and whenever there is union not very firm, and may also modify some of our opinions on atomic weights and the motion of gases.

Of course, I cannot pretend to give the result of these results; but as we have here the building up of a molecule by volumes, so as to form an equivalent of physical combination analogous to the chemical equivalent, it is impossible to avoid seeing that it indicates the possibility of our present equivalents being made up in a similar manner.

I did not expect these numbers; but I certainly, as my previous paper showed, had in full view a necessity for some connexion between physical and chemical phenomena more decided than we possessed.

February 13, 1879.

W. SPOTTISWOODE, M.A., D.C.L., President, in the Chair.

The Presents received were laid on the table and thanks ordered for them.

The following Papers were read:—

I. "Note on the Development of the Olfactory Nerve and Olfactory Organ of Vertebrates." By A. MILNES MARSHALL, M.A., D.Sc., Fellow of St. John's College, Cambridge. Communicated by W. S. SAVORY, F.R.S., Surgeon to and Lecturer on Surgery at St. Bartholomew's Hospital. Received January 30, 1879.

In the course of an investigation into the development of the cranial nerves of the chick, certain facts came to light indicating that the olfactory nerve, instead of being, as usually described, a structure differing totally in its mode of origin from all the other nerves in the body, in reality "exactly corresponds in mode of development and in appearance with the other cranial nerves, and with the posterior roots of the spinal nerves."*

The present paper contains the results of further investigations on this point; it deals also with some features in the development of the vertebrate olfactory organ, and with certain questions of a more general nature affected by the conclusions arrived at.

* "Proc. Roy. Soc.," vol. xxvi, p. 50, and "Quarterly Journal of Microscopical Science," January, 1878, pp. 17–23.

The Development of the Olfactory Nerve.

For the sake of clearness the more important conclusions are stated in the form of propositions:—

a. The olfactory nerves do not arise from the cerebral hemispheres, but from the single unpaired forebrain.

In chick embryos of about the fiftieth hour, or a little older, the olfactory nerves can be clearly recognized arising from the upper part of the sides of the forebrain. At this stage there is no trace whatever of the cerebral hemispheres. The olfactory nerves then come into existence before the cerebral hemispheres, and therefore cannot be derived from them. The hemispheres are developed in the chick as lateral outgrowths from the upper part of the forebrain; at first the olfactory nerves have no connexion with them, beyond that of close proximity; but very soon the hemispheres, by their rapid growth forwards, drive the nerves down to the base of the brain, and so make the nerves appear to arise from their under and anterior part.

This account is confirmed in all points by observations on duck embryos, which show clearly that the connexion of the olfactory nerves with the cerebral hemispheres is not of a primary but of a secondary or adaptative nature.

In the dogfish (*Scyllium*) the forebrain is, as has been already shown by Balfour,* single and unpaired up to stage O, presenting till then no trace whatever of a division into cerebral hemispheres: the olfactory nerves are, however, well developed structures by stage M; at which period they can be seen, in transverse sections through the anterior part of the head, arising from the upper part of the sides of the forebrain and running downwards to the olfactory pits. The nerves can be recognized, though with less distinctness, at still earlier stages.

The olfactory nerves of the salmon and of the trout can, in a similar manner, be identified before the cerebral hemispheres have come into existence; and the same statement applies to the axolotl.

b. There is no trace of an olfactory lobe in the early stages of development of the olfactory nerve.

Since the olfactory lobes are commonly described as "hollow outgrowths of the cerebral hemispheres," and the olfactory nerves have just been shown to arise quite independently of the cerebral hemispheres, this second proposition is in reality already proved by the first. However, as the existence of olfactory lobes has been supposed to separate the olfactory from the other cranial nerves, it becomes necessary to investigate carefully the time and conditions of their appearance.

In the chick the olfactory nerve is in its early stages solid, and

* "Elasmobranch Fishes," p. 178.

from a histological point of view differs in no appreciable respect from the other cranial nerves at corresponding stages of their development. At the end of the sixth day of incubation the nerve, which is now of some length, has acquired its secondary connexion with the cerebral hemisphere in the manner described above; yet the nerve is still solid along its whole length, and presents no trace whatever of an olfactory lobe, or hollow outgrowth from the brain. By the end of the seventh day a very small conical pit is visible in the wall of the cerebral hemisphere at the point of origin of the olfactory nerve. This pit, which is the earliest rudiment of the olfactory lobe, is formed almost entirely at the expense of the inner wall of the hemisphere, so that there is hardly any corresponding projection on the outside of the brain.

