
PATRE SVO
A CAROLO DARWIN
LEGATVM ACCEPIT
FRANCISCVS DARWIN
Harry Soane. 1888.

ELEMENTS OF PHYSIOLOGY.

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TRANSLATED FROM THE GERMAN,

WITH NOTES,

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ILLUSTRATED WITH STEEL PLATES AND NUMEROUS WOOD ENGRAVINGS.

VOL. II.

CONTAINING CILIARY MOTION, MUSCULAR AND THE ALLIED MOTIONS, VOICE AND SPEECH, MIND, GENERATION, AND DEVELOPMENT.

LONDON:
PRINTED FOR TAYLOR AND WALTON,
BOOKSELLERS AND PUBLISHERS TO UNIVERSITY COLLEGE,
UPPER GOWER STREET.

1842.

LONDON:
PRINTED BY SAMUEL BENTLEY,
Bangor House, Shoe Lane.

BOOK IV.

Of motion; of voice and speech.

SECTION I.

Of the organs, phenomena, and causes of motion in animals.

SECTION II.

Of the different muscular movements.

SECTION III.

Of voice and speech.

ADDENDUM.

Page 1223, line 21. Compare Valentin's account of the structure of the retina in his Repertorium for 1837, p. 251. [Valentin believes that the primitive fibres of the optic nerve terminate in the retina by forming loops with each other. The papillæ of Treviranus he describes as granules arranged closely side by side in a distinct layer, which is only loosely connected with the stratum of the retina beneath them.]

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Preliminary considerations.

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Of the sense of Smell.

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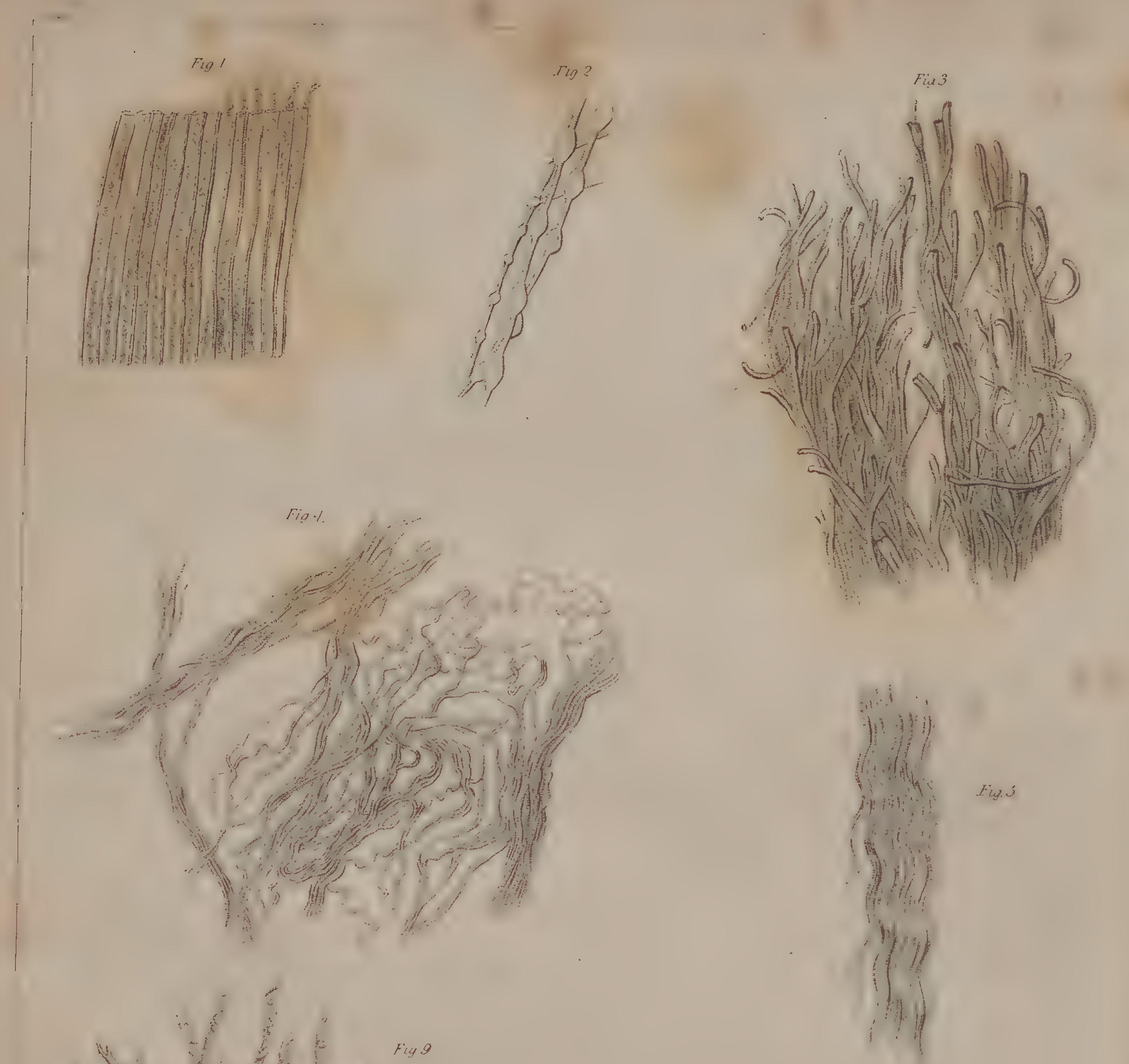


London: Taylor & Walton, Upper Gower Street.

EXPLANATION OF PLATE II.

[Fig. 1. Primitive nervous fibres, after Ehrenberg.

Some of the tubes are nearly empty, and from others their contents are escaping. (See page 596.)

Fig. 2. Primitive fibres from the spinal cord, after Ehrenberg; showing the varicose form which the fibres of the nerves, and still more frequently those of the brain, are prone to assume. (See page 598.)

Fig. 3. Fibres of elastic tissue from the ligamentum flavum of the vertebræ (magnified about three hundred and eighty diameters), showing their dark outline and *apparent* anastomosis and division, and the curved position of their free ends. (See page 875.) These characters of elastic tissue have been pointed out by Lauth, Schwann, and Räuschel (De Arteriarum et Venarum Structurâ Diss. Vratisl. 1836). The curling back of the broken fibres is figured and described by Mr. Skey (Phil. Transact. pt. ii. 1837). The translator doubts the real branching and coalescence of the fibres; for, where two united, the fibre resulting from their union has always appeared to him to be twice as large; and he has in nearly every instance been able to trace a line of separation between them after their seeming union.

Fig. 4. Fasciculi and fibres of cellular tissue, magnified about six hundred diameters. (See pages 432 and 871.)

Fig. 5. Portion of tendon, magnified about six hundred diameters, showing the parallel waving position of the smooth cylindrical fibres, described and figured by Jordan. (See page 873.)

Fig. 6. Portion of the middle fibrous coat of the aorta, magnified about three hundred and eighty diameters; the characters of the fibres identical with those of the fibres of elastic tissue generally. (See page 876.) The apparent anastomosis and division of the fibres is sometimes much more marked than is here represented; their size is greater towards the external surface of the vessels than near their internal surface; but they are generally smaller than those of the ligamentum flavum.

Fig. 7. Muscular fibres of animal life, magnified about two hundred diameters. The broken ends of the fibres show some of the appearances mentioned by Mr. Skey as proving their tubular nature. (See page 881.) In many instances, however, the whole thickness of the fibre at its extremity has appeared to the translator to be formed of beaded filaments. According to the recent important investigations of Dr. Schwann on the developement of the tissues from cells, (Froriep's Neue Notiz. Bd. v. pp. 33 and 225,) an account of which will be given in a future part of the work, the fibres are at first membranous tubes without transverse striæ, and the beaded filaments are deposited on the internal surface, and at last completely fill them.

Fig. 8. Portion of a broken muscular fibre of animal life, magnified about seven hundred diameters; showing the *apparently* beaded form of the filaments, and the production of the transverse striæ by the transverse parallel apposition of the beads of the different filaments. The beads are here represented as bright parts of the filaments separated by narrow dark intervals; by a variation of the light and focus of the instrument, they assume the appearance of dark points separated by longer and narrower portions, as described in the text. (See page 880.) Both these appearances might be produced in such soft pellucid filaments, even though they were cylindrical, by a succession of more dense points in their substance. Sometimes the filaments appear cylindrical, not beaded; and in

such cases the striæ of the fibre they compose are generally, if not always, very close to each other, and difficult to be discerned.

Fig. 9. Organic muscular fibre magnified about three hundred and eighty diameters.

The muscular fibres of organic life have hitherto been described, for the most part, merely by negative characters; namely, by the absence of striæ on their fasciculi, and the non-beaded form of their ultimate filaments. (See page 882.) After repeated observations, however, the translator is satisfied that they have characters as distinctive as those by which the muscular fibres of animal life are known from every other tissue. The organic muscular fibres are *flat bands* varying greatly in breadth, and having in the large bundles which they compose a perfectly parallel arrangement. At successive points, though not at regular distances, transparent bodies of various form, — sometimes oval, at other times linear or semilunar, like flat bodies viewed edgeways and placed transversely or obliquely across the fibre, — are seen sometimes apparently merely attached to their surface; in other instances, manifestly contained within them. (See fig. 9. A.) Occasionally the fibres are destitute of these bodies, and their surface merely presents a number of small irregularities. (See fig. 9, B.) Sometimes faint longitudinal striæ are seen in the fibre, particularly after having been some time in spirit; more frequently the edges of the flat bands appear thicker than the middle portion, and the fine granular membrane composing them presents small rugæ or folds, suggesting the idea of their being flattened tubes. The parts which the translator has found to be composed of fibres of this kind, are the muscular coat of the œsophagus, stomach, whole intestinal canal, bladder, pregnant uterus, trachea, and the red muscular substance of the gizzard of the common fowl. The fibres of the alimentary canal and bladder vary in diameter from $\frac{1}{5000}$ to $\frac{1}{2500}$ of an inch; those of the trachea are smaller.

The fibres of the uterus differ somewhat in aspect from those of the other parts; they are in part much broader, namely, $\frac{1}{1000}$ of an inch in diameter, and taper towards their extremity until their diameter is scarcely more than $\frac{1}{10000}$ of an inch, appearing when thus narrowed nearly cylindrical; the corpuscules are smaller in proportion to the breadth of the fibre, and less prominent than they frequently are in the fibres of the intestinal canal, &c. Frequently the fibres of the uterus appear split at their extremity into two or three. The parts in which it is mentioned that this tissue was found, were all examined in the perfectly fresh state. Maceration for a short period in dilute alcohol does not, however, materially alter its characters; the fibres merely become contracted in breadth, and frequently thrown into zigzag inflexions; the corpuscules are still less affected. These bodies are most probably analogous to the nuclei of the cells, from which not only the scales of the epidermis, but, according to M. Schwann's observations, all the tissues of the body, are developed, or to the cells themselves. M. Schwann, in the papers already referred to, does not speak of the organic muscular fibre; but, in a more recent paper by him in the same journal, (Froriep's Neue Notiz. Bd. vi. p. 21,) the translator finds the following isolated passage. "In the uterus of a woman who had borne a child at the full time of pregnancy, I found immediately under the peritoneal coat, not muscular fibres with transverse striæ, but long, very flat bands of different breadth, which presented very indistinct longitudinal striæ (Langstreifung). In some few I could distinguish a flat, pale nucleus very much elongated, and containing a smaller corpuscule."]

Fig. 2

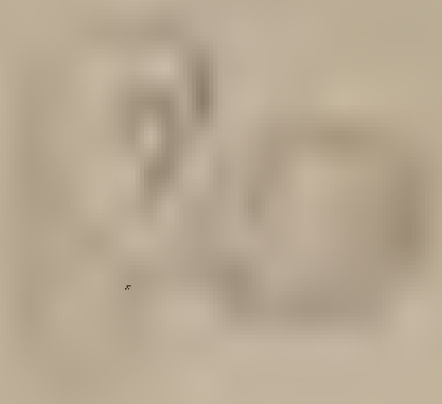


Fig. 3

Fig. 4.

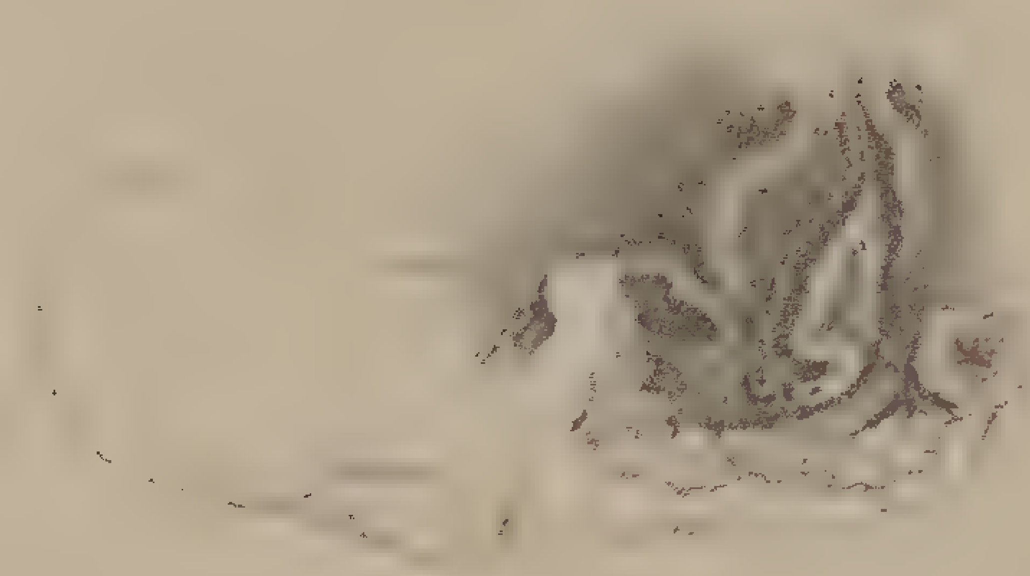


Fig. 5

Fig. 1

EXPLANATION OF PLATE III.

[This is the drawing of an embryo with its membranes, in the possession of Dr. Sharpey, of which an outline copy and a full description are given in the note at page 1581.]

EXPLANATION OF PLATE IV.

[Figures 1, 2, and 3 are drawings of the ovum and embryo to which reference is made by the author at page 1587.

Fig. 4 represents the second embryo belonging to Dr. Sharpey, described in the note at page 1582.

Fig. 5 represents the mesentery and intestine of the embryo shown in plate iii., spread out so as to display the mesenteric vessels and the origin of the omphalo-mesenteric artery from one of the main branches. See the description in the note at page 1581.]

BOOK THE FOURTH.

Of Motion; of Voice and Speech.

SECTION I.

Of the Organs, Phenomena, and Causes of Motion in Animals.

CHAPTER 1.

OF THE DIFFERENT KINDS OF MOTION AND MOTOR ORGANS.

The vital motions of the solid parts of animals present two principal kinds, differing in the organs of their production, in their phenomena, and their causes: they are, the motion from contraction of fibres, and the oscillatory motion of cilia with free extremities, in which no other organic apparatus of motion can be distinctly demonstrated. The first kind of motion is produced by the shortening of fibres, which either have a longitudinal direction and are fixed at both extremities, or form circular bands; the contraction or shortening of the fibres bringing the fixed parts nearer to each other. This kind of motion is generally effected by means of muscular fibres; in some few instances it is produced by fibres which differ from the muscular in structure and chemical properties. The second kind of motion consists in the vibration, in a determinate direction, of microscopic cilia with which the surfaces of certain membranes are beset. Here only the base of the motor organ is attached. By the motion of the contractile fibres, and especially by muscular motion, solid parts of the body are approximated to each other, or fluids are impelled onwards in muscular tubes. By the motion of cilia, fluids and minute microscopic particles of solid matter are merely made to move over the surface of membranes; the fluids do not here fill the entire cavity of the tubes, nor do the membranes themselves contract. The motion due to contractile fibres prevails much more extensively through the body than the ciliary motion.

The muscular fibrous structure is distributed in three strata, the arrangement of which is connected with the earliest process of organisation. All the systems of the body are developed from the laminæ of the germinal membrane, which originally covers the yolk in the form of a disk; this membrane is formed of three layers, the external or serous, the internal or mucous, and the middle or vascular layer: and when the embryonic portion has become separated from the rest of the germinal membrane by a constriction corresponding to the future umbilicus, the parts of the body endowed with animal or voluntary motion are developed in the external layer; those endowed with organic or involuntary motion in the internal layer; and in the middle or vascular layer is formed the heart, together with all the parts belonging to the vascular system, which, at a later period, ramify in the structures developed in the external and internal laminæ. The portion of the body formed in the external layer of the germinal membrane separates into the different structures of the animal nervous system, the osseous system, the system of voluntary muscles, and the skin. The portion of the body developed from the mucous layer separates into the different structures of organic life, namely, the fibrous structures forming the support of the different organs, such as the fibrous tunic of the intestinal tube, (the tunica nervea of the older anatomists,) the serous membranes, the mucous membranes, the muscular coat lying between the fibrous and the serous, and, lastly, the organic nervous system.* This organic portion of the body includes the intestinal tube, the urinary and the generative apparatus, all of which have in nearly their whole extent an organic muscular layer, which is the sole cause of all the motions they exhibit. The proper pharyngeal muscles and the perinæal muscles, which are endowed with voluntary motion, and belong to the animal portion of the body developed in the external lamina, are not here included. Even the efferent ducts of the accessory glands of the organic system have a muscular coat continued on them from the muscular layer of the great tubes; for, though the muscular coat of these ducts has not, it is true, from their delicacy, been demonstrated so plainly as the other membranes, yet its presence is certain: the ductus communis choledochus, the ureters, and the vasa deferentia have been seen to contract, both spontaneously and under the application of stimuli (see page 475). That the efferent ducts and their glands are originally developed from the walls of the tubes into which they open is an ascertained fact, at least, with regard to the glandular apparatus of the intestinal tube.

The muscles of animal life are distinguished from the pale muscular coats of the organs of the organic portion of the body which are not subject to volition, not merely by their moving under the influence of volition, by their red colour, and their solidity, but even by the great difference of their microscopic character. We shall see that the primitive muscular fasciculi of the animal system present, under the microscope, transverse markings, and that the primitive fibres of these muscles have regular varicose enlargements following each other in

* Von Baer, Entwickelungs-geschichte. Scholien.

close succession; while the fasciculi of the muscular coats of the intestines, urinary bladder, and uterus are destitute of those cross markings, and their primitive fibrils uniform, not varicose, threads. In the œsophagus the two systems border closely on each other; the muscles of the pharynx belong to the animal system, those of the œsophagus to the organic: but the first fourth of the proper œsophagus receives an investment from a stratum of muscular fasciculi, descending on it in an arched form to a defined limit, in which Schwann has discovered the transverse markings and the varicose structure of the fibrils; these, however, belong to the pharyngeal muscular apparatus: no such fasciculi are met with on the rest of the œsophagus. [According to M. Ficinus* and M. Valentin,† the latter part of this statement is incorrect; the muscular fibres of animal life descend on the œsophagus even to the cardia, and in man as well as many mammalia can be seen radiating out on the cardiac extremity of the stomach. Ficinus has also found the animal fibres in the intestine near the rectum, and in the stomach of birds.

The animal system of perinæal muscles, with the sphincter ani, also comes into contact with the organic system of the intestinal canal at the anus. The same is the case in the urinary apparatus; for, according to my observation, the red muscular fasciculi which surround the membranous part of the urethra present the cross markings, and their primitive fibrils are varicose; while the proper muscular fibres of the urethra are pale, and without transverse markings, and their primitive fibrils like those of the intestines.

From the middle lamina of the germinal membrane is formed the vascular system, with the heart. This system, which, in the course of its developement, ramifies in the other two laminæ, is furnished with contractile fibres at certain points only; namely, in the heart, at the commencement of the venæ cavæ and pulmonary veins, and in the lymph-hearts of reptiles and amphibia. All other parts of the vascular system are devoid of muscular fibres, though the whole arterial system possesses in its middle coat a highly elastic structure, which must not, however, on account of its extraordinary elasticity, be confounded with the contractile muscular fibre. The muscular tissue developed in the vascular layer of the germinal membrane, although its motion is not under the influence of the will, does not belong to the same class of muscular tissue as the involuntary muscles of the organic system; it is red, and its whole structure is exactly similar to that of the muscles of animal life: the primitive fasciculi have the transverse markings, and the primitive fibrils are varicose.

The muscular are not the only fibres endowed with vital contractility; there are other fibres, of quite a different nature, which

* De Fibræ Muscular. formâ et structurâ. Lips. 1836. p. 13.

† Repertorium, 1837. Bd. i. p. 86.

resemble those of cellular tissue both in microscopic appearance and chemical properties, and are chemically wholly unlike muscular fibre. The parts in which this tissue occurs evince a slight and imperceptible degree of contractility, and are not capable of sudden contractions, such as can be excited in muscles: electricity also does not excite their contraction, but cold and mechanical stimuli cause it to ensue frequently with considerable rapidity. As an example of such parts, the tunica dartos of the scrotum may be instanced; there are, however, many others with a similar property, which will be mentioned separately hereafter. How far this insensible contractility may be possessed by other tissues, it has not hitherto been possible sufficiently to investigate; for an insurmountable difficulty in the inquiry arises from the slight results produced where the contraction is not very marked. It appears, however, that just as there are very few membranes containing cellular tissue, that have not the property of undergoing a change of cohesion under the influence of chemical substances used in medicine, so a slight degree of contractility also is probably enjoyed by these tissues. Membranes which are permeable by fluids do not permit their passage during life: in disease this power of resisting imbibition is frequently lost, and after death it always ceases. Our ideas of increased laxity of tissues and of astringent substances, as far as they are founded on observations, presuppose a variability in the power of opposing the permeation of fluids, which, according to physical laws, must ensue.

The second primary kind of motion in animals, that of vibrating cilia, is observed on certain membranes both in the animal and in the organic portion of the body; and it is in some measure probable that it exists, at least in some of the lower animals, in the vascular system also, namely, in the interior of the vessels. It is seen in many of the lower animals in the animal part of the body, namely, over the entire surface. In the higher animals it is seen on the surface of the body during the embryo state only, as in the embryo of the frog; and, in some animals, in the larva state, as in the tadpole; [but it has been discovered by Purkinje to exist in the parietes of the ventricles of the brain, both in the embryonic and adult state of mammalia.] In the organic portions of the body the mucous membranes (not all of them) present it, even in the highest animals, up to man himself. It is possible that the motion of nutritive fluids which is observed in the lower animals where there is no heart and no distinctly contracting vessels, is, in all cases, merely the effect of the motion of cilia; and the circular motion of the sap in the cells of many plants may be produced in a similar way. The phenomena of this kind have been described at pages 45 & 155; they do not in any way tend to confirm the notion of a spontaneous motion of fluids.

CHAPTER II.

OF CILIARY MOTION.*

The phenomena of ciliary motion were observed in the Mollusca by De Heide, Leeuwenhoek, Baker, Swammerdam, and Baster, although the mode of their production was not explained until a much later period. [The cilia on the surface of the infusory animalcules were distinguished by Leeuwenhoek,† who described their motion and use. They were afterwards observed by Baker.‡] De Heide and Leeuwenhoek noticed the currents on the surface of the branchia of Mussels; Swammerdam, Leeuwenhoek, and Baster observed the whirling motion of the embryo of Mollusca in the ovum. The former phenomenon has recently been minutely described by M. Erman § and Dr. Sharpey, the latter by Carus.|| The cilia on the tentacula of the Plumed polype (Plumatella) had been described by Steinbuch, and more recently by Meyen. Gruithuisen ¶ discovered them in the Planariæ and a freshwater snail; [Dr. Fleming had noticed them vibrating on the branchiæ of another gasteropod (Tritonia;)] and Dr. Grant first recognised them as the cause of the motion of the embryos of Mollusca in the ovum, and of the ova (or rather embryos) of the Polypifera [and Sponges. The cilia of the Medusæ have been described by Tilesius, Eschscholtz, and Dr. Grant.] The ciliary motion has been further discovered by Ehrenberg to prevail through the whole group of invertebrate animals, which he names Turbellaria, (including the Gordius, Nemertes, Planaria, Naides fluviatiles, &c.) occupying the surface of their body, and he has seen it in the intestinal cavity of the Wheel animalcules and Naides. [Dr. Sharpey has discovered the existence of the ciliary motion in the Actiniæ and Asterias, and in the internal cavities of the Echinus, on the surface of which it has been noticed by M. Ehrenberg. Mr. Lister has described the ciliary motion as existing in the Ascidiæ. And very recently it has been observed on the exter-

* The principal writings on ciliary motion are those of Purkinje and Valentin, in Müller's Archiv. i. p. 391. ii. 159; their work, De Phænomeno generali et fundamentali motus vibratorii continui in membranis, &c. Vratisl. 1835. 4; and a paper in the Nova Acta Nat. Cur. t. xvii.; Sharpey, in Edinb. Med. and Surg. Journ. vol. xxxiv. July 1830; Edinb. New Phil. Journ. vol. xix. July 1835; and Cyclopedia of Anat. and Phys. Art. Cilia; Grant, Edinb. New Philos. Journ. 1826; Edinburgh Journal of Science, 1827.

