenital system, as Professor His at first supposed.

Professor His is astonished to notice that his views on this
mature have been “völlig unbeachtet,” and finds,—though this discovery is not likely to be accepted by anyone competent to judge the question,—that his original views are practically identical with the generally accepted account of Balfour.

Now, among those naturalists who have worked on the development of the peripheral nervous system, Balfour stands pre-eminent in the precise formulation of his conclusions. I am bound to maintain that on many of the most fundamental questions Balfour’s observations cannot be longer upheld, while I am also sure that none would be more ready than he to accept the facts I am about to record.¹ Balfour says (No. 2, p. 369): “All the nerves are outgrowths of the central nervous system.” How this statement can be reconciled with his Zwischenrinne hypothesis (for it is nothing more than an hypothesis) it is for Professor His to determine. The matter need not trouble us much, for, as I shall afterwards show, the Zwischenstrang (there is no Zwischenrinne!) is just that portion of the epiblast or ectoderm which takes no part at all in the ganglionic formation. All I here wish to do is to enter a protest against the way in which Professor His attempts to convert all previous work on the early development of the ganglia into a mere confirmation of his own more or less

¹ It is certain that Balfour had an idea of the true facts, for he closes his account of the peripheral nerves on page 383 of the ‘Comparative Embryology,’ vol. ii, with this passage: “Situation of the dorsal roots of the cranial and spinal nerves. The probable explanation of the origin of nerves from the neural crest has already been briefly given. It is that the neural crest represents the original lateral borders of the nervous plate, and that, in the mechanical folding of the nervous plate to form the cerebrospinal canal, its two lateral borders have become approximated in the median dorsal line to form the neural crest. The subsequent shifting of the nerves I am unable to explain, and the meaning of the transient longitudinal commissure connecting the nerves is also unknown. The folding of the neural plate must have extended to the region of the olfactory nerves, so that, as just stated, there would be no special probability of the olfactory nerves belonging to the same category as the other dorsal nerves, from the fact of their springing from the neural crest.” The reader may compare the first sentences of this passage with the results recorded in the following pages.
hypothetical views on this matter. That the Zwischenstrang has any concern in the formation of the ganglia is a baseless assumption.

In his 'Lehrbuch der Entwickelungsgeschichte,' &c., Bd. ii, Professor O. Hertwig has made an attempt to extract a little light from the chaos which reigns over our knowledge of the development of the peripheral nervous system. For Professor Hertwig, the most important researches are those made by his pupils and by Sagemehl. As he mainly relies upon these and ignores for all practical purposes almost entirely the more recent work on the matter, it is not unnatural that the chapter on the peripheral nervous system is one of the most unsatisfactory in the whole work. As an instance of Professor Hertwig’s treatment of recent authors, I may mention that for him our knowledge of the formation of the lateral nerve of Amphibians and Silachians is confined to the older observations of Semper and Goette, and he only mentions incidentally that van Wijhe has seen similar fusions of epiblast and sensory nerves in the head of Elasmobranchs (No. 23, p. 338).

Professor Hertwig has thought fit to illustrate his account with one or two figures from as yet unpublished researches of Professor Rabl. If Professor Rabl is to pose as an authority on the formation of spinal ganglia, one may at least ask for tolerably correct figures in illustration of his work. The two figures 175 and 171 given by Hertwig are among the most incorrect that have been published till now on this matter. As the climax to Professor Hertwig’s appreciation of work on the peripheral nervous system, let me add that he is of opinion that "um auf dem schwierigen Gebiete vorwärts zu kommen, muss man . . . . . . bei der Untersuchung von Embryonen nicht nur Schnittserien, sondern auch andere histologische Methoden zu Rathe ziehen" (p. 337). It is to be hoped that besides giving the advice Professor Hertwig will also show us the way to use his "andere histologische Methoden." From these citations the reader will, I think, be convinced that from the researches till now published, we may form very different conceptions of the results
obtained according as one belongs to this that or the other
school of embryologists. For myself, for the better compre-
hension of my work on later stages, it was absolutely essential
that a clear, precise, and uncontradictory account of the very
first stages of the peripheral nervous system, and of the rela-
tions of the latter to the central nervous system, should be
worked out. It was necessary to attempt to do for the Verte-
brate nervous system what Kleinenberg has done for that of
the Annelid. Not that the following researches make any
pretence to being an account comparable in minuteness of
detail with Kleinenberg's work, they are rather the beginnings
of work on the matter; for there is still much to be done in
the early development of both central and peripheral nervous
systems of Vertebrates.

According to Professor Wiedersheim's opinion and my own,
the most lasting results were likely to be obtained by drawing
within the sphere of investigation as many types of Vertebrates
as possible, and hence, although my original intention regarding
this and other researches was to consider only Elasmobranchs
and Ganoids, in aid of which researches the Government Grant
Committee of the Royal Society of London made a grant of
money from the fund at their disposal, I nevertheless thought
it in the interest of science to extend my observations to various
classes of Vertebrates. So far I have had at my disposal embryos
of (various genera) Elasmobranchs, Teleostei, of Amphibia,
Reptiles, Birds, and Mammals. Researches on Ganoids and one
or two other types as yet unattainable, I hope in the course
of the year to be able to carry out. For the moment in con-
sequence of the time necessary for the preparation of the
numerous indispensable drawings, I publish the results obtained
on Elasmobranchii and Birds.

1 The development in Ganoids conforms exactly to those in other types.
ELASMOBRANCHII.

The researches on this group were made on embryos of *Torpedo ocellata*, *Pristiurus melanostomus*, *Acanthias vulgaris*, *Mustelus lævis*, and *Scyllium canicula*. Of the first-named form especially a very large and complete series of stages was at my disposal. This genus, *Torpedo*, is, in my experience, the best suited for researches on the early development, for the cell elements are larger, and the appearances presented in sections much clearer than those of any of the other forms mentioned. Of the other forms a sufficient number of stages was at my disposal to show that there is no essential difference in the development. And, in fact, for both cranial and spinal ganglia of all the Vertebrates which have till now come into my hands, including Teleostei, *Rana*, and even the Chick, I may with full confidence say that the appearances presented are all easily reducible to one type—to that of the Elasmobranchii. The differences observed in different forms are in reality very slight, and are readily explicable as variations in the time of development. As in the case of other organs, the development may be either retarded or accelerated. As a striking example of the way in which, for instance, the spinal ganglia agree in development in *Torpedo* and the Chick, I may mention that in sketches of portions of sections of the two forms drawn under high power it is often difficult, if not impossible, to find any differences, even in detail; and if the reader will compare figs. 37 a, 42, and 68, 69, he will, I think, find it impossible of his own knowledge to say definitely that the former are figures of *Torpedo* sections, the latter of Chick sections.

A. Spinal Ganglia of Elasmobranchii.

Balfour is mainly responsible for our knowledge of the development of the spinal nerves and ganglia in Elasmobranchs (Nos. 1, 2, and 3).

1 The development in Ganoids conforms exactly to that in other types.
The stages of development which Balfour described as the earliest are, however, by no means such, for I can demonstrate the first traces of ganglia some time before the neural canal closes. Neither Balfour nor Onodi, nor any other observer, has seen the stages which I figure in Pl. XVI, and in figs. 37—42 of Pl. XVIII.

Figs. 1—4 of Pl. XVI are taken from various parts of one embryo of Torpedo ocellata. Figs. 1—3 are the only ones which at the moment concern us, for they are all three from the trunk, and hence from the region of the spinal ganglia.

In Prof. His's recent paper (No. 34, p. 445) the author remarks: "Der Zeitfolge nach entwickeln sich die peripherischen Nerven spät. Am Rumpf treten sie später auf als die Urwirbel, am Kopf fällt die Zeit ihrer Bildung zum nahe an diejenige des Visceralbogen, aber da geht die Gliederung des End-gebietes dem Vordringen der Stämme voraus."

I am not quite sure that Professor His means these remarks also to apply to the ganglia. But however that may be, I will at once assert that the "Anlagen" 2 of the spinal ganglia are formed very much earlier than has hitherto been supposed, and, indeed, that the first traces of them appear when only two or three of the mesoblastic somites 3 have been entirely segmented off from the main mesoblast (figs. 2 and 3). Generally speaking, the first differentiation of the spinal ganglia may be said to occur at about the time of separation of the notochord from the hypoblast. In earlier stages than this fig. 1 (here the

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1 Onodi's researches, so far as they relate to the posterior root-ganglia of Elasmobranchs after exclusion of the sympathetic, contain no new results. And their author was entirely in the dark as to the relations of the ganglia to the lateral sense organs. Though he must have seen the skin fusions he entirely ignores them.

2 I use the word Anlage or Anlagen (plural) throughout this paper instead of our only term rudiment, which has a double meaning.

3 In agreement with van Wijhe, Wiedersheim, and others, I use here the word somites, or body-somite, instead of the older and incorrect term protvertebrc. In the same way I shall call the "head-cavities," with van Wijhe, the head-somites. With Dr. Eisig I use the terms hemal and neural instead of ventral and dorsal.
The notochord is already partly separated off; the neural plate is a broad, slightly-grooved, shallow structure, which presents no appearance of differentiation. Very soon the invagination process begins, and with it the Anlagen of the spinal ganglia begin at once to be distinguishable from the rest of the neural plate. At the extreme outer boundary of what is really the "Anlage" of the spinal cord a commencing proliferation of the deeper layers of the epiblast is observable (fig. 2). This leads to the appearance of a bud-like outgrowth of cells at each side of the spinal cord Anlage. On the one hand this outgrowth is very soon sharply distinguishable from the spinal cord Anlage; on the other hand, it begins to separate somewhat from the rest of the epiblast in the form of a somewhat wedge-shaped mass of cells. In figs. 3, 5, 9, this process is readily made out. From an inspection of these figures it will be obvious that the whole thickness of the epiblast is not concerned in this outgrowth. The outer layer of epiblast is quite indifferent, and neither takes share in the Anlage, nor presents any resemblance at all to a sense epithelium, a point on which I shall have more to say in connection with Dr. Eisig's comparisons. The epiblast in the region of the ganglionic Anlage, and for some distance lateral of this, is composed of several cell layers (fig. 1). Now, the way in which the ganglionic Anlage separates from the rest of the epiblast is such that a triangular wedge of epiblast is left as the limit of the ganglionic formation. The point of this wedge, which exists in much the same form for a considerably later period of development, projects towards the mesoblast. It is somewhat difficult to describe these appearances in words; a glance at figs. 2, 14, 38 suffice, I think, to make clear the meaning of the Zwischenstrang of His, for that is what this portion of indifferent epiblast really is. Let us follow the lateral epiblast upwards from the side of the trunk to the lips of the neural plate. At first it is for some distance neuralwards only one layer thick; soon this changes, and it becomes gradually thicker; and if we follow it in such a section as is figured in figs. 14, 38, we see that at
some little distance from the infolding neural plate it attains its maximum thickness (leaving the neural plate itself out of question as part of the epiblast). Beyond this point it abruptly becomes one-layered again, and remains one-layered till it ends also abruptly in the neural plate. The region of this one-layered epiblast is that from which the ganglionic Anlage has been cut out. The point of maximum thickness is that portion of epiblast which has just failed to take any share in the formation of the ganglion. This point was one which gave me a good deal of trouble in the course of the researches, but the explanation of it gave the key to the origin of the ganglionic Anlagen. In fact the first rudiments of the ganglia are formed from the deeper layers of the epiblast just outside the limits of the neural plate.

These stages in the formation of the spinal ganglia have never yet been seen or figured by any observer.

The involution of the neural plate now begins to take place very rapidly (fig. 15). Along with it the ganglionic Anlagen get carried upwards. It seems as though they had not time to get out of the way of the infolding process, and in missing the chance to get out before the involution begins they are bound, on account of pure mechanical processes—the explanation and description of which I leave over to others—to follow the neural plate, and thus they come to a somewhat abnormal position at and between the dorsal lips of the neural plate. The steps of this process are shown successively in figs. 14, 15, 5, 9, 21, 32.

Some figures of the head region (Nos. 38—42) are given under high magnification, and tell their own tale in justification of my statements of the very early appearance of the ganglia as epiblastic proliferations and their independence of the neural plate. They lie close to the latter, but can no more be regarded as outgrowths of it than any other two organs which lie close to each other in development can be considered, for that reason, as derivatives one of the other. I have nearly always been able, after the first traces of the ganglia were visible, to distinguish the lateral limits of the neural plate,
and I think the reader will also have no difficulty in doing this in very many of the figures given in Pls. XVI, XVII, and XVIII.

In such figures as figs. 21, 33—36, 49, 50, 52, one sees that the lips of the neural plate are very sharply defined. This appearance was one which struck me as remarkable in the very beginning of the investigations, all the more as till now no observer seemed to have noticed it, and, so far as I am aware, there is only one figure of it in existence, pl. xvii, fig. 12, in Professor His's paper on the peripheral nervous system (No. 29). This figure also is taken from the spinal region of an Elasmobranch embryo, and tallies almost exactly with my figs. 22 and 32. Professor His, though he long ago noticed the appearance, incorrectly interpreted it, and attached no particular importance to it. I shall refer to it again in reviewing the work of previous observers.

To me it was the key to the origin of the ganglionic Anlage, for it showed me unmistakably that this Anlage was not, as all authors except His had supposed, an outgrowth of the spinal cord. The identification of this sharp line of division, however, was by no means a solution of the problem, for it was now a question of where the ganglionic Anlage really arises. The thin one-layered epiblast above the lips of the neural canal when contrasted with the many-layered epiblast in the region of His's Zwischenstrang, suggests at once a possible point of origin; but in Elasmobranchs at first no proof of this could be found, and so I had to look further back in earlier developmental stages before the neural plate is involuted. The results of this search are given above, and indeed it bears out my statement that this thin-layered epiblast above the neural lips is really the point from which the ganglionic Anlage has taken its origin. There is no need to demonstrate, by means of mathematical formulæ, &c., that the one-layered epiblast has during the involution of the neural plate undergone a good deal of tension,—a tension which no doubt helps to separate the ganglionic Anlage on each side from the epiblast.

We have now arrived at a stage such as is figured in figs.
32—36, 21, 13, 17, 43—45, where the Anlage of the ganglia sits upon and between the dorsal lips of the neural plate and prevents the closure and fusion of the latter.