The development of the olfactory lobe in the dogfish closely resembles that in the chick: at stage M there is no trace whatever of a lobe, though the olfactory nerves are large and conspicuous structures. At a stage a little younger than Balfour's stage O, the first rudiment of an olfactory lobe appears, as a slight lateral bulging of the side of the forebrain, at the point of origin of the olfactory nerve: this increases rapidly, much more so indeed than the nerve itself; by stage O it is a tolerably prominent structure, and in the later stages it becomes considerably larger than the nerve proper.*

Stage O in the development of a dogfish embryo corresponds to about the sixth day in the chick, so that there is a close agreement in time as well as in mode of development of the olfactory lobe in these two types. In the dogfish, however, the olfactory lobes appear before the cerebral hemispheres are differentiated, and consequently arise from the forebrain; while in the chick the hemispheres are developed rather earlier, and the olfactory lobes arise as direct outgrowths from them, and not from the original forebrain.

In the salmon and trout, from the earliest period at which the existence of an olfactory nerve can be recognized up to the time of hatching, and indeed for some little time afterwards, there is no trace of an olfactory lobe.

The existence of an olfactory nerve without any trace of an olfactory lobe has also been established in the earlier embryonic stages of the axolotl, of the common frog, and of the green lizard.

The olfactory nerve of an adult vertebrate is commonly described as consisting of three parts, a proximal element or *olfactory tract*, an intermediate *olfactory bulb*, and a distal *olfactory nerve proper*, the two former of these corresponding to the olfactory lobe or vesicle of the embryo. From the descriptions given above it would appear that the

* Cf. Balfour, *op. cit.*, p. 178, and Plate 15, figs. 2 and 8*a*. Balfour has not observed the olfactory nerves earlier than stage O, and therefore describes them as outgrowths from the olfactory lobes.

third of these elements—the olfactory nerve proper—is the earliest to be developed, and that the olfactory tract and bulb, when present at all, do not appear till an exceedingly late period of development—a period so late indeed that their ultimate presence affords no ground whatever for separating the olfactory from the other cranial nerves.

c. The olfactory nerve is a primary nerve, comparable to the segmental cranial nerves.

Certain of the cranial nerves, *e.g.*, the facial and glossopharyngeal, have long been recognized as possessing segmental value. These segmental nerves in the early stages of their development possess certain characters in common, which serve to distinguish them sharply from other nerves or branches of nerves; of these characters the following are the most important:—(1) They appear very early; (2) they arise (at least in the chick) from the neural ridge on the mid-dorsal surface of the brain; (3) shortly after their appearance their roots undergo a shifting downward of their points of attachment, so that they no longer arise from the dorsal surface, but from the sides of the brain; (4) they present, at least in their early stages, ganglionic enlargements on, or close to, their roots of origin; (5) their course is at right angles to the longitudinal axis of the head; (6) and, finally, they have very definite relations to the segments as indicated by the visceral clefts, each nerve supplying the two sides of a cleft.

In all these points the olfactory nerve agrees very closely with the segmental nerves:—(1) It appears very early in all the types examined, and in the chick it seems to be one of the very first nerves in the body to be developed; (2) there is also strong reason for thinking that, in the chick, the olfactory nerve is developed from the neural ridge;* (3) its point of attachment to the brain undergoes a shifting of precisely similar nature to that presented by the segmental nerves; (4) its direction is at right angles to the longitudinal axis of the head, so that were the cranial flexure to be corrected, and the head straightened out, the course of the olfactory nerve would be parallel to that of the segmental nerves; (5) it possesses a ganglionic enlargement at its point of origin from the brain; (6) and, finally, an attempt will be made in the second part of this paper to show that it supplies the two sides of a visceral cleft.

Since, then, the olfactory nerves do not differ embryologically in any material respect from the segmental cranial nerves, they must be regarded as the first or most anterior pair of true segmental cranial nerves.

The Development of the Olfactory Organ.

This will, in the absence of figures, be treated very briefly; those

* For a discussion of this point, *vide* "Quart. Journ. Micro. Science," January, 1878, pp. 18, 19.

points only being noticed which are of special interest in connexion with the conclusions arrived at in the preceding part of the paper.

The olfactory pits appear at almost the same time as the visceral clefts; or, to speak more accurately, they first become conspicuous objects at, or very shortly after, the time when the anterior visceral clefts become open to the exterior. This occurs about stage K in the dogfish, and about the fiftieth hour in the chick.