† Contin. Arcan. Natur. p. 382.—Dr. Sharpey's article, "Cilia," Cyclopedia of Anat.

‡ On Microscopes. London, 1743, p. 72.

§ Abh. d. Acad. zu Berlin. 1816, 1817.

|| Nova Act. N. C. t. xvi.

¶ Salzb. Med. Zeit. 1818. 4. 286.—Nov. Act. N. C. t. x.

nal surface of the Spermatozoa of the Newt by Mayer,* and of those of the land Salamander also by Wagner.†]

The first observations relative to the existence of the phenomenon in vertebrate animals were made by Steinbuch, who remarked the currents in the water around the branchiæ of the Batrachia, but did not recognise their cause, and sought in vain for cilia. Gruithuisen discovered the phenomenon on the tail of the larva of the frog; and Dr. Sharpey described the existence of the currents not only around the branchiæ, but over the whole surface of the body of the tadpole; similar observations with respect to the branchiæ were made by Huschke, Raspail, and myself. It remained, however, for Purkinje and Valentin ‡ to make the important discovery, not only that the phenomenon in question was in the Batrachia, as in the invertebrata, dependent on the oscillation of cilia, but that it exists, from the same cause, on the surface of the mucous membranes of birds, reptiles, mammalia, and man. It appeared to be absent in fishes; it exists, however, in them also. I will now give an account of the most important facts relating to this subject, with some remarks upon them.

a. Of the different parts of animals in which the ciliary motion exists.

The ciliary motion has in different animals been observed on the external surface, in the alimentary canal, the respiratory system, generative organs [in the cavities of the nervous system, and on the surface of serous membranes].

1. *The external surface* presents the ciliary motion in the Infusoria, the coralline Polypifera (the Bryozoa, in contradistinction to the Anthozoa,§ of Ehrenberg); [in the Actiniæ and Asterias also, according to Dr. Sharpey; in the Echinus, according to Ehrenberg;] in the Acalepha; in the Mussel (on the mantle); in the Gasteropods (snails), terrestrial and aquatic (over the whole surface); in the Turbellaria of Ehrenberg [and in the Spermatozoa]. In the higher animals the ciliary motion is not observed on the external surface, except in the embryo, and in the very young larvæ of amphibia. During the earliest period of the larva state, the whole superficies of the body was seen by

* Froriep's Notiz. 1836. No. 1089. p. 165.

† Fragmente zur Physiologie der Zeugung. München. 1836.

‡ Müller's Archiv. 1834; and afterwards in their work, De Phænomeno, &c.

§ [M. Ehrenberg (Symbolæ Physicæ, and Müller's Archiv. 1834, p. 578,) divided the polypi into two groups, the Bryozoa and the Anthozoa. The Bryozoa are those which have a perfect intestinal canal, with a ciliated surface (whence they are called ciliobrachiata by Dr. A. Farre, Philos. Transact. 1837). The Anthozoa have merely a digestive sac with one opening, and their surface is destitute of cilia. M. Ehrenberg has since made a further division of these Anthozoa. A similar arrangement of the Polypifera, showing the coincidence of a complete intestinal canal, with the presence of cilia on their surface, was given by Dr. Sharpey in his article, "Cilia," in the Cyclop. of Anat.]

Dr. Sharpey, and by Valentin and Purkinje, to present the ciliary motion; afterwards, the extent to which the phenomenon is observed, becomes gradually less, until it is confined to the root of the tail and the sides of the head; and when the extremities have become developed it has wholly disappeared.

2. *Alimentary canal.*—Purkinje and Valentin have discovered the ciliary motion in the alimentary tube of reptiles; but only at its upper part, namely, on the internal surface of the mouth, the Eustachian tube, the pharynx, and in the chelonia, (turtles and tortoises,) and serpents in the œsophagus also. In the œsophagus of serpents the ciliary motion is described by the observers above mentioned to cease at the point where the longitudinal folds of the mucous membrane of the stomach commence; in the chelonia the phenomenon ceases to present itself at a defined line where the stomach commences. In mammalia and birds the ciliary motion does not exist either in the cavity of the mouth, or in the pharynx and œsophagus.

In the mollusca the ciliary motion prevails, according to Purkinje and Valentin, throughout the whole alimentary canal, and even in the biliary ducts; it was observed by Ehrenberg in the alimentary canal of Rotatoria (wheel animalcules) and Naides (a genus of annelida, or red-blooded worms); and Dr. Sharpey has seen it in the stomach and cæca of the Asterias, in the intestinal canal of Annelida, and in the stomach of Actiniæ; lastly, the movements of granules in the digestive cavity of the polypifera, which was described by Meyen and Mr. Lister,* are of this nature.

3. *Respiratory organs.*—The mucous membrane of the larynx, trachea, and bronchi, has been found by Purkinje and Valentin to present the ciliary motions in all the air-breathing vertebrata. In mammalia and birds the phenomenon commences at the glottis, not existing in the cavity of the mouth and pharynx in these classes. In birds it extends into the air-sacs which communicate with the lungs. The external branchiæ of the larvæ of the amphibia present the ciliary motion; but on the internal branchiæ, which these larvæ have in the second stage of their developement, and on the branchiæ of fishes, the phenomenon is, as Dr. Sharpey observed, absent. It is probable that the external gills of the embryo shark and skate would present the ciliary motion. [Dr. Allen Thomson, however, failed to perceive any appearance of it on those parts in the skate.†]

The motion is universally present over the surface of the branchiæ of the mollusca, and also over that of the accessory branchiæ or labial appendages of the conchifera (mussels). But Purkinje and Valentin could not detect it on the inner surface of the pulmonary sacs of the

* Philos. Transact. 1834.

† Dr. Sharpey's article, "Cilia"; Cyclopedia of Anat. vol. i. p. 632.

pulmoniferous gasteropods (common snail and slug). They also failed to discover the slightest motion on the surface of the branchiæ of the true crustacea (crab or lobster). Steinbuch distinguished the cilia, and described their motion, on the arms of the Plumatella. Henle and I have seen the ciliary motion on the branchiæ of Sabellæ (marine annelida); [Dr. Sharpey has observed it on the gills of the Serpula and another annelide; and on the parietes of the visceral cavity, to which the water has free access, in the Aphrodita aculeata (sea-mouse), as well as in the Asterias, Echinus, and Actinia.]

4. *Nasal cavity.*—In this situation the ciliary motion is constantly present. It was discovered there by Purkinje and Valentin. In reptiles and amphibia, birds and mammalia, it occupies both the external and internal wall of the nasal cavity; and in mammalia the observers just named have detected it also on the mucous membrane of the sinuses opening into the nostrils, the frontal and maxillary sinuses, and in the Eustachian tube. In the rabbit the lining membrane of the lachrymal canal and sac presents no ciliary motion, though the phenomenon exists in the nasal cavity; the ciliary motion is also not present on the conjunctiva. This is certainly not what we should have expected, for had the ciliary motion existed on the surface of the conjunctiva, or even in the lachrymal canals and sac merely, it would have afforded an easy explanation of the absorption of the tears. The ciliary motion is very evident in the nasal cavities of fishes.

5. *Generative organs.*—In vertebrate animals the ciliary motion has been found by Purkinje and Valentin to occupy the mucous surfaces of the female generative organs only. It is observed in the oviducts, the uterus and vagina of mammalia (not in young animals); it persists even during pregnancy on those parts of the uterus which are not occupied by the chorion. [Professor Wagner* could not detect any ciliary motion on a portion of mucous membrane taken from the upper part of the vagina of a woman labouring under gonorrhœa; and Dr. Henle † states that cilia do not exist on the mucous membrane of the genital organs of the human female lower than the middle of the neck of the uterus.] In birds, reptiles, and amphibia it extends to the very extremity of the oviducts. I have seen the phenomenon in mammalia, as well as in birds, reptiles, and amphibia. It is probable that the motion of the cilia has some share in effecting the transmission of the ovum to the oviduct in amphibia: how the ova reach the oviduct, the abdominal extremity of which in the frog and salamander lies so much higher in the abdominal cavity than the ovarium, is, it is well known, at present quite enigmatical; but it is possible that this object may be aided by the mucous membrane of the oviduct being protruded from the abdo-

* Froriep's Notiz. 1837. Bd. i. p. 227. † Müller's Archiv. 1838, p. 113.

minal extremity of the tube, so as to turn the vibrating surface to the ovary, and to the ova escaping into the abdominal cavity. In fishes also the ciliary motion exists in the female organs of generation, namely, on the inner surface of the oviduct, extending very distinctly as far as the external opening of the generative apparatus.

In the mollusca, Henle found the ciliary motion distinct in the female organs of generation, that is to say, in the organ called by Cuvier the ovary of the snail, and on the inner surface of the cavities of the ovary of the mussel. The male organs do not present any ciliary motion in vertebrate animals, and it has not been observed in any organs of the invertebrata, which indubitably belong to the male sexual apparatus.

6. *Urinary apparatus.*—In the vertebrata the ciliary motion is entirely wanting in the urinary organs. But Purkinje and Valentin have detected it in the saccus calcareus of snails, an organ which opens upon the surface of the body near the anal aperture, and which, from containing uric acid, may be regarded as the kidney of these animals. Henle also has seen the ciliary motion in this organ. In the conchifera the ciliary motion has been observed by Purkinje and Valentin on the inner surface of the saclike organ described by Bojanus, which opens near the orifice of the ovaries: this organ has been compared to the kidney; but it might with equal reason be regarded as the testis, until some other organ is clearly proved to be the testis of these animals. [This question is now decided; the conchiferous mollusca are male and female; the organ hitherto generally supposed to be in all individuals the ovary, produces in one sex the ova, in the other a fluid containing spermatic animalcules. This was known to Leeuwenhoek, and was again discovered by Prevost in 1825, but the fact was overlooked until recently confirmed by Wagner.*]

7. [*The ventricles of the brain.*—The ciliary motion has been discovered on the lining membrane of the ventricles of the brain by Purkinje, who has with M. Valentin examined it in this situation in man, many mammalia, birds, amphibia, and fishes. It extends through all the ventricles of the brain, and all the cavities of the brain and spinal cord in the fœtus and embryo.†]

8. *The serous membranes* (the pericardium and peritoneum in the frog) have been stated by Mayer ‡ to present the phenomenon, and the observation has been confirmed by M. Valentin.§]

From the review which we have thus taken of the parts which pre-

* See Wagner's Lehrbuch der Vergleichenden Anatomie; and Siebold über die Spermatozoen der Wirbellosen Thiere, in Müller's Archiv. 1837, p. 381. The bivalves of the genus Cyclas are an exception to the order. They are hermaphrodite, each individual having distinct double ovaries and testes.

† Müller's Archiv. 1836, 289, and Valentin's Repert. 1837, Bd. i. p. 156.

‡ Supplemente zur Lehre vom Kreislaufe, Pt. ii. p. 7. Froriep's Notiz. No. 1024.

§ Repertorium, Bd. i. p. 149.

sent the ciliary motion, it is evident that it is a phenomenon which exists very generally in the animal kingdom; but that the extent to which it prevails in the different classes of animals is very various. In no class of animals [except the crustacea?*] is it entirely wanting.

The vibrations of cilia are also the cause of the motions of the embryos of many animals in the ovum, and of the motion of the free ova (or, more correctly, embryos,) of several of the lower animals, as the Radiata and Polypifera. Cavolini observed the motions of the ova of Gorgoniæ; Tilesius, those of the ova of the Millepores; Dr. Grant, those of the ova of Campanulariæ, Gorgoniæ, Caryophylli, Spongiæ, and Plumulariæ. The ova, escaped from the capsules, move along with one end forward. Rapp discovered cilia on the ova of the Corynæ likewise. Dr. Grant has also discovered the cilia on the embryos of Gasteropods, which are the cause of their motions in the ovum.

b. Of the phenomena of ciliary motion.

It requires a high magnifying power to perceive the ciliary motion in most animals. To see it, a very small piece of any mucous membrane on which it exists should be moistened with water and covered with a plate of glass, by which it is spread out, and its border rendered clearly visible. With the aid of a powerful microscope the phenomenon of the ciliary motion may then be seen. First, there is the appearance of an undulation, and the small bodies floating in the water are seen near the border of the membrane to be driven along in a determinate direction. With a still higher magnifying power, the cilia themselves may sometimes be recognised, although seldom very distinctly, on account of the great rapidity of the motion. Often the effect of the action of the innumerable moving organs is so great, that it is necessary to be quick in making the observation, lest the entire portion of membrane should escape from the field of vision. The influence of the ciliary motion on the fluids and small bodies which are in contact with the ciliated membranes may also be very well shown by strewing on the surface a fine powder. The motion of the cilia is so active on the branchiæ of the larva of the salamander, or of the mussel, that small portions of those organs, when placed in water, are regularly whirled round.

The motion of the cilia, having a uniform direction, gives rise to currents over the surface of the mucous membranes. The direction of these currents on most parts has been already determined by the labours of Dr. Sharpey, and of Purkinje and Valentin. The direction of the current in the trachea of a hen was found by Purkinje and Valentin to be from without inwards; in the oviduct it was from within outwards: the supposition, therefore, that the semen is conveyed to the ovum by

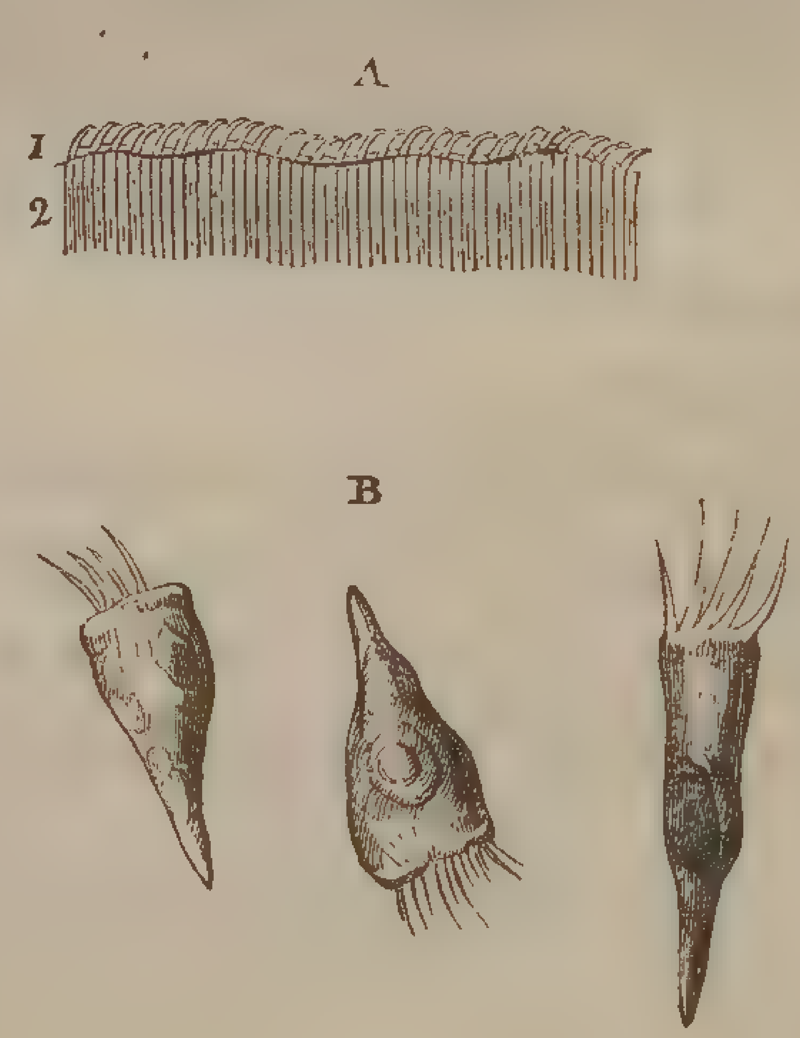
* See Dr. Sharpey's article, "Cilia," in the Cyclop. of Anat. vol. i.; the note at p. 628.

ciliary motion, is not capable of proof. On the inferior turbinated bone of a rabbit the current was ascertained by Dr. Sharpey to be directed from behind forwards; in the antrum it appeared to be directed towards the opening of the cavity. In the cavity of the mouth of the batrachian amphibia the current produced by the ciliary motion is, both on the floor and roof of the cavity, directed towards the œsophagus. At the palatal entrance of the nostril, in a lizard, the current on the inner side of the opening carried small particles of powder into it; on the outer side it carried them out into the mouth.

c. Of the organs which produce the ciliary motion.

The organs of the ciliary motion are, according to Purkinje and Valentin, delicate transparent filaments, varying in length from 0·000075 to 0·000908 of a French inch [from $\frac{1}{12307}$ to $\frac{1}{1016}$ of an English inch]. They are generally thicker at their base than at their free extremity: this is the form that they generally appeared to me also to present on the mucous membranes; on the branchiæ of a new genus of annelide, allied to the sabella, which exists in the Baltic, they were more club-shaped. [The cilia in invetebrate animals are generally cylindrical, acutely pointed filaments; but in the vertebrata they are, according to MM. Purkinje and Valentin, more or less flattened processes, of which the free extremity is in man and mammalia cut off or rounded; in birds and reptiles more pointed.* The cilia which these observers discovered in the ventricles of the brain of mammalia were, however, tapering pointed filaments, resembling those on the vibrating membranes of mollusca.†] It is very difficult to determine the form of the cilia, but easy to ascertain their presence. I have seen them very distinctly in the fresh-water mussel (Anodon), on the branchiæ of the annelide just mentioned, in the mouth of the frog, in the oviducts of rabbits, frogs, and fishes, and in the trachea of birds and mammalia; and I cannot understand how Treviranus (L. Chr.) could fail to discover them. The surface of the membranes which present the ciliary motion is, according to Purkinje and Valentin, composed of minute straight fibres, arranged parallel to each other, and united by an intermediate connecting matter (see fig. 54, A). A similar stratum of fibres, how-

Fig. 54.‡



* Nov. Act. Nat. Cur. t. xvii. pt. ii. p. 846.

† Repertorium für Anat. & Physiol. Bd. i. p. 158.

‡ [Fig. 54, A, from Valentin, Nov. Act. t. xvii.; cilia vibrating on mucous mem-

ever, exists on the surface of the mucous membrane of the jejunum of the turtle, on which there is no ciliary motion. If we understand MM. Purkinje and Valentin, these fibres are arranged perpendicularly upon the surface of the mucous membrane. [These are the same nucleated bodies that have been found by M. Henle forming the epithelium of various mucous membranes, as described and figured at p. 435 (fig. 32). From the form of the component particles, he calls the epithelium which it forms, the "cylinder epithelium," to distinguish it from the epithelium which is formed of flattened cells (see p. 435, fig. 31). In membranes which present the ciliary motion, the epithelium is formed of the cylindrical particles, on the free extremity of which the cilia are seated (see fig. 54, B). The cylinders of the ciliary epithelium of the nasal cavities measure about $\frac{1}{72}$ of an English line in length. Their mean length in the uterus is $\frac{1}{105}$ of an English line. The length of the cilia which these cylinders bear in the Fallopian tubes is $\frac{1}{505}$ of an English line.* M. Henle describes the cylinders of the ciliary epithelium as containing each a nucleus, like the particles of the epithelium in other parts. The account which M. Valentin gives of the separated cylinders is somewhat different. "If," he says, "we scrape from the Schneiderian membrane of the horse some of the half fluid mass which covers it, and examine it with the microscope, we shall perceive a number of bodies, like pedunculated vorticellæ, consisting of an elongated cylindrical body, rounded at its posterior extremity, from the centre of which a delicate, soft filament issues, and more flattened at its anterior extremity, on which from six to thirteen cilia are seated in a circle upon a slightly arched surface. Within the cylinder, and beneath the general granulated investment, are seen granular striæ, probably muscular fibres, for the movement of each of the cilia. The same parts may be distinguished in the ciliary epithelium of the trachea and uterus, (in which Purkinje also has seen them.")†]

The researches of Ehrenberg have made us most intimately acquainted with the cilia as they exist in the infusoria. In the genera Stylonychia and Kerona, which are of large size, he distinguished that each of the revolving cilia has a bulbous enlargement at its base; and he satisfied himself that a slight turning of the bulbs upon their fixed points causes the extremity of the cilia to move round in larger circles, each of the cilia describing a cone, the apex of which is the bulb. In the polygastric infusoria the cilia sometimes occupy the whole surface of the body; sometimes they are

brane of trachea of rabbit: 1. cilia; 2. fibres of epithelium.—B, from Henle, Symbolæ, &c.; cylinders of epithelium with cilia, abraded immediately after death from the trachea of a cat.]

* See Henle, Symbolæ ad Anat. Villor. Intest. &c.; and Muller's Archiv. 1838, p. 114.

† Valentin's Repertorium, 1837. p. 207.

entirely absent; and in other instances they are confined to the circumference of the mouth. When they are distributed over the whole surface, Ehrenberg found them very regularly arranged, generally in longitudinal, but frequently also in transverse series. This arrangement of the cilia in rows has also been some few times observed by Purkinje and Valentin; and the wave-like motion of series of cilia, which they observed also, renders it probable that the cilia are thus arranged. The rotatory organs of the Wheel animalcules do not, according to Ehrenberg, differ essentially from other cilia. The Hydatina senta has seventeen rotatory organs arranged in a circle, each organ consisting of six cilia, which are seated upon a roundish muscle. The muscles are surrounded by sheaths, and fixed by two ligamentous fasciculi to two points of the general investment of the body.* The same organs, when not aggregated together, as in the wheel animalcule, do not give rise to the appearance of rotatory motion.†

d. Nature of the ciliary motion.

In inquiring into the nature of the ciliary motion, we have first to consider its duration and its connection with other vital phenomena. It continues, after death, at least as long as the animal tissues retain their irritability, and often much longer. In frogs and lizards it ceases, according to the observation of Purkinje and Valentin, in from one to two hours after death; in a fresh-water tortoise, the Emys Europæa, it continued in different parts from nine to fifteen days after decapitation. It is true the muscles preserved their irritability, and reflex movements could be excited for seven days; but the ciliary motion continued equally long in parts which had been quite separated from the body of the animal and been placed in water. In birds and mammalia Purkinje and Valentin found that the vibrations of the cilia continued from three quarters of an hour to four hours. Light has no influence on the motions of the cilia; but the influence of heat is considerable. The ciliary motion will continue in mammalia and birds, although the parts in which it is seated be immersed for a moment in water of a temperature of $180\frac{3}{4}°$ Fahrenheit; but, if the immersion be protracted for a longer period, the motions of the cilia are abolished. The discharge of a Leyden jar does not put a stop to the motion in the bivalve Unio, nor does the influence of a galvanic battery of thirty pairs of plates, except at the spot where the wires are applied, and the cessation of the motion there is owing to the decomposition of the tissues. The ciliary

* Abhandl. der Acad. zu Berlin, 1830.

† In a second paper, published in 1831, Ehrenberg has pointed out many variations in the structure of the rotatory organs.

motions are not affected by prussic acid, extract of aloes or belladonna, catechu, musk, acetate of morphia, opium, salicin, strychnine, nor by decoction of capsicum, even though the most concentrated solutions of these substances be used. The salts of alkalies, earths, and metals, the alkalies and the acids, put a stop to the motion after a longer or shorter period, according to the strength of the solution applied. Blood maintains the cilia in activity longer than any other fluid; but the serum of the blood of vertebrate animals causes the ciliary motion in mussels to cease immediately; bile also puts a stop to the ciliary motion. It is very remarkable that those substances which have a particular action on the nervous system—the narcotics, namely,—have not the slightest influence on the ciliary motion, which is thus distinguished as a peculiar phenomenon not dependent on nervous energy. Purkinje and Valentin have killed pigeons and rabbits by means of prussic acid and strychnine, either introduced into the pharynx or inserted into fresh wounds of the skin; and they never perceived the slightest change in the ciliary motion in consequence of the poisoning, although they used the precaution not merely not to open the animals before all motion had ceased in every part of the body, but even to wait until pinching the limbs no longer excited automatic movements. To render the result more certain indeed, they, in their experiments on pigeons, killed a second bird, of the same kind and age, by bleeding; and the differences which were observed with reference to the ciliary motion in those experiments were only such as were owing to the individual peculiarities and age of the animals, and the peculiarities of the parts examined. There was, in all cases, the same absence of all effects from the narcotisation.* These latter experiments are evidently less conclusive as to the independence of the ciliary motion from the nervous system than those in which the poisonous substances were applied directly to the vibrating surface; for in frogs killed by narcotics the muscles and nerves retain their susceptibility of the influence of stimuli locally applied for a long period, while both nerves and muscles to which narcotics are directly applied soon lose their irritability. The heart alone is an exception to this rule; it continues to beat for a long time after solution of opium or of the extract of nux vomica has been applied to its external surface, but is immediately paralysed when the same poison is applied to its internal surface.