The next step is the further proliferation and removal of the Anlagen to the sides of the spinal cord. In the words of most authors, we have now got to Marshall’s neural ridge or crest, and the Anlagen “begin to grow out of the spinal cord” (Marshall, Nos. 45, 46).

I think that in the preceding lines I have shown clearly enough that there is really no outgrowth from the spinal cord, nor do I find myself in the position to support Marshall’s view of the origin of the ganglia from a neural ridge. From the time of their first formation the ganglionic Anlagen appear to me to be segmented, and if the Anlage of one segment passes over into that of another in this and some of the following stages, I can see in this no reason for saying that the spinal ganglia arise from an unsegmented ridge of cells. No one attaches great morphological importance to the origin of the muscle-somites from an apparently unsegmented structure, an origin which is conditioned by the mode of formation of the cell elements, and as all traces of such a continuous structure soon disappear, the whole of its elements passing over into the various spinal ganglia without leaving any permanent “commissure.” I must hold that if we are to say that the spinal ganglia are outgrowths of a neural ridge, we must not forget two things: that the outgrowths begin as epiblastic buds long before the neural ridge stage; and secondly, that the whole of the neural ridge is absorbed by the various spinal ganglia. This latter point is all the more necessary seeing that at least one observer has suggested as an hypothesis worthy of proof the origin of the lateral nerve of fishes from the remains of the neural ridge. M. Julin says (No. 39, p. 31), “Dans mon idée le nerf latéral, tel qu’il se trouve constitué chez l’Ammocoetes ne serait que le reste de la crête neurale, ce qui expliquerait ses rapports avec les racines du vague et les branches dorsales des nerfs spinaux dorsaux.” He is further of opinion that this
avowed hypothesis "m’ériterait d’être soumise à un contrôle rigoureux, par des recherches embryogéniques." In face of the known facts concerning the morphology of the lateral nerve as detected by van Wijhe and myself, we may regard with perfect indifference M. Julin’s researches in the direction of the above hypothesis. Such researches will turn out to be neither more nor less than a wild-goose chase.

In my statements that the whole of the so-called "neural ridge" passes over into the ganglionic formations, I agree completely with Sagemehl, Onodi, and His. Balfour and Marshall held different opinions which now can no longer be maintained.

The ganglionic Anlage—now that it lies on the lips of the neural plate, seems often to possess an unpaired character, but from its subsequent fate, and from the appearances presented in such figures as my figs. 21 and 29, it must really be considered as a paired structure, a point of the truth of which the lateral origin of the Anlagen is sufficient evidence. The Anlagen now begin to grow out from their position above and between the lips of the neural plate (figs. 22, 23, 33—36), and wander to their permanent position at the lateral portion of the spinal cord (figs. 8 and 30).

We are now treading on ground which has been fairly worked, but there are none the less one or two points of extreme importance to which a few words must be devoted. As we have seen, until now the ganglionic Anlagen have really no attachment to the spinal cord; and during the growth downwards to its lateral side they are, as Sagemehl (No. 56, p. 30) first showed, quite independent of that structure (fig. 57). The difference between Sagemehl’s account and my own is obvious when we remember that he, along with most other observers, regarded the ganglia as outgrowths of the spinal cord. I maintain—and the figures prove the truth of my view—that neither now nor before are the ganglia attached to the spinal cord. The first and only attachment to the spinal cord is the permanent one now soon to be acquired. Before the attachment takes place the ganglionic Anlage of each side divides into two portions,
the definite spinal ganglion and the sympathetic ganglion (fig. 59). The latter will not concern us here, though on this system of ganglia I shall later on have more to say. The development of the sympathetic has been worked by Balfour (Nos. 1 and 2), and more fully by Onodi (No. 52).

Arrived at the lateral surface of the spinal cord (figs. 28, 31, 61) the attachment\(^1\) to the latter takes place. On this point, which in my opinion it is difficult to decide for the spinal ganglia by direct observation, differences of view also obtain. Sagemehl (No. 56, p. 31) and others hold that the connecting fibres grow out from the spinal cord, while Professor His (No. 34, p. 373), with great confidence, says, "Die sensibeln Nerven, der N. acustieus, und die Geschmacksnerven entspringen in dem Ganglion und sie wachsen mit ihren centralen Wurzeln in das Rückenmark und in das Gehirn herein. Diesen Satz, den ich früher nur indirect zu stützen vermocht hatte, vermag ich nun mit grosser Sicherheit zu beweisen."

His was the first to apply the physiological laws of the trophic properties of the ganglia to the solution of this question. He says (No. 29, p. 477), "Die Frage, ob die hinteren Wurzeln vom Rückenmark aus nach den Ganglien hin wachsen, oder von den Ganglien aus nach dem Rückenmark, ist bis jetzt noch ziemlich unerortet geblieben. In meinem Augen spricht das Uebergewicht der Gründe für die letztere Alternative. Als einen dieser Gründe betrachte ich die durch Waller und durch Cl. Bernard (No. 12) nachgewiesene Trophische Abhängigkeit der hinteren Wurzeln vom Ganglion. Bei Durchschneidung der hinteren Wurzeln zwischen Rückenmark und Ganglion degenerirt nach den Ergebnissen jener Forscher der mit dem Rückenmark in Verbindung stehende Stumpf; der mit dem Ganglion verbundene bleibt intakt (No. 12, Bd. I, p. 237). Jede Zelle eines Ganglions nimmt nämlich zunächst eine spindelförmige Gestalt an, dann aber wächst sie in zwei Fasern aus, die nach entgegen-gesetzten

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\(^1\) Marshall (Nos. 46, 49) held this to be a secondary attachment. It is the first and only connection with the central organ.
Richtungen vom Zellkörper abgehen, &c.” I am inclined, and was so before reading these words, to agree with Professor His in his conclusions that the growth is a centripetal one; indeed, as Dr. Hill (‘Three Lectures;’ p. 3, No. 27) also has insisted, the matter is one of which the physiologists have already furnished the solution. He says, “It appears probable that the fibres of the posterior roots also grow from the cells of the ganglion centralwards into the cord, instead of from the cord to the ganglion as usually supposed. A consideration of the effects of cutting nerves in such cases as have been hitherto described leads me to formulate the law that nerve-fibres die when cut off from the cells of which they are processes, and from which they derive their nutrient supply. It is well known that, when the posterior roots are cut, the fibres which remain attached to the root-ganglia live; those entering the cord die.”

I will not cast any doubt on Professor His’s very positive statements on this point, indeed, I believe they represent the facts of the case, but I must again say that the question is difficult, if not impossible, to decide for the spinal ganglia by direct observation, and for myself, I must admit that I have not been able to make more of it as yet.¹

The mode in which the connection between the ganglia and their peripheral end organs takes place, is one on which there is also much dispute. For His (No. 33, p. 375) and Kölliker (Nos. 42, 44) hold, as against all other observers, that the nerves are processes of the ganglionic cells, without any intervention of ganglionic cells or ganglionic cell nuclei in the course of the nerve. I shall have occasion to discuss this question more fully in connection with the anterior roots of spinal and cranial nerves, and content myself here with the remark that I believe Professor His’s and Kölliker’s conclusions cannot be maintained, and that the peripheral connection in the case of sensory or

¹ As an absolute maxim I am only inclined to support this as regards the spinal ganglia; in the case of the cranial ganglia, as we shall see, there are reasons for holding this view only with regard to the sensory part of the root.
motor nerves is brought about rather by a chain of ganglionic cells.


Compared with the development of the cranial ganglia that of the spinal ganglia previously described is simplicity itself. For just as the head of Vertebrates presents, when compared with the trunk, a complexity of problems, the solution of which, in the opinion of morphologists like Huxley, Dohrn, Froriep, and others, will take years of careful work, so also the cranial ganglia present a number of problems, towards the solution of which I only can hope to go a little way in the following pages.

While there can be no sort of doubt that the spinal ganglia are strictly segmental in their origin—indeed, that such is the case is easily demonstrable—the reduction of the cranial ganglia to segmental order is a task of great difficulty. It has been objected by Dohrn and others that the setting up of tables showing the segmental nature of the head nerves is a proceeding which is to be deprecated, and that the true problem is the reduction of the components of the head to simpler Annelidan structures. To which one may reply that, according to Dohrn, such Annelid ancestors were segmented animals, and no matter how complex the Vertebrate head may now be, it is at its basis composed of a number of Annelid metameres, and the unravelling and ordering of the existing complex, as far as it is possible, is the real task of the morphologist.

I shall not at the moment attempt to discuss again the claims of the various cranial nerves to “segmental rank,” a proceeding which, to my mind, is entirely justifiable, for it has its meaning in the sorting of the cranial nerves for morphological (and physiological) considerations. Still, in the following account of the very first signs of the cranial ganglia, I must insist on such points of development as support, for instance, the comparison of the auditory and olfactory ganglia and sense organs with those of, for example, such a typical
cranial nerve, its ganglion, &c., as the glossopharyngeus. This is all the more in place, as Professor His, in his recent note of warning against the speculations of us unfortunate younger morphologists, does not hesitate to maintain as a fact the derivation of the auditory and olfactory organs from what he calls the "ganglion Leiste," which also gives origin to such ganglia as facial, glossopharyngeus, &c. I hope to show to Professor His's satisfaction that this "fact" is as little a fact as his derivation of the spinal ganglia from the "Zwischenstrang," which is the continuation backwards of the "ganglion Leiste" of the head.

A further complication is presented by the superaddition of the sense organs of the head (and their ganglia), excepting the eye, which all enter into relationships with those portions of the head ganglia which appear morphologically to correspond to the spinal ganglia. These complications will be more clearly explained in the course of the work.

I have mentioned in a recent paper (No. 8) that the cranial ganglia are made up of more form elements than the spinal, and I observe that Professor Gegenbaur, without investigating the development, comes to the same conclusion (No. 21).

The first traces of the cranial ganglia Anlagen are formed in exactly the same fashion as those of the spinal ganglia, and it is much easier, on account of their greater distinctness, to make out the earliest stages. In the embryo in which I described the first traces of the spinal ganglia such Anlagen can also be distinguished in the head region. As the mesoblast has not yet divided up into the body-somites, or so-called protovertebræ, the head-somites are also not formed, and so we are entitled to say generally, the traces of the posterior root ganglia of cranial and spinal nerves are formed very early and long before the closure of the neural plate.

A figure through the head region of an embryo, as early as the one depicted in fig. 4, has been given by Professor Marshall in one of his papers (No. 48, fig. 1), but he gave no trace of any ganglionic formation, and, indeed, it is quite possible that
such traces were not differentiated in the section from which he figured. In his monograph of the development of Elasmobranch fishes, Balfour has also given, on Pl. IX, many figures of stages corresponding to those on my Pl. XVI; but here again no trace of the ganglionic Anlage, which is seen in all my figures, has been represented.

In fact, of the cranial, just as of the spinal ganglia, no observer has hitherto seen the very first stages which I am about to describe, and the last observer, Onodi (No. 51), who has given no figures at all, has, judging from his description, only seen the Anlagen in much later stages, and, as we shall afterwards see, has not interpreted rightly or seen all that is to be seen in fairly decent sections.

Returning to fig. 4, we find, on examination, the same appearances (g. a.) as were met with in the developing spinal ganglion. If we examined an earlier stage than this we should meet with no trace of the Anlagen of the cranial ganglia. We see now a central portion which represents the brain part of the neural plate in section. At each side of this, but independent of it, one notices the budding out and separation, so far as the lateral epiblast is concerned, of a process which is, as we shall see, the first trace of a cranial ganglion, or rather of part of one. Soon after this phase the involution of the neural plate begins just as in the case of the spinal cord, and along with the involution the ganglionic Anlagen are also carried upwards. I have figured these stages in figs. 6, 10—12, 16, 19, 20, 39—43, taken from various parts of the brain, in order to show that this mode of development holds for portions of the olfactory ganglion (figs. 19, 20), mesocephalic or ganglion of the ophthalmicus profundus (No. 7), trigeminus, facialis, auditory, glossopharyngeus, and vagus.

The involution of the neural plate, on its completion, encloses the cranial ganglionic Anlage just as occurs in the spinal cord. A number of figures of this stage are given in figs. 18, 21, 24, 25, 29, 45, 48, g. a.

The Anlage is now separated from the skin, and in the head of Elasmobranchs no trace of a Zwischenstrang is left behind.
If in such stages it is difficult in the trunk to be always quite certain of the sharp boundary line separating the ganglionic Anlagen from the closing neural plate, such is never the case in the head. I cannot remember having seen a single Elasmobranch section in which for the head it was at all a difficult matter to distinguish the limits of the two; and in spite of this fact there are no figures in existence which show this separation such as I depict it in figs. 44—48, 24—27, 29. Here, as in the trunk, the position of the ganglionic Anlagen between the lips of the neural tube (figs. 25, 44, 47) prevents their complete closure. But soon the Anlagen begins to grow downwards and outwards towards the lateral surface of the body. This outward growth leads, as is well known from the researches of recent years, to a difference in position between the ganglia of the head and those of the trunk. For while the latter lie between the muscle-plates and the spinal cord, the former take up a position outside the mesoblast and close to the skin.

The portion of the ganglionic Anlagen of the head derived from the neural epiblast corresponds, in development at least, with the Anlagen of the spinal ganglia, but the cranial ganglia of (apparently) all Vertebrates acquire a further form-element derived from the lateral epiblast above the gill-clefts, and at about the level of the notochord. For the formation of this element I have not in this paper given any figures, but I think such figures can be here entirely dispensed with, seeing that in a former paper (No. 6) treating of the branchial sense organs and their ganglia I figured a great many stages of this ganglionic formation, for, what I there called the branchial ganglia make up this additional form-element of which I just wrote. I believe I showed conclusively enough in that paper that above the gill-cleft ganglionic elements were given off into the main ganglion—indeed, it then seemed to me that most, if not all, the ganglion was formed there. As even such a severe critic as Professor Gegenbaur expresses himself satisfied that such form-elements of the ganglion take their origin above the gill-cleft, I may assume it to be unnecessary
to give a very detailed account of such formation in individual cases. From Professor Gegenbaur one must apparently be thankful for small mercies, and as this is the one thing in my researches which he admits unreservedly that I have seen, I quote his testimony in my favour. He says (No. 21, p. 41), "Die Beziehung des Ganglions zu dem Ektoderm ist von Beard richtig erkannt worden: er sagt, 'The proliferated cells form a mass of actively dividing elements still connected with the skin and fused with the dorsal root; . . . . for some time the cells continue to be given off, and of those already given off many show nuclear figures.' Die epitheliale Verdickung hat also die Bedeutung einer Quelle der Ganglienbildung. Das geht auch aus den bezüglichen Figuren Beard's hervor, die zudem in der Anordnung der Elemente der am Ganglion befindlichen Ektodermsschichte gar nichts aufweisen, was man auf ein hier sich bildendes Sinnesorgan beziehen könnte. Wenn die Thatsachen, wie sie in Wirklichkeit bestehen, die Grundlage der Forschung abgeben, so kann man hier nur sagen: der Nerv wächst vom Centralorgane aus unter dem Ektoderm bis zu einer Stelle, an der ihm aus dem Ektoderm ein Zufluss von Formelementen zu Theil wird.'