In their early stages the olfactory pits present a striking resemblance to the visceral clefts in position, shape, size, and general relations; their external apertures elongate and become slit-like, and the direction of the slit, like that of the visceral clefts, is at right angles to the longitudinal axis of the head. These facts are best illustrated by the study of whole embryos, and of longitudinal vertical sections.* They come out with great clearness in all the types of vertebrates examined, but with especial distinctness in the axolotl and salmon.

The development of the Schneiderian folds presents several points of great interest, which can be most favourably studied in the Elasmobranchs. Attention has already been directed by Balfour† to the very early appearance of these folds. The important point, so far as the present question is concerned, is that these Schneiderian folds appear at the same time as, or very shortly after, the first rudiments of the gills. In addition to this identity in time, there is also identity in structure; in both cases development consists in the formation of a series of equal, closely apposed folds, mainly epithelial, but involving the underlying mesoblast to a certain extent. These folds are in the two cases—gills and Schneiderian folds—of the same width, the same distance apart, have epithelium of the same thickness and same histological character, involve the mesoblast to exactly the same extent, and in exactly the same manner; in a word, are structurally identical.

In the later stages the Schneiderian folds, like the gills, receive a very abundant supply of blood-vessels; and the relations of these vessels to the folds, which are very peculiar and characteristic, are identical in the two cases. Even in the adult Elasmobranch there is a remarkable histological resemblance between the gills and the nose.

The facts above recorded concerning the development of the olfactory nerve and olfactory organ point towards the same conclusions as to morphology of these structures, viz., that the olfactory organ is the visceral cleft; that the olfactory nerve is the segmental nerve supplying that cleft in a manner precisely similar to that in which the hinder

* For figures of whole embryos illustrating the points referred to, *vide* Parker, "On the Structure and Development of the Skull in Sharks and Skates," "Trans. Zool. Soc.," vol. x, part iv, 1878, Pl. 25, fig. 1; Pl. 39, figs. 1 and 2; Pl. 40, fig. 1; and Balfour, *op. cit.*, Pl. 7, Stage L.

† *Op. cit.*, p. 184, and Pl. 44. fig. 14.

clefts are supplied by their respective nerves; and that the Schneiderian folds are gills.*

These conclusions, if accepted, will considerably simplify our conception of the segmentation of the vertebrate head. As there are no nerves or clefts in front of the olfactory segment, the olfactory nerve must be taken as the most anterior nerve, and the nose as the most anterior cleft. The next cleft is that in front of the maxillo-palatine arch, of which a part probably persists in the adult as the lachrymal duct: the segmental nerve corresponding to this cleft is the *third*, or oculomotor nerve. Next comes the mouth cleft, supplied by the *fifth*, or trigeminal, nerve; and then in succession the clefts supplied by the facial, glossopharyngeal, and pneumogastric nerves. This view of the constitution of the vertebrate head is found to accord well with the later researches of Professor Parker on the morphology of the skeletal elements of the head.

Some at least of the labial cartilages will probably prove, on this view, to be homologues of the extrabranchials, a comparison that has already been made by Professor Parker.†

If the olfactory organs are visceral clefts, they must originally have communicated with the mouth cavity. Indications of a former connexion of this kind are by no means wanting; thus in salmon embryos the alimentary canal extends forwards, so as to underlie the nasal sacs: as development proceeds, this anterior prolongation of the mouth cavity gradually shrinks; it persists for a short time as a pair of cæcal diverticula, which ultimately disappear altogether.

In conclusion, it may be noted that the Schneiderian folds afford an instance, on the theory here maintained, of structures originally hypoblastic in nature becoming, from changed circumstances, epiblastic.

II. "On the Development of the Skull and its Nerves in the Green Turtle (*Chelone midas*), with Remarks on the Segmentation seen in the Skull of various types." By Professor W. K. Parker, F.R.S. Received February 3, 1879.

In the first paper on the development of the skull of the Vertebrata, published in "Phil. Trans.," I figured and described certain modifications of the skull in the embryos of the African ostrich, which have only received their explanation lately, and this has become possible through what I see in the embryos of the green turtle.

For these embryos I am indebted to two of our Fellows, namely,

* Cf. Dohrn, "Ursprung der Wirbelthiere," p. 23.

† "Proc. Zool. Soc.," vol. x, part iv, 1878, p. 212.