We do not regard the minuteness of the vibrating organs in comparison with the primitive fibres of the nerves as any argument against their phenomena being dependent on the nervous system; for the muscular fibrils themselves are much more minute than the nervous fibres, and the latter fibres are distributed in such small number in the muscles,

* Müller's Archiv. 1835, p. 159.

and the mass of muscular substance which is seen by means of the microscope to intervene between the nervous fibres is so great, that the existence of an influence exerted at a distance is a necessary supposition in accounting for the action of the nervous fibres on muscles. Moreover, there are parts in which, though not in the muscles, a much more minute ramification of the nervous fibres appears to take place.* The persistence of the ciliary motion, however, after the direct application of narcotic poisons, sufficiently proves the peculiarity of this phenomenon, and its independence of any immediate influence of the nervous system. An equally important fact in relation to this question is, the existence of the ciliary motion on the surface of the so-named ova of polypiferous animals, which are however the animated, though undeveloped embryos. The extreme conditions of the phenomenon afford here the most interesting subject of comparison: the lowest condition is that of the ciliary motion on the undeveloped embryos of polypi; the most perfect that of the motion of the rotatory organs of the wheel animalcules. In the former instance we have the phenomenon taking place on membranes devoid of special structure, and allied to this condition is that of the vibratory motion of cilia on the mucous membranes of the higher animals, which is not arrested by the action of strychnine and other narcotic poisons; the motion of the cilia of the rotatory organs, on the contrary, is effected distinctly by muscular action, and is subject to the will; hence certainly dependent on the nervous system: strychnine also, as Ehrenberg has shown, arrests this form of ciliary motion.

The question now arises, Does the ciliary motion throughout the animal kingdom owe its production to a very delicate contractile tissue lying at the base of the cilia, and contracting after the manner of muscular fibres, as is the case with the rotatory organs of the wheel animalcules? Does this contractile tissue of the wheel animalcules (rotatoria), which Ehrenberg has discovered, constitute a peculiar system, forming part in the vibrating membranes even of the higher animals, the delicate structure of the infusoria being preserved in the cilia, while all other tissues of the higher animals have a coarser structure? Or is the motion of the rotatory organs of the wheel animalcules alone allied to muscular motion, and the ciliary motion of all other animals essentially different? I must give Ehrenberg's own words in describing the mechanism of the ciliary motion of the rotatoria. "If the creatures are observed when they commence their motion, there is always seen a distinct extension and retraction of the curved cilia, a true grasping movement (greifen), which however is soon succeeded by the rotatory motion, which is a totally different kind of movement. The grasping

* See page 604.

motion is seen likewise when the animalcules are made to die in a tetanic state, by putting strychnine into the water; the action of the rotatory organs then gradually ceasing, the proper rotatory motion first." Ehrenberg endeavoured to explain the phenomenon in the following manner: "Each of the cilia is moved separately by the muscle situated at its base, and single muscular bands may probably go simultaneously to many or perhaps all the cilia of the same series, and give them all a motion towards one side. If, now, this one muscular band is opposed by a second attached to the opposite side of the bulbous root of the cilium, if the two are fixed to the cilia at somewhat different heights and act alternately, an alternate motion in four different directions will result; in consequence of which the free extremity of each of the cilia will be made to move in a circle, the entire cilium describing a cone, the apex of which is at the base of the moving filament. If, during this motion of the individual cilia, the rotatory organs be regarded partially or entirely from the side, the cilia will be alternately nearer and more distant from the eye, and will consequently be alternately seen distinctly and indistinctly. This alternation in the degree of distinctness of the single cilia appears to me," says M. Ehrenberg, "to be the cause of the apparent rotatory motion of the entire organ; for such a motion of the cilia must certainly give rise to the appearance of active motion of the whole circle." We can easily understand how a muscular action such as Ehrenberg supposes to be exerted would cause the cilia to describe a cone; for the recti muscles of the eye of the higher animals can move the eyeball in a similar manner. In fact, the voluntary power of the wheel animalcules over their rotatory organs, and the motor apparatus demonstrated by Ehrenberg, places it almost beyond a doubt that the motion of those organs belongs to the class of the true muscular motions. But how is it with the ciliary motions of the mucous membranes which are not subject to the will, and continue unaffected when the animals presenting them are poisoned by narcotics, and which are not affected even by the local application of strychnine or other narcotics? Again, how can we account for the existence of the ciliary motion on the ova of corals? Do these ova retain a portion of the vital energy which was infused into them when they were exposed to the vital influence of the ovary; and is it this remaining portion of vital energy which they thus manifest for a certain period, just as is the case with separated portions of mucous membrane taken from any of the higher animals? Are these vital phenomena analogous to the motions of the ovi-capsules of the Cercariæ observed by Bojanus and Von Baer? (See p. 17.) It is much more rational to regard these ova as animated, though undeveloped embryos. However this may be, it appears to us certain that, in the present state of our knowledge, the ciliary motions of the rotatory organs of the wheel animalcules must be considered as different from the vibratory motions of the cilia of the mucous membranes. The former are subject to the influence of the will; the latter are independent both of the will and of any direct influence of the nervous system. In the rotatory organ the cilia are apparently passive, and the muscular apparatus is alone the active agent in producing the motion. No muscular apparatus has at present been discovered in connection with the cilia of the mucous membranes and those of the surface of the infusoria; and it is not at present known whether the cilia themselves move and bend, or whether they act as mere oars by virtue of a contractile tissue at their root. Meyen has seen the cilia of the Leucophrys sol (a polygastric infusory animalcule) continue to move when separated from the animal. Gruithuisen has observed the cilia of Planariæ in the separated state, and has seen them continue to move in parts where the substance of the animal was undergoing decomposition. [One kind of motion of the cilia described by Purkinje and Valentin* is that of uncination, the cilia becoming flexed, particularly near their point, as represented at fig. 54, A. Dr. Sharpey, too, says: the cilia most commonly "have a fanning or lashing motion; that is, the cilium is bent in one direction, and returns again to its original state;" and "the more elastic cilia," he says, "when their motion abates in intensity, appear sometimes to bend only near the point, the base and adjoining part remaining motionless."†] On the other hand, some animals present organs acting like oars or paddles, which in their involuntary and constant action greatly resemble cilia, but yet differ from them in their form; and the motions of these organs can scarcely be explained except by the presence of a contractile tissue at their root. In the genus Beroe (one of the Acalephæ) there are, according to Dr. Grant's observations, bands running longitudinally from the mouth to the anus, each bearing forty laminæ, which are the organs of motion or cilia. These laminæ are formed of parallel fibres connected together by a membrane. Indeed, the laminæ, which are very easily seen with the naked eye, constantly moving at the abdominal surface of the gammarus pulex and other of the lower crustacea, must be referred to the same class of organs, although the motions of these laminæ are certainly effected by muscles,—a different tissue perhaps from that which produces the ciliary motions on the mucous membranes.

In the present state of our knowledge, thus much may be advanced:

1. That the ciliary motion of the mucous membranes is due to the action of some unknown contractile tissue;

2. Which lies either in the substance of the cilia or at their base;

* Nov. Act. Nat. Cur. vol. xvii. pt. ii.

† Article "Cilia," Cyclopedia of Anatomy, pp. 634, 635.

3. That this tissue resembles in its contractility the muscular and other contractile tissues of animals;

4. That its properties in so far agree with those of the muscular tissue, at all events with that of the involuntary muscles of the heart; and with the vibrating laminæ of the lower crustacea, that the motions which it produces continue without ceasing with an equable rhythm;

5. That its properties agree also with those of the muscular tissue of the heart, in its motions continuing long after the separation of the part from the rest of the animal body;

6. That this tissue differs essentially, however, from muscle, in the circumstance of its motions not being arrested by the local application of narcotics;

7. That the ciliary motion presents itself under conditions where it is not probable that a complicated organisation exists, namely, in the undeveloped embryos of polypiferous animals.

The circumstance of the ciliary motions not being immediately dependent on the influence of nerves, constitutes a point of resemblance between them and the oscillatory motions of certain plants, for example, the Oscillatoria. How far this comparison is correct must be determined by further research. But, however this may be, there certainly exists in the mucous membranes that present the ciliary motion, an active force which regulates the mode of action of these microscopic organs, since the cilia are very frequently observed to act simultaneously in regular series. There is here a force, the influence of which extends beyond individual cilia; for though the simultaneous action of a series of cilia producing waves might be explained by supposing many cilia to be attached to one contractile band, yet there is also frequently observed a certain remission and acceleration of the ciliary motion over considerable tracts of a vibrating membrane, which must have a more general cause. I have sometimes seen a total rest of the cilia for a considerable interval over a large extent of the surface of the branchiæ of an annelide allied to the genus Sabella, which I brought with me in sea-water from Copenhagen, this state of rest being again succeeded by a state of activity. Analogous phenomena are frequently enough observed in the vegetable kingdom; they are not necessarily therefore to be referred to a variation in the nervous influence.

The explanation of the production of currents by the ciliary motion is also attended with difficulty. The mere vibration of cilia from one side to another cannot give any particular direction to a fluid. The motion of the cilia, too, in a conical space, which, according to the observation of Purkinje and Valentin, is the most frequent kind of motion, can merely give rise to the motion of the fluid in a circle around the cilium. For the cilia to give rise to a current of the fluid in a certain direction, it is necessary that they should strike and bend in one direction; such, indeed, was the motion which Purkinje and Valentin observed sometimes, and that which I saw in most cases. But even with this motion it is necessary, to produce a current, that the cilia in returning to their erect position should present a smaller surface to the fluid than they do in making the stroke. [According to the observation of MM. Purkinje and Valentin,* it is the return of the cilia from their bent to the erect state which gives the impulse to the water, and produces the current.]

CHAPTER III.

OF THE MUSCULAR, AND THE ALLIED MOTIONS.

1. *Of the contractile tissues.*

If we leave out of consideration the enigmatical tissue which is the cause of the ciliary motion, four forms of contractile tissue may be distinguished; namely, the contractile tissue of vegetables, the contractile tissue of animals which yields gelatin by boiling, the arterial contractile tissue, and the muscular tissue.

a. Of the contractile vegetable tissue.

The most remarkable of the phenomena of irritability presented by plants have been already described at page 40. We have here merely to institute a comparison between the contractile tissue of plants and that of animals.

Fig. 55.

The leaves of the sensitive plant (Mimosa sensitiva) are supported upon a long petiole, at the base of which, as well as at the junction of each leaflet with the petiole, an elongated intumescence exists, the seat of the power by which the petiole and leaflets are moved. In the natural state during the day the petiole is elevated, the leaves expanded, and the intumescence elongated, but equally convex superiorly and inferiorly. (Fig. 55. 1.) But at night, or when irritated, the petiole is depressed, the leaves applied to each other in pairs, and the intumescence at the base of the petiole curved so as to be convex superiorly, concave inferiorly (as at fig. 55. 2). The structure of this intumescence has been investigated by M. Dutrochet. He [formerly] †

* Nov. Act. lxvii. pt. ii.

† Recherches Anat. et Physiol. sur la structure intime des Animaux et des Végétaux. Paris, 1824.

described it to be in greater part composed of globular cells arranged in longitudinal series, but separated from each other by considerable intervals, the interspaces being occupied by much more delicate cellular tissue which contained numerous dark bodies. The centre of the intumescence he stated to be traversed by tracheæ which maintained the vascular communication between the leaves and stem. [Professor Müller, believing from M. Dutrochet's account of his experiments that the curving of the intumescence was probably owing to the approximation of rows of the globular cells, remarked that, were such the fact,] a great similarity would seem to exist between the contractility of plants and animals; there being, however, this difference, that the elements, which in animals attract each other to produce the contraction, form continuous threads, while in the Mimosa they are separated from each other by intervals. [More recently,* however, M. Dutrochet has given a different account of the structure of the motor organ of the mimosa. According to his later description, the external portion of the intumescence is seen in a transverse section to be formed of hexagonal cellular tissue, which, with the exception of the most internal cells, which are filled with air, contains a fluid coagulable by acids. Within the cellular portion is a ring formed of tubular fibres; within this again a thin layer of tubes and tracheæ (*d*); and in the centre a bundle of fibres similar to those of the layer within the cellular substance. When, by a longitudinal section the upper half of the intumescence is removed, the lower half, which remains, becomes permanently curved, so as to throw the petiole upwards. When, on the other hand, the lower half is removed, the intumescence curves so as to depress the petiole. The facts which M. Dutrochet has ascertained relative to the properties of the different tissues composing the intumescence are the following:—A segment cut from the outer cellular portion, when placed in water, becomes curved with the concavity inwards, whether the water be deprived of its air or not. A portion of the fibrous layer also becomes curved in the same direction when immersed in water containing air, but remains straight if the water have been deprived of its air. A leaf of robinia pseudo-acacia, placed in water containing air, presented the phenomena of periodical sleep, as in the air; but, in water which contained no air, it remained permanently in the position which the plant has in the air during day. A sensitive plant also did not sleep in the vacuum of an air-pump. From these facts M. Dutrochet concludes that the change to the position of sleep must be effected by the fibrous tissue, and that it is the cellular tissue which causes the expansion of the leaves and elevation of the petiole during the day. M. Dutrochet now proceeds to inquire how the cellular and fibrous parts of the intumescence respec-

* Mém. pour servir à l'Histoire Anat. et Physiol. des Végétaux et des Animaux, 1837.

tively produce the results which he thus traces to their action. Now, the cellular layer of the intumescence has its cells larger externally than internally; hence each portion of its circumference might be expected, if rendered turgid by endosmose, to have a tendency to bend towards the axis of the petiole, the larger cells being more distended than the smaller; and it is thus, according to M. Dutrochet, that the water acts in causing a segment of the cellular portion of the intumescence to become curved.

The cause which influences the motion of the plants so as to induce the expansion of the leaves and rising of the petiole is the augmentation of light during the day; the light favours the ascent of the sap, and thus must produce turgescence of the cellular portion of the motor intumescence. Each portion of the cellular cylinder in the mimosa has a tendency to curve towards the centre or axis of the petiole; but the lower part is the thickest, and hence the tendency will there be strongest, and will, when the intumescence is rendered turgid by the influence of light, cause the elevation of the petiole. If, however, the lower half of the intumescence be removed, the tendency of the upper half, being no longer counterbalanced, will come into play, and depress the petiole: if the upper half only is removed, the lower will act with increased force, and raise the petiole still more, as in the experiment already mentioned.

The fibrous tissue has the property of curving when submitted to the action of atmospheric air or oxygen (" par oxigenation"). Each segment of the layer of fibrous tissue has a tendency to curve with the concavity towards the axis of the petiole; the central bundle of fibrous tissue has, M. Dutrochet supposes, though he does not demonstrate this, a tendency when oxygen unites with it to curve downwards, in the same direction therefore as the upper part of the hollow cylinder of fibres, with which it would co-operate in depressing the petiole, overcoming the force of the lower portion of the fibrous layer, the tendency of which is to raise the petiole. It is thus, according to M. Dutrochet, that the depression of the petiole is effected in the evening, when the turgescence of the cellular portion of the intumescence becomes less from the absence of light; while oxygen, having accumulated in the fibrous tissue, increases its incurvating tendency. Even the fibrous tubular tissue is supposed by M. Dutrochet to become curved by virtue of a state of impletion caused by the union of oxygen with the contents of the tubular fibres. The tubular fibres of the fibrous layer of the intumescence increase in size, he says, from within outwards; and hence, when distended, would give to each part of the fibrous cylinder a tendency to curve towards the axis of the petiole.

The depression of the petiole, and the folding of the leaves of the mimosa and other plants when irritated mechanically, or by heat or acids, is, according to M. Dutrochet, also the result of the same action of the fibrous tissue, which becomes oxygenated whenever the plant is irritated in any way, it being a fundamental theory with this physiologist that excitation is in all cases merely oxydation of the living tissue, animal or vegetable.

In other plants,—as the Phaseolus vulgaris, or haricot bean, and the Robinia pseudo-acacia,—though the structure of the motor intumescence is generally the same, there are differences in the relations of the cellular and fibrous tissues which render M. Dutrochet's theory insufficient to explain their action. These difficulties he attempts to overcome by other suppositions, which are not always satisfactory. Professor Müller, opposing the idea of endosmosis and expansion being the cause of the motion of the intumescence, remarks]: The sudden expansion of the cellular tissue is not demonstrated, nor is it indeed probable; the cells cannot so rapidly attract through their parietes the fluids necessary to produce their turgescence; and Dutrochet does not state that the portions cut from the intumescence became expanded, but that they became curved; these reasons induce me to regard the explanation of these motions of vegetables by contraction as more probable. We are acquainted with no other instance of rapid motion by expansion than that of erection, which is effected by the effusion of a fluid into cavities previously collapsed; but such a rapid effusion into the closed cells of the intumescence of the Mimosa cannot easily be conceived; nor can an active, rapid expansion of the parietes of the cells be imagined to take place.

Supposing the phenomena to be owing to contraction, two modes of explaining them might be adopted. Either we may suppose that there are two active parts,—one acting under the influence of the general vital stimuli, and producing the elevation of the petiole, but ceasing to act when the plant receives any shock,—the other evidencing its irritability only under the influence of external shocks or irritation, and causing the depression of the petiole; or we may suppose the petiole to be kept erect during the waking state by a vital action of the intumescence, and external stimuli to cause the depression of the petiole by annulling for a period the vital contractility, and allowing an elastic force to come into play. Were this latter explanation correct, the contractility of plants would be distinguished from that of animals in being abolished by disturbing influences, and not excited by them as in animals,—that is to say, beings furnished with nerves. The former explanation is, however, the most probable, since the depression of the petiole excited by external shocks has been observed by many physiologists to resist any attempt to raise it; it is, therefore, an active movement.

To excite the motion of the leaflets and petiole of the mimosa, it is not necessary that either the intumescence itself, or even the leaves, should be touched. The stimulus may be applied to a more or less distant part. [Even the roots transmit the excitation to the leaves; M. Dutrochet moistened a small portion of the roots of the mimosa with sulphuric acid, and, before there was time for absorption of the acid to have taken place, the leaves became folded.] M. Dutrochet has satisfied himself that the transmission of the excitation is effected by the woody part of the plant, not by the cortical or medullary parts; for these he found might be entirely removed, and irritation above or below the spot would still be propagated beyond it. The excitation extends gradually from the points to which the stimulus is applied; first the nearest leaves, and then the most distant, becoming folded. The excitability is greatly influenced by light and temperature, as well as by the presence or absence of atmospheric air. Both the excitability and mobility of the mimosa are lost after a few days, when the plant is deprived of light; the susceptibility of external stimulus being lost before the movements of sleep and waking cease. Variations in the temperature of the atmosphere also cause the quickness of the transmission of the excitation from one part of the plant to others to vary, and at $47\frac{3}{4}°$ Fahr. no motions can be excited.

b.—Of the contractile tissue of animals which yields gelatin by boiling.

The first traces of vital contractility in animals are presented by a tissue so similar in the structure of its fibres, as well as its chemical properties, to cellular tissue, that it might almost lead us to regard them as identical, and to ascribe to cellular tissue not merely the property of elasticity which it retains after death, but also an organic contractile power. Until more is known of the tissue in question, we designate it the contractile tissue yielding gelatin, by which we sufficiently distinguish it from the fibrinous muscular tissue.

In addition to their transparency and smoothness, the fibres of the cellular tissue, which have been described at page 432, have a very peculiar character in their convoluted disposition. When not artificially extended, they are not straight, but have an arched or waving direction (plate ii. fig. 4). The fibres of each primitive fasciculus are, however, always parallel; it is the fasciculi which are thus waving. This character of the cellular tissue is owing to its great elasticity. If the fasciculi be extended and straightened, they return, as soon as the extension is remitted, to their original curved state. A chemical examination of cellular tissue, after it is freed by washing from blood or lymph, shows that it belongs to the class of tissues that are converted by boiling into gelatin; and its fibres are, in this circumstance, again distinguished from muscular fibre which belongs to the albuminous tissues.* This is important, as affording a means of distinguishing the contractile cellular tissue from those muscular fibres which have not the varicose structure; for example, the muscular fibres of the uterus. The latter fibres, however, differ from the fibres of cellular tissue by another character, namely, by the want of the curved and waving position of their fasciculi.

The contractile property of the tissue allied to cellular membrane has been long known; but it has, in many parts of the body, been frequently confounded with muscular action; and, on the other hand, in consequence of the slight change of diameter produced by this kind of contraction, the phenomenon has by some been quite neglected, or even denied to exist. To verify the existence of the phenomenon in question, it is best to study it first in those parts in which it is presented in the most marked degree, and in which the tissue can be submitted to an accurate microscopic and chemical analysis. The tunica dartos has a very active contractile property, which is most frequently excited by cold. The structure of this tunic and the nature of its tissue have been recently determined by M. Jordan. The following is extracted from his paper.†

At the point where the surface of the scrotum begins to present folds or wrinkles, the subcutaneous cellular membrane likewise changes its aspect and structure; the adipose tissue so abundant on the mons Veneris is suddenly lost, and in its place is seen in men who have strength of body, and whose scrotum is very rugose, a fibrous tissue of reddish colour. The fibres of this tissue are extensile and elastic, and are collected into small fasciculi, and these again into thicker bundles. These bundles of fibres run from above downwards, at right angles, therefore, with the folds of the scrotum, with which they are so closely connected, that it requires great trouble and caution to separate them. The larger fasciculi do not all follow a parallel course; but, by frequent anastomoses, a portion of the fibres being given off from one fasciculus to another, form a dense and strong reticular tissue, of which the numerous elongated meshes have all their longest diameter directed from above downwards. This tissue is, like the folds of the skin, most distinct on the anterior surface of the scrotum, and generally cannot be distinguished on the posterior surface; it exists in young children, and even in newborn infants. Similar reddish fibres are found under the skin of the penis; but they here form a more irregular and much thinner tissue. Besides the fibres already described, the dartos contains many long and narrow cylinders of a faint yellow colour, very elastic,

* See the Appendix to the chapter on Nutrition. † Müller's Archiv. 1834.

but little ramified, and following a course from above downwards. M. Jordan convinced himself by injection that these are branches of the external pudic and posterior scrotal arteries. Between the skin and the dartos there is no cellular tissue; the two are so intimately connected, that the one must follow the movements of the other. But between the inner surface of the dartos, and the cremaster and tunica vaginalis communis, there lies a quantity of cellular tissue, so loose that, as M. Jordan has observed in experiments on dead bodies and living animals, the testis with its coverings can be drawn up towards the inguinal ring, leaving the lower part of the scrotum empty.

The primitive fibres of the fasciculi which compose the tunica dartos are excessively delicate and elastic. When examined with the compound microscope, they are seen to be uniform cylindrical filaments, with a serpentine waving disposition. Their diameter, as determined by M. Jordan, varied from $\frac{1}{2000}$ to $\frac{1}{1111}$, and in the mean $\frac{1}{1430}$ of an English line. The fibres of cellular tissue had the same diameter. On the other hand, the fibres of the dartos differ in diameter from the muscular fibres. The varicose muscular fibres are smaller, the cylindrical muscular fibres of the colon are larger, and those of the iris are much more minute. But, independently of their size, the fibres of the dartos exactly resemble the fibres of cellular tissue in their serpentine disposition and elasticity, and are by these characters distinguished from ordinary muscular fibres. The reddish-grey colour, however, which the fibres of the dartos in a mass present, and the regularly longitudinal direction of their fasciculi, distinguish them, although they form a reticular tissue, from the fibres of cellular tissue, of which the fasciculi have a whitish-grey colour, and are interlaced in all directions. It is a question, therefore, whether the similarity in the appearance of these fibres under the microscope is sufficient to identify the dartos with cellular tissue. The decision of this question is rendered still more difficult by the circumstance of the fibres of tendon, which is in its properties so totally different from the dartos, being very similar, when seen with the microscope, to those of cellular tissue (see plate ii. fig. 5). Another difficulty is, the existence of a class of muscles of which the primitive fibres are not varicose like those of the muscles of the limbs, &c. but uniformly cylindrical, in which character the fibre of the dartos resembles them, and thus far seems to stand very near to them. Moreover, the motion of the dartos, though generally excited by the stimulus of cold, yet sometimes is produced by certain internal conditions of the nervous system; the same state of the nerves giving rise sometimes to the contraction of a true muscle,—the cremaster,—as well as to the wrinkling of the scrotum; which latter phenomenon can be proved distinctly not to depend on the action of the cremaster.