For the present moment I leave entirely alone Professor Gegenbaur's doubts about the sense organs. Such doubts are entirely unjustifiable. To return to the ganglionic Anlagen derived from the epiblast at the neural side of the head. These Anlagen grow outwards and downwards towards the lateral surface of the body. Just above the gill-cleft there is here a small portion of neuro-epithelium (figs. 94, 95), which is the Anlage of the branchial sense organs or lateral sense organs. This neuro-epithelium has begun to extend its growth before the ganglionic Anlage fuses with it.1 In figs. 94, a and 95, a, I have represented this. The growth has

1 Fig. 101 shows this growth for the auditory epithelium of a lizard. Just as all the lateral sense-organs are formed from a certain limited number of pieces of neuro-epithelium, so all the sensory cells of the ear arise from the extension of one little bit of neuro-epithelium (o. e.)
already extended behind the gill-cleft (fig. 95, $b$), and also in front of the gill-cleft (fig. 94, $a$). In connection with the morphology of nose and ear this point is one of considerable importance, and I shall have occasion to refer to it again. The ganglionic Anlage now fuses with neuro-epithelium at one point. At the point of fusion a proliferation of the cells of the neuro-epithelium takes place into the ganglionic Anlage. The proliferated cells form a mass of actively dividing elements still connected with the skin, and fused with the rest of the ganglionic Anlage. Externally to this thickening is situate what Professor Froriep (No. 17) and I regard as the primitive branchial sense organ of this segment. Here again I refrain from discussing any of the questions connected with the formation and morphology of these sense organs.

One fact at least holds as the result of this skin fusion, and this is that a number of form-elements are given off into the ganglion. The recognition of this fact does not come to me after reading Professor Gegenbaur's paper quoted above. I had long before seeing that written as a note, on p. 21 of my paper (No. 8), on the "Old Mouth and the New," "The cranial ganglia of Vertebrates are far more complicated morphologically than has hitherto been recognised. In addition to parts which appear to correspond morphologically to the posterior root ganglia of the spinal nerves plus the sympathetic ganglia, they also contain the special ganglia which are formed in connection with the gill sense organs."

The ganglion complex soon begins to leave the skin, and in doing so a number of cellular fibrous cords are left behind connecting the sensory epithelium with the ganglion complex.

The sensory epithelium has, briefly stated, usually grown in three directions in front of the gill-cleft, behind the gill-cleft, and above the gill-cleft, either in a neural, or a forward, or a backward direction. The nerves connecting these various sensory elements with the ganglion appear to me to be all derived as splittings off from the inner layer of the sensory epi-
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this view, which I formerly only mentioned as true for the suprabranchial nerves, I must now also extend to the prebranchial and the sensory part of each postbranchial nerve. The ganglion complex has also to acquire its first and permanent connection with the central nervous system, and of the mode in which this takes place there can be no sort of doubt. The main trunk of the nerve and its connection with the central nervous system are formed respectively by the formation of nerve-chains from some of the ganglion-cells, and by the growth of fibres into the central nervous system.

Here again, however, the cranial ganglia present us with complications as compared with the spinal. It is well known that the whole of the motor fibres of the spinal nerves (those to the voluntary and the visceral muscles derived respectively from the anterior and lateral horns) pass out in the anterior roots. Now, there can be no doubt that the whole of the anterior root of a spinal nerve is a direct outgrowth from the central nervous system. All observers are agreed on this point. Quite other conditions obtain in the head. In the oculomotorius, trochlearis, and abducens, the only nerves which are comparable at all to anterior roots of spinal nerves, no fibres are derived from the homologue in the head of the lateral horn of the spinal cord; in other words, the anterior roots of the head give no fibres to visceral muscles, and—a fact which is well known—the fibres to the visceral muscles of the head pass out with the posterior roots of the cranial nerves. It appears also that these fibres take their origin in the continuation of the lateral horn in the head. This being so, and it being also true that all other motor nerves, including those of the spinal cord and the three eye-muscle nerves, certainly occur as outgrowths of ganglia situated within the central nervous system, it becomes a question whether the motor fibres of the gill-cleft muscles are not also direct outgrowths of the central nervous system. I must confess that I have not as yet been able to settle this point by

1 See fig. 100, which depicts the third and its central ganglionic origin as seen in *Lacerta agilis*.
direct observation, but I do not hesitate for a moment in expressing the opinion that such is the case. If this be true it follows that a typical posterior root of a cranial nerve, that is, a root passing to a gill-cleft, is composed of elements derived from at least three sources: there is, firstly, the portion which corresponds to the true spinal ganglion¹ in its derivation from the epiblast just outside the neural plate (neural ganglion); secondly, a portion formed in connection with the branchial sense organs (lateral ganglion); and thirdly, a portion derived from the continuation of the lateral column in the head.

In addition, a part must be added comparable to the sympathetic ganglia of the trunk, and this portion is probably, as occurs in the case of spinal ganglia, contained in the portion of the ganglion derived from the epiblast, just outside the neural plate.

Here we are faced by some interesting problems, which I will afterwards discuss.

His (No. 34, p. 394) and others have raised objections to the view of Balfour, that the cells derived from the neural ridge or crust are the Anlage of the posterior roots of the cranial nerves. Balfour's phraseology has been used by Marshall, Spencer, van Wijhe, myself, and others. No doubt objections may be urged against the use of this phraseology as accurately representing all the facts.

While I admit that these cells are more a ganglionic Anlage than that of a nerve, there are two points which must be urged in extenuation of the offence, if offence it be. In the first place, Balfour, Marshall, van Wijhe, and all of us who have used this phraseology, have done so, in the sense of the inclusion in the term posterior root, both root and ganglion of the nerve; and secondly, in the head at any rate, in addition to the cell processes which grow from the ganglion into the central organ, it can be demonstrated (fig. 103) that some of the cells of the ganglionic Anlage pass over into the root of the nerve, and take a direct share in its formation. This question

¹ This portion of the cranial ganglion is possibly only morphologically an equivalent to the sympathetic part of a spinal ganglion.
of the formation of nerves is one on which, along with most observers, I am completely at variance with His (Nos. 29 and 34) and Kölliker\(^1\) (Nos. 42 and 44); and I refer the reader to a fuller discussion of it in another part of this paper.

With this I close my account of the very earliest stages of the cranial ganglia in Elasmobranchii. The mode of development here described from at least two sources is characteristic for the ganglia of all the branchial nerves, facial, glossopharyngeus and vagus (fig. 24), and also for the trigeminus. Mutatis mutandis it also holds for the olfactory (figs. 19, 20), mesocephalic, and auditory (figs. 25, 29) ganglia. Here I will only emphasize this point, reserving to myself the right to return to it on a subsequent occasion. To go further into the matter here would lead to the discussion of a great many disputed points, and for the moment I wish to lay more stress on the absolute facts of the development which can be demonstrated. The conclusions which I feel entitled to draw from those facts can for the moment be postponed.

II. THE PERIPHERAL NERVOUS SYSTEM OF THE CHICK.

Our knowledge of the development of the peripheral nervous system in Birds is almost entirely due to His (No. 29), Marshall (No. 46), and Onodi (No. 51). Kastschenko (No. 40) has also contributed his item, which, so far as nerves or ganglia are concerned, is of no particular value, for it contains no new facts and throws no new light on the morphology of either cranial or spinal nerves and ganglia.

For many reasons I was obliged to include the Chick in the sphere of my observations. For one thing His’s remarkable observations and hypotheses were mainly established for this animal (Nos. 28, 31), and I could not feel satisfied until the explanation of His’s Zwischenstrang was got at the bottom of. The striking manner in which the epiblastic origin of the

\(^1\) Kölliker has upheld his views in several papers.
ganglia in the head of the Chick attracts the attention in good sections was also a reason for fully investigating the development in this animal; for the question naturally arises, Are these appearances primitive, or is the development modified in some way or other in the Chick? One could hardly hope to maintain, as a strict morphologist would be almost bound to do, if he had only Onodi's researches to go upon, that the mode of development of the cranial ganglia in the Chick is a more primitive one than that in Sharks. The facts, which I had discovered before seeing Onodi's paper, were at first a great puzzle to me, a puzzle to which Onodi's researches have given no solution; for, according to him, and so far he agrees with Marshall (No. 46), the cranial ganglia of the Chick differ entirely in mode of development from the ganglia, cranial and spinal, of all the other forms, Sharks, Lizards, Mammals, &c., which he had examined. Indeed, he maintains—and I find this attitude a surprising one in the man who had seen the true development in the cranial ganglia of the Chick—he maintains that in all other cases the ganglia, both cranial and spinal, are developed as outgrowths of a ganglion ridge (neural ridge of Marshall), and this in its turn owes its origin to the central nervous system.

Seeing that my researches on the cranial ganglia of the Chick are partly a confirmation of Onodi's, it might be supposed that there was no necessity for giving them in detail. However, I am of a different opinion, for they do not agree with Onodi's results on all points, and on the fundamental question whether the ganglionic Anlagen of the head are or are not parts of the central nervous system, Onodi says nothing. As he holds that in all other cases the ganglia, spinal and cranial, are outgrowths of the central nervous system, his position as a comparative embryologist is not a very logical one. The first traces of the ganglia, both cranial and spinal, are met with in the Chick between the twenty-second and twenty-sixth hours of incubation. In such embryos there are on the average from two to ten body-somites or protovertebræ, and it is in such embryos that evidence of the epiblastic origin
of both cranial and spinal ganglia can nearly always be obtained.

The mode of preparation, which in Sharks is not of such importance, is here a very weighty factor. My embryos were all prepared by immersion for from half an hour to two hours in Flemming’s chromic-osmic-acetic acid mixture, and afterwards stained with borax carmine or picro-borax carmine. Osmic acid must be used here, and used very carefully, or otherwise no guarantee can be given that all the appearances depicted by me in Plates XIX, XX, XXI will be visible. Thin sections are of course also of importance, and I must express the opinion that the results obtained by Professor His ten years ago (No. 29) are vitiated by improper treatment of the embryos and by the thickness—at that time unavoidable—of the sections. My sections are mostly \( \frac{1}{200} \) mm. thick. As was the case in the account of Elasmobranchs, I shall begin this part of the paper also with the


The appearances about to be described may be even seen sometimes in embryos in which no body-somites are as yet formed, and, speaking generally, an embryo with about six body-somites will show in different regions the appearances presented in seven sections (figs. 70—76) taken from the spinal region of such an embryo with six mesoblastic somites. It will be noticed that the medullary canal is everywhere open, and, in fact, here, as in Sharks, the first traces of the cranial and spinal ganglia are formed long before the closure of the neural plate. The first section is in the region of the primitive streak—and here no trace of ganglionic Anlagen is to be seen (fig. 70). The next section (fig. 71) is taken much farther forwards, and on the left side of the section, at any rate, the commencement of the ganglionic differentiation (fig. 72, g. a.) can be seen. The third section (fig. 72) passes through the middle of a meso-
blastic somite on the right—and here it is difficult to distinguish a ganglionic Anlage—but on the left it has cut the segment near its end and the ganglionic Anlagen is distinctly seen at g. a. as a small plug of cells being cut out of the epiblast just outside of the neural plate.

The fourth section (fig. 73) shows very distinctly on both side the spinal ganglionic Anlagen (g. a.). The boundaries of the infolding spinal cord are sharply marked off at o from the ganglionic Anlagen, which lies just outside them at g. a. This figure shows that the spinal ganglia in the Chick take their origin in exactly the same way as those of Elasmobranchii, and that by the cutting out of the ganglionic Anlagen at g. the epiblast to the outer sides of them is left as a somewhat triangular body, which, as in Sharks, where it is not so distinct, represents the "Zwischenstrang" of His. The following three figures, taken still farther forwards from the embryo, show the same appearances even better. On examining, for example, the six figures (fig. 75, 76, 80, 81, 85, 89), one sees the following things:—The spinal cord is rapidly closing in, and its lips are sharply defined from the ganglionic Anlagen (g. a.) just outside them. With the lateral epiblast (e.) the Anlagen of the ganglia have lost all connection, and only retain it with the epiblast at the re-entering angle between spinal cord and skin. The epiblast at i.e, of which the Anlagen, as in figs. 70, 71, originally formed a part, is, ever since the separation, only composed of a single layer of cells, which, in consequence of the tensions arising in connection with the infolding process, has become much lengthened. Outside this thin-layered part the epiblast passes almost abruptly into a much thicker-layered portion of the outer layer, which has taken no share at all in the formation of the ganglia. This thicker portion (fig. 68) forms a somewhat triangular mass of cells, the apex of which is directed towards the mesoblast. From a consideration of these figures (figs. 75, 76, 80, 81, 85, 89,), and of several other figures (figs. 98, 99, 102), to be afterwards noticed more in detail, the conclusion is forced upon any unbiased observer that the triangular mass of cells is identical with the so-called "Zwischenstrang" of His. The
consequences of this conclusion are fatal to the observations which His recorded nearly ten years ago, and to which he has been true for nearly twenty years.

The next stages in the formation of the spinal ganglia which we need consider are represented in Pls. XVIII, XIX, and XX, figs. 51, 55, 98, 99.