On the other hand, traces of contractility are displayed in true cellular tissue in other parts of the body; for example, in the subcutaneous cellular tissue between the folds of the prepuce, which frequently in irritable individuals contracts very strongly in the cold bath. The phenomenon of "cutis anserina" seems to be one of an analogous nature (see page 227). The sudden erection of the nipple is probably produced in the same way; for I have good grounds for questioning the correctness of the common opinion, that the latter phenomenon is the result of vascular turgescence, or true vascular "erection." In the first place, the nipple does not contain any of the spongy tissue which forms the corpora cavernosa penis; those anastomosing veins and sinuses, and the arteriæ helicinæ projecting into the venous sinuses, which characterise the true erectile tissues (see page 227). Secondly, the erection of the nipple is perceptible not only in females when it is handled during the existence of the sexual excitement, but also in men, quite independently of sexual feeling. Thirdly, the nipple in man becomes erected almost instantaneously and quite visibly when it is suddenly and roughly handled in one's own person; the same takes place in a less degree also when the nipple is exposed to the contact of cold water, and in a more marked degree when the individual suddenly enters a cold bath. Fourthly, the erection of the nipple is not attended with any increased fulness; on the contrary, while it is becoming erect, which occupies a few seconds only, it becomes narrower, and loses in breadth what it gains in length. Now, in all these circumstances there is great similarity to the phenomena of the elevation of the cutaneous follicles in "cutis anserina," and to those of the contraction and wrinkling of the prepuce in cold water. The erection of the nipple is, therefore, most probably the effect of contraction of the subcutaneous cellular tissue which surrounds it. It is remarkable that the contractile cellular tissue exists principally beneath or in those parts of the skin which have a dark tint, as, for example, the skin of the penis, the scrotum, and nipple. If, in addition to what we have already stated, it be recollected that the skin in its whole extent, independently of any cutaneous muscle, manifests a certain degree of contractility,—a phenomenon which cannot be owing to the admixture of muscular fibres in its tissue,—it will appear very probable that all the parts which we have mentioned,—the scrotum, skin of the penis and nipple,—owe their contractility to a contractile cellular tissue, which, in the structure of its primitive fibres, does not differ from ordinary cellular tissue. The similarity of the chemical properties of the dartos, and its difference in chemical composition from muscular fibre, strengthen this opinion; for M. Jordan has shown that the dartos is partially converted into gelatin by three hours' boiling; and that its solution in acetic acid, like that of cellular membrane and all tissues which yield gelatin, is not precipitated, nor rendered turbid by ferrocyanide of potassium.

M. Jordan has likewise instituted some experiments relative to the nature of the contractile property of the dartos. The stimulus which most usually excites its contraction is cold; warmth relaxes it; galvanism does not affect it; and this fact is the more interesting, as it affords a means of distinguishing the contractility of cellular tissue from that of muscular fibre. The dartos has no share in producing the retraction of the testis towards the abdominal ring; this is effected solely by the cremaster. In animals in which the scrotum has no folds or rugæ, as in rabbits and dogs, M. Jordan found the dartos replaced by ordinary cellular tissue; while, on the contrary, in the ram, which has a very strongly though irregularly wrinkled scrotum, the dartos is very much developed. The scrotum of the ram became contracted and wrinkled under the application of cold water; but the cremaster at the same time contracted suddenly, drawing the testes upwards, and leaving the lower part of the scrotum, which contracted more slowly, empty. When the application of the cold water was desisted from, the scrotum as it recovered its warmth gradually relaxed, and its rugæ became unfolded; while, long before that had taken place, the testes had descended again as quickly as they had been retracted. The action of a galvanic battery of sixty-five pairs of plates, the wires being applied to the inner surface of the scrotum, had no influence on its contractility; while the testes were instantaneously drawn up by the contraction of the cremaster. The mode in which the shortening of the fibres of the contractile tissues, which we have been considering, is effected, is probably their inflexion into waving lines by the reciprocal attraction of aliquot parts of the fibres.

c. Of the elastic and contractile tissue of arteries.

It has been already shown, at page 202, from the results of galvanic experiments as well as from the real properties of the elastic coat of arteries, that this tissue does not possess muscular contractility. The yellow fibres which compose it are of the same class as those of all other elastic yellow membranes and ligaments, such as the ligamentum nuchæ of mammalia, the ligamenta flava of the vertebræ, the yellow ligaments of the larynx, the yellow fibres of the membranous part of the trachea and bronchi, the elastic ligament of the wing of birds, the elastic ligaments of the last phalanx of the toes in feline animals, &c. The elastic tissues are distinguished from all other tissues, not only by their yellow colour, but more especially by the character of their fibres, which, unlike all other known animal fibres, have been observed by

Lauth* and Schwann† to divide and anastomose (plate ii. fig. 6). In chemical properties the elastic tissues resemble the cellular and other tissues which yield gelatin by boiling, and of which the solution in acetic acid is not precipitated by ferrocyanide of potassium. (See Appendix to the Chapter on Nutrition.) Eulenberg‡ has recently discovered that, after long-continued (many days') boiling, they give out some gelatin, which differs, however, from the ordinary gelatin, being more like the "chondrin" which I have remarked to be afforded by cartilages and the cornea in boiling. The elasticity of the middle coat of arteries, the influence of which on the circulation of the blood has been described at page 199 et seq. is preserved for many years in alcohol. A portion of the aorta of a young whale, which I have received from my friend Professor Eschricht, is still highly elastic, although it has been several years in alcohol. Thin laminæ cut from it, are found, when extended, to have the same elasticity as caoutchouc. All elastic tissue retains its elasticity in the same way; this I have ascertained by experiment on all the elastic ligaments above-mentioned, after they had been kept in alcohol. In fact, the contractility of the fibrous coat of arteries is physical elasticity, not a vital property: it is exerted only after previous distension; for example, after the distension of the arteries by the blood impelled into them by the heart's contraction. Dr. Parry and Tiedemann have ascribed to arteries, in addition to their elasticity, a vital tonicity,—"tonus," a power of contracting, which does not essentially aid the rhythmic motion of the blood, but which is seen to be exerted in arteries which are laid bare, giving rise to a gradual narrowing of them: by virtue of this contractility, also, they supposed arteries to become narrowed at the time of death, before all circulation has ceased, to a greater degree than mere elasticity would account for. It has been long known that cold water is of use in arresting hemorrhage from divided arteries. Dr. Schwann has succeeded in affording an explanation of this important fact by an interesting experiment. He has found that in transparent parts, in which the arteries are not fixed, and nearly free from any dense tissue around them, the application of cold water can be seen to excite a very slow vital contraction of the small arteries. His experiment is detailed at page 206: the mesentery of the Rana bombina is best adapted for it, being more easily spread out than the mesentery of the frog. Dr. Schwann's experiment was repeated so many times that the fact is placed beyond a doubt. I have myself verified it in the Rana bombina, or brown toad. The arteries which manifested this contractility measured about $\frac{1}{10}$ of a line in diameter. Dr. Schwann has observed a slight degree of this contractility in arteries of some-

* Müller's Archiv. 1835, p. 4 —L'Institut, Jun. 14, 1834.

† Eulenberg, de Telâ elasticâ. Berol. 1836.—Müller's Archiv. 1836, p. xxv.

‡ Loc. cit.

what larger size. We have already shown (at page 206), that the experiments to determine the contractility of arteries, which were instituted with chemical agents, were of no value. [Dr. Hastings* observed contraction of the small vessels in the web of the frog's foot, as the first effect of the application of ice; but, from the too protracted action of the cold, the vessels afterwards became dilated, and the motion of the blood retarded.] By the aid of a high magnifying power, delicate and indistinct transverse fibres can be distinguished in the parietes of the smallest arteries of the mesentery of the frog; and Dr. Schwann has discovered that even the capillary vessels in the mesentery of the frog have similar fibres,—a fact which decides the question as to capillaries having distinct parietes. Since these transverse fibres of the minute arteries have the same direction and arrangement as the fibres of the elastic coat of arteries generally, it is doubtful whether the vital contraction which is excited in small arteries by cold be due to these fibres,—whether the elastic tissue of arteries, which retains its elasticity for years when kept in spirit, possesses during life that vital contractility, or "tonus," which is lost at the time of death; or whether the latter vital contractility of the smaller arteries is the property of unknown elements in their structure. We hesitate to ascribe the tone or vital contractility of arteries to their cellular sheath, because the small veins were observed by Dr. Schwann not to present that contractility. The "tone" of arteries differs from muscular contractility in not giving rise to sudden contractions, and also in not being distinctly excited by galvanism; cold being the stimulus by which most frequently the arteries, as well as the other contractile tissues which yield gelatin, are excited to contract.

d. Of the muscular tissue.

1. *Chemical properties of muscle.*—In respect to its chemical properties, muscle belongs to the class of animal tissues which cannot be made to yield gelatin by boiling, and of which the solution in acetic acid is precipitated by the red ferrocyanide of potassium: all the gelatin extracted from muscle by boiling is due to the cellular tissue which unites the muscular fasciculi. By these chemical characters muscular fibre may be easily distinguished from the different elastic tissues, including the elastic tissue of arteries, which yield gelatin in boiling, and of which the solution in acetic acid is not precipitated by ferrocyanide of potassium; whereas it is difficult and often impossible to distinguish chemically whether a body which belongs to the class of albuminous substances be muscle or not. Uncoagulated albumen may, it is true, be recog-

* Treatise on Inflammation, p. 55.

nised by its solubility in cold and lukewarm water, and by its property of being coagulated by a temperature of from 158° to 167° Fahr., by alcohol, and by metallic salts; uncoagulated fibrin may be known by its spontaneous coagulation when removed from the animal body; uncoagulated casein by its solubility in boiling as well as in cold water: but coagulated albumen and the coagulated fibrin of the blood and muscles cannot be distinguished from each other further than that fibrin decomposes the peroxide of hydrogen, while albumen has not that property. There is no chemical means of distinguishing the fibrin of the blood from that of muscle.

Those fibrous tissues, such as the fibrous tissue of the corpora cavernosa of the penis of the horse, which agree with muscle in their chemical characters, can be distinguished from it only by observing their vital properties; the red fibrous tissue of the penis does not contract when irritated (see the note at p. 226). If all muscular fibres were beaded or varicose, it would be easy to distinguish them by the aid of the microscope, but that is not the case. Even the contractility of the muscular fibres is not always sufficient to distinguish them; some fibrous tissues, as the dartos, have a slight degree of contractility; but these tissues are readily known by their chemical character of yielding gelatin.

The red colour of muscle has been ascribed to the presence of cruorin, the colouring matter of the blood; and the colour of muscle is, like that of the blood, rendered brighter by exposure to the air. But Dr. Schwann has once observed the naturally pale muscles of the carp become of a dark red during maceration for a short time in the cold in winter; a fact which seems opposed to the idea of the colouring matter of muscle and that of the blood being identical.

2. *Structure of muscle.*—The elementary parts of muscles are either beaded or cylindrical fibres, which are unbranched, and are arranged parallel to each other in fasciculi. According to Professor Krause, they are united together in the primitive fasciculi by a transparent tenacious fluid. The diameter of the primitive fasciculi, which contain from five to eight hundred fibres, is stated by Professor Krause to be from $\frac{1}{240}$ to $\frac{1}{29}$ of an English line. The diameter of fasciculi taken from the pharynx of the human subject was found by Dr. Schwann to be from $\frac{1}{47}$ to $\frac{1}{40}$ of an English line. The primitive fasciculi are invested and connected together by cellular tissue, so as to form larger secondary fasciculi, which are again connected together by cellular membrane. Anatomists differ very much in their accounts of the form of the primitive fibrils. Some, as Professor Schultze, describe them to be simple, uniform filaments; others, as Bauer, Home, Milne Edwards, Prevost and Dumas, and Professor Krause, regard them as composed of globules; while others, again, describe them to be beaded threads. The first and last

of these descriptions, though apparently contradictory, are both correct, these two forms existing in different kinds of muscle.

1. *Muscles, of which the primitive fibres have a varicose or beaded structure; the primitive fasciculi, cross markings.* (Plate ii. fig. 7 and 8.)—It is this class of muscles that has been the most examined. It includes those muscles of voluntary as well as involuntary motion which are more remarkable for their red colour; all the voluntary muscles, namely, except the expulsor muscle of the urinary bladder; and among the involuntary muscles, the heart. All red muscles, however, are not of this kind; thus, the red muscular substance of the gizzard of the bird belongs, together with the muscular coat of the whole intestinal canal, to the second class of muscles. [According to Ficinus, the stomach of the bird contains varicose muscular fibres.*] The muscles of this first class are moreover not always red. The muscles of fishes are generally pale; the muscles of the gill-covers alone are frequently red; and a thin layer beneath the lateral line of the body in the carp is red. The red and pale muscles of fishes do not differ in the slightest respect in their structure; examined with the microscope, they are seen to be formed of fasciculi with cross markings and beaded primitive fibres. All the muscles of this class are remarkable, not only for the strength, but also for the rapidity of their contractions, which ensue instantaneously on the application of the stimulus.

The transverse striæ of the primitive fasciculi, seen when a portion of these muscles is examined with the microscope, follow each other very closely, are always quite parallel, and generally pass in a straight line across the fasciculus; occasionally, but rarely, they are a little curved. On the primitive fasciculi of the heart the transverse striæ are much less distinctly visible, but nevertheless exist, as Professor R. Wagner correctly remarks. The fasciculi occasionally present a waved outline. The primitive fibres present a regular succession of bead-like enlargements, which are somewhat darker than the very short constrictions which intervene between them. It is not correct, however, to assert that these fibres consist of a mere aggregation of globules, for there is a distinct continuation of the fibre intervening between the enlargements; and the opinion that they are formed by the aggregation of the nuclei of the blood particles is quite untenable, for their size has been found both by Professor R. Wagner † and myself to be in many animals different from that of the nuclei of the red particles of the blood (see p. 360). The diameter of the beaded muscular fibrils is stated by MM. Prevost and Dumas to be 0·00012 of a French inch [$\frac{1}{641}$ of an English line]. In the frog I found their diameter from $\frac{1}{461}$ to $\frac{1}{738}$; that of the most minute fibrils in the parrot, $\frac{1}{385}$ of an English line. Their size was found by Professor Wagner to be very nearly the same

* See page 85.

† Burdach's Physiologie, 5.

in all vertebrata, in insects and in the craw-fish, as well as in the heart of the Helix pomatia; namely, from $\frac{1}{738}$ to $\frac{1}{923}$ of an English line. Professor Krause estimates the size of the fibrils at from $\frac{1}{738}$ to $\frac{1}{978}$ of an English line. The red particles of the blood of the rabbit are five or six times larger than the primitive fibres of its muscles.

Dr. Schwann has applied himself during an entire winter to the microscopic examination of muscle; the following are the results at which he has arrived. The diameter of the primitive fasciculi varies from $\frac{1}{46}$ to $\frac{1}{40}$ of an English line. To obtain the primitive fibrils in an isolated state, the muscles should be macerated at a low temperature varying from 34° to 50° of Fahr. during a period of from eight to twenty-one days. If macerated at a higher temperature, they are converted into a pulp in which the original structure cannot be recognised; but even at the temperature above mentioned the maceration affects the muscles of different animals differently. Sometimes the transverse striæ disappear before the primitive fibres separate; sometimes the muscle divides in the direction of its length rather than into its primitive fibres, although the transverse striæ remain distinct. The fibres are most easily examined in the muscles of the rabbit. They are beaded filaments, presenting under the microscope a succession of dark points from $\frac{1}{1666}$ to $\frac{1}{1250}$ of an English line in breadth, separated by bright and somewhat narrower portions of the filament. The distance of the points from each other is not everywhere the same; it can be estimated very accurately by measuring the length of a portion of a fibre which contains a known number of points. Thus a portion of a fibre from the human pharynx, containing five of the dark points or enlargements, measured 0·0060 of a line: one of the enlargements, therefore, with the transparent narrow portion belonging to it, measured 0·0012 of a line; of which about 0·0004 was occupied by the dark enlargement, 0·0008 by the narrow part. The appearance of transverse striæ on the primitive fasciculi is produced by the dark points of the fibrils being arranged side by side in the fasciculus; this is proved by the following circumstances. 1. The distance of the striæ and that of the dark points of the fibrils from each other is exactly the same. 2. The primitive fibrils sometimes become spread out at the end of a fasciculus of macerated muscle, without their relative position in the longitudinal direction being altered. The transverse striæ are then still seen in these expanded parts of the fasciculus; they correspond exactly in their degree of separation from each other with the striæ of other parts of the fasciculus, but are here distinctly seen to be formed of dark points, not sufficiently approximated to constitute a continuous line. 3. Lastly, the relation of the fibrils in the longitudinal position is sometimes disturbed; and the primitive fasciculus then appears at the first view to be dotted, not marked with transverse striæ. On a more close examination, however, it is seen that the dark points, when traced in the direction of the fibres, succeed each other at regular intervals, while in the transverse direction the series of points is irregularly interrupted.* The appearance of transverse striæ being produced by the dark points of the primitive fibres, it necessarily follows that the distance at which the striæ are separated from each other indicates the distance between the dark points of the fibres. In any single primitive muscular fasciculus the transverse striæ are all parallel; the dark points of all the primitive fibres of a fasciculus, therefore, are at equal distances. But the degree of separation of the transverse striæ may be very different in different fasciculi which lie close side by side with each other. This last circumstance is seen very remarkably in the muscles of the human pharynx. The space included by five transverse striæ of these muscles was in one fasciculus from 0·0065 to 0·0068; in another, from 0·0053 to 0·0056 of a line; in a third fasciculus the striæ were even much closer, so that they could not be counted. In a muscular fasciculus from the pharynx of another subject, the space occupied by five striæ was found by Dr. Schwann to be 0·0034; in another fasciculus, which lay quite close to the former, 0·0080 of a line. [According to Mr. Skey's observation, the distance of the striæ from each other is sometimes very different, even in the same fasciculus, at different parts.] The usual space occupied by five striæ in the voluntary muscles of the rabbit was from 0·0043 to 0·0046 of a line.

The limits to which this class of muscular fibres encroaches on the sphere of the organic muscles with uniform cylindrical fibres, has been already detailed at page 850.

[The primitive fasciculi are, as Mr. Skey has observed and figured, smaller in the fœtus; their diameter being about one third of that which they have in adult age.]

* [In a paper in the Philosophical Transactions for 1837, Mr. Skey has given an account of the muscular fibre, which differs in some respects from the descriptions of previous anatomists. Mr. Skey believes the striæ of the fibres (primitive fasciculi of Müller) to be independent of the filaments (primitive fibrils); the beaded appearance of the latter is owing, he thinks, to indentations made upon them by the striæ. Mr. Skey believes also that the fibres are really tubes, containing in their interior a semi-transparent amorphous substance, around which the filaments are arranged. The principal arguments which he adduces in support of this opinion are: — first, that the extremity of a divided fibre sometimes presents the appearance of a jagged circle terminating an apparently hollow tube; — second, that the fibre is frequently elongated to a point, up to the extremity of which the external surface presents the transverse striæ;— third, that when a fibre is separated into its filaments at its extremity, he sees no filaments projecting from its centre, but only from its borders;—fourth, that when dried on glass, the dark outline only of the fibre remains apparent, the centre is obliterated; — fifth, that the separation of a few filaments from the surface of the fibre never exposes other filaments beneath them.]

The beaded muscular fibres with primitive fasciculi marked with transverse striæ are not confined to vertebrate animals. The voluntary muscles of insects, for example, are wholly constituted by them. Each primitive fasciculus has a very delicate sheath, which can often be perceived forming a transparent border to the fasciculus.

Professor R. Wagner* has examined the structure of the muscles in many of the lower animals. He met with muscles of which the primitive fasciculi presented cross striæ, in insects, crustacea, cirropods, and arachnida.

2. *Muscles with uniformly cylindrical primitive fibres and primitive fasciculi devoid of transverse striæ.* (Plate ii. fig. 9.) — These fibres are found to compose the muscular coat of the whole intestinal canal of the higher animals from the œsophagus to the anus.

This is the more remarkable, as the muscles of the pharynx belong to the former class,—the muscles with beaded fibres. The diameter of the primitive muscular fibre from the large intestine of the human subject was found by Dr. Schwann to be 0·0007, 0·0011, and 0·0013; in the mean, about $\frac{1}{1000}$ of an English line. Their border or outline was quite smooth and even. In the uterus of the human subject, in the pregnant uterus of the rabbit, and in the urinary bladder, Schwann could detect no fasciculi marked with transverse striæ. From the human iris, and that of the rabbit, he was unable to obtain any isolated fibres; although he, as well as M. Lauth,† perceived in the iris a distinct appearance of fibres, which had a concentric arrangement near the pupillar margin, and a radiate disposition in the periphery. The circular fibres in the iris of the ox consist, according to Lauth, of fibrils collected into fasciculi which interlace one with another; M. Lauth perceived no other than the circular fibres. Dr. Schwann was able by traction to distinguish very easily the separate fibres of the iris of the pig without any previous maceration. They were very minute, $\frac{1}{5000}$ to $\frac{1}{3333}$ of an English line in diameter, and perfectly cylindrical, not beaded.‡

The muscular fibres of this second class occur among the invertebrata, according to Professor Wagner, in all mollusca in which he has examined the muscles, (in cephalopods, gasteropods, testaceous acephala, and ascidiæ,) and likewise in the echinodermata.¶

* Müller's Archiv. 1835, p. 318.

† L'Institut, No. 57. 70. 73. 1834.

‡ [The muscular filaments of organic life are not regularly aggregated together into cylindrical fibres, like those of animal life; the fasciculi into which they are collected have a much more loose and confused structure, as is described and represented by Mr. Skey. Philos. Trans. 1837.]

¶ For the account of the developement of muscles, and of Valentin's labours on that subject, see page 384. For a detail of the physical properties of muscle, we refer to Haller's Elementa Physiol. lib. xi. s. 2. § 2. and Weber's Anat. i. 396.

2. *Of the vital properties of muscle.*

In addition to the vital properties common to all animal tissues, muscles possess sensibility and contractility. The sensibility of muscles is seated in the sensitive nervous fibres distributed to them, and not in the muscular fibrils themselves: the contractility is the essential property of muscles, which manifest it under the influence of every stimulus; while other organs, not muscular, are by the same stimuli excited to the manifestation of other properties, such as sensation, secretion, &c. Muscles possess but slight sensibility to external impressions, such as cuts and punctures. A needle passed through the skin may be carried deeply into the substance of a muscle without pain being produced; the heart laid bare has been observed to possess a very slight degree of sensibility. The muscles, however, are endowed with a very delicate sense of their internal condition; or rather, their nerves communicate accurately to the sensorium a knowledge of the states induced in them by their contraction: by virtue of this property we are not only made conscious of the sensations of fatigue and cramp in muscles, but acquire through muscular action a knowledge of the distance of bodies and their relation to each other, and are also enabled to estimate and compare their weight and resistance. This muscular sense cannot, however, be seated in the same nervous fibrils which excite the motions. If, in a frog, the posterior roots of the nerves for the hinder extremity be divided, and the anterior left uninjured, all trace of sensibility is lost in the muscles as well as in the skin of the leg and foot, while the power of voluntary motion continues perfect. A portion of the leg may be cut off without exciting any motion of the animal. On the other hand, by dividing the anterior roots only, the power of motion may be taken away and the sensibility left.

Muscles are thrown into action by any stimulus applied to themselves or to their motor nerves. All stimuli, as mechanical or chemical influences, cold, heat, or electricity, produce the same effect. They all excite contraction of the muscles even when applied to their nerves. Acids act more readily when applied to the muscles themselves than when applied to the nerves; it is not, however, as we remarked at page 615, a constant rule that acids excite no muscular contractions, when they act on the nerves alone. Dr. Bischoff and Professor Windischmann have at all events frequently seen muscular contraction produced in the latter case. The property which muscles possess of contracting under the influence of any stimulus was made the subject of special study by Haller,* who called it "irritability," in contradistinction to the sensibility of nerves. There are, however, so

* Deux Mémoires sur les parties sensibles et irritables. Lausanne, 1756.

many hypothetical notions and false ideas connected with the name "irritability" in this sense, that it figures better in the history of medicine than in discussions on physiology itself.

Muscles retain their property of contracting under the influence of stimuli applied to them or to their nerves for some time after death; the period varying with the degree of complexity of the organisation of the animal. The more complex the structure of the body, the more dependent are its different parts on each other, and the sooner are the vital properties of individual tissues lost after the vital action of the system has ceased. The contractility of muscles is preserved for a longer time by cold-blooded than by warm-blooded vertebrata. The contractility of the heart is retained for several hours in fishes, reptiles, and amphibia; and in the frog the other muscles also retain their contractility for several hours, particularly in the colder season of the year: a tortoise for a week after decapitation presents some contractility in its muscles. In higher animals the muscular contractility is seldom retained more than one or two hours after death; there are instances, however, in which it is not lost for many hours, an example of which is afforded by the cutaneous muscle of the hedgehog. Nysten,* in his experiments on the bodies of executed criminals who were previously in good health, found that the different muscles lost their contractile property in the following order: the left ventricle of the heart first, the intestinal canal at the end of forty-five or fifty-five minutes, the urinary bladder nearly at the same time, the right ventricle of the heart after the lapse of an hour, the œsophagus at the expiration of one hour and a half, the iris fifteen minutes later, the muscles of animal life still later, and last the auricles of the heart; the right auricle being the part which retained its contractility longest, in one instance contracting under the influence of galvanism sixteen hours and a half after death. In birds the muscular contractility is lost sooner than in mammalia, — namely, in from thirty or forty minutes to an hour, after death. The muscles of young animals retain their contractility in general longer than those of adults. In new-born kittens Nysten excited contraction in the muscles by the application of stimuli three hours and forty-five minutes after death; and at the end of six hours and a half the right auricle was still irritable. A general conclusion which may be drawn from the preceding observation is, that the greater the influence of respiration on the animal, and the greater the necessity of aerated blood to the system, the shorter is the time of duration of the irritability in the muscles after death.

There are many substances which have the property of deadening the muscular irritability. The muscles of animals killed by immersion

* Rech. de Physiol. et de Chim. Path. 321.

in carbonic acid gas, hydrogen, carbonic oxide, or by the vapours of sulphur, contract very feebly, or not at all, when stimulated; while in the atmosphere, or oxygen, muscles retain their contractility much longer.* The action of pure water on muscles for any length of time diminishes their irritability in a remarkable degree. This was first observed by Nasse, and has been recently confirmed by Dr. Stannius. The legs of frogs freed from the skin, and laid for a short time in water, are no longer adapted for delicate experiments on the excitability of nerves and muscles.† Narcotic substances, applied directly to the muscles, destroy their irritability; applied to the nerves, they deprive the nerve, at the point which they have acted on, of the property of exciting muscles to contraction; but, between that point and the muscle, the motor power of the nerve is preserved. When animals are killed by the introduction of narcotic poisons into the blood, the irritability is not affected in so great a degree as by the local application of the narcotic in a concentrated state; muscular contractions can be excited by irritating the muscles or nerves for several hours after death in frogs poisoned by narcotics. Substances which have a decomposing chemical action on animal matters—the caustic alkalies, concentrated acids, and chlorine, for example,—annihilate the irritability of muscles instantaneously at the point which they touch. There are no bodies known to have the property of heightening the irritability of muscles.

Muscular contractility is subject to the general laws of animal excitability. Muscles become feeble if seldom excited to action; and a great exertion of their contractile power always induces temporary exhaustion of it. Excitement and rest are, therefore, equally necessary for the maintenance and increase of the muscular power. The excitement seems to cause the organic processes necessary for the nutrition and formation of muscular tissue to go on more quickly during the succeeding state of rest. Temporary exhaustion is, however, a necessary consequence of the state of activity, action and excitement being themselves always attended with changes of composition of the tissue (see p. 52). These facts may be demonstrated, to a certain extent, in the muscles even of a dead frog. The contractions of the muscles of the frog, if at first feeble, may be rendered more energetic by moderate and occasional applications of the galvanic stimulus; but the stimulus, being too frequently applied, exhausts the power of the muscles rapidly; and when the repeated action of the stimulus has caused the contractions to become feeble, rest often restores, in some measure, the irritability.

The state of contraction of muscles, which renders them firmer and harder, is alone the active condition; in their more elongated state they

* Tiedemann's Physiol. i. p. 551.—Nysten, loc. cit. p. 328.

† Hecker's Annal. Dec. 1832.

are relaxed. There is no fact to justify the supposition that muscles possess a power of active expansion. The opinion that the heart has such a power has been refuted by Oesterreicher (see p. 173). The living muscles must not, however, be supposed to be at any time in a state of complete relaxation. They are constantly, even in the state of rest, subject to the influence of the nervous principle; this is seen in the retraction of divided muscles, in the slight tremors of muscles laid bare during life, and in the distortion of the features, and drawing of the tongue to one side, in hemiplegia.

If a muscle be observed at the moment of its contraction, it is seen to become thicker in the same proportion as it is shortened; and very often its fasciculi are seen to be for an instant bent into waving lines. The circumstance of the muscles becoming firmer in the state of contraction might naturally induce the conjecture that their substance becomes condensed so as to occupy a smaller volume; although, without this being the case, the mere strength of the attraction of certain parts of the muscle towards each other would explain the increased firmness. I will pass over the less perfect observations of Glisson and Swammerdam,* and will detail merely the more accurate experiments of later date. The muscular part, which is to be experimented upon, is introduced into a cylinder filled with water, which is at one extremity elongated into a fine tube, in which the height of the water is noticed at the moment of the contraction of the muscles excited by galvanism. In such experiments, Barzellotti, Mayo, and Prevost and Dumas, who employed muscular parts of small volume, observed no change in the level of the fluid; while, by Professors Gruithuisen and Ermann,† a fall of the fluid was perceived. The change in the level of the fluid, observed by M. Ermann, was very slight. He introduced into a glass vessel the hinder half of an eel without the viscera, one wire of a galvanic battery being connected with the spinal cord, and another with the muscles of the body. The vessel was then filled with water to such an extent that a narrow glass tube, in which the apparatus terminated superiorly, was partly filled. The wires being connected with the poles of a galvanic battery, the water in the glass tube fell about four or five lines each time that the circle was closed and contraction of the muscles produced, and rose again when the circle was interrupted. The condensation of the muscular substance during its contraction is, therefore, far too slight to aid us in explaining the phenomena of muscular contraction. And it is possible that the condensation which took place in these experiments was owing to the air contained in the divided vessels being pressed out of them by their contraction; it might certainly be thus completely accounted for. When the experiment of M. Ermann is repeated, the portion of eel

* Haller's Element. lib. xi. s. 2. § 22.

† Gilbert's Annal. 40.

should be prepared under water, and introduced into the tube without coming into contact with the air.

The modes in which the muscles could become shorter during their contraction are threefold. 1. The zigzag inflexion of the muscular fasciculi. This can be seen with the naked eye in muscles during contraction, but may be more accurately observed with the aid of a lens. The fasciculi of muscular fibres are thrown into zigzag inflexions (fig. 56). MM. Prevost and Dumas* have in particular studied this phenomenon. They regard each muscular fibre as composed of a number of short lines (*a*, *b*, *c*, *d*,) disposed in a series, which can be approximated to each other. The length of these short lines, in the muscle of the leg of a frog, was from ten to twelve millim.;† the distance between the angles of inflexion of the same side, from sixteen to seventeen millim.; the space occupied by sixteen such inflected portions, when the fibre was straight, 172·5 millim.; and the space which they occupied in the contracted or bent state of the fibre, 130 millim. The degree in which the fibre became shortened was, therefore, $\frac{23}{100}$ of its length. Prevost and Dumas, moreover, measured the degree of shortening of the entire mass of the same muscle, and found it amount to $\frac{27}{100}$ of its length. Since this and the foregoing measurements nearly agree, MM. Prevost and Dumas concluded that the shortening of the muscle during its contraction was due to the above described angular inflexions of the muscular fibres. It is, however, from many reasons probable that the angular inflexion of the fibres observed by these physiologists, and so easily seen even with the naked eye, is not the sole, and perhaps not even the most essential cause of the shortening of the muscles.‡

Fig. 56.

* Journ. de Physiol. iii. p. 311.

† A millimetre is 0·03937, or nearly $\frac{1}{25}$ of an English inch.

‡ [Prof. Owen and Dr. A. Thompson doubt the accuracy of the observation, that muscular fibres, at the moment of contraction, are thrown from a straight to a zigzag line. Prof. Owen was led to doubt it, "from observing the contraction of the muscular fibres in small filariæ, (such as commonly infest the abdominal cavity of the cod,) and more especially from observing the contraction of the retractor muscles of a species of vesicularia." * * "Here each separate fibre of the retractor muscle is seen with great distinctness, and is characterized by a single knot or swelling in the middle. In the act of retracting the tentacles, the fibres become shorter and thicker, especially at

2. M. Lauth has made some important observations with regard to muscular contraction.* Exposing a muscle, which still preserved its irritability, to the action of galvanism under the microscope, he perceived that its contraction was effected in two ways. When the muscle contracted most forcibly, its whole secondary fibre or primitive fasciculus was thrown into angular inflexions; a more feeble galvanic stimulus caused a shortening of the entire secondary fibre, without any zigzag inflexion. In the latter case, the surface of the secondary fibres, or primitive fasciculi, is not smooth, but presents, in its whole extent, transverse rugæ (rides), which are also visible in the fibres while bent into zigzag lines, but are quite independent of that zigzag inflexion. It is probable, therefore, says M. Lauth, that this slighter degree of shortening is due to the contraction of the primitive fibres; and this contraction he supposes to be effected by the approximation of globules composing the fibres. In the primitive muscular fasciculi of insects I have observed a kind of cross marking, which is different from the ordinary close transverse striæ; it is seen most distinctly in those muscular fasciculi of insects which have lain in spirit, but is also frequently to be seen here and there in the fresh muscles. These (secondary) cross striæ are much more distant from each other than the primitive transverse striæ, but they occur at regular intervals; and the primitive fasciculus of muscle macerated in spirit often appears as if regularly articulated, and in such muscle the primitive fasciculi easily break at these points. The space between two of the secondary transverse striæ measures somewhat less than half the breadth of the primitive fasciculus. Five of the spaces measured $\frac{1}{100}$ of an English line; each space, therefore, would be $\frac{1}{500}$ of an English line. The secondary cross striæ were generally straight, sometimes rather oblique or curved, but always parallel to each other for a considerable extent of the fasciculi. In the muscles of insects which had

the central knot, but do not fall out of the straight line." (This mode of contraction of the muscular fibres of polypifera has also been observed by Dr. A. Farre, Philos. Transact. 1837, pp. 394 and 396.) "After the retraction has been effected, the fibres fall into a wavy or zigzag position; but this is characteristic of their state of relaxation under the circumstances which bring their two attached extremities nearer each other. In like manner, in the parallel longitudinal fibres of the filariæ, it is most evident that at the moment of contraction they become shorter and thicker, but do not alter their rectilinear position until the action has ceased, when they fall, like the parallel nervous chord, into zigzag folds, which continue until effaced by the restoration of the part to its usual length through the action of the exterior transverse fibres." Dr. Allen Thompson, on repeating the experiment of Hales and Prevost on the frog, "observed single fibres continuing in contraction, and being simply shortened, and not falling into the zigzag plicæ: and he was led to suspect, from this and other circumstances, that the zigzag arrangement was not produced until after the act of contraction had ceased." (Hunter's Works, vol. iv. with notes, by R. Owen, F.R.S. 1837.)]

* L'Institut, No. 57. 70. 73. 1834.—Müller's Archiv. 1835, p. 4.

been kept in spirit the fasciculi were distinctly constricted at these secondary cross striæ, and enlarged in their intervals; the constricted and tumid parts appearing dark or bright according to the variation of the light. Sometimes the constriction appeared light, the tumid part dark; sometimes, the focus of the microscope being slightly altered, the constricted part appeared dark. The light portion of the transverse constriction measured $\frac{1}{1429}$ of an English line; the dark intervening portion, $\frac{1}{769}$. These constrictions of the primitive fasciculi are certainly not due to the mere wrinkling of their sheath; for the sheath can be distinguished forming a transparent border to the fasciculus, and the constriction is seen to affect, not it only, but the muscular substance of the fasciculus formed of primitive fibres with primitive transverse striæ. The muscular fasciculi of insects being so similar in the form of their fibres and in the existence of the primitive transverse striæ to those of the higher animals, the appearance of secondary constrictions on the former is a circumstance of importance with reference to the explanation of muscular contraction; and the fact of the secondary transverse striæ or constrictions being present only in parts, renders it still more probable that they are due to the contraction of the primitive fasciculi. A fasciculus of fibres can, it is plain, become shorter in two ways; either by the whole fasciculus being bent alternately in opposite directions, the fibres in the intervals of the flexure remaining parallel to each other, which mode of shortening takes place visibly in the larger muscular fasciculi, or by the fibres of the fasciculus spreading out in the intervals of transverse lines which divide the fasciculus into aliquot parts. The latter mode of contraction takes place, very probably, together with the first, in the muscles of insects, and perhaps also in those of the higher animals.

3. It is possible that the muscular fibres of the second class (those of the organic parts of the body) contract both in the first and the second mode simultaneously; but there is a third manner in which the muscular fibres of the animal system may shorten themselves,—namely, the approximation of the bead-like enlargements, and contraction of the interspaces between these enlargements of the primitive fibres. Such a mode of contraction can neither be demonstrated, nor proved not to take place. The absence of the beaded enlargements in an entire class of muscles would render any theory of muscular contraction defective, which was based on them. Still, the approximation of the globules of the primitive fibre may very possibly take place in the muscles of animal life, in addition to the other modes of contraction which are seen in the primitive and secondary fasciculi; and there are, in fact, some reasons for believing that in them it actually does occur. These reasons are,—first, the circumstance that the beaded enlargements of the primitive fibres are not necessary either to the contraction of the primitive fasci-

culi into belly-like portions, or to their zigzag inflexion; for a whole series of the bead-like enlargements intervene between the flexures:—secondly, the positive argument that, according to Dr. Schwann's observations on contiguous fasciculi, the enlargements of the primitive fibres and the corresponding transverse striæ of the fasciculi are not always separated by equal intervals. This is all that can be said in support of the hypothesis of the approximation of the globular enlargements of the primitive fibres. There are, however, two ways in which such an action might be supposed to be effected,—namely, by the reciprocal attraction of the globules towards each other; or, supposing the primitive fibres to be hollow, by the distension of their varicose enlargements with a fluid so as to increase their size at the expense of the intervening parts of the fibre. It would be useless and rash to hazard any more remarks on this question. It is impossible, in the present imperfect state of our instruments, to determine whether such excessively delicate threads as the primitive muscular fibrils are solid or hollow; and an account of the opinions and bold hypotheses of the earlier anatomists regarding them would be misplaced in this work.*

The rigidity of muscles after death, rigor mortis.†—This phenomenon is due to a particular state of the muscles, which ensues at a certain period after death, giving rise to stiffness of the limbs, and after a time ceases. The rigidity affects the neck and lower jaw first, according to M. Sommer; next, the upper extremities, extending from above downwards; and lastly, reaches the lower limbs: in some instances it begins in the lower extremities, or affects them simultaneously with the upper extremities. Out of two hundred cases, M. Sommer only observed one in which the rigidity did not commence in the neck.

When the limbs have become rigid, the muscles, flexors as well as extensors, feel firmer. M. Sommer states that a slight motion takes place when the muscles become rigid; he affirms that Nysten was incorrect in stating that the position of the limbs always remains unchanged. The lower jaw, he says, though it be separated from the upper jaw at the time of death, becomes afterwards firmly drawn up towards it. The extremities also become more strongly flexed; thus the thumb is drawn towards the palm, and even the fore-arm is a little bent on the arm. If the rigidity of any part after it is fully developed be forcibly overcome, it is not reproduced; but, if the part be not yet in its complete state of rigidity, forcibly flexing it will not prevent its again becoming stiff. The rigidity usually ceases as it began; first at

* See Haller's Elementa, lib. xi. s. 3.

† Nysten, Rech. de Physiol. et de Chim. Pathol.—Guentz, der Leichnam des Meuschen, Leipz. 1827. — Burdach, Physiol. Bd. 3. — Nicolai, Rust's Magazin, 34. 2. — A. G. Sommer, Diss. de signis mortem hominis absolutam indicantibus. Pars. 2. Havniæ, 1833. 8.

the head, then in the upper extremities, and lastly, in the lower extremities. The rigidity, according to Sommer, never commences earlier than ten minutes, and never later than seven hours, after death. Both Nysten and Sommer state that its duration is greater in proportion to the lateness of its accession. If the muscular energy was undiminished at the period of death, as in men killed by asphyxia, the rigidity of the limbs ensues later and continues longer: while, on the contrary, in bodies of persons who have died of acute diseases attended with great depression of the vital powers, it comes on more rapidly; after death from typhus, for example, M. Sommer has sometimes known it to be developed in fifteen or twenty minutes. In the bodies of individuals exhausted by chronic diseases, the same fact is observed. After sudden death from acute diseases, the rigid state of the limbs continues for a long time, even though it be rapidly developed. Hunter and Himly have remarked that, in the bodies of persons killed by lightning, no rigidity of the muscles takes place; M. Sommer, however, states that, in a dog killed by an electric shock, the phenomenon ensued at the ordinary period after death. The remark of Orfila, also, that after death from the vapour of charcoal the limbs do not become rigid till after a longer period than usual, was found by M. Sommer to be incorrect: he remarks that, if in some cases the rigidity of the limbs appears to be late in being developed, this is owing not so much to the mode of death, as to a state of apparent death preceding the real cessation of life. The assertion that the muscles do not become rigid after poisoning with narcotic substances, is also contradicted by the experiments both of Nysten and Sommer on animals. Nysten had made the remark that the rigidity is equally intense in muscles paralysed by hemiplegia: this is confirmed by Sommer, with the provision that the paralysis must not have been attended with any considerable modification of nutrition, or with serous effusion of the muscles; for, in such a case, Sommer has once observed an entire absence of rigidity on the paralysed side. Nysten remarked that death from tetanus was attended with or quickly followed by a cessation of the spasms, and that the body then remained in a flexible state for some hours before the rigidity of the corpse ensued: in one case observed by Sommer, however, the tetanic cramp of the muscles of the jaw passed immediately into the rigidity of death. In new-born infants and old people, the rigidity of the limbs generally comes on earlier, is less intense, and lasts a shorter time. Sommer observed that, contrary to the statement of Nysten, the body in many instances becomes rigid before it is completely cold, and sometimes even while still warm. The body becomes rigid after death in water as well as in the air; but in water of the temperature of 32° to 66° Fahr. the rigidity is greater and of longer duration than in air of the same temperature. With reference to the question of the influence of the brain and spinal cord on the production of the phenomenon which we are considering, Sommer confirms Nysten's observations as to the fact that destruction of the central organs of the nervous system in animals has no influence on the developement, degree, or duration of the subsequent rigidity of the body.

The cause of the rigidity is, according to Nysten, seated in the muscles; for the limbs still remain stiff, though the fasciæ and even the lateral ligaments of the joints be divided, but become flexible as soon as the muscles are cut through. This statement is confirmed by Sommer, who adds that, although the limb recovers its mobility from the division of the muscles, still the divided muscles themselves remain firm and rigid,—a fact previously noticed by Rudolphi. Nysten referred the rigidity of dead bodies to the organic contractility of the muscular fibres. Of his grounds for this opinion, the most important is, that when the rigidity affects a limb which is completely flexed, the flexor muscles are found to be in exactly the same condition as during their voluntary contraction; they are not relaxed, but shortened, and thicker than in the ordinary condition. Sommer, however, does not admit the correctness of this statement. If one arm of a corpse be, at the time that it becomes rigid, in the state of flexion, the other extended, the biceps of the arm thus extended will, he says, become rigid as well as the other, though its rigidity does not resemble the state of voluntary contraction. With reference to this question, it is important to know whether the muscles, when rigid, still present signs of contractility under the influence of stimuli. Nysten had, in some instances, observed that a slight degree of contractility was preserved. Sommer found that generally the application of stimuli excited no contraction; sometimes distinct contractions were produced, without, however, influencing the position of the limbs. It is generally found, that the quicker the muscles lose their irritability, the sooner do they become rigid; thus the rigidity affects them soonest in birds: in reptiles and amphibia, in which the muscles retain their irritability for a long period, they are late in becoming rigid, and remain so a shorter time. Sommer ascribes the rigidity to a physical contractility of the muscles, distinct from their organic contractility or irritability; for it does not take place, he remarks, until all the vital phenomena have become faint: and a similar contraction of physical nature is seen after death in parts not muscular,—in the skin, in cellular tissue, in the fasciæ and ligaments. Orfila, Beclard, and Treviranus believed the phenomenon to be dependent on the coagulation of the blood. But M. Sommer thinks this opinion incorrect, since the body sometimes becomes very rigid when the blood has not coagulated, or but imperfectly: thus, in persons drowned, the rigidity of the limbs is very great, while the blood is often fluid; and the same is the case in men and animals killed by prussic acid. Sommer, however, admits the resemblance of the two phenomena,—that coagulation is the death of the blood, the state of rigidity the death of the muscles. I regard the correctness of the explanation of the phenomenon by the coagulation of the blood in the small vessels as by no means disproved. The coagulation of the blood and lymph in the small blood-vessels and lymphatics must render the muscles more firm; and it is a question only whether this increased cohesion of the muscles would alone suffice to explain the phenomena. This cannot be proved; but the hypothesis is so far tenable as it affords an explanation of the subsequent solution of the rigidity. The blood and lymph in coagulating become a solid, gelatinous mass; but after a time, and frequently after a considerable interval, the coagulum of fibrin, which includes the more fluid parts, contracts so as to expel the serum. As soon as this has taken place in the coagulated blood and lymph of the small vessels, the cohesion of all the textures must be diminished. The coagulation of the blood, and the coagulation of the adipose matter after death, in warm-blooded animals, both render the textures more firm; but, while the firmness produced by the coagulated blood is lost again, the adipose substance retains its coagulated condition. I do not, however, by any means affirm that the explanation of the post-mortem rigidity by the coagulation of the blood is correct, or that it is the one which I adopt. I merely say, that, in the present state of our knowledge, it seems to me impossible to prove either its correctness or its fallacy. Should it at a future time be determined that the rigidity of the corpse is owing to a physical contractile property of the muscular fibres exerted at the time of the loss of their vitality, and ceasing with their decomposition, the phenomenon would be more analogous to the physical contraction of the fibrinous coagulum to a smaller and denser substance.

CHAPTER IV.

OF THE CAUSES OF MOTION IN ANIMALS.

In an inquiry into the causes on which the motion of the solid textures of organic bodies depend, it is necessary in the first place to distinguish between the motions of parts devoid of nerves, and those which are consequent on a reciprocal action exerted between the contractile tissue and the nervous system. Motions of the first kind are presented by plants, and perhaps also by some parts of animals which are not muscular. The first traces of organic contractility in its simplest condition are observed in the Oscillatoria,—those simple vegetable filaments which consist of a tube filled with granules closely arranged in a linear order. These granules are at certain periods expelled from the tube, which does not thereby lose its contractility. On account of the simplicity of their structure, the motions of these vegetables are of great importance with reference to the theory of motion in organic bodies. I have seen them under the microscope at the house of Professor Meyen. When the filaments begin to move, they slowly, and with scarcely perceptible motion, bend to one side, and then after some time bend back again, and become curved in the opposite direction, the granules in the interior of the tube remaining all the time quite motionless. Since these movements take place independently of any attraction exerted by neighbouring filaments, and since no circulation or motion of sap can be detected in the interior of the filaments, we can conceive no other explanation of the phenomenon than that the component particles of the parietes of the tube, in consequence of an exaltation of vitality alternately on the two sides of the filament or tube, attract each other at those parts, so as to become condensed, or that the sides of the tube alternately at different parts attract and imbibe water, so as to become swollen with it. The idea of the walls of the tube becoming contracted by a wrinkling (Kräuselung) is quite incompatible with the appearance presented by the plant in motion. The spontaneous rhythmic motions of the leaves of the Hedysarum gyrans, which occur independently of external excitement, present us with the same phenomenon in a more highly developed vegetable.