The separation of the neural tube from the epiblast has now taken place, and the ganglionic Anlagen have also no longer any connection with the epiblast. The spinal cord has not yet really closed, for its lips have not met, and in all the figures they are sharply defined from the fused ganglionic Anlagen which lie between and above them. In all the figures, but especially in 55, 98, 99, the Zwischenstrang of His (z.) is a prominent object. It is represented under very high power in figs. 98 and 99. As in Elasmobranchs, the ganglionic Anlagen now begin to grow down the sides of the cord, leaving their position above the lips of the neural tube; a stage of this process, showing that they are still unconnected with the cord, is given in fig. 102. When the Anlagen leave the lips of the neural tube the latter close together, and all subsequent stages go on exactly as described in Elasmobranchs. As I can here record no new facts I leave the development of the spinal ganglia of the Chick at this stage. I have proved at least three things for the spinal ganglia of the Chick. (1) That they are direct epiblastic proliferations formed very early outside the limits of the spinal cord Anlagen; (2) that there is no outgrowth of cells from the spinal cord to form them; (3) that the Zwischenstrang of His is that part of the epiblast which just fails to play any part in the formation of the ganglia. A fourth conclusion may be drawn, and this also holds for Elasmobranchs and other forms. It is that there is no form element in the spinal ganglia corresponding to that portion of the cranial ganglia which is derived from the sensory epithelium of lateral sense organs.
II, b. The Cranial Ganglia in the Chick.

As we have seen, the development of the cranial ganglia in the Chick was described by Marshall (No. 46) just ten years ago. He says, p. 15, "About the twenty-second hour a small outgrowth of cells appears along the mid-brain on each side, at the angle between the external epiblast and the neural canal—the neural ridge. This rapidly extends both forwards and backwards; forwards as far as the anterior part of the optic vesicles; backwards, along the whole length of the brain, and a certain distance down the spinal cord. Its first appearance precedes the closure of the neural canal." And on p. 12 (1), "The neural ridge appears before closure of the neural canal is effected, so that the ridges of the two sides are primitively independent of each other." (2) "The ridge is not developed directly from the external epiblast or from the neural canal, but from the re-entering angle between the two."

His (No. 29) has also given some partially correct figures of the first origin of the cranial ganglia in the Chick (Taf. xvii, fig. 3, a—f). The remaining figures of the series g and h are, I think, not correct; and the interpretation put on the (only partially correct) figures by His is one which, along with Balfour, I cannot accept.

His himself (No. 29, pp. 464—465) summarises his conclusions as follows:


"Nach meiner Ansicht gliedert sich demnach das obere Grenzblatt oder Ectoderm in dreierlei Anlagen; in die Medullarplatte, in die beiden Zwischenstrang-platten und in
das Hornblatt. Nach vollendem Rückenschluss ist auch die Zwischenstrang-Anlage vom Hornblatt überdeckt, ihre Stellung aber zur Medullardecke wechselt in den verschiedenen Bezirken, indem sie in dem einen über, in den anderen neben dieselben zu liegen kommt.


My account of the cranial ganglia of the Chick is in most points in agreement with that given by Onodi (No. 51, p. 260), to whom the reader may refer for a fuller account. In a later paper (No. 52) Onodi himself describes his results in the Chick briefly as follows (p. 553) :—"Beim Huhn stammt das Ganglion intervertebrale² am Kopfe theils von der Zellenproliferation, theils von der gleichseitigen Abschnürung des der

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1 The italics are mine.

2 When, as here and elsewhere in his papers on nerve development, Onodi speaks of the cranial ganglia as "spinal ganglia of the head," he is begging entirely the question of the homology of the two sets of ganglia. There is no discussion of the homology in any of his papers (see list at end of this work), neither do his researches contain any facts which justify this baseless assumption of their homology.
Umbiegungsstelle in das Gehirurohr naheliegenden Abschnittes des Ectoderma."

As in Elasmobranchs the first traces of the cranial ganglia Anlagen in the Chick are found in embryos in which as yet no division of the mesoblast has taken place. Marshall's statement of the time of first appearance, viz. the twenty-second hour, may be taken to be as nearly correct as one can determine.

The neural tube is still quite widely open.

Figs. 86, 87, and 67 are sections through the head region of three such embryos. In fig. 86 no trace of the ganglion Anlagen is to be seen, but the epiblast is much thickened, especially in the region of the future central nervous system and ganglionic Anlagen.

In fig. 87 traces may be seen of the ganglionic Anlagen at g. a., and one sees that they occupy practically the same position in reference to the central nervous system as the spinal ganglion Anlagen. In figs. 82, 83, and 84 are figured three sections through different regions of the head of a Chick embryo with seven body-somites. In all these sections the origin of the ganglia is very easily distinguishable. In fig. 82, which is through the region of the fore-brain, the limits of the neural plate are already marked out, and outside this the ganglionic Anlagen of each side are visible as special differentiations of the epiblast of the re-entering angle between the neural canal and the external epiblast, and also of a portion of the lateral epiblast beyond this. One notices that here, as in the spinal cord, the separation of the ganglionic Anlagen will cut out a particular region of the inner epiblast, and will leave a structure at Z. which is comparable to, and, indeed, identical with, the Zwischenstrang of His in the region of the spinal cord. Fig. 83 is in the region of the mid-brain, while fig. 84 is taken farther back from the hind-brain; these two sections present exactly the same appearances, and in a more marked degree than fig. 82. Figs. 77—81 are taken through the hinder head region of a Chick embryo with nine body-somites or so-called protovertebræ. Here the development of the ganglia has
advanced a step farther. The boundaries of the central nervous system are well marked in all the sections, and one can see that the latter is not connected with the ganglionic Anlagen. In this series of figures, which go backwards to the hind-brain, the ganglia Anlagen are already separated from the epiblast outside the re-entering angle between brain and epiblast, but still connected with the epiblast of the re-entering angle. For Professor His's satisfaction it may be added that in all the sections a Zwischenstrang is more or less developed. The next stages are shown in figs. 97, 46, 63, 65, 66, which are taken through embryos with, on the average, eight to ten mesoblast somites. The central nervous system with the ganglionic Anlagen are now shut off from the outside by the meeting and fusion of the external epiblast.

The lips of the neural tube itself have not yet closed, because the ganglionic Anlagen, which in some of the figures (figs. 97, 88, 46) have still a distinctly bilateral character, still exist between and above them. The ganglionic Anlagen soon become entirely separated from the epiblast, and in doing this leave behind them the traces of the limits of their epiblastic origin in the shape of a three-cornered ridge of cells which is identical with His's "Zwischenstrang" of the spinal region. It is figured at Z. in figs. 88 and 89. By the growth outwards from their position above and between the lips of the neural canal, the latter is able to close, and does so without having contributed a single cell to the formation of the ganglia.

The ganglionic Anlagen now begin to grow downwards towards the lateral surface of the brain to the point at which they acquire their permanent and only roots of attachment. The attachment takes place as in Elasmobranchs, and what I said about these forms on this subject may be taken as holding for the Chick also.

On the other hand, a portion of the "Anlagen" grows towards the lateral epiblast at about the level of the noto-

1 There is no such structure in the head of the Chick or any other Vertebrate I have as yet examined as His's Zwischenrinne.
chord and fuses with it (figs. 90, 91, 92, 93). I have not seen any reason for giving numerous figures of this point; those represented appear to me sufficient for the purpose. We are now concerned with the rudiments of the branchial sense organs. These structures were first described for Mammals by Professor Froriep (No. 17), and very shortly after his discovery my own preliminary researches independently announcing almost the same facts for Elasmobranchs appeared (No. 5). In the full account I afterwards gave of them I also mentioned the finding of similar rudiments in three-days-Chick embryos (figs. 90, 91, 92, 93). Béraneck (No. 10) afterwards confirmed the discovery, and Kastschenko (No. 40) in the account he more recently gave of them, with his characteristic failing, conveniently forgot to mention that either Béraneck or I had ever seen the structures which he described.¹

However, the following conclusions regarding the importance of the rudimentary branchial sense organs for the embryo Chick are peculiarly my own.

We saw that in Elasmobranchii the fusion of the ganglionic Anlagen with the neuro-epithelium which forms the Anlagen of the branchial sense organs leads to a certain amount of ganglion form-elements passing from the neuro-epithelium to the main ganglion. Such portion is really the ganglion of the branchial sense organs or sense organs of the lateral line (figs. 92, 93) (lateral ganglion).

It can be demonstrated also for the Chick that such form-elements pass by proliferation from the rudimentary sense organ into the ganglion (figs. 92, 93). This being so, and it being also capable of demonstration that the sense organs, with

¹ As Herr Kastschenko quotes my paper, I presume he was aware of the discovery; this conclusion is all the more justified as Professor Wiedersheim also briefly mentions my discovery in the last edition of his 'Lehrbuch der Vergleichenden Anatomie der Wirbelthiere' (p. 332). Professor Strasser also recently accuses Herr Kastschenko of a similar absent-mindedness in connection with another matter (Strasser, 'Ueber die Methoden der Plastischen Rekonstruktionen,' 'Zeitschr. f. Wiss. Mikros.,' Bd. iv, 1887, Hefte 2 and 3).
certain exceptions, connected with the cranial ganglia of Ver-
tebrates above Ichthyopsida, are rudimentary organs which only
present themselves during embryonic life (Froriep (No. 17),
Beard (No. 6), Béraneck (No. 10), and Kastschenko (No. 40).

The explanation so frequently given of such phenomena as
this, viz. that such organs reappear in the ontogeny as pleasing
reminiscences of the ancestral forms, if it has any claim to
pass as an explanation at all, is only a partial one. There are
many reasons for the reappearance of such rudimentary organs,
one of which is the part they play in contributing to the for-
formation of other organs. In fact, to come to the point, we
are here dealing with cases of Kleinenberg's law of the de-
velopment of organs by substitution (No. 41). I will not
enter at length here into the application of Kleinenberg's law to
the nervous system of Vertebrates. For a full comparison of
the phenomena presented in the development of the Vertebrate
nervous system with analogous and homologous phenomena in
that of Annelids (No. 41), our knowledge of the former is as
yet not sufficient. Some comparisons can even now be made,
but the time for their consideration had better be deferred.

The neuro-epithelia of the rudiments of the branchial sense
organs appear in the ontogeny of the higher Vertebrates, be-
cause they contribute certain form elements to the cranial
ganglia, and very probably also to some, at least, of the sensory
cranial nerves.

In the Chick (figs. 90—93, 96) such sense-organ rudiments
are found in connection with the mesocephalic (figs.90,93, m.g.),
trigeminus (figs. 90, 92, 94, v), facial (90, vii), glossopharyngeus
(figs. 90, 91, ix), and vagus ganglia. In Mammals (sheep em-
byros) Froriep (No. 17) has described them in connection with
the facial, glossopharyngeus, and vagus ganglia. In Mammals
they have not as yet been described for the mesocephalic and

1 The exception here has reference to the nose and ear, for both of which
organs evidence is accumulating for the views of their homology with the
sense organs of the lateral line which I originally expressed (Nos. 4, 5, 6). I
believe the organs of taste also arise from such neuroepithelium and wander
through one, or in some cases perhaps two, gill-clefts on each side into the mouth
cavity. My evidence for this conclusion will be produced in another Study.
trigeminus ganglia, but there can be little doubt that they also exist for these at some stage or other.

After the fusion of the mass of each cranial ganglion with the skin, form-elements are, as we have seen, given off into it. The ganglion leaves the skin, and, as in Sharks, almost certainly leaves sensory nerve branches behind it. The sense-organ rudiments afterwards disappear. I have not followed the steps of this process in the Chick, but I cannot doubt the general accuracy of Kastschenko's account (No. 40, pp. 281—284), for it agrees fairly well with Professor Froriep's earlier researches (No. 17) on the fate of the rudiments in Mammals.

This finishes the general account of the first formation of cranial ganglia in the Chick.

III. THE DEVELOPMENT OF THE ANTERIOR ROOTS OF SPINAL NERVES IN ELASMOBRANCHS.

In Balfour's account of the spinal nerves in Elasmobranchii (Nos. 1 and 2), he described the anterior roots as direct cellular outgrowths from the lateral ventral region of the spinal cord, and in the second volume of the 'Comparative Embryology,' p. 372, he says: "The anterior roots of the spinal nerves appear somewhat later than the posterior roots, but while the latter are still quite small each of them arises as a small but distinct concise outgrowth from the ventral corner of the spinal cord, before the latter has acquired its covering of white matter. From the very first the rudiments of the anterior roots have a somewhat fibrous appearance and an indefinite form of peripheral termination, while the protoplasm of which they are composed becomes attenuated towards its end. They differ from the posterior roots in never shifting their point of attachment to the spinal cord, in not being united to each other by a commissure, and in never developing a ganglion." The anterior roots grow rapidly, and soon form elongated cords of spindle-shaped cells with wide attachments to the spinal cord." And in a note at the foot of p. 372: "The cellular structure of embryonic nerves is a point on which I
should have anticipated that a difference of opinion was impossible, had it not been for the fact that His and Kölliker, following Remak and the older embryologists, absolutely deny the fact. I feel quite sure that no one studying the development of the nerves in Elasmobranchii with well-preserved specimens could for a moment be doubtful on this point. And I can only explain His's denial on the supposition that his specimens were utterly unsuited to the investigation of the nerves. I do not propose in this work entering into the histogenesis of nerves, but may say that for the earlier stages of their growth, at any rate, my observations have led me in many respects to the same results as Götte (‘Entwickl. d. Unke,’ pp. 482—483), except that I hold that adequate proof is supplied by my investigations to demonstrate that the nerves are for their whole length originally formed as outgrowths of the central nervous system. As the nerve-fibres become differentiated from the primitive spindle-shaped cells, the nuclei become relatively more sparse, and this fact has probably misled Kölliker. Löwe, while admitting the existence of nuclei in the nerves, states that they belong to mesoblastic cells which have wandered into the nerves. This is a purely gratuitous assumption, not supported by observation of the development."

I could have been content to leave this matter of the anterior roots unnoticed but for two circumstances. In the first place the figures which Balfour has given of their development in the ‘Comparative Embryology’ (vol. ii, p. 371, fig. 267), “Elasmobranch Fishes” (Pl. X, fig. 7), and in the paper on the spinal nerves (No. 1, Pl. XVI, figs. Da. b. and c. Pl. XVII, figs. H 11, I 11, and E. b.) are very diagrammatic, and His would be justified from his standpoint in objecting to their representing the true facts. On the other hand, I can raise the same objection to the diagrammatic figure of the development of anterior roots in Pristius, which His represents on p. 393 (No. 34, fig. 1) of his recent work. Nay, I cannot help insisting that if Balfour's figures were not what one might expect, His's figure is incorrect to a far greater degree, and the “Ehren-
Wache" of parablast cells which Professor His, in conformity with his peculiar doctrines, gives the nerve, has, so far as I can find out in Pristiurus and other Elasmobranchii, no real existence in the world of fact. I should have been quite satisfied but for these considerations to merely echo Dr. van Wijhe's recent remark on this point (No. 63, p. 76, Anmerkung). He says, "In Betreff der zelligen nicht faserigen Struktur der ventralen Wurzeln bei ihrem ersten Auftreten muss ich Balfour vollständig Recht geben."