The time has not arrived for inquiring into the causes of the ciliary motion. We do not even know by what mechanism it is produced. In its great independence of the influence of the nervous system it resembles the motions of plants. The motions of cellular tissue, or the contractile animal tissue which yields gelatin,—motions which are readily produced by the action of stimuli, particularly cold, heat, and mechanical influences, on the tissue itself,—in some degree resemble those of plants and the cilia, which are independent of the influence of the nervous system. They resemble the motions of plants in another circumstance also, namely, in not being perceptibly excited by electricity. The motions of the cellular and allied contractile tissues are not, however, entirely withdrawn from the influence of the nerves. The contraction of the skin and dartos is excited not only by external stimuli, but frequently also by causes seated in the nervous system. The dartos is frequently contracted, and the scrotum thrown into wrinkles, under circumstances where the presence of nervous excitement in the genital organs cannot be doubted, and where the cremaster is at the same time in action; the contractility of the skin also is frequently manifested under the influence of affections of the nervous system quite as manifest, —for example, it accompanies rigors (where there is both sensation and motion at the same time produced). Since, however, in the case of these motions, the nature of the influence exerted by the nervous system is not easily ascertained, our whole attention must be directed to the muscles, in which a most marked reciprocal action between the contractile tissue and the nerves is manifest.

The contractile property of the muscles is intimately dependent on two different influences,—the influence of the blood, and that of the nerves.

1. *Influence of the blood.*—Stenson first pointed out that muscles lose their power of motion when the current of blood (that is, of arterial blood) towards them is obstructed. This phenomenon is sometimes observed when a ligature is applied to a large arterial trunk in the human subject; the power of moving the muscles under the influence of the will is either partially or wholly lost, until the collateral circulation is developed. This fact has been confirmed by Arnemann, Bichât, and Emmert.* Segalas † also has observed that, when the abdominal aorta is tied in animals, the hind-legs are rendered so weak, that after eight or ten minutes they can scarcely be dragged along. Whether the principal influence of the blood consist in its maintaining the contractility of the muscles, or in its enabling the nerves to convey the influence of the will, has not been investigated. Treviranus argued, in opposition to M. Percy, that the blood is shown to be necessary to the muscles, since the division of the great arteries of the limbs into numerous anastomosing branches in some animals which use their muscles much in climbing,—for instance, the lemur and sloth,—seems to be a provision for the maintenance of an uninterrupted circulation during muscular action.‡ It is probable that the influence of the blood is necessary both to the muscles and nerves; yet it is certain that even after complete arrest of the circulation in dead animals, and in amputated limbs, the nerves are still capable, when irritated, of exciting the muscles to action; and the muscles also, when the stimuli are applied immediately to them, of contracting. The ligature of an artery does not altogether put a stop to the influence of the blood,—this fluid is still present in the small vessels; but the afflux of fresh arterial blood to the muscles and nerves is arrested. The experiments of Segalas also show, that when the capillary vessels are completely filled with blood, the circulation being nearly stopped by ligature of the lower part of the vena cava, the power of motion is still enfeebled. It is therefore certain that the arterial blood undergoes in the motor organs a change, which, while it gives the blood the venous character, renders it unfit to maintain in the muscles their contractile property,—in other words, that the property of con-

* Treviranus, Biologie, v. p. 281. † Journ. de Physiol. 1824.

‡ The arterial plexuses, or retia mirabilia, are as frequent in parts not muscular as in muscular organs; we may instance the rete mirabile of the internal carotid artery in ruminants, and the largest of all known vascular plexuses, that connected with the portal vessels in the tunny (thynnus), which has been discovered by Eschricht and myself.

tractility requires for its perfect preservation the constant action of arterial blood on the muscular fibre. This is confirmed by the phenomena observed in the subjects of the cœrulean disease; in whom, on account either of a patent state of the foramen ovale, or ductus arteriosus, or a narrow condition of the pulmonary artery, the arterial and the venous blood are mixed, or the process of arterialisation imperfectly performed. Such persons are incapable of any great muscular exertion. In reptiles and amphibia the necessity of the influence of the blood upon the nerves and muscles, for the maintenance of the power of voluntary motion, is not so great. Frogs are still capable of voluntary movements when their heart is cut out; they can even move limbs which are connected with the trunk by the nerves alone; and even after I had expelled all the blood, by forcing a current of water into an artery till it escaped from the divided veins, I found that the muscles still contracted when irritated.

2. *Influence of the nerves upon the contractility of muscles.*—The question of the action of the nerves in exciting the muscles to contraction must not be confounded with that of their influence in the maintenance of the muscular contractility. Haller regarded the contractility of muscles as a vital property peculiar to them, and independent of the nerves; he named it "irritability." This great physiologist, whose theory was adopted by Fontana, Soemmering, Nysten, Bichat, and others, taught that all stimuli acting on muscles excite their contractility without necessarily exerting their influence primarily on the nerves, and through them upon the muscles; and that the nervous stimulus is in fact merely one kind of the many stimuli by which the contractility of the muscular fibre may be excited. The proofs which Haller and his followers adduced in support of this theory have long lost their weight. The heart does not, as they supposed, act independently of all nervous influence, and its nerves are not insensible to external stimuli. The heart is, with reference to nervous influence, in the same condition as all other parts supplied by the sympathetic nerve. Not only can it be excited to contraction by galvanism, as has been observed by Von Humboldt, Pfaff, Fowler, Wedemeyer, and myself; but Humboldt and Burdach have succeeded in influencing its mode of action by irritating the cardiac nerves (see pages 191 & 663). The influence of the nerves on organic muscles can be demonstrated very distinctly also, as my experiments show, by irritating the cœliac ganglion, which causes the peristaltic motions of the intestines to become much accelerated (see p. 664). My own researches, and those of Wutzer, Retzius, and Mayer, have moreover sufficiently refuted Scarpa's opinion that the sympathetic nerve has no connection with the anterior motor root of the spinal nerves and the motor cerebral nerves. These facts, however, merely lead us to conclude that the nerves of the heart,

as well as the nerves of other muscles, transmit motor influence; they still leave undecided the question, whether in the sound body, and in a heart removed from the body, the cardiac nerves are necessary for the maintenance of the contractile power of the organ. The correctness of Haller's theory has been disputed by other physiologists,—as Whytt, Monro, Prochaska, Legallois, and Reil,—who contended that the motor power depends on a reciprocal action exerted between the nerves and muscles. Were such the case, the contractility of muscles would differ essentially from that of plants, which is excited directly by external stimuli, without the aid of nervous influence. In support of this opinion it is urged, that stimuli applied to the nerves excite the muscles to action; that narcotic substances, which seem to have a special action on the nervous system, when applied to the muscles, destroy their contractility; and that destruction of the brain and spinal cord also has the effect of diminishing the contractile power of the muscles. It must, however, be confessed that these arguments are by no means weighty. The duration of the muscular irritability is not less after the destruction of the brain and spinal cord, than after death from other causes; and poisoning with narcotic substances merely causes the influence of the brain and spinal cord to be no longer transmitted to the muscles. The irritability of the nerves and muscles is far from being destroyed in frogs by narcotic poisoning; I have seen the usual phenomena produced by the application of stimuli to the nerves or muscles for a very long time in frogs thus poisoned. Treviranus has adopted a middle course with regard to this question; and in accordance with what is observed in plants, which owe their irritability to the influence of light, but yet are excitable by other stimuli, believes that the influence of the nerves is a necessary condition for muscular irritability, but that all stimuli do not act by their intervention on the muscles. Tiedemann* agrees with Haller in regarding the muscular contractility as a peculiar property inherent in the muscles themselves, but believes the maintenance of this property in them to be dependent on nutrition and nervous influence; and further holds that the nerves do not merely conduct the stimulus which excites the muscular contraction, but afford an essential condition for the manifestation of the vital property of the muscles. This essential influence of the nerves may consist either in their imparting to the muscles their property of being affected by stimuli, in other words, of manifesting irritability; or it may be, that stimuli, even when applied to the muscles, must act first upon the nerves, and through their medium excite the contraction of the muscular fibre. It is evident, from the foregoing remarks of Tiedemann, that there are here involved two perfectly distinct questions: 1. Is the influence of the nerves necessary for the preservation of the vital pro-

* Physiologie. i. p. 547.—Transaction by Gully and Lane, p. 295.

perty of the muscles by virtue of which they contract, and is this property lost when the nervous influence is cut off? 2. Are the nerves conductors, through the medium of which all stimuli act upon the muscles? does even the apparently direct irritation of the muscles themselves act first on the nervous fibrils distributed in the muscular substance, and only through the medium of them affect the contractile tissue? The first question may be decided in the affirmative, without the second proposition being necessarily admitted; but if the second receive an affirmative answer, the admission of the first is a necessary consequence.

1. Is the integrity of the nerves necessary for the preservation of the vital contractility in muscles? Nysten had observed, that, a short time after an apoplectic seizure, the muscles paralysed in consequence of the cerebral lesion still contracted under the influence of galvanism; and Wilson, on the authority of Sir B. Brodie, asserted that a nerve, whose communication with the brain and spinal cord was cut off, retained, for a considerable time, its faculty of exciting the muscles to contraction when irritated.* I had reasons for suspecting that the persistence of this excitability of a divided nerve, when its continuity had not been restored by regeneration, is not without its limits; and several experiments instituted with reference to this question by me, in conjunction with Dr. Sticker, (see page 632,) have proved that, when the communication with the central organs of the nervous system is completely interrupted, not only the power of the nerves to excite muscular contractions, but with it the irritability of the muscles themselves, also, is gradually lost.

2. Are the nerves the sole conductors, through the medium of which all stimuli necessarily act on the muscles? The reasons for admitting such to be the case are the following:

a. The stimuli which excite the contractions of muscles, when applied directly to their tissue, are the same that produce the like effect when applied to the nerves. I have, it is true, frequently observed a difference in the action of stimuli on nerves and muscles; the mineral acids and alcohol namely, which, when applied immediately to the muscles, cause them to contract, had not the same effect when applied to the nerves. This difference does not, however, appear to be constant; for M. Humboldt has produced a tremor of the muscles by the application of alcohol, chloric acid, arsenic, and even of the metallic salts to the nerves; and Dr. Bischoff and Professor C. Windischmann have, I learn by private communication, in some instances seen muscular contractions produced in frogs by the application of mineral acids to the nerves.

b. The substances which destroy the contractility of muscles are also destructive of the excitability of nerves; for, although narcotic substances

* Phil. Transact. 1833, pt. i. p. 62.

taken into the circulation, and destroying life by their action on the brain and spinal cord, do not immediately annul the excitability of the nerves and muscles of the body,—the muscles and nerves of frogs thus killed retaining their excitability for a long period,—yet the immediate application of these substances to the nerves and muscles destroys locally the muscular contractility and nervous excitability. Nerves immersed for a short time in a solution of opium lose their susceptibility of stimuli to the extent to which the fluid has acted on them; while between this part and the muscle they retain their property of exciting muscular contractions under the influence of stimuli. Muscle also immersed in solution of opium loses its vital properties to the extent to which the contact with the poison has reached. This similarity of action of narcotics on nerves and muscles renders it probable, that the effect of such substances in making muscles to which they are applied insensible to the influence of stimuli, is owing to their destroying the excitability of the nervous filaments distributed in the muscular substance.

c. M. Humboldt dissected away the finest branches of the nerves from muscles (those of the upper parts of the legs of frogs and the fins of fishes), and then found that they were no longer sensible of the stimulus of galvanism.

d. Very powerful electric discharges, acting either upon the muscles or upon the nerves alone, are stated to destroy very quickly the susceptibility of the muscles for external stimuli.*

e. The fact which I have observed relative to the different effects of the application of galvanism or mechanical irritation to the motor and to the sensitive nerves distributed in muscles, may also be adduced as an argument. Irritation of the gustatory branch of the fifth, namely, excited no contractions of the lingual muscles, nor irritation of the infraorbital nerve any motion of the muscles of the nostrils and lips of animals. This fact proves that mere nervous influence, as a general property, does not act as a stimulus for muscular contractions in the manner of other stimuli; but that, for the excitement of muscles to contraction, a specific action of a special class of nerves is necessary.

f. Lastly, the extinction of the muscular irritability after a time, when the nerves have been paralysed by division, and their accidental union prevented, is another, and perhaps the most conclusive argument in favour of the opinion that, for the excitement of muscular contractions, the integrity of the nerves ramifying in the muscles is necessary, and that the muscles themselves are not susceptible of the direct action of stimuli.

Although the conclusion just stated seems to be proved by the arguments which we have adduced, yet it is evident that the contractility

* Tiedemann's Physiologie. i. p. 551.—Translation, p. 297.

must be a property of the muscles themselves, and that the nerves cannot even during life impart to them a power which they do not themselves possess. But the manifestation of the contractile property of muscles presupposes a concurrent action of the nerves; the discharge of an imponderable agent by the nerves is indeed as necessary for causing certain portions or minute elementary parts of the muscular fibres to be attracted towards each other, as this attraction of the parts of the fibre towards each other is essential for the shortening of the whole fibre. The modes of contraction of the fibres under the influence of nervous energy have been considered and illustrated by facts in the preceding chapter. The strength of the attraction between the angles of the inflected fibres may be best estimated from the power which the living muscles possess of resisting in their contracted state the greatest extending force; while after death, when this power of reciprocal attraction in their particles is lost, they are very easily lacerated and torn asunder.*

Of the mode of action of the nerves on the muscles in exciting their contractions we are at present quite ignorant. MM. Prevost and Dumas † have described the nerves to be so distributed in the muscles that at each of the angles of the muscular fasciculi formed by their zigzag inflexion in the act of contraction, that is to say, at each of the points towards which other parts of the muscular fasciculus are attracted, or which attract each other, there is a nervous fibre running transversely across (see fig. 56, p. 887). These transverse nervous filaments, according to MM. Prevost and Dumas, form loops, returning to the nervous trunk after having passed across the muscular fasciculi at the points of their angular inflexion. Dr. Schwann has examined with the microscope the distribution of the nerves in one of the lateral abdominal muscles of a frog, which are so thin that even with a magnifying power of 450 diameters the light which is transmitted is sufficient to make the whole structure visible. A magnifying power of 100 diameters only, however, was found necessary. The following was the structure observed:—The nerve entering the muscle gave off numerous branches, which very soon divided into smaller branches, and so on, until from the smallest fasciculi the primitive fibres themselves issued. The smaller fasciculi, as well as the primitive fibres, were frequently seen to be given off at right angles. Very frequently the nervous fasciculi, and still more the primitive fibres, united in their course with other fasciculi, both with those running in the opposite direction, as well as with those following the same course. This anastomosis of the fasciculi rendered it impossible to discern whether any of the fibres, after forming a loop, did really return to the nervous trunk

* Compare the observations of Tiedemann, Physiol. p. 553.—Translation, p. 299.
† Magendie's Journ. de Physiol. t. iii.

whence they arose. The anastomosis of the fasciculi was so frequent that the muscle appeared interwoven, as it were, with an irregular nervous net-work. There was no determinate relation as to position, however, observed between the nervous fibres forming this net-work and the muscular fasciculi. Some few times Dr. Schwann perceived the following arrangement: A fasciculus containing four nervous fibrils, for example, ran transversely across a muscular bundle; it gave off, at a right angle, first a primitive nervous fibre to the space between two primitive muscular fasciculi; then a second primitive fibre to the space between one of these muscular fasciculi and a third; a third nervous fibre came off from the nervous fasciculus, and entered the space between the third muscular fasciculus and a fourth; and the fourth nervous fibre was continued on to form an anastomosis with another nervous fasciculus. The three single primitive nervous fibres given off to the muscular fasciculi ran a certain distance parallel with them, and then disappeared without its being possible to ascertain what became of them. Perhaps they divided into much finer fibrillæ, like those which Dr. Schwann has discovered issuing from the ordinary nervous fibres, and forming a delicate anastomosis in the mesentery of the frog and the tail of the larva of the toad (see p. 604).

[MM. Prevost and Dumas observed only the smaller nervous fasciculi, not the primitive fibres. The later investigations of Emmert* and Valentin,† confirmed by E. Burdach,‡ have shown, however, that the nerves do really terminate in muscles by their primitive fibres forming loops or arches, the concavity of which is directed towards the nervous stem. According to Valentin and Burdach, the smaller ramifications of the nerve in the muscle, by a frequent interchange of filaments, constitute a plexus, from which the filaments forming the loops issue, and which they re-enter to return to the trunk of the nerve. Burdach states that this terminal plexus exists only near the extremity of the muscle not equally throughout its whole extent.]

The observation of MM. Prevost and Dumas, that the nervous fibres form loops running transversely across the muscular fasciculi at the points of their angular inflexion, serves as the basis for their theory of muscular motion, according to which these transverse nervous loops are supposed to attract each other, and thus shorten the muscular fibre. But in repeating their observations on living muscle it is evident that the parts of the nerves which in their transverse course are said to correspond to the angles of the zigzag inflexion of the muscular fasciculi, cannot be the primitive nervous fibres, but are entire fasciculi: for a portion of muscle in which it is possible to excite contraction

* Ueber die Endegungsweise der Nerven in den Muskeln. Bern. 1836.

† Nova Acta. Nat. Cur. t. xviii. pt. i.

‡ Beitrag zur Mikroskopischen Anatomie der Nerven. Konigsburg, 1837.

must be too thick to allow the primitive fibres of nerves to be seen; the primitive nervous fibres can be seen only by examining very thin laminæ of muscle with the compound microscope. The drawings which MM. Prevost and Dumas have given prove that they used only a simple lens. The observations, therefore, on which their theory is based, do not refer to the ultimate elements of the nerves and muscles. A part of their hypothesis consists in supposing that the nervous loops are traversed by electric currents; but, as we have seen at page 636, the existence of such currents of electricity in the nerves cannot be demonstrated. To obviate this main objection to their theory, MM. Prevost and Dumas suppose that the current of electricity in the nervous loops is double; and that for this reason, the two currents neutralising each other, the electricity cannot be detected by the galvanometer. They compare the fasciculi of muscular fibres to the magnetic needle of the galvanometer, which, like the muscular fibre, being subject to the action of opposite electric currents, is thrown into motion. Moreover, another inconsistency in the theory of MM. Prevost and Dumas is, that it attributes the shortening of the muscular fibre to the attraction of the nervous loops towards each other; and that the muscular fibre itself is consequently regarded as passive, and of no importance in the production of the phenomenon. This objection would, it is true, be avoided, were the hypothesis so far modified as to suppose the muscles to be charged with one kind of electricity, and a current of the other to be brought by the nervous fibres, the meeting of the positive and negative electricity causing the nervous loops and the muscular fibres to be attracted towards each other. In this case, however, the comparison of the muscular fibres with the needle of a galvanometer, which MM. Prevost and Dumas introduced into their theory, must be given up; and it is not easy to understand why the meeting of the two kinds of electricity should cause any attraction of the nervous and muscular fibre, why they should not neutralise each other as in other animal tissues without causing a reciprocal attraction of the component particles.

The same remarks apply to the theory of Meissner* (see p. 73), which supposes an electric atmosphere to be communicated by the nerves to the muscular fibres, and to cause these fibres to repel each other, like the electrified pith-balls on different threads fixed to an electric conductor; the two ends of the fibres being fixed must be approximated when the fibres are thus spread asunder at their middle by electric repulsion. Such a theory would afford an explanation of the appearance of alternate expansion and constriction of the primitive fasciculi of the muscles of insects. But, for electricity to have the effect here described, it is necessary that, like the pith-balls on the threads, the

* System d. Heilkunde aus allgemeinen Naturgesetzen. Wien, 1832.

fibres should be bad conductors of electricity; otherwise the equilibrium of the electricity would be restored without any motion being produced. The muscular fibres, however, are good conductors of electricity.

If, indeed, we reflect that the whole hypothesis of the similarity of the electric and the nervous principles is unsupported by any facts, and that, as we have shown at pages 634 and 635, these principles differ essentially as to their conductors and insulators, the theory of Prevost Dumas, and any other modified theory of muscular motion as due to electric action, will be perceived to be baseless.

The muscular fibres certainly appear to become shortened during contraction in the intervals of the nervous loops which cross the fasciculi; it is probable, therefore, that the parts of the muscle which are traversed by the nervous loops, and which are principally exposed to the nervous influence, attract each other, and thus give rise to the zigzag inflexion of the muscular fasciculi. The regular succession of intumescences and constrictions of the primitive fasciculi of the muscles of insects also afford evidence of an attractive force exerted in the direction of the length of the fibre between smaller segments of it, than in the production of the zigzag inflexion. This attraction also will depend on aliquot parts of the fibre being thrown into a state of attractive energy by the nervous influence. In the present state of our knowledge, it is impossible to go further than this in explaining muscular contraction. The contractile tissue of some plants,—the oscillatoria, mimosa," &c.—and the contractile animal tissue which yields gelatin in boiling, seem to be enabled to curve, contract, or shorten themselves by virtue of a property, like the contractility of muscles, peculiar to these tissues in their vital condition. But the vital property of muscular fibres differs from the endowments of those other contractile tissues in requiring the influence or discharge of the nervous principle to set it in action.

Dr. Schwann is engaged in performing some experiments with the view of ascertaining whether the contractile force of a muscle diminishes or increases as the contraction of the muscle is greater. He employs, in these experiments, the musc. gastrocnemius of a frog with the following apparatus. The frog being fixed upon a board with the thigh in the horizontal position, its leg is raised so as to be perpendicular to the board, and the foot again flexed to the horizontal direction, in which position the limb is firmly fixed. The ischiadic nerve is then divided high up in the thigh, and dissected out as low as the knee, the greatest care being used not to injure any vessels: the nerve is drawn out towards the side, where it can be laid upon two wires which first run horizontally along the surface of the board, but soon turn down and perforate it, passing without coming in contact with each other to a galvanic battery of a single pair of plates, with one pole of which one of the wires is connected, while with the other pole the second wire can be made to communicate by a slight pressure. The skin of the leg is left entire except at the heel, where a small incision is made for the passage of the tendo Achillis previously cut through in the foot. A thread tied to this tendon is connected with one arm of the beam of a balance suspended over the board. To the other arm of the balance a scale is attached. The arm of the balance which is connected with the tendon is lengthened to six times the length of the other arm by means of a straight wire attached to it; a slight contraction of the muscle producing, by means of this contrivance, a considerable motion of the balance-beam. The scale is now charged until it slightly overbalances the lengthened arm of the beam, which is prevented by a horizontal rod from rising, but can be carried downwards without meeting with any obstacle. The rod which stops the rise of the lengthened arm of the beam is so arranged that it can, with great accuracy, be altered by means of a screw to any higher or lower point, and is provided with a graduated measure to indicate the extent of its change of height. The apparatus being prepared with the long arm of the beam somewhat raised above the horizontal line, and the thread connecting it with the muscle being tense, the galvanic stimulus of a pair of plates of one square inch surface is applied to the ischiadic nerve. The contraction of the muscle causes the lengthened beam of the scale to be depressed. The level of the horizontal rod is now lowered to such an extent, that the contraction of the muscle can depress the arm of the balance but a very slight extent from the rod. The slight overbalance of the scale being regarded as 0, the extreme degree of contraction of the muscle is thus found. On the addition of weight to the scale, the beam could no longer be moved by the contraction of the muscle. At this point of its contraction, therefore, the power of the muscle was = 0. If, however, the level of the horizontal rod was gradually raised, there was found a point at which the contraction of the muscle moved the beam. At this less degree of contraction, therefore, the power of the muscle equalled the weight added to the scale. The amount of shortening, however, equalled one-sixth only of the extent to which the rod was raised. If double the former weight was laid in the scale, it was necessary to screw the rod up to a still higher level. Here then the power of the muscle was double that which it exerted at the former level, and the degree of shortening could be again found by referring to the instrument measuring the height of the rod. In this way the power exerted by a muscle under the influence of a determinate stimulus could be compared with the degree of its contraction. In performing the experiments, Dr. Schwann observed the precaution of applying the stimulus at equal intervals, and of ascertaining, after each circle of experiments, whether the muscle would again contract to the same point as before, the weight in the scale being as 0, or even of repeating each experiment in the reversed order; for example, first noting the height of the instrument with the weights in the scale, 0; then 50; and then 100 grains; and afterwards again 50, and at last 0 grain; taking the mean between the two numbers indicated at the same weight. The results of experiments instituted on a frog during the space of twelve hours in winter, a certain interval of time being allowed to elapse between the different experiments, were the following:

Experiments.	*Weight in the scale of the balance, showing the force of the contraction.*	*Comparative elongation of the muscle, as measured by the elevation of the horizontal rod.*	*Rate of increase in length of the muscle, compared with the progressive increase of force.*	
			Elongation of the muscle.	*Weight indicating the increase of power.*
Exp. 1.	0 grains . .	14·1		
	60 ,, . .	17·1	3·	from 0 to 60 grains
	120 ,, . .	19·7	2·6	,, 60 to 120 ,,
	180 ,, . .	22·6	2·11	,, 120 to 180 ,,
	0 at end of expt.	13·7		
Exp. 2.	0 grains . .	13·5		
	100 ,, . .	18·8	4·3	,, 0 to 100 ,,
	200 ,, . .	23·4	4·6	,, 100 to 200 ,,
	0 at end of expt.	14·4		
Exp. 3.	0 grains . .	13·7		
	50 ,, . .	18·7	4·3	,, 0 to 50 ,,
	100 ,, . .	20·3	2·1	,, 50 to 100 ,,
	50 ,, . .	17·7		
	0 ,, . .	14·1		
Exp. 4.	0 grains . .	13·5		
	100 ,, . .	19·1	5.6	,, 0 to 100 ,,
	200 ,, . .	23·2	4·1	,, 100 to 200 ,,
Exp. 5.	100 grains . .	16·8		
	0 ,, . .	12·7	4·1	,, 0 to 100 ,,
	100 ,, . .	16·1	2·4	,, 100 to 200 ,,
	200 ,, . .	18·7		
	100 ,, . .	16·1		
	0 ,, . .	11·7		

In the first two experiments, it appears, an uniform increase of force was attended with a nearly uniform increase of length of the muscle. In the last three, the rate of increase of force being uniform, the length of the muscle did not increase in the same proportion; but while the weight in the scales which balanced the power of the muscle was increased in a uniform ratio, the elongation of the muscle became less. The rest of the experiments instituted by M. Schwann afforded a precisely similar result. In those experiments, namely, which were performed earliest after the preparation of the frog, and in which, therefore, the normal conditions of the system were least disturbed, the power of the muscles was found constantly to become greater in the same ratio as they were less contracted, or to diminish as the contraction of the muscle was greater. The later the experiments were performed, the more did the results differ from this law, which may therefore be regarded as pretty exact for the normal condition. The same law regulates the force of elastic bodies. In the case of the muscles, it affords a refutation of every theory which supposes the force of muscular contractility to be due to any one of the forces of attraction already known to us, all of which increase in energy as the attracted parts approach each other, in the ratio of the square of the distance; for, did such a force of attraction exist in the particles of the muscles in such intensity as to cause the approximation of these particles when distant from each other, its intensity should be still greater when the particles were already approximated, or, in other words, the muscle already somewhat shortened. The power of the muscle ought therefore to be least when it is in its ordinary elongated state, to increase as it contracts, and be greatest when the contraction has reached its extreme degree. The experiments of Dr. Schwann, however, prove that the very reverse of this is the case, that the power of the muscle is greatest when it is least contracted, and is 0 when the contraction has reached its greatest degree. The hypothesis of MM. Prevost and Dumas does not accord with this law demonstrated by Dr. Schwann, since the magnetic attraction increases in force the more nearly the attracted bodies approach each other. The theory of Meissner is less opposed to the facts. It supposes, not a direct attraction of particles, but a repulsion in the transverse direction of the muscle. The more the muscle is shortened by such repulsion, the more distant would the repelled particles be from each other, and the less effective would become the repelling force. Here, therefore, the contractile power would diminish as the contraction increased. Dr. Schwann has, however, ascertained, by mathematical calculation, that did the contraction take place, as Meissner supposes, the force would not decrease in equal proportion with the shortening of the muscle.