There are three investigators who have regarded the motor-nerve formation as entirely due to fibres alone, without the inclusion of any nuclei. The view is one which can only be accepted if rigidly proved, and this in my opinion has not yet been done. His holds that the anterior root-fibres are prolongations of cells which lie in the anterior cornu of the spinal cord. Thus, according to him, a motor nerve-fibre passing from the spinal cord to a muscle in the foot would be a direct prolongation of a ganglion-cell within the cord, and no cell nuclei would at any time intervene in its course (Nos. 32 and 33, p. 375).

He asserts (No. 29, p. 475), "Mit Beginn des vierten Bebrütungstages, sind vordere Wurzeln erkennbar als Bündel seiner, vom Rückenmark aus in die Leibeswand tretenden Fäden. Vom ersten Moment an, da sie überhaupt sichtbar sind, haben sie die angegebenen Eigenschaften und ihrem Auftreten gehen keine zelligen Urgebilde voraus."

And again, in the more recent work (No. 33, p. 375), "Die peripherisch auswachsenden Fasern, sowohl die motorischen, als die sensibeln, sammeln sich als kurzen Stämmen. Jeder dieselben besteht aus einer Anzahl feiner kernloser Fäden, die in der Nähe des Ursprungs eine deutlich fibrilläre Streifung zeigen. Innerhalb eines Stammes zeigen die Fasern theilweise verschränkten Verlauf. Parablasticshe (!) Zellen zeigen sich beim menschlichen Embryo Anfangs nur sparsam zwischen den Nervenfasern zerstreut . . . . . Je jünger ein Nervenstamm, um so kürzer ist er, das Auswachsen geschieht allmählich und es vergehen einige Wochen bis z. B.
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die letzten Enden der Finger und der Zehen ihre Nerven erhalten haben."

To return to my own observations. I have as yet only investigated Sharks and Lizards on this point. The results, so far as they concern the latter group, will be given later along with observations on the anterior roots of the cranial nerves. Figs. 58, 60, 62, 53, 54, 56 and 61, on Pl. XIX, are intended to illustrate the development of anterior roots of spinal nerves in Elasmobranchii. One of the very earliest stages in the development of an anterior root (a) is shown in fig. 58 (Pristiurus), and it possibly corresponds to the stage figured by Professor His in the paper quoted above (No. 34, fig. 1). There is no possibility of recognising "parablastic" cells in this section, and one sees that while the root is partially fibrous there is at least one nucleus passing out of the spinal cord, either entirely or partly after cell division. A slighter later stage is represented in figs. 60 and 61. The fibres of the nerve have reached the muscle-plate,¹ but there are also two nuclei visible in the nerve-cord lying partly also in the cord. There are here also plenty of mesoblast—pardon, "parablast" cells in the neighbourhood. But they are not destined for the nerve, but are about to enclose the notochord to form the body of the vertebra.

Later stages in the development are figured in figs. 54, 56. Here, too, the fibrous nature of the nerve is very obvious, but one also observes a vast number of nuclei within the nerve, which one cannot regard, from their form and characters, as otherwise than offsprings of the nuclei which have passed at earlier stages, and even still continue to do so (figs. 60, 54, 61), from the anterior cornu to the nerve. When His regards the nuclei here present as mesoblastic or "parablastic" cells, his view is just as much a gratuitous assumption as the whole parablastic doctrine, as the Zwischenstrang ganglionic formation in the trunk, and as the identification of a certain ganglion

¹ The end plates of muscles (and of the electric organ) are derived from ganglionic cells, which wander in this way in these early stages from the anterior horn to the muscle-plate. Several figures show this, and I shall treat of the matter at length elsewhere.
to be mentioned elsewhere as the ciliary ganglion. A figure such as Professor His gives in his recent work of two fibres passing out from two nuclei in the anterior cornu of the head, outside which they receive an "Ehren-Wache" of four "parablastic" cells, two on each side, is one which, in spite of much search, I have never seen. On the other hand, the figures I give in Pl. XIX could be multiplied by the dozen, and figs. 53 and 58 are representations of an appearance which I have often met, and which Dr. van Wijhe assures me he also has very frequently seen. From these facts, and from facts regarding the development of anterior roots of cranial nerves, and nerves of the sense organs of the lateral line or branchial sense organs, I do not for a moment hesitate to declare that the facts of development are contradictory to (1) Professor His's view of the absence of nuclei in the anterior roots, and (2) his assumption that when such nuclei are present they are of "parablastic" origin. It is worthy of notice that in his original assertions Professor His absolutely (vide supra) denied the presence of nuclei in the anterior roots, and only now that their presence in those structures in Elasmobranchii is obvious to every observer, including Professor His, does it occur to him to make use of that wonderful doctrine of parablast to explain their presence. Professor His's attempt to get out of a false position here is only a little more dignified than his endeavour to explain away the meaning he attached to the Zwischenstrang.

IV. THE GANGLIONIC DEVELOPMENT IN DIFFERENT GROUPS OF VERTEBRATES.

Without anticipating the results of my researches on other groups, which so far include Teleostei, Lizards, Frog, Newt, and Rabbit, I may be at least allowed to say now that the above mode of development of cranial and spinal ganglia holds, with very slight and unimportant modifications, for all these forms also. I might have left these forms undescribed but that for the certainty that some observer or other would by-and-by quote
their development according to his ideas, as opposed to the facts I have here described for Elasmobranchii and Birds. The conviction was very early in the research forced upon me that the development of spinal and cranial ganglia in all Vertebrates must take place after one type, and any differences found in different groups must be referable to variations or changes rung on that type. And as an example, the investigation of the development of cranial ganglia in the Anuranous Amphibians was one I could not leave unnoticed on account of Spencer's notes on the matter (No. 59). All the more, as in my paper on the branchial sense organs (No. 6) I felt obliged, after the examination of some of Spencer's preparations, and of a few I made myself, to support his conclusions. We were then both in error on one point—of that I am now quite sure—and that is in reference to the deeper layer of epiblast above the level of the lateral sense-organ thickening, and which connects the latter in early stages with the neural plate. We both believed it gave origin to the trunk of the nerve. This is not so. That layer is indifferent except at two points corresponding exactly to the two points at which the ganglionic form elements arise in Elasmobranchs. In fact, as a preliminary note I take the opportunity of saying that the cranial ganglia of the Frog develop in exactly the same way as those of Elasmobranchii. Among other forms examined the Lizard is one of the most favorable for such investigations. It also agrees essentially in the mode of development of cranial and spinal ganglia with Elasmobranchii.

The Newt has been mainly studied by Bedot (No. 9), and Misses Johnson and Sheldon (No. 38).

In both of these works I shall have occasion to underline a number of mistakes and false interpretations; here I will only remark that I am somewhat surprised that none of these investigators have seen the epiblastic origin of the spinal ganglia in this animal. I know no animal in which such origin is easier to identify. The criticisms with which the two latter authors have seen fit to honour my work may also be here left unnoticed. The only one whose justification I will acknowledge.

ledge is their doubt of the accuracy of Spencer’s and my investigations on the origin of the root of a cranial nerve in the Frog. I have admitted the error above, and need not here mention the matter further. To one assumption of these two authors (No. 38, p. 11) I must, however, be allowed here to reply. They remark: “More recently the theory of the derivation of the whole or greater part of the cranial nerves from the epiblast has been supported by Mr. Spencer and Mr. Beard. This view is a revival of that held by Götte.”

(1) The origin of a part of each of the cranial ganglia, and of what I called the suprabranchial nerves, was no longer a theory after the publication of my paper on the branchial sense organs (No. 6). It was then demonstrated for certain parts of the cranial ganglia and for certain nerves that they have an epiblastic origin, and the matter could for these hardly be called a “theory.” I can now demonstrate that the whole of the components of the various cranial ganglia are epiblastic in origin, and not wholly or in part outgrowths of the central nervous system.

(2) Götte never held this view, whatever may now be the case. I can only suppose that the two ladies never read the passages in his work which bear upon the question. The following quotation from Götte’s ‘Unke’ (No. 22, p. 719) gives a clear statement of Götte’s conclusions at that time:—Bei der Untersuchung der Kopfnerven handelt es sich zunächst um ihre Zugehörigkeit zu den ganzen hintereinander liegenden segmentalen Abteilungen des Kopfes ferner um ihre Unterscheidung nach dem Ursprunge aus dem inneren oder äusseren Segmente des mittleren Keimblattes oder aus anderen Embryonalanlagen jeder Abtheilung. Zu den letzteren gehören der Sehnerv und die Seitenennerven als Erzeugnisse des oberen Keimblattes, die übrigen Kopfnerven entstehen aus dem mittleren Keimblatte.”

I was inclined then to regard the whole of the ganglion as arising from the epiblastic sense thickening, and the cells derived from the “neural crest” as forming the root of the nerve. The point is a very difficult one to decide, and I refer the reader to a discussion of it in another part of these researches.
V. The Neural Ridge.

The reader may have remarked in the preceding pages that the terms neural ridge and neural crest have been banished from my account of the development of the ganglia, both cranial and spinal. The reasons for this may now be explained, and hand in hand with this explanation one may compare the origin of the ganglionic Anlagen as described here with the accounts of previous observers.

Considering for a moment the neural ridge without prejudice as to its origin, most authors, following Marshall (No. 46, p. 15), regard the neural ridge as a continuous structure passing forwards from the mid-brain right away backwards through the head and along the whole spinal cord as a continuous structure; and from its continuity in all parts, of which in a certain sense there can be no doubt, Balfour and Marshall were inclined to attach great morphological importance to it. The continuity of the neural ridge is originally most marked in the head, in which the ganglia show tendencies to concentration and fusion, and where also the ganglionic Anlagen are very large.

In the spinal cord, on the other hand, where the ganglionic Anlagen are not so massive, the continuity of the neural ridge is by no means so evident as in the brain. Indeed, from the neural-ridge stage onwards, and even from the very first formation of the spinal ganglia Anlagen, the segmental nature of the latter is one about which a careful investigator can make no mistake. For this reason, and the additional one that all the cell elements of the neural ridge in both head and trunk undoubtedly, as His insists (No. 34, p. 393), pass over into the ganglia, I can see no particular advantage in the use of the term. And when one comes to consider, as we shall presently do, the origin of the neural crest, my objections to the term as at present used are intensified. Marshall, from the apparent fusion of the neural ridges of the two sides, gave to the single structure thus formed the name of neural crest. Here, again, as the structure is certainly a bilateral one and not unpaired, and as in many cases its bilateral structure is
very evident (figs. 21, 24, 46, 51), I confess I see no conve-
nience in the use of a name to which doubtful morphological
characteristics are attached.

We are now met by the question, Assuming that the ganglia
arise as outgrowths of the neural ridge, what is the ultimate
origin of the structure, and are the ganglia first visible in the
neural-ridge stage?

The foregoing researches give the answer to this question,
and in anything like a complete and correct form they are the
first researches which can lay claim to decide the question. Six
years ago Sagemehl (No. 56), in a prize research, published
observations which he believed, and apparently the judges of
the competition also, to be a solution of the problem, so far as
the spinal ganglia are concerned. How little claim his
researches have to pass as a last word on the origin of the
ganglia will be evident to the reader of this paper, and if he
will take the additional trouble to compare the numerous
figures I have given here of Elasmobranchii and the Chick
with the nineteen figures of Sagemehl’s work, he will, I think,
admit the correctness of my conclusion, that Sagemehl never
saw any of the earliest stages of the formation of spinal ganglia.
Except for Marshall’s and Onodi’s researches on the cranial
ganglia of the Chick, this remark applies to all the observa-
tions of various investigators of the development of cranial
and spinal ganglia. His (No. 29) has also seen, but only
partially interpreted in a correct sense, some of the earliest
stages in the cranial nerves of the Chick. As His’s Zwischen-
rinne theory was one of the earliest on the development of
cranial nerves, we can at once consider his claims to having
furnished the solution to the above question in the wider sense
of the origin of the ganglia Anlagen. Remak’s (No. 54)
older observations, originally supported by Balfour and Foster,
may be here passed over, for no one now believes that the
ganglia arise as differentiations of the “protovertebræ.” And
the same also holds for Hensen’s conclusions (No. 24), which
are more of a theoretical nature than results of actual investi-
gation; still, as I shall elsewhere show, there is an element of
truth in Hensen's suggestions, though not quite the same Hensen thought.

It is perhaps unkind to remind Professor His that his "Zwischenstrang" was originally believed by him to be concerned in the formation of the urogenital system. The Zwischenstrang was afterwards converted in the basis of a theory of the origin of the spinal ganglia. In spite of the persistent way in which Professor His, without full and complete investigation of the matter, holds to this Zwischenstrang theory of the proved origin of spinal ganglia, a persistence which leads him in his recent work (No. 34, pp. 391 and 416) to identify it with what Balfour, Marshall, Sagemehl, and others have regarded as the first stages in the formation of the ganglia, and to rebaptize the structure, which undoubtedly exists (figs. 97, 98, 99, z.), under the name of "Ganglionstrang," I do not see how Professor His can escape the fatal consequences of the researches I now record.

I think I have demonstrated, even to Professor His's satisfaction, that the Zwischenstrang is just that part of the epiblast which takes no part in the ganglionic formation, and that it owes its formation to the cutting out of ganglionic Anlagen between it and the neural plate. As the crowning proof that the Zwischenstrang is not identical with the neural ridge or the

1 Professor His (No. 34, p. 417) states that both olfactory and auditory organs of Vertebrates take their origin from parts of the "Zwischenrinne" or "Ganglienrinne" which remain open. This is absolutely incorrect. The views of the homology of both these organs with the lateral or branchial sense organs, which I formerly advocated (Nos. 6, 5, 4), can be still maintained. From figures in my former work (No. 6) and figs. 25, 27, 46 of this paper, it is obvious to any unprejudiced observer that the auditory organ develops ganglionic elements from two sources, just as occurs in a typical gill-bearing segment. The same holds for the olfactory organ. I postpone for the time the further elucidation of my views of the homology of these two sense organs, but only for a time, for I intend shortly to discuss the problems they present more fully; here I will only say that no one has as yet urged unanswerable arguments against my views. Personally, I may remark, I care nothing about the quondam existence of gill-clefts for ear and nose; the important points to me are those which make the nose and ear parts of the system of lateral or branchial sense organs.
ganglionic Anlagen, I may refer to figs. 97, 98, 99 and others, more especially figs. 97 and 98, in which the "Zwischenstrang" and the ganglionic Anlagen can be seen in the same figure, and where they are entirely distinct and separate.

When we turn to Professor His's researches on the cranial ganglia of the Chick (Nos. 28 and 29), we find that he was a little more fortunate in seeing some of the true facts. But here again his theory influenced his interpretation of the facts. The foldings of an elastic plate by which, as is well known, Professor His explained all embryonic phenomena\(^1\) (No. 31), must also find their application in the formation of the cranial ganglia. It is not merely in the assumption of such a folding in of the epiblast of the head to form the ganglionic Anlagen in his "Zwischenrinne" that His is in the wrong; he has actually figured such a Zwischenrinne (No. 29, Pl. XVII, figs. 3, 6, 7, 8, 9).

I have made a very large number of sections through the head region of Chick embryos (well preserved) in this stage, and as the result I do not for a moment hesitate to say that the Zwischenrinne of His has no existence. On the contrary, in the head just as in the trunk, as the result of the separation of the ganglionic Anlagen from the epiblast, a "Zwischenstrang" may be formed (figs. 63, 97, 88); but this structure also plays no part in the formation of the ganglia. If Professor His had not assumed or believed in the existence of this "Zwischenrinne," and if he had left the "elastic plate" out of question and acknowledged the proliferation of a certain portion of the inner epiblastic layers to form the ganglia, he, who certainly was the first to see some of the true appearances on the Chick, would also have been the first to ascribe their true epiblastic origin to the cranial ganglia. But under the dominance of his theory he believed he saw structures\(^2\) which

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\(^1\) This "Mechanische Auffassung" has unfortunately more influence on Professor His's results than his conception of the great value of comparative embryology, to which he lays claim in p. 405 of his recent critical study.

\(^2\) One must bear in mind that the sections of those days were nothing like as good as those a fair worker can now make.
have no existence; and he says in a passage which on another
page I have quoted in full, "Ich verwerfe überdies, wie
ich schon an anderem Orte ausgesprochen habe, das von
manchen Embryologen so freigebig benutzte Princip der lokalen
Wucherungen" (No. 34, p. 465). The reference to another
place in this passage is to the "Briefe über unsere Körperform"
p. 67, u. f.—a work in which the foldings, &c., of an elastic
plate are used to explain fully the development of all the organs
of a Vertebrate embryo. By this declaration Professor His
gives the coup de grâce to any possibility of the acceptance
of his account of the cranial ganglia in the Chick as a solution
of their origin. The two diagrammatic figures which are re-
presented on p. 465 of Professor His's paper on the peripheral
nervous system have been referred to recently (No. 34, p. 394,
Anmerkung) by him as representing really the true facts, and
as agreeing essentially with the results of other investigators;
but that I may not be accused of an unfairness, which is far
from my thoughts, I quote the passage: "Wie jedes Schema,
so ist auch dieses in Betreff absoluter Correctheit1 anfechtbar,
aber, dass die untere Lamelle des dort ausgebogenen Streifens
mit der von Kölliker, Sagemehl, u. A. abgebildeten Ganglien-
anlage zusammenfällt, bedarf kaum eine Erläuterung." As
these figures show an epiblastic invagination to form the
ganglionic Anlagen, in conformity with the elastic plate theory,
—an appearance which has no existence in fact,—it is difficult
to see how the lower layer of this structure can be identical
with the ganglionic Anlagen of Kölliker, Sagemehl, and others.
This is as near being the case as any fancy figure drawn in the
same position would be. The principle of the epiblastic origin
of the ganglia, apart from the central nervous system, is one on
which His has long been in the right; the mode in which he
believes this origin takes place is one in which he has been
further from the true facts than anyone else. I have quoted
before the following passage from Professor His's recent paper
(p. 380), and as we now see that the facts are not so much

1 This "Schema" of His's is not relatively correct, it is absolutely
incorrect!
matters of agreement as Professor His supposes, one may quote it again with the request to Professor His to furnish us with the evidence in which he bases his opinions on the origin of the ganglia from the Zwischenstrang and Zwischenrinne, and of the olfactory and auditory organs from parts of the latter structure which remain open (No. 34, p. 417). These are questions of facts whose accuracy I challenge. Nor are they the only points of fact on which I (and many others) disagree with Professor His. Of that more elsewhere.

The passage reads: "Bei genauerem Zusehen findet man eben, dass die Differenzen nicht in dem liegen, was der eine und der andere Beobachtungskreis an thatsächlichen Befunden ergiebt, sondern in demjenigen, was die Vertreter der einen und der anderen Schule zwischen die Zeilen zu lesen sich bemühen. Nun sind aber die jüngeren vergleichend morphologischen Schulen in der Lektüre zwischen den Zeilen über die Maasen weit gegangen, und ich halte es für eine Pflicht, meinen Bedenken hiergegen offenen Ausdruck zu geben."

However it may be with the hypotheses, &c., one thing is certain, that some of Professor His's most fundamental facts are no facts at all, and we may not unnaturally ask whether the reproach intended for us younger morphologists does not partially recoil on Professor His himself?

All other observers, excepting Spencer for the cranial ganglia of Amphibia, are agreed in referring the source of the posterior roots and ganglia to the neural ridge of Marshall, and nearly all agree with Balfour's maxim of the origin of the latter structure as an outgrowth from the central nervous system.

On p. 369 of the 'Comparative Embryology' of Balfour, vol. ii—a book which represents his latest views on the question—we read: "All the nerves are outgrowths of the central nervous system;" and on p. 374, "The neural crest clearly belongs to the brain, from the fact of its remaining connected with the latter when the medullary tube separates from the external epiblast."
Marshall's position is not quite so simple. The cranial nerves (and ganglia) of the Chick Marshall (No. 46) refers to the re-entering angle between the neural plate and external epiblast, but nothing definite is stated as to the relations of this portion of the epiblast to the external epiblast on the one hand or to the brain on the other. In other words, if we are entitled to conclude that Professor Marshall held the independent epiblastic origin of cranial nerves and ganglia, we miss in the account the necessary denial of Balfour's view as stated above. If Marshall recognised the epiblastic origin of the neural ridge he did not tell us whether or not he holds with Balfour that it "clearly belongs to the brain." This is important, for taken in connection with his acceptance of Balfour's view of the origin of spinal ganglia, it does not preclude the possibility of the assumption that the neural ridge in the Chick arose from a portion of the brain which has not got shut in. Professor Marshall has indeed seen and described part of the true origin of the cells which form the neural ridge in the Chick. The whole of the source he has not identified, and he did to draw the conclusions of the independent origin of the ganglia to which he was entitled.

The part he had not seen is that portion of the cranial ganglion Anlage which is formed from the external epiblast outside the angle between epiblast and brain. This was first seen by Onodi (No. 51).

Judging from the following passage, it would appear as though Professor Marshall held the origin of the ganglia to be the same in both brain and cord, and the difference to be only as to the time of closure of the neural canal. He says (No. 46, p. 16): "Its (the neural ridge) first appearance precedes the closure of the neural canal, but after about the fortieth hour the closure of the canal proceeds backwards more rapidly than the growth of the neural ridge, so that in the greater part of the length of the spinal cord the ridge is developed as an outgrowth from the summit of the cord itself, and never has any connection with the external epiblast."

In order to get a little nearer Marshall's position I turned to
his latest statements on the development of nerves, and find (No. 50, p. 9) that he quotes with approval Balfour’s views. He says, “Balfour showed that, contrary to the generally accepted theory, the nerves are outgrowths from the central nervous system, and therefore of epiblastic origin, instead of being, as formerly supposed, structures arising independently in the mesoblast and only acquiring a secondary connection with the brain and cord.” Hensen (No. 25), Kölliker (No. 43, p. 621), Sagemehl (No. 56, p. 33), van Wijhe (Nos. 60, p. 18), Bedot (No. 9, p. 186), Shipley (No. 58), Béranec (Nos. 10, 11), and Misses Johnson and Sheldon (No. 38), have practically accepted Balfour’s and Marshall’s views; and van Wijhe (No. 61, p. 4) has used the conclusion as an argument against my views of the epiblastic origin of the sensory nerves of the branchial sense organs (Beard, No. 6, p. 69). He remarks, “Wenn Beard jetzt, seiner früheren Behauptung entgegen, den Olfactorius und die Seitennerven nebst ihren Ganglien allein aus der Epidermis entstehen lässt, so kann er dies wohl nei beweisen weil der Stamm der Nerven sich ursprünglich aus dem Medullarrohre entwickelt.”

It is not difficult from the researches I have here recorded—and others as yet unpublished—to conclude that all these authors have been mistaken in describing the ganglia as outgrowths of the central nervous system. The figures I have given demonstrate the justice of this criticism, and as a final argument, which more especially negatives Balfour’s remark (quoted earlier), that the neural crest clearly belongs to the brain, I will point out that the limits of the two structures, brain and ganglionic Anlagen, are very early sharply separated off by a well-defined line (figs. 45, 51, 32—36 and others), and only in those stages in which the neural plate is quite open, in fact only during the primitive-streak period can one really, with any pretence to accuracy, speak of a common Anlage for both structures, of an encephalo-ganglionic Anlage. But this is a stage at which the embryo is barely differentiated into the three embryonic layers.

Onodi (No. 51) has shown the true source of origin of
the main portion of each cranial ganglion in the Chick,—of that portion which is not derived from the remains of the branchial sense organs. The rest of his researches, on the cranial and spinal ganglia of Elasmobranchii, Teleostei, Lizards, and Mammals, and on the spinal ganglia of the Chick, lead him to the same results as Balfour, Marshall, and others. His researches hence agree partially with my own for parts of the cranial ganglia of the Chick, but for all other types he has failed to see the true epiblastic origin of both cranial and spinal ganglia.

Hoffmann (No. 36, pp. 45—49) while supporting Balfour's views of the outgrowth of spinal ganglia from the cord, considers it probable that the posterior root ganglia of the cranial nerves of Teleostei arise from the epiblast beyond the limits of the neural plate, and before the closure of the latter. He did not prove that such was the case.

In later researches (No. 37, p. 204) he again refers to the neural ridge, but says nothing of its origin.

VI. THE GROWTH OF OUR KNOWLEDGE OF THE INDEPENDENT EPIBLASTIC ORIGIN OF THE PERIPHERAL NERVOUS SYSTEM.

The first conclusions on this question were arrived at by Götte (No. 22, p. 72) and Semper (No. 57, p. 256), both of whom stated that the lateral nerve has an epiblastic origin and arises pari passu with the growth of the lateral line as a differentiation of the epiblast. Götte (p. 719) extended this mode of development to the nerves of the lateral sense organs of the head. These statements, on which doubt was cast by Balfour, were practically confirmed by van Wijhe (No. 60, p. 35) and Hoffmann (No. 36, p. 89,) for Teleostei. I (No. 4) believed Balfour's doubts to be well founded, but in two subsequent publications I was able to prove, for Elasmobranchii the accuracy of Semper's account. Just before my paper on the origin of the cranial ganglia (No. 5) appeared Professor
Froriep published his researches on the rudiments of sense organs in connection with several cranial ganglia in Mammalia (No. 17). Without committing himself very definitely to the matter Professor Froriep did not think it impossible that the ganglia derived form-elements from the epiblastic fusion (No. 17, p. 40), and the cranial ganglia concerned were regarded by him as the remains of the ganglia of sense organs which in the course of phylogenetic development had got lost.

He says (p. 45): “An der drei Nerven übereinstimmend gehen aus der Kiemenspaltenorganen keine definitiven Bildungen hervor, was von ihnen übrigbleibt, ist lediglich die gangliöse Anschwellung des Nerven, welche ursprünglich die nervöse Unterlage des Sinnesepitheliums gewesen ist. Diese Ganglien, Ggl. genicule, Ggl. petrorsum, und Ggl. nodosum, sind demnach als rudimentäre Organe zu betrachten, sie stellen die Ueberreste phylogenetisch verlorengegangener Sinneswerkzeuge dar.”

Professor Froriep was undoubtedly the first in point of time to describe this fusion of cranial ganglia with the epiblast, and to draw the conclusion that the modified epiblast at the point of fusion was the remains of a special branchial sense organ. He hesitated (p. 35, et seq.) to homologise them with the sense organs of the lateral line in Fishes, considering it possible that they corresponded with rudiments of other sense organs connected with the ventral branches in Fishes as in Mammalia, and which, as in Mammalia, probably disappeared in later development.

The identification of the ganglion fusion with the “Anlagen” of the sense organs of the lateral line for head and trunk in Elasmobranchii, was first made by me (No. 5) independently of Professor Froriep, and at that time also—a point which I afterwards developed more fully—I was quite aware of the relations of the sense organs to the gill-clefts, for I homologised the nose with such a ganglionic epiblastic fusion, and called it “the modified sense organ of a gill-cleft rather than a gill-cleft itself;” and in my note-book there still stands the notice from which I wrote that conclusion, which shows, I
think, very clearly that, contrary to Professor Froriep's recent criticism (No. 19, p. 821), I was then fully aware of a point to which he attaches a very great deal of importance, viz. their typical position over a gill-cleft. The note is, "The nose is not a gill-slit but the sense organ which sits above a cleft."

In my paper on the branchial sense organs (No. 6) I showed that out of this epiblastic fusion, which (No. 5) I had described independently of Froriep, the sense organs of the lateral line or branchial sense organs take their origin. The sensory epithelium grows in various directions by division of its cells, and it pushes away the indifferent epiblast. From the sensory epithelium arise both sense organs and the nerves which supply them and connect them with the ganglia. The ganglia were considered as mainly arising from the thickenings, the cells derived from the neural ridge only forming the root of the nerve. Whether the latter conclusion is true or not I cannot say, certainly some of those cells do take part in the formation of the nerve, and their nuclei may be found along the course of the nerve. The suprabranchial nerves were distinguished from the præbrachial and postbranchial, and a morphological importance was attached to the former. At the present time I regard the nature and mode of origin of suprabranchial, præbrachial, and postbranchial nerves, so far as the latter innervate the sense organs (for, as is well known, they also contain motor fibres to the muscles of the gill-cleft) as entirely the same, and would now say all the nerves to the sense organs of the lateral line or branchial sense organs are derived from the neuro-epithelial "Anlagen" of the latter.