In concluding this discussion on muscular contractility, it appears necessary to direct attention to the fact that any sudden change in the condition of the nerves of muscles, by whatever cause it be produced, is productive of a shock to the muscles. The closing or interruption of the galvanic circle, sudden destruction of the nervous tissue, burning, chemical influence, mechanical stretching, and all such influences, appear to give an impulse to the imponderable principle of the nerves, by which either a current or oscillation of that principle towards the muscle is excited, whether the external influence heighten or depress the vital energy of the nerves themselves. Hence muscular contractions may attend any, even the most feeble state of the vital forces, the nervous principle being capable of such motion or oscillation as excites the muscles to action, when any change is produced in the state of the nerves, even though the activity of the nervous principle is upon the point of being annihilated. We have here an opportunity of verifying the law laid down in the Prolegomena, that excitation is perfectly different from augmentation of the vital forces, — that an animal system may be stimulated to death, and that even the narcotic substances (the alterantia nervina), which have the property of producing so great a change in the nervous matter, give rise to symptoms of irritation or excitation, while they destroy the vital properties of the nerves.

SECTION II.

Of the different muscular movements.

CHAPTER I.

OF THE INVOLUNTARY AND THE VOLUNTARY MOVEMENTS.

The most obvious distinction which presents itself in classifying the different muscular movements, is that between the voluntary and the involuntary. On closer examination, however, this division is found to be less natural than it at first appears. It does not agree with the differences in the forms of the muscular tissue; and there are many involuntary movements performed by muscles which are subject to the will,—movements in some cases following as regular a rhythm as the motions of the heart. Certain muscles also, which are quite independent of the influence of the will, are nevertheless influenced by particular states of the mind; and lastly, the fact that the nerves have as great an influence over the involuntary as over the voluntary movements, deprives such a classification of much of its interest. The facts stated at page 850, were sufficient to show that a division of muscular movements into the voluntary and involuntary would not find any support in the anatomical structure of the muscular tissue; for, although the muscles of the organic parts of the system are distinguished by the absence of transverse striæ on the primitive fasciculi, and by the uniform cylindrical character of their fibres, while they act also independently of the will, yet the urinary bladder, which in respect to structure belongs to the organic muscles, is capable of some degree of voluntary motion. The fasciculi of the fibres of the iris again have not the cross striæ, and nevertheless a voluntary influence can be exerted indirectly upon the iris by turning the eye inward (see page 684). On the other hand, though the muscles of the animal parts of the system are characterised by the transverse markings of the primitive fasciculi, and the beaded form of their fibres, at the same time that they are subject to the will, yet the heart here constitutes an exception, it being referable by the structure of its fibres to the animal muscles, but with respect to its involuntary motion to the organic. There is no correspondence also between the colour of the muscles and their division into involuntary and voluntary. The voluntary muscles are generally red; but those of fishes are, for the most part, white. The muscles not subject to volition, as the muscular coat of the intestines, are generally of a pale colour; but the muscular gizzard of birds and the heart are composed of muscle of a deep red colour; while the muscular coat of the bladder, which is in some measure under the influence of the will, is as pale as that of the intestines. This difference of colour is certainly not merely owing to the greater or less abundance of blood-vessels, and of the red colouring matter of the blood. The peculiarity appears to reside in the muscular substance itself, which agrees with the cruorin of the blood in being rendered of a brighter red by the action of the atmosphere. The division of the muscular movements into the voluntary and involuntary finds, it is true, better support in the difference of the nerves supplying the different muscles; but even in this point of view it is subject to exceptions, the urinary bladder and iris, though supplied by the sympathetic, being capable of some voluntary motion.

If, indeed, we reflect that many muscles, which are ordinarily under the influence of the will, are nevertheless constantly being thrown into contractions in opposition to the will, as is the case, for example, with the sphincter ani; that some muscles belonging to the animal system, are incapable of being made to act voluntarily, except in very few individuals, of which we have examples in the cremaster, &c.; and lastly, that all the voluntary muscles are also frequently excited to involuntary action, whether in consequence of "nervous reflection," or "associate nervous action," or by mere mental conceptions,—as in laughing, yawning, or sighing, and still more frequently by passions of the mind,—it will be seen that we have reasons sufficient for adopting a classification in which the internal causes of the different motions are more kept in view. Since the class of involuntary motions is founded on a negative character, some physiologists have more aptly divided the animal movements into the voluntary and automatic. The involuntary motions are, however, with reference to their causes, of such various kinds, that this division also appears to me to be objectionable: for what constitutes the difference between the automatic rhythmic movements of the heart and respiratory muscles, and the movements from reflex nervous action? The different causes of the muscular motions seem to be best kept in view in the following classes.

1. *Movements excited by heterogeneous stimuli, external or internal.*

By heterogeneous stimuli I understand here all other causes of muscular contractions than the mere impulse of the nervous principle itself. There are but very few instances in which such stimuli give rise to muscular actions in the normal state of the body: such is the case, however, for example, with the stimulus of the bile and fæces, which excite the movements of the intestines; with the stimulus of the urine causing the bladder to contract, &c. For the production of muscular motion, a change in the state of the nerve supplying the muscle is necessary. It is indifferent whether this change in the nerve be effected through the medium of its anatomical connections with the central organs, or from its own blood-vessels, or whether the influence which produces it be derived entirely from without. All muscles, animal as well as organic, are equally capable of being excited to motion in this manner; but the movements thus produced are always involuntary, whether the muscle be ordinarily withdrawn from the influence of the will or not. The point at which the stimulus may act is threefold.

a. It may act on the muscle itself.—In this case, the nervous fibrils distributed in the muscle are primarily affected, and through their influence the muscular fibre is made to contract (see page 898). The direct application of an external stimulus causes the heart, the intestinal canal, the urinary bladder, and all the involuntary as well as the voluntary muscles, to contract. There is, however, this difference to be observed, that the movements thus excited in the organic muscles, which are under the influence of the sympathetic nerve, are not always a rapid momentary contraction immediately following the application of the stimulus, as is the case in the animal muscles, but either a gradual increasing contraction, ensuing more slowly, enduring longer, and reaching its maximum when the action of the stimulus has ceased,—which mode of contraction is seen in the intestinal canal and uterus,—or a long-continued modification of the ordinary rhythmic action of the organ,—as when the heart is irritated. (See page 731).

b. On the nerve. — The application of a stimulus to the nerve before it has reached the muscle has the same effect as irritating it in the muscle itself. This is a fact well known with regard to the cerebro-spinal nerves; but that it is true of the organic or sympathetic nerves also has been more recently discovered. (See pages 732 and 733.)

c. On the central organs of the nervous system.—Irritation of the brain and spinal cord always gives rise to contractions in the muscles which derive their nerves from the irritated part of the nervous centres. The influence of the brain and spinal marrow on the movements of parts supplied with cerebro-spinal nerves has been considered at page 840; and the influence of the same parts on the organs of which the nerves belong to the sympathetic system, at page 730. The experiments of Dr. Wilson Philip tend to show that every part of the brain and spinal cord can exert an influence on the motions of the heart; while, in the case of the muscles supplied by cerebro-spinal nerves, particular parts of the brain and spinal cord are always connected with particular muscles.

An important difference is found to exist in the action of irritating agents. Many stimuli — as mechanical irritants, heat, electricity, the alkalies, and other substances, — excite muscular contractions when applied directly either to the muscles themselves, to the nerves, or to the central organs of the nervous system. Other substances, on the contrary, excite no contraction of the muscles, unless when they act on the central organs of the nervous system through the medium of the circulation: thus the local application of narcotics to a muscle or nerve destroys their irritability or excitability at the part acted on, but gives rise to no muscular contractions; while the same substances produce the most violent convulsions, when, mixed with the blood, they exert their influence on the brain and spinal cord. That in animals poisoned by narcotics the convulsions are due to the irritation of the great nervous centres, is evident from the fact that division of a nerve puts a stop to the tetanic convulsions in the part which it supplies. (See page 629.)

2. *Automatic movements.*

By automatic movements it is intended here to designate all those muscular actions which are not dependent on the mind, and which are either persistent or take place periodically with a regular rhythm, and are dependent on normal natural causes seated in the nerves or the central organs of the nervous system. The cause of the rhythmic movements may be either in the sympathetic nerve or the great nervous centres, but never in mere cerebro-spinal nerves.

a. Of the automatic movements dependent on the sympathetic.

These movements are presented, 1, by muscles of which the primitive fasciculi are marked by transverse striæ,—namely, by the heart; and 2, by muscles of which the fasciculi have no transverse markings, —as the intestinal canal, uterus, and urinary bladder.

The automatic movements of the heart, like those of the animal muscles of the body, are contractions of momentary duration succeeding each other quickly. The automatic motions of the muscles of the second series are more gradual and more enduring, and their intervals of rest are much longer. Whether this difference be owing to the different structure of the muscle, or to the nature of the nervous influence, is not known. The fact that the bladder, although it may be made to contract voluntarily, yet is not capable of a rapid contraction, is in favour of the kind of motion being due to a peculiarity of the muscular tissue. The action of the urinary bladder being, when the viscus is distended, periodically increased in force, is so far referrible to the automatic movements, but otherwise does not belong to them.

In all the automatic movements of the viscera of organic life, without exception, there is observed a certain order of succession in the contractions; one part of the viscus contracts before another, and the motion thus traverses the organ in a determinate direction during each period of the rhythm. In the heart of the frog, the motion is seen to commence in the venæ cavæ, and to proceed through the auricles and ventricle till it reaches the bulbus aortæ, which contracts last. In the intestine, the movement travels in a vermicular manner from above downwards; and a second movement, beginning at the upper part of the intestine before the first has completed its course, affects the parts in the same order. The rhythmic motion is seen even in the lower part of the œsophagus. It is proportionally very feeble in the morning. The contractions even of the uterus of animals is vermicular; at least they are so, as I have witnessed, in the rat when excited by irritants locally applied. The periodic contractions of the uterus are generally observed to occur only during parturition; they in rare instances take place during pregnancy, but are then more feeble. The action of stimuli on organs endowed with automatic motion does not generally alter the order of the contractions; to produce such an effect, the irritation must increase to a great degree, and an antiperistaltic motion is then produced; but this reversed order of the automatic movements may also attend the interruption of nervous influence in cerebral affections. Irritation of organs presenting the automatic movements has also an influence on the rapidity and force of the contractions; stimuli, whether external or internal, acting on the heart, cause it to beat quicker and more forcibly. In acute diseases of great intensity, which make such an impression on the central organs of the nervous system as to give rise to fever, the heart not only acts more frequently than natural, but even the mode of contraction of its fibres is altered, causing hardness of the pulse; hence in fever, while the powers of the system are unimpaired, the pulse is hard, strong, and quick. In proportion as the powers of the system decline, the impression of the disease on the central organs continuing, the beat of the heart, though it retains its altered character, becomes feeble; and the pulse accordingly, still hard, also becomes weak, while it increases in frequency. A hard, full, and frequent pulse, therefore, is in acute disease an indication that a violent impression is made on the nervous centres, the vital powers not being essentially impaired; while, in proportion as the pulse, still hard, becomes more feeble and frequent, we know that the vital powers are sinking. The pulse becomes slower in many affections, not inflammatory, but attended with interruption of the functions of the central organs of the nervous system, — such as syncope and apoplexy. The motions of the intestinal canal are rendered both more energetic and quicker by external irritation, as when the intestine is exposed to the air; or by internal irritation of its mucous membrane, as in diarrhœa: irritation of the spinal cord also is productive of spasmodic automatic movements of the intestinal canal and uterus. The same increase of the automatic movements is produced by irritation of the sympathetic nerve; such, at least, is the effect of irritation of the cœliac ganglion by the application of caustic potash on the intestines of the rabbit.

Many of the organs which present the automatic movements are provided with sphincters. While the automatic contractions of these muscular tubes or sacs become periodically stronger, the sphincters, as for example the sphincter vesicæ or os uteri, remain for a time constantly closed; but their resistance is at last overcome, and they are dilated by the contents of the viscera, which are thus driven against them with increasing force. The antagonism which subsists between the sphincters and the muscular coats of the viscera is evidently not so much due to any cause seated in the muscles themselves, as to the mode of action of the nerves in them. Reil* supposed that there was a polarity of action between the fundus and the cervix uteri; but this supposition does not make the matter clearer. The dilatation of the sphincters appears to be for the most part the consequence of the pressure exerted against them from within. After the expulsion of their contents both the muscular viscera and the sphincters gradually contract again,—the sphincters, as before, uninterruptedly, and equably, and the coat of the hollow viscus with periodic increase of intensity. The *after-pains* of the parturient woman seem to be the expression of the rhythmic contractions of the uterus.

The primary cause of the rhythmic contractions of the organic muscles is connected with the mode of action of the sympathetic nerve on the muscles; it is not seated in the brain or spinal cord. This constitutes an essential distinction between the automatic movements of the organic and those of the animal muscles. The rhythmic contractions of the heart continue even when it is removed from its connections in the body. This continued action of the organ is not due to the stimulus of blood, for it is kept up with the same regularity when the heart is emptied of all its blood. The action of the heart continues also in vacuo; it cannot, therefore, be owing to the stimulus of the air. The intestinal canal likewise still presents its peristaltic motions when removed from the body; and the separated oviduct of a turtle has been seen to contract so as to expel the ova.

The inquiry as to the cause of muscular contractility (see p. 896)

* Reil's Archiv. Bd. 7.

leads to the conclusion that a concurrent action of the nerves is always necessary for the act of muscular contraction; and hence, as well as from the fact that stimuli applied to the cœliac ganglion produce a change of some duration in the peristaltic movements of the intestine, we must infer that the organic nerves distributed in the muscular substance have a principal share in the production of these automatic movements, and that the rhythmic contractions of these organic muscles are not independent of the nerves, as Haller believed. The cause of the rhythm may be in the muscular fibres themselves, or it may be in the nerves. If it be in the muscular fibres, we must suppose that while the action of the nerves is constant, the muscular fibres of the heart lose for a time their capability of contracting, which is restored during a short repose. If the cause of the rhythm have its seat in the nervous fibres, the susceptibility of the muscle must be persistent; but the current of nervous principle must, from some causes appertaining to the nerves, be emitted from them so as to act on the muscles only periodically. The hypothesis that the heart each moment, or eighty times in a minute, loses its susceptibility of the still constant influence of the nervous principle, and as often regains it, is improbable, from the circumstance that all other muscles are capable of persistent action if the stimulus be continued. So rapid a restoration of the excitability also is as improbable as the frequent loss of it, for the renovation of the excitability in exhausted muscles requires not repose alone, but also the action of the arterial blood circulating in them; and arterial blood can no longer circulate in the vessels of a heart cut from the body, and nevertheless its rhythmic movements continue under such circumstances, even when the blood is removed from its cavities. The second hypothesis, namely, that the excitability of the heart is persistent, but the action of the nerves on it periodic, is more probably correct.

This second hypothesis requires a more close consideration. The effect which irritation of the cœliac ganglion produces on the motions of the intestines renders it probable that this ganglion has a share in the production of the rhythmic motion; but even after the caustic potash used to irritate the ganglion has destroyed its structure, the rhythmic motions still continue for a long period, and even the intestine alone, separated from the mesentery, continues its peristaltic contractions, the power of determining the muscular fibres to peristaltic motion must therefore be possessed by the sympathetic nerves of the intestines after they have issued from the ganglion,—indeed, by their branches contained in the coats of the intestines. Confirmatory of the conclusion that the branches of the sympathetic nerves distributed to the organic muscles have the same influence on the peristaltic motions as the cœliac ganglion is proved to have, is the fact that a minute examination of the branches of the sympathetic often detects the presence of very small secondary ganglia distributed irregularly in them. Retzius* has observed such minute ganglia on the twigs from the sympathetic, which accompany the divisions of the fifth nerve (see p. 668). I have once seen such small ganglionic enlargements on the communicating branch between the sympathetic and a dorsal nerve, and, in the neighbourhood of the posterior extremity of the prostate, in those branches of the hypogastric plexus which I have discovered to enter the posterior part of the corpora cavernosa penis, both in the human subject and in the horse. If portions of the sympathetic nerve of considerable length be minutely examined, small knot-like enlargements, which might easily be overlooked, are not unfrequently seen, when the fasciculi are separated from each other to some extent. Remak has frequently isolated such minute knots, which are easily discoverable by the naked eye. On the minute microscopic filaments of the sympathetic nerve discovered by Dr. Schwann in the mesentery of the brown or fire-toad (rana bombina), he has seen small enlargements separated by considerable intervals. These small enlargements of the sympathetic are not identical with the varicosities observed by Ehrenberg on the primitive fibres of that nerve.

It has been proved that the automatic motions of the organic muscles, like all muscular motion, depend primarily on the influence of the nervous principle; that the cause of the rhythm of these automatic motions is not connected with the nature of the muscular fibres, but with the peculiarity of the nervous system of the organic muscles; and that the cœliac ganglion has the property of exciting, when irritated, the peristaltic motions of the intestines. It appears, moreover, that the sympathetic nerve retains its ganglionic structure even in its more minute ramifications; and the power of the intestine to perform its peristaltic motions is found to be preserved even when it is separated from the mesentery. From these facts, then, I conclude that even the minute branches of the sympathetic which ramify in the intestinal coats have the same power of causing periodic contractions as the cœliac ganglion was proved to possess. The explanation that applies to the peristaltic movements of the intestines has the same force with relation to the rhythmic motion of the heart; the first observed motion of the heart in its simple tubular condition is indeed of a peristaltic nature. Since, therefore, not merely the larger ganglions of the sympathetic, but even its ultimate ramifications in the tissues of organs, seem to possess the power of giving rise to periodic motions, we can understand how the rhythmic movements of the heart, intestine, and oviduct of the turtle are enabled to continue when these organs are removed from their connections in the body.

Hypothetical explanation of periodic movements.—Let us now inquire

* Isis, 1827.

whether it be not possible to frame an hypothesis which shall afford some explanation of the periodic action of the nervous principle in parts under the influence of the sympathetic. When a definitive explanation of phenomena is yet impossible, an hypothesis which is not opposed to the facts, but on the contrary accords with them, and which opens a new field for further research, is admissible even in an exact science founded on facts. Such an hypothesis appears to be the following:—It being supposed that the sympathetic nerve is the seat of constant currents of the imponderable nervous principle transmitted from the centre, or point of origin, to the periphery in the organs supplied by the nerve, the question is, How can the constant motion of the nervous fluid be changed to a periodic motion? This may be illustrated by comparing it with what takes place when a constant current of electricity meets with an imperfect conductor. Thus, when a conductor of electricity is held at some distance from the electric machine, which is kept in a state of constant electric excitement, the electricity is given off periodically in sparks. The dry air, which intervenes between the conductor of the machine and the conducting substance held near it, is an imperfect conductor of electricity, and impedes the progress of the electricity from the machine to the conducting body, until it accumulates in such quantity as to overcome the impediment thus offered to its course; hence the electricity escapes in a succession of sparks. We intend this merely as an illustration of the mode in which the current of the nervous principle may be rendered periodic: we have refuted the idea of the identity of the nervous and electric principles in another part of the work (see p. 634). The ganglia of the sympathetic nerve have frequently been compared to imperfect conductors; and we have seen that the nervous principle certainly travels much less rapidly in the sympathetic than in the cerebro-spinal nerves (see p. 731, parag. vi.): some impediment, therefore, to the motion of the nervous principle must exist in the sympathetic which is not present in other nerves, where the influence of a stimulus applied to the nerve is communicated with immeasurable rapidity to the muscle so as to cause its instantaneous contraction. The sympathetic nerves may therefore be compared to imperfect conductors, whether the insulating influence be seated in the ganglia or in the nervous fibres themselves. This being granted, the cause of the periodic action, or periodically increased action of the nervous principle on the muscular fibre, is obvious. The ganglionic parts of the sympathetic nerve will, as imperfect conductors, tend to arrest the current of the nervous fluid. The general current, on the other hand, following the peripheral distribution of the nerve, strives to reach the organic muscles. As soon as the insulating particles of the sympathetic have in this way received the maximum of the nervous principle of which they can resist the progress, they suddenly communicate it to the organic muscles; the current of nervous influence then begins again to be arrested for a time. Did such a process take place in the sympathetic nerve, even to its peripheral ramification in the muscles, the ganglia, which are met with in such frequency on a small scale in it, must play an important part as imperfect conductors or partial insulators of the nervous principle.

The muscular movements dependent on the sympathetic nerve have not universally an intermittent type; the sphincters, which are subject to the influence of the sympathetic, have, for example, a persistent type of action. In these last muscles, then, the current of the nervous principle is uninterrupted. The sphincter of the urinary bladder is almost constantly in action; it is subject to only occasional relaxation. It is remarkable that the bladder, which presents this constant muscular action, receives, not merely organic nerves, but also cerebro-spinal nerves, in which the current of nervous influence can go on uninterruptedly. The nerves of the urinary bladder are derived not merely from the hypogastric plexus, but in part from the third and fourth sacral nerves. The persistent contraction of the sphincter of the bladder is, in fact, not so much dependent on the sympathetic nerve as on the cerebro-spinal nervous system. The sphincter is paralysed by diseases seated in the brain or spinal cord. Division of the spinal cord paralyses the sphincter vesicæ as well as the sphincter ani, which is under the influence of the will; while the motions dependent solely on the sympathetic nerve go on independently of the brain and spinal cord even when these organs are removed from the body.

Admitting that the organic nerves have really the property of arresting the transmission of the nervous principle for a time, so as to prevent its rapid escape, the continuance of the motions in viscera supplied with nervous influence by these nerves for a considerable time after their connection with the brain and spinal cord is at an end, will be intelligible. The organs under the influence of the sympathetic are not, however, wholly and permanently independent of the brain and spinal cord. When these central organs of the nervous system are exhausted by want of rest and sleep, or by the impression of acute diseases, the dependence of the organic viscera on them, which is not observable when the supply of nervous influence to the sympathetic is arrested only for a short period, becomes as evident as in parts supplied by cerebro-spinal nerves; the power of the heart and other organic muscles becomes exhausted.

b. Of the automatic movements dependent on the central organs of the nervous system.