Nothing was said in my former paper of the origin of the neural-ridge of the spinal nerves, which lay beyond the scope of my researches at that time. Nose and ear were considered as modified branchial sense organs and their ganglia (for, in spite of Gegenbaur, the nose has a ganglion) as differentiations of the sensory epithelium. Rudiments of such branchial sense organs and their ganglionic fusion were described in three-days'-Chick embryos. Spencer (No. 59) on Amphibia (Frog),

\footnote{See No. IV of these Studies.}
derived the cranial ganglia from the epiblastic thickenings which form the lateral sense organs, and the main roots of the nerves from the inner epiblast connecting this thickening with the neural plate. This latter conclusion, which I formerly supported, is wrong.

Onodi (No. 51) extended Marshall's (No. 46) description of the origin of the cranial ganglia in the Chick from the angle between the epiblast and the neural plate, in that he stated that the epiblast outside this also shares in the formation. Neither Onodi nor Marshall distinctly say whether they regard this portion of epiblast as part of the central nervous system or not. And, as we have seen for the cranial and spinal ganglia of other forms, they supported Balfour's views.

In a note which I quoted in the introduction, van Wijhe (No. 61) mentions that the olfactory nerve arises from an epiblastic differentiation at the lips of the anterior neuropore. The present research, taken in connection with my former paper on the branchial sense organs, shows that the sensory nerve-elements of the whole of the peripheral nervous system arise as epiblastic differentiations independently of the central nervous system.

VII. THE RELATIONS OF CRANIAL TO SPINAL GANGLIA AND OF THE "SEITENORGANE" OF ANNELIDS TO THE SENSE ORGANS OF VERTEBRATES.

It is far from my intention to enter here into the discussion of morphological questions. My contribution to recent controversy may fitly find a place in a special paper in which I intend to analyse the recent critical studies of Professors Gegenbaur and His on Vertebrate morphology, and especially on the nervous system.

But still, the conclusions to which Froriep and I arrived at regarding the fundamental differences which obtain between the head and trunk regions of Vertebrates may be here slightly reviewed, and, so far as I am concerned, revised in the light of the facts recorded in the preceding pages. Gegenbaur
(No. 20), and in a certain sense Dohrn and others, regard the head as a specially modified portion of the trunk, and, as is well known, Gegenbaur (No. 20) considered that certain of the cranial nerves could be reduced to spinal nerves. His present position with regard to recent researches is defined more or less clearly in his recent paper (No. 21). I cannot now enter into a criticism of that—the limits of my space forbid it,—and, as far as possible, I have endeavoured to shut speculative matter out of this research.

Dohrn (No. 13, p. 471) has formulated his conclusions as to the relations of the spinal and cranial nerves and ganglia in the following passages:

"Die Hirnnerven haben diejenigen Leitungsbahnen verloren, welche die Urwirbel und deren Derivate innervirten; sie haben aber in Folge der ausserordentlichen Vergrösserung und Complicationen der visceralen, i.e. ventralen Theile des Kopfes um so mehr gewonnen und sind durch die vielfachen Verschiebungen der bezüglichen Theile in ihrem Verlaufe sehr verwickelt geworden.

Die Spinalnerven ihrerseits haben am Rumpfe in ihren viszeralen Verrichtungen Verschiedenes verändert (—auf welche Weise soll später dargestellt werden—,) haben aber durch die Entwicklung der Körper—und Extremitäten—Musculatur im Umfang im Allgemeinen nicht vermindert, und sind in gewissen Sinne weniger modificirt, als die Cranialnerven. Am Schwanz dagegen haben sie durch die Einbusse der gesammten Viseralpartien die stärksten Verluste erlitten und sind dort demgemäß am wenigsten complicirt."

While there are some points in the above statements with which I can express my agreement, my standpoint is more on Froriep's side than on that of Dohrn. For a general survey of Froriep's views I must refer the reader to that investigator's recent utterances (No. 19, p. 833, et seq.).

I agree with Professor Froriep that at present we cannot see much beyond the primitive separation of the Vertebrate body into two sharply-defined regions,—a respiratory region the head, and a locomotive (and digestive) region the trunk.
We have hardly begun to get any idea of the more primitive structures from which these two regions are derived.

I have previously with Froriep, much to the disapproval of Gegenbaur, His, Dohrn, and Eisig (No. 15), sharply contrasted the cranial and spinal nerves and ganglia, and declared my conviction (No. 6) that it is a very doubtful question whether the two sets of organs ever had the same primitive characters. The development of the branchial sense organs and ganglia, in connection with the cranial ganglia, was my main consideration for saying this. And the same considerations appeared to Froriep (independently) to add strength to this conclusion at which he had arrived some years ago (No. 16).

The question arises, How is the position altered by the researches I now record?

Eisig (No. 15, p. 542) had, perhaps rightly, urged against my views that it was not impossible that the spinal ganglia of Vertebrates represent the "Seitenorganen ganglia" of Capitellidae. Without devoting here the time which a thorough examination of Dr. Eisig's comparisons entails, I cannot omit a partial discussion of this point. The exact weighing of the pros and cons of Dr. Eisig's views must be left over for another publication, in which we must examine more closely the lateral sense organs of Vertebrates.

I quote the following passage from Eisig's great work1 (No. 15, p. 542), in spite of its length, because it touches upon the proposed homology between the spinal and cranial ganglia on the one hand, and the parapodial ganglia of Annelids on the other. This homology, as I previously mentioned, was suggested by Kleinenberg (No. 41, p. 220), and in a strict morphological sense I think, as the result of my researches, it can be accepted.

The passage runs thus (p. 542): "Es muss dagegen speziell der Punkt von mir erörtert werden auf den sich Beard zum Behufe der Perhorrescirrung der Homologie von Gehirn und Spinalnerven stützt: nämlich, die Thatsache, dass die Spinal-

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1 I take this opportunity of expressing my gratitude to Dr. Eisig for the generous gift of a copy of his immense monograph.
nerven nicht ebenso wie die Hirnnerven mit Hautsinnes-
organen (Seitenorganen), respective mit Ganglien solcher in
Verbindung traten. Um so mehr muss dieser Punkt ins Auge
gefasst werden, als ich davon überzeugt bin, dass die in ihm
enthaltenden Probleme auf dem Boden der Vertebraten-mor-
phologie allein nicht gelöst werden können, indem es sich um
Verhältnisse handelt, welche phylogenetisch so weit zurückliegen,
dass uns nur die den vermuthlichen Ascendenten der Verte-
braten näher stehenden Wirbellosen noch Anhalts-punkte
für den Ausgang und die Richtung der bezüglichen Entwick-
elungen zu bieten vermögen.

"Wenn die Spinalnerven gegenwärtig nicht mehr ähnlich wie
die Hirnnerven mit Seitenorganen, respective mit Ganglien
solcher im Bereiche der Haut in Verbindung treten, so frage ich
zunächst Beard, woher er denn weiss, dass dies auch früher nie
der Fall gewesen sei, ferner frage ich ihn, ob er irgend einen
triftigen Einwand gegen die Vorstellung gebracht hat oder
beibringen kann, dass die Ganglien der hinteren Spinalnerven
wurzeln möglicherweise den Seitenorganganglien der Hirn-
nerven entsprechen? Wie berechtigt diese Frage ist, geht
daraus hervor, dass nicht etwa nur Thatsachen der Vertebraten
—sondern auch solche der Anneliden-Morphologie zu Gunsten
einer solchen Vorstellung oder Hypothese sich anführen
lassen."

Then follows the citation of Kleinenberg's views respecting
the homology of the parapodial ganglia of Annelids and the
spinal ganglia of Vertebrates, which I have already quoted in
the introduction of this paper.

Dr. Eisig continues (p. 542): "Wenn man erinnert, dass ich
ganz unabhängig von der vorliegenden Frage dazu gekommen
bin, die Seitenorganenganglien der Anneliden von den Parapo-
dialganglien der Anneliden abzuleiten, so wird man einsehen,
dass unserem weiteren Schlussverfahren schon der Weg vorge-
zeichnet ist. Es entsprechen nämlich aller Wahrschein-
llichkeit nach im Vertebratenrumpfe die Spinalganglien den
Seitenorganganglien (Parapodialganglien) der Anneliden.

"Und auch die Frage, warum denn erstere Ganglien bei den

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Vertebraten nicht mehr so wie diejenigen der Hirnnerven zu der Haut, respective den Seitenorganen ontogenetische Beziehungen aufweisen, lässt sich beantworten. Derselbe durch die Concentrirung des Kopfes oder Gehirnes hervorgerufene Prozess, der an den übrigen Bestandtheilen des Seitenorgan-systemes so tiefgreifende Veränderungen hervorrief, nämlich, die Anbahnung einer einheitlichen und directen (Gehirn-) Leitung an Stelle der segmentalen, hat auch die ursprünglichen Hautbeziehungen der Seitenorganganglien (Spinalganglien) allmählich zum Schwinden gebracht. Nachdem einmal die directe Leitung zwischen dem Gehirne und dem Seitenorgansysteme des Rumpfes hergestellt, und die Innervation durch Spinalnerven zurückgetreten war, so lag auch keine Veranlassung mehr für Verbindungen zwischen Spinalnerven und Haut vor, und so können wir einschen, dass die nunmehr für ihre Sinnesorgane ebenfalls bedeutungslos gewordenen Seitenorganganglien des Vertebratenrumpfes immer unabhängig von den Seitenorganen und schliesslich den Spinalnervenwurzeln, respective dem Rückenmarke, einverleibt werden. Alles das ist zwar—es sei wiederholt—vorläufig noch durchaus hypothetisch, aber es gewinne schon in dem Moment, solide Boden, wo in der Entwicklungsgeschichte der Spinalganglien irgend eines Vertebraten noch Anzeichen von Hautverbindungen nachgewiesen würden, und wer möchte behaupten, dass unsere Kenntnisse bereits hinreichen, um die Existenz-möglichkeit einer derartigen Recapitulation a priori verneinen zu können? Wie dem aber auch sei, diese auf Thatsachen beruhende Hypothese zeigt, dass es angesichts der so verwickelten Verhältnisse doch nicht an Anhaltspunkten für eine mögliche Lösung fehlt, und die Aussicht auf eine mit Schwierigkeiten verbundene Lösung ist doch erfreulicher, als die gar keiner Aussicht auf Lösung kommt aber die Auffassung Beard's gleich, welche, da sich zwischen Rumpf und Kopf zahlreiche Divergenzen ausgebildet haben, die Vergleichbarkeit beider überhaupt n Frage stellt."

The above extracts naturally fall into two divisions. In the first place there is the question of the actual facts of develop-
ment which Dr. Eisig puts to me, and in the second place there is the answer which Dr. Eisig from his standpoint gives to these questions. With the latter I am here little concerned, for the answer is purely hypothetical, as Dr. Eisig admits, and no one can object to his right to establish as an admitted hypothesis the view that the lateral sense organs were once connected with spinal nerves. According to my ideas the evidence is entirely wanting, and the quotations from three or four authors which Dr. Eisig makes to show that even now spinal nerves send branches to the sense organs situate in the trunk, do not seem to me to affect the question; for, as I shall elsewhere show, they are all either vague or of a very doubtful character, and as yet no one has figured these connections.

These remarks also answer his questions as to whence I know that such connection was never the case. We know nothing of such connection of spinal nerves with the sense organs of the lateral line, either now or in the past, and any opinion one may express in favour of such a view is only an assumption.

To the second question, whether the spinal ganglia are not homologous with the sense-organ ganglia of the head, I think the answer must be decidedly in the negative.

I regret to be compelled to this result, but I see no way out of the conclusion that the spinal ganglia of the trunk are homologous with those portions of the cranial ganglia which take their origin in the similar position to the spinal, viz. just outside the lips of the neural plate. I have never as yet seen a trace of the sensory epithelium and ganglia of the sense organs in the trunk region of a Vertebrate embryo. Here, of course, I except the sense organs derived from the vagus which wander into the trunk, as I have shown elsewhere (No. 6, p. 19), by displacing the indifferent epiblast.

I have, moreover, never seen a trace of a sensory epithelium

1 The authors quoted are Julin (No. 39), Ransome and Thompson (No. 53), and Ryder (No. 55). While this paper was passing through the press, the supposed connection between spinal nerves and lateral nerve has been totally refuted by Professor Dohrn ("Studien, &c.," No. xiii, "Mittheil. a. d. Zool. Station zu Ncapel," Bd. viii, Hft. ii).
in connection with the neural ganglia, i.e. in connection with those ganglia in head and trunk which are formed just outside the limits of the neural plate; and, as Froriep and I have indirectly shown, the lateral sense organ Anlagen in higher Vertebrates show no disposition to leave their original home above the gill-clefts, and to wander into the epiblastic Anlagen of the neural ganglia, but force the latter, as it were, to come to them to receive their contingent of nerve-cells.

Like Dr. Eisig I support, as the result of these researches, Kleinenberg’s view of the homology of the spinal ganglia of Vertebrates, and the parapodial ganglia of Annelids. But I go further, and say that what in the sense given above may be called the cranial neural ganglia of Vertebrates, are also morphologically equivalent to parapodial ganglia of Annelids. I also am fully prepared now to accept with Eisig the homology of the branchial sense organs of Vertebrates with the Seitenorgane of Annelida; but from the nature of the case it will be obvious that at present I cannot admit the unproved homology of the “Seitenorganen” ganglia of Annelids with the entire parapodial ganglia of Annelids. To meet the conditions of the Vertebrate head the parapodial ganglion must at some time or other have divided into two parts, one remaining neural and corresponding to the neural ganglia of Vertebrates, and one becoming lateral above the gill-clefts (and connected with them), which would correspond to the lateral sense-organ ganglia of Vertebrates, and to the same ganglia of Annelids. At present such a view would be merely speculative.

VIII. The Functional Distribution of the Cranial Nerves.

The recent researches of Gaskell (No. 19 a, p. 58) lead him to divide the anterior and posterior roots of each spinal nerve into two sets of fibres, which are visceral and somatic respectively.

Somatic motor nerves are those fibres derived from the anterior horn; somatic sensory nerves are those derived from the posterior horn; while the motor visceral nerves arise in
the lateral horn and pass out with the other motor nerves in the anterior root; and the sensory visceral fibres take their origin in Clark's column and pass out with the posterior root.

Both sets of sensory fibres possess ganglia, the motor fibres being unganglionated.

I do not propose to devote any great amount of space to the examination of the bearings of Dr. Gaskell's results on the cranial nerves as given by himself, or as they appear to me; still, a few morphological conclusions can be drawn from those researches just as my results may be of use to the physiologist. The oculomotorius, trochlearis and abducens correspond morphologically and physiologically, as van Wijhe (No. 61), Hill (26), Gaskell (19), and His (34) have insisted, to the motor somatic roots of spinal nerves. They arise in the combination of the anterior horn in the head, and they are distributed to muscles of the somatic system. Thus one is faced at once by the conclusion that the motor visceral fibres do not enter anterior roots in the head, and, on the contrary, they pass through the posterior roots, which are mainly sensory.

Now, these motor somatic fibres in the trunk develop as direct outgrowths of the spinal cord, and as the ganglia which form them lie in the cord they ought also to arise in the head as direct outgrowths of cells in the brain, and in the homologies of anterior root of spinal nerves. The latter is certainly not the case, for they pass out with the posterior roots: and the question arises, How do they develop in the head? Either the old course with anterior roots in the head never existed, or it has been lost, and they have acquired new paths through the afferent fibres of the posterior root.

Which of these things is really the case I cannot decide, for as yet I have been unable to prove the first by the demonstration of an element of the posterior root of a cranial nerve which develops as a direct outgrowth of cells from the brain.

1 Gaskell has quite recently arrived at very different conclusions (Proc. Roy. Soc., Feb. 9th, 1888), which appear to be largely erroneous. I shall consider them in the second part of this work, after Dr. Gaskell has published the complete paper.
From what is known about the development of all other motor nerves, we may expect that such is the case; and I believe that sooner or later it will be shown that these fibres, which are the nerves to the muscles of the gill-clefts, do develop as direct outgrowths of cells in the brain like the anterior roots of spinal nerves.

When one also considers that to those four groups of nerves distinguished by Gaskell there must be added a fifth ganglionated sensory element connected with the lateral sense organs, the exceedingly complicated nature of the problems presented by the cranial nerves of any Vertebrate higher than Amphi-oxus will be very evident.

**Résumé of Results.**

The spinal ganglia of Vertebrates are formed as differentiations of the inner layers of the epiblast just outside the limits of the neural plate. As the result of the cutting out from the epiblast of these ganglionic elements an appearance is presented by the epiblast which is left, to which Professor His gave the name of "Zwischenstrang." This has no share in the formation of the ganglia. "The Zwischenrinne" of His has no existence, but certain portions of the cranial ganglia, called here neural ganglia, are developed from the epiblast before closure of the neural tube in exactly the same way as the spinal ganglia. These portions of cranial ganglia are more or less homologous with spinal ganglia, possibly only with the sympathetic portion of the spinal ganglia Anlagen. After separation from the epiblast the neural cranial ganglia and the spinal ganglia get carried up with the closing in of the neural tube, and come to lie between its lips, but are quite distinct from the central nervous system, and the line of boundary between the two can always be distinguished. After the closure of the epiblastic folds the Anlagen grow out of their position between the lips of neural tube, which then also closes. They grow downwards and to the sides of the neural tube, and acquire their first and only connection with it by the
probable growth of fibres from the ganglia into the central nervous system. The neural cranial ganglia also grow towards the lateral epiblast at the level of the notochord and fuse with it. Here are the Anlagen of the lateral or branchial sense organs of Froriep and myself. From this fusion in all Vertebrates form-elements pass into the cranial ganglia; these form-elements I distinguish as lateral ganglia. The parapodial ganglia of Annelids appear to be homologous with the spinal ganglia of Vertebrates, as Kleinenberg suggested, and also more or less with the neural cranial ganglia.

The anterior roots of cranial and spinal nerves arise as outgrowths of ganglia situate in the central nervous system. To form them cells leave the nervous system, and are distributed in the nerve. All the anterior roots at first contain many nuclei, which are of nervous and not parablastic origin. These statements on the anterior roots are only a confirmation of Balfour's researches.

In addition to the four elements of the anterior and posterior roots, two ganglionated and sensory, two motor and unganglionated, distinguished by Gaskell, Hill, and partially by His, the cranial nerves contain a fifth element, derived from the lateral or branchial sense organs. Such are, in very brief form, the main results of the researches recorded in the preceding paper.

It is with more than ordinary feelings that I desire to record here my most heartfelt gratitude to Professor Wiedersheim, in whose laboratory I carried out the above researches, for the generosity and kindness with which he in many ways supported my work. I owe him many thanks for his advice and criticism, and for the use of his valuable library, and, not least, for the gift of various material which was of great use to me.
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DESCRIPTION OF PLATES XVI—XXI,
Illustrating the Memoir by Dr. Beard on "The Development of the Peripheral Nervous System of Vertebrates. Part I."

List of References.
1. iii, v, vii, &c. Olfactory, motoroculi, trigeminal, facial, &c., nerves.
   br. gl. Branchial or lateral ganglion.  cl. Cleft.  e. Epiblast.  f. br. fore-brain.
   h. br. Hind-brain.  h. c. Head-cavity, or head-somite.
   i. e. Indifferent epiblast.  m. Mesencephalic ganglion.  m. br. Mid-brain.  me.
   Parapodial ganglion.  s. e. Neuroepithelium.  sp. Spinal.  sp. c. Spinal cord.

All figures, except Fig. 64, are drawn under Zeiss's camera lucida. The magnification is indicated by such letters as Z. D, oc. 2, which signifies Zeiss's objective D, ocular No. 2. The objectives used were those of Zeiss and Hartnack, and are distinguished as Z. and H. respectively. Except Figs. 90—93, 96, 100, 101, which are from longitudinal frontal sections, the figures represent transverse sections.

All figures are reduced in the plates to two-thirds of their original size.

PLATE XVI.

Figs. 1—3.—Sections through the trunk of a Torpedo embryo.  Z. D, oc. 2.
Fig. 4.—Section through the head region of Torpedo ocellata.  Z. D, oc. 2.

Fig. 5.—Section, trunk region, T. ocellata.  Z. D, oc. 2.
Figs. 6 and 7.—Sections, head region, T. ocellata.  Z. D, oc. 2.
Figs. 8 and 9.—Sections, trunk region, T. ocellata.  Z. D, oc. 2.
Fig. 10.—Section, mid-brain region, T. ocellata.  Z. D, oc. 2.
Fig. 11.—Section, head region, T. ocellata.  Z. D, oc. 2.
Fig. 12.—Section, head region, T. ocellata.  Z. D, oc. 2.
Fig. 13.—Section, trunk region, T. ocellata.  H. 8, oc. 2.
Fig. 14.—Section, trunk region, T. ocellata.  Z. D, oc. 2.
Fig. 15.—Section, trunk region, T. ocellata.  Z. D, oc. 2.
Fig. 16.—Section, trunk region, T. ocellata.  Z. D, oc. 2.
Fig. 17.—Section, trunk region, T. ocellata.  H. 8, oc. 2.
Fig. 18.—Section, head region, T. ocellata.  Z. D, oc. 2.
Figs. 19 and 20.—Sections, brain region, of two Torpedo embryos. Origin of olfactory neural ganglion.  Z. D, oc. 2.
PLATE XVII.

Fig. 21.—Section through facial ganglion anlage, T. ocellata. Z. D, oc. 2.
Fig. 22.—Section, trunk region, Mustelus levis. Z. D, oc. 2.
Fig. 23.—Section, trunk region, M. levis. Z. F, oc. 2.
Fig. 24.—Section, vagus ganglion, T. ocellata. Z. D, oc. 2.
Fig. 25.—Section, auditory organ and ganglion, T. ocellata. Z. D, oc. 2.
Fig. 26.—Section, spinal cord region, Pristiurus. Z. F, oc. 2.
Fig. 27.—Section, auditory region, T. ocellata. Z. F, oc. 2.
Fig. 28.—Section, trunk region, Pristiurus. Z. D, oc. 2.
Fig. 29.—Section, vagus region of head, T. ocellata. Z. D, oc. 2.
Fig. 30.—Section, trunk region, T. ocellata. Z. D, oc. 2.
Fig. 31.—Section, trunk region, T. ocellata. Z. D, oc. 2.
Figs. 32—36.—Sections, trunk region, Pristiurus. Z. D, oc. 2.
The order from before backwards is 33, 34, 35, 36, 32.

PLATE XVIII.

Fig. 37.—Section, anterior head region, T. ocellata. Z. C, oc. 2.
Fig. 37a.—The small figure marked out in preceding section under high power, to show anlage of a cranial ganglion. Z. F, oc. 2.
Fig. 38.—Portion of a section of head region, T. ocellata. Z. F, oc. 2.
Fig. 39.—Section, head region, T. ocellata. Z. F, oc. 2.
Figs. 40—42.—Portions of sections through head region of three Torpedo embryos. Z. F, oc. 2.
Fig. 43.—Section, trunk region, Mustelus. Z. D, oc. 2.
Fig. 44.—Portion of a section, trunk, T. ocellata. Z. F, oc. 2.
Fig. 45.—Portion of a section of Mustelus through vagus region. Z. F, oc. 2.
Fig. 46.—Section through auditory region of a Chick embryo. H. 9, oc. 2.
Fig. 47.—Section, head region, T. ocellata. Z. F, oc. 2.
Fig. 48.—Section, mid-brain region, Mustelus. Z. F, oc. 2.
Fig. 49.—Section, region of anus, Mustelus. Z. D, oc. 2.
Fig. 50.—Section, region of head, Mustelus. Z. C, oc. 2.
Fig. 51.—Section, trunk region, Chick, eight somites. Z. F, oc. 2.

PLATE XIX.

Fig. 52.—Section, anus region, T. ocellata. Z. D, oc. 2.
Fig. 53.—Section, trunk region, T. ocellata. Z. D, oc. 2.
Fig. 54.—Section, trunk region, T. ocellata. Z. D, oc. 2.
Fig. 55.—Section, trunk region, Chick, eight somites. Z. F, oc. 2.
Fig. 56.—Section, trunk region, T. ocellata. Z. D, oc. 2.

Fig. 57.—Section, spinal cord region, Scyllium canicula. The epiblast is not represented. Z. D, oc. 2.

Fig. 58.—Section through developing anterior root of a spinal nerve, Mustelus. Z. F, oc. 2.

Fig. 59.—Section through tail region, T. ocellata. H. 8, oc. 2.

Fig. 60.—Section of developing anterior root (near anus), Mustelus, Z. D, oc. 2.

Fig. 61.—Section through trunk region, T. ocellata. Z. D, oc. 2.

Fig. 62.—Section, head region, Chick with no somites. Z. D, oc. 2.

Fig. 63.—Section in region of infundibulum, Chick, nine somites. Z. D, oc. 2.

Fig. 64.—Copy of Kleinenberg's figure of developing parapodial ganglion (p.g.) of Lopadorynchus. The sketch has been turned through 180 degrees.

Fig. 65 and 66.—Section, head region, Chick embryo with nine somites.

Fig. 67.—Section, head region, Chick embryo with four somites. Z. D, oc. 2.

Figs. 68 and 69.—Two sections through trunk and head regions respectively of a Chick embryo with four somites. Z. D, oc. 2.

PLATE XX.

All the figures on this Plate are from Chick embryos. All are under Zeiss's D, oc. 2.

Figs. 70—76.—Series of sections through trunk region, from behind forwards, of an embryo with six somites.

Figs. 77—79.—Series of sections from before backwards through brain region of an embryo with nine somites.

Fig. 80.—From same embryo, but through first somite.

Fig. 81.—From same embryo, but through end of second somite.

Figs. 82—84.—Three sections through brain region of an embryo with seven somites.

Fig. 85.—Section through spinal region of same embryo.

Figs. 86 and 87.—Two sections through brain region of two embryos with no somites.

Fig. 88.—Section, hind-brain region of a Chick embryo with ten somites.

Fig. 89.—Section, trunk region of a Chick with eight somites.

PLATE XXI.

Figs. 90 and 91.—Two longitudinal frontal sections through the head of a three-days' Chick embryo, showing the rudiments of branchial sense organs. Z. A, oc. 2.

m = Mesocephalic ganglion and sense organ.

v. Trigeminus " "

vi. Facial " "

ix. Glossopharyngeal " "

m l e G o s s o p h a r y n g e a l
MORPHOLOGICAL STUDIES.

Fig. 92.—Trigeminus ganglion and sense organ from Fig. 91, highly magnified. Z. F, oc. 2.

Fig. 93.—Mesocephalic ganglion and its sense organ from Fig. 91, highly magnified. Z. F, oc. 2.

Fig. 94.—Section in front of a gill-cleft of T. ocellata. Z. A, oc. 2.

Fig. 94 a.—The black portion of this section highly magnified to show growth and extension of the lateral sense-organ epithelium.

Fig. 95.—Section behind a gill-cleft of T. ocellata. Z. A, oc. 2.

Fig. 95 a.—The blackened portion of this section highly magnified, to show growth and extension of lateral sense-organ epithelium. Some cells wander into mesoblast to form ganglion-cells.

Fig. 96.—Glossopharyngeal ganglion and its sense organ in three-days' Chick, from Fig. 90. Z. C, oc. 2.

Fig. 97.—Section of hind-brain of a Chick embryo with nine somites, showing "Zwischenstrang" (Z.) and its relation to ganglion Anlage, Z. F, oc. 2.

Figs. 98 and 99.—Sections of trunk region of Chick embryo of second day. Z. F, oc. 2.

Fig. 100.—Portion of longitudinal vertical section of mid-brain of a lizard embryo (L. agilis), showing origin of oculomotorius and its "ganglion" in brain. Z. D, oc. 2.

Fig. 101.—Portion of longitudinal vertical section of the auditory epithelium of a lizard embryo (L. agilis). Z. F, oc. 2.

Fig. 102.—Section, trunk region of a Chick embryo of second day. Z. F, oc. 2.

Fig. 103.—Section through glossopharyngeus nerve and ganglion of an advanced Torpedo ocellata embryo. Z. C, oc. 2.
Fig. 37-65 ELASMOBRANCHII. Fig. 46-51 CHICK.
All the Figures are from CHICK EMBRYOS.