The same muscles being engaged both in the involuntary movements of respiration and in voluntary movements, it would naturally occur to the mind that these different modes of action of the same muscles were determined by different nerves. Sir C. Bell* endeavoured to prove by experiment that the power of performing one of these kinds of movements may be lost, the muscles still preserving their capability for movements of the other kind. He told a patient with hemiplegia to raise his shoulders; in spite of the greatest effort, the shoulder of the sound side only was raised. The voluntary motions of the thorax appeared to be lost on the paralysed side; but, when the patient was directed to take a deep inspiration, the shoulder of the paralysed side was raised as well as that of the sound side. This, however, merely proves that a patient who has the power of taking a deep inspiration, still possesses voluntary influence over the muscles which raise the shoulder. Sir Charles Bell, however, explained the result of this experiment by supposing that the nervus accessorius, which is distributed to the trapezius and levator scapulæ muscles, may retain its power as a respiratory nerve, while the branches of the spinal nerves sent to the same muscles are paralysed; and thus that the power of elevating the shoulder during respiration, to free the thorax from the weight of the shoulders, which is due to the influence of the spinal accessory nerve, may be retained while the same movement as a mere voluntary effort cannot be performed, and *vice versâ*. The same physiologist divided the nervus accessorius in an ass, and states that the action of the trapezius and levator scapulæ in respiration was lost, but that the animal still possessed voluntary power over those muscles. This statement with regard to the nervus accessorius may be granted to be true, though it is not yet sufficiently confirmed: the nervus accessorius has certainly, however, equal power with the spinal nerves in exciting the trapezius muscle to simple voluntary motion. Many respiratory muscles — as the diaphragm, for example,—have but one kind of nerves, and it is not in the most remote degree probable that these nerves contain special fibres for the respiratory movements, and others for the excitement of voluntary motion. The same nervous fibres are engaged in regulating the rhythmic movements of involuntary respiration, and in determining the muscular actions by which we voluntarily alter the mode of respiration.

The type and rhythm of these movements have their source, not in the nerves, but in the brain and spinal cord themselves. The cerebral and spinal nerves are merely conductors of the influences emitted by the central organs; if the conducting nerves be divided, the automatic movement ceases. This is the case with the motions of the diaphragm and all the other respiratory muscles, and also with those of the sphincter ani and other sphincters of the animal system.

The automatic movements dependent on the influence of the central organs have, like those regulated by the sympathetic nerve, in part an intermittent, and in part a persistent type. The respiratory movements

* Natural System of the Nerves, 8vo. 1824, p. 212 to 215.

are automatic and intermittent; the action of the animal sphincters is automatic, but persistent. All the movements of the group we are now considering are executed by muscles which are also subject to the will.

Automatic movements of muscles of the animal system with an intermitting type. The respiratory movements.—The respiratory movements include motions of the diaphragm, the abdominal and thoracic muscles, and the laryngeal muscles by which the glottis is dilated and closed. Under some circumstances, respiratory movements affect the muscles of the face, and those of the soft palate in many persons during sleep. The nerves engaged in the production of these movements are the phrenic, the spinal accessory, the vagus, (for the muscles of the larynx,) a great part of the spinal nerves, and, for the respiratory movements of the face, the portio dura of the seventh. The source of the nervous influence for all the respiratory motions is the medulla oblongata (see page 348). But how is their rhythmic character to be explained? Does it consist in a periodic action of the inspiratory muscles only, or in two alternate actions of the inspiratory and expiratory muscles? The problem would be more simple were the first the case. In fact, during ordinary perfectly tranquil respiration, the muscular movements do consist only of periodic inspiratory efforts of the diaphragm, the thoracic and laryngeal muscles; expiration is effected by the return of the parts by virtue of their elasticity to their former state. The pressure of the abdominal muscles has a share in the production of expiration, but probably only so far as their constant pressure on the abdominal viscera tends to force up the diaphragm and diminish the cavity of the thorax. Sometimes when from internal causes the inspiration takes place abruptly and suddenly, the expiration remains unaffected, and follows gradually as usual. In very frequent and laboured respiration, however, during a state of excitement, the movement of expiration becomes active, and the rhythm of the respiratory movements consists of two distinct acts: in the frog it consists of three acts (see page 345). To express these facts in physiological terms: the medulla oblongata, in giving rise to the movements of respiration, is the seat of a periodic discharge of the nervous principle towards all the muscles of inspiration, and alternating with this,—in many cases, at least,—a movement of the nervous principle, whether a current or oscillation, towards the expiratory muscles. In seeking the causes of this action of the medulla oblongata, two questions present themselves:

1. What is it that excites the medulla oblongata to determine the respiratory nerves to action in the human subject after birth, while in the fœtus it does not exert this influence? The exciting cause must either be sensations arising in the respiratory organs, and making an impression through the medium of the vagus (which is the sensitive nerve of the lungs) on the medulla oblongata, or it must be the impres-

sion made by the arterial blood on this highly excitable part of the nervous system. Neither the sensitive impressions produced by the atmospheric air in the lungs, nor a sense of the want of air, can be the cause of exciting the medulla oblongata to action; for I have divided both vagi nerves and both superior laryngeal nerves, and have even entirely separated the larynx, and still the respiratory movements continued in regular order up to the time of death. The theory of M. Kind, that it is the stimulus of the air acting on the cutaneous nerves, and transmitted to the spinal cord, which gives rise to respiration as a reflected movement, is not very probable; for a frog wholly deprived of its skin continues to respire as before; and a frog with its head only in the air will breathe equally well, whether the skin of its body be immersed in water or surrounded with air. If the stimulus of water acting on the skin were sufficient to excite the respiratory movements, the fœtus of mammalia ought to perform them in the uterus. It is evident, therefore, that the cause of the first respiration of the infant, as well as of the continued respiratory movements, must be some influence which could not act in the fœtal state, but which comes into operation immediately after birth; and this influence is not the stimulus of atmospheric air either in the lungs or on the skin. The cause of the first respiration can only be the impression made on the medulla oblongata by the arterial blood, which is formed in consequence of the first entrance of the air into the respiratory organs, and in less than a minute reaches the primum movens of the respiratory movements in the central organs of the nervous system. The arterial blood is also very beautifully shown to be the cause of the continuance of the respiratory movements throughout life by my experiments on frogs, in which I made the animals breathe for several hours in hydrogen; after a time respiration ceased, although life was not extinct. For a time the respiratory movements were renewed when the vessel in which the animals were included was agitated; but, after a longer period had elapsed, this was no longer the case. If, after being thus confined in hydrogen for two or three hours, the frogs are taken out and exposed to the atmosphere, they appear perfectly dead; not the least sign of motion or sensation is observable in them. The heart being laid bare, if it is found to have ceased to beat, the animal will not revive. If it still beats, though at intervals of half a minute or a minute, the frog will generally recover without any external stimuli being applied, merely from the gradual oxidation of the blood in the vessels of the lungs, the want of which arterialisation was the cause of the asphyxia. The blood impregnated with oxygen, however slow the action of the heart, must at length reach the brain and the medulla oblongata, which then begins again to emit nervous influence. The first signs of the revival of the frog, which lies quite motionless, is the retraction of the extremities when the skin is pinched; after a short time it is seen to respire at long intervals, and in a few hours is quite lively. The cause, therefore, of the first excitement, and of the continued action of the medulla oblongata in determining the respiratory muscles to action, is the arterial blood.*

2. What regulates the rhythm of the respiratory movements? The action of the arterial blood on the medulla oblongata is constant; and though the motion of the blood in the small arteries be accelerated from time to time synchronously with the heart's action, yet this pulsatory motion does not bear any relation to the rhythm of the respiratory movements: how then does the continual excitement of the medulla oblongata give rise to a periodic action of this centre of nervous influence on the respiratory nerves? The rhythm here might be supposed to be owing to a similar cause with the rhythmic automatic motions of organic muscles, namely to the nervous influence destined for the respiratory nerves being arrested in the medulla oblongata by some insulating power, which is only overcome when the nervous influence constantly excited has accumulated to a certain degree: or it might be thought connected with the fact that the power of nerves to

* [The arguments adduced by Professor Müller appear to the translator to be by no means sufficient to refute the opinion, that the respiratory movements are the result of reflex nervous action excited at first by the contact of the air with the surface of the new-born infant, and afterwards by sensitive impressions in the lungs. The continuance of the respiratory movements in animals after the division of the nervi vagi may be due, as Dr. Hall supposes, to the transmission of voluntary influence from the brain to the respiratory muscles; since respiration will not go on, he states, when both nerves are divided and the cerebrum removed, though either of these operations may be performed singly without checking the movements; or, what is perhaps more probable, the sensitive impressions in the lungs, which are usually conveyed to the medulla oblongata by the nervi vagi and sympathetic simultaneously, may now be transmitted solely by the pulmonary branches of the latter nerve, which is the explanation proposed by Mr. Grainger (on the Spinal Cord, p. 89), and Dr. J. Reid. (Edin. Med. and Surg. Journ. No. xlix.) The last named physiologists have shown by experiments that after the nervi vagi have been divided, animals still feel the sense of suffocation, the "besoin de respirer," when the supply of air to their lungs is interrupted. Again, the fact that a frog denuded of its skin or immersed in water will continue to breathe, and the circumstance of the liquor amnios,—a fluid of the same or nearly the same temperature as the body of the fœtus, — not exciting in it respiratory movements, do not prove that the impression made on the cutaneous nerves by the cooler air when the fœtus escapes from the uterus, may not be the exciting cause of the first inspiration. Such was the explanation of the first inspiration proposed by Sir G. Blane, and it is in some measure confirmed by the well-known fact that cold water or cold air suddenly coming in contact with the surface of the body gives rise to a deep inspiration, and by an interesting observation made by Dr. Heming, of a child just born apparently asphyxiated beginning to breathe when the cool air was admitted by raising the bedclothes. (Dr. Hall's Memoirs on the Nervous System, p. 88. A similar but more extraordinary case is related by Dr. Wagner. Medicin. Zeitung. Jan. 1838. Brit. and For. Med. Rev. April, 1838.) The theory of Professor Müller, that the cause of the first respiration is the impression made on the medulla oblongata by the arterial

transmit nervous currents or vibrations, or the power of muscles to contract under the influence of the nervous impulse, has a certain limit, ceasing after a certain time until restored by the vital process going on in the capillary blood-vessels.

In the muscles of the extremities the power of continued action is evidently much greater than in the muscles engaged in respiration; thus we can continue standing or bear a weight for a long period, but can prolong the movement of inspiration or that of expiration only for a very limited time. Any muscular motion, however, may be persisted in for a very long period, if made to alternate with other motions. It is not, therefore, the nervous principle that is deficient in these causes, for there is nervous influence sufficient for other muscular actions: the defect must be either in the conducting power of the nerves, or in the contractility of the muscles; one or the other of which, or perhaps both, are exhausted by the movement performed. The regular alternation of inspiration and expiration, and the regular succession of the three acts in the respiration of frogs, show pretty distinctly that neither

blood, is clearly open to the objection that the blood could not be rendered arterial, and therefore could not excite the medulla oblongata, until respiration had been at least once performed. The phenomena presented by the frogs asphyxiated by immersion in hydrogen gas, the last argument brought forward by Professor Müller, are perfectly in accordance with the theory which attributes the continuance of respiration to the transmission of sensitive impressions from the lungs to the medulla oblongata, and a consequent reflected action; for while venous blood was circulating in the vessels of the brain and spinal cord, they were incapable of reflex action, no motion could be excited in the apparently dead animal; but, when the circulating blood became arterialised, pinching the skin, we are told, excited a retraction of the limbs, which, whether a reflected or voluntary motion, showed that the nervous centres had regained their sensibility of impressions, and it is very possible that the restorative action of the arterial blood on the medulla oblongata consisted merely in its rendering it susceptible of the sensitive impressions transmitted from the lungs. It appears also to the translator to be more probable that the blood was arterialised in this experiment chiefly through the medium of the skin; for we know that frogs will live many hours after their lungs are extirpated; while, immersed in oil, they die in less than an hour (see page 294); and in an asphyxiated frog the entrance of air to the lungs, and its renewal, must be very limited. The cause of the respiratory movements was supposed by Dr. Whytt (Works, p. 94,) to be an uneasy sensation in the lungs produced by the accumulation of blood in them at the end of each expiration, and exciting the act of inspiration through the intervention of the brain and spinal cord. Expiration he believed to be the result of the reaction of the parietes of the thorax previously stretched. The exciting cause of the reflex nervous action for each inspiration is now supposed to be either the influx of venous blood into the lungs, or the presence of carbonic acid in the air-cells. Dr. Whytt referred the commencement of respiration in animals to the same cause as its continuance,—namely, an uneasy sensation in the lungs arising from a great quantity of blood which before passed through the aorta being now, on account of the interruption of the placental circulation, thrown into the vessels of the lungs through the pulmonary artery. Other physiologists regard the cessation of the supply of partially arterialised blood, which the lungs previously received from the placenta, as the exciting cause of the first inspiration; it has probably some influence.]

of the preceding modes of explanation is sufficient to account for them; but that some unknown influence is in operation in the medulla oblongata, which causes each movement of the nervous principle towards the inspiratory muscles to be followed by a motion of the same principle towards the muscles of expiration, and *vice versâ*; so that, as in a pendulum or balance, the movement in one direction necessitates the movement in the opposite direction. In fact, at the end of a voluntarily prolonged inspiration, we feel not merely exhaustion of the inspiratory muscles, but the striving of an irresistible force opposed to the movement of inspiration; and so likewise, after a long-continued expiration, the necessity of inspiring is felt; and, though this may be delayed for a time by an increased voluntary effort, the inspiratory movement at length necessarily ensues. Were the cause of the alternation of the respiratory movements not seated in the medulla oblongata itself,—were it merely the temporary exhaustion of the nerves and muscles,—the inspiratory and the expiratory muscles might voluntarily be made to act simultaneously, and both to desist from action simultaneously, and again act at the same time. Moreover, the regular alternation of inspiration and expiration cannot be occasioned by the communication to the central organs of the nervous system of a feeling of the necessity of expelling the air impregnated with carbonic acid, and of taking in pure air; for after the division of both vagi nerves in the neck, and of both superior laryngeal nerves, all sensations in the lungs must be lost, still more completely even than in sleep, and nevertheless the regular respiratory movements continue in animals after this operation (see note to page 920). It has been supposed (see page 355) that the different states of fulness of the great venous trunks and of the veins of the brain, consequent on the diminished and increased capacity of the thorax in respiration, may be the cause of the rhythm of the respiratory movements. But this is evidently arguing in a circle. Besides, the periodic motion of the branchial opercula in fishes, where no pressure is by this means excited on the veins, proves the impulse to respiration to be completely independent of external influences. In consequence of the continual excitement of the medulla oblongata by arterial blood, therefore, a periodic discharge of the nervous influence upon the nervous fibres alternately of the inspiratory and expiratory muscles takes place; the excitement of one of these sets of muscles to action being followed, as a necessary consequence, by the antagonistic excitement of the other set. Irritation in the respiratory organs is capable of giving rise sometimes to a disturbance of this order of movements,—the irritation itself exciting movements by reflexion from the medulla oblongata; thus, in cough, several expirations occur without each being preceded and induced by an inspiration. Other periodic inspiratory movements sometimes occur in certain states of the nervous system, namely, during fatigue, and in the state preceding and immediately succeeding sleep;

such is yawning. Of similar nature are the periodic sighing and hiccough which attend certain nervous affections.

The respiratory movements are not the only periodic automatic muscular actions of daily occurrence which are due to the influence of the central organs of the nervous system. The motions of the muscles of the eye and the iris during sleep present us with another example of these automatic muscular actions. During sleep the eye is turned somewhat inwards and upwards, and the iris is much contracted, although light is quite excluded. The eye takes this position even before sleep has come on; and the position of the double images which a person sees when he finds himself on the point of falling asleep, proves that the eyes are turned inwards. Their position is the same as that which they hold whenever the eyes are made to converge to a focus in front of any object; the image seen by the right eye lies to the right, that seen by the left eye to the left. It has been already shown that when the eye is directed inwards, whether voluntarily or involuntarily, the pupil is at the same time contracted. Both these phenomena are dependent on the action of the third nerve, and they both occur during sleep. The nervous principle, which in the waking state is expended on so many functions, is, in the production of these motions of the eye and iris, directed to a special region of the brain, and to the nerves which conduct the nervous influence to the muscles by which the motions are effected. It is possible, however, that the position which the eyes assume when sleep comes on, and the contracted state of the pupil during sleep, are merely the results of an antagonistic relation subsisting between the different branches of the third nerve; in consequence of which, the motions referred to necessarily take place whenever the levator palpebræ superioris ceases to act.

Automatic movements of the animal system with a persistent type. The sphincters of the animal system.—Although we have voluntary power over these muscles to strengthen their contraction, yet their action continues independently of volition during sleep as well as in the waking state, and it cannot be voluntarily interrupted, except by exerting a counter pressure against them by their antagonist muscles. The principal sphincters of the animal system are the sphincter ani and the sphincter vesicæ, which is to a certain extent subject to the animal system of nerves. The force and impulse to contraction of these muscles are derived from the spinal cord. Injuries of the spinal cord cause their permanent relaxation, and the consequent involuntary escape of the fæces and urine; this relaxation of the sphincters sometimes also occurs under the influence of depressing passions, which have the effect of weakening the power of the cord. Dr. Hall has shown that the sphincter ani of the turtle remains contracted as long, but only so long, as the lowest portion of the spinal cord is left uninjured.

The action of the sphincters must be owing to an incessant motor excitement of their nerves. In considering the antagonistic muscular action, however, we shall become acquainted with facts which prove that not the sphincters alone, but indeed all the muscles of the animal system, are subject to this constant motor excitement.

We have thus seen involuntary movements partly of periodic character, partly persistent, which are dependent on the influence of the brain and spinal cord. The same phenomena are observed as symptoms of disease of the central organs of the nervous system; persistent as well as intermittent muscular spasms, muscular contractions often occurring at very regular intervals, involuntary motion of the head to and fro, trembling of the limbs and the tonic cramps returning at regular periods, are expressions of morbid states of those organs. It is not known why the motions assume these characters; it has been observed merely that the enduring contractions more generally attend the diseases of a completely local and fixed nature, although every kind of disease of these organs is capable of giving rise to periodic convulsive affections. As a general rule, indeed, nearly all affections of the nervous system which are attended with muscular contractions come on in paroxysms; and even inflammation of the spinal cord, though the cause has here a uniform action, gives rise to tetanic convulsions, which occur in paroxysms. These phenomena, together with the periodic character of the attacks of epilepsy, while the operation of their causes is constant, seem to show that the excitability of the nervous centres is exhausted by the constant impression of morbid irritation, just as the excitability of the nerves is temporarily lost under the influence of impressions which excite them, in consequence of the change produced in the nervous matter by the excitement, and that the power of reacting depends in both cases on the excitability being restored by rest. The fading away of the image of a coloured spot on which the eyes are long fixed, and its reappearance after an interval, and the periodic daily return of the states of sleep and waking in the sensorium, are phenomena which are typical of all such healthy or morbid periodic actions; for in these instances also the reaction ceases at intervals for a time, although the exciting impressions are constantly the same.

3. *Antagonistic movements.*

The action of muscles is not restricted to their occasional contraction when excited by discharges of nervous influence. There are grounds for believing that the muscular fibres, particularly those of the animal system of muscles, are constantly in a state of slight contraction, even during their apparent repose. The retraction of divided muscles in a living body, and, still more, the manifest contraction of muscles of which the antagonists are divided or paralysed, are in favour of this opinion.

When the muscles of one lateral half of the face are paralysed, those of the opposite half draw the features towards their side. The tongue, when one half of it is paralysed, is always drawn to the opposite side; and in cases of removal of the middle portion of the lower jaw, whereby the muscles which draw the os hyoides and tongue forwards,—namely, the anterior belly of the digastricus, the mylo-hyoideus, the genio-hyoideus, and the genio-glossus,—lose their fixed point of attachment, the os hyoides is drawn backwards by the stylo-hyoideus, and the tongue by the stylo-glossus, so forcibly, that great danger of suffocation arises. Hence it would appear that the state of inaction of the different parts of our body does not indicate an absolutely relaxed condition of the muscles, but rather that the different groups of muscles antagonise and balance each other; and that when the position of a part is changed from the medium state of apparent rest, one or more of the muscles, already in a state of antagonistic action, are merely thrown into more powerful contraction.

There are groups of muscles opposed to each other in their action in almost all parts of the body. The extremities have flexors and extensors, supinators and pronators, abductors and adductors, and rotators inwards and rotators outwards. Frequently the opposed groups of muscles have different nerves. Thus the flexors of the hand and fingers derive their nervous fibrils from the median and ulnar nerves; the extensors theirs from the radial nerve; the flexors of the fore-arm are supplied by the musculo-cutaneous; the extensors by the radial nerve. The crural nerve supplies the nervous fibres for the extensors of the leg; the ischiadic those for the flexors. The peroneal muscles, which raise the outer border of the foot, derive their nervous fibres from the peroneal nerve; the tibialis posticus, which raises the inner border of the foot, is supplied by the tibial nerve. The muscles which move the foot and toes backwards and downwards are supplied by the tibial nerve; those which move them in the opposite direction, by the peroneal nerve. The circumstance of the convulsive motions in affections of the spinal cord being frequently such as to curve the body in a particular direction,—a fact exemplified by the opisthotonus, emprosthotonus, and pleurotonus of traumatic tetanus,—shows that there must be something in the disposition of the nervous fibres in the central organs which facilitates the simultaneous incitement to action of particular sets of muscles, as the flexors or extensors, &c.; although Bellingeri's opinion that the anterior columns of the spinal cord serve for the motions of flexion, the posterior for those of extension, is based on no sufficient facts. Too much importance, however, must not be given to the above remark relative to distinct nerves supplying the different groups of muscles; it is not a constant fact. Sometimes the same nerve gives branches to muscles opposed in action; thus the ninth, or hypo-glossal nerve, supplies both the muscles which draw the hyoid bone forwards, and one muscle which retracts it; the peroneal nerve supplies the peroneal muscles, which raise the outer border of the foot, and the tibialis anticus, which opposes this motion. Antagonist muscles can, moreover, be most easily made to combine in action; thus the peroneal muscles and the anterior tibial, acting together, raise the foot. The flexor carpi radialis and the extensores carpi radiales can combine so as to abduct the hand. The opinion of Ritter, that galvanism has a different action on the flexors and the extensors, has not been confirmed.

There are many muscles which have but few or no antagonists; such muscles always tend to give to the parts on which they act a determinate position. Thus there are numerous muscles which rotate the thigh outwards, while the rotation inwards can be effected but feebly by the tensor vaginæ femoris. Hence arises the involuntary tendency to the turning outwards of the whole limb in walking, sitting, or lying. The sphincters are also muscles which have no proper antagonists. The constant occlusion of the orifices of the viscera by the sphincters can be accounted for, therefore, solely by the fact of the contraction of muscles not wholly ceasing in the state of apparent rest, and of their having no antagonising muscles, without its being necessary to suppose that a constant current of nervous influence is transmitted specially to them. The sphincters give way when the contents of the bladder or rectum have accumulated, so as to excite a stronger contraction of the muscular coat of the viscus, which then impels these accumulated contents against the sphincter, and dilates it. The iris, which is also a sphincter, is constantly in the state of contraction during the waking state, and still more strongly so during sleep. During the act of awakening from sleep the pupil is seen to contract and dilate alternately, though the intensity of the light remains the same.*

The antagonism of muscular motions is of great pathological importance. Distortions are produced by the balance of the action of muscles being destroyed. Clubfoot, for example, which may take its rise during the first months of pregnancy as well as after birth, is frequently owing to the proper balance in the antagonistic action of the muscles which elevate the inner and outer borders of the foot being lost, and is often cured by restoring the balance of action. Either the peroneal muscles which elevate the outer border of the foot are partially paralysed, or the muscles which raise the inner border are in a state of "paralytic contraction." In either case the foot rests on its outer margin, and is drawn inwards by the tibialis posticus muscle. After a time, however, the position of the bones forming the joints is altered; the os naviculare is generally turned inwards, and the head of the astragalus, left partly exposed, forms a prominence on the dorsum of the foot. In pes equinus, in which the heel is drawn up and the foot rests on the toes, the gastrocnemii are tensely contracted, and nevertheless

* See Henle's article, "Gedächtniss," in the Encyclop. Wörterb. d. Med. Wissenschaft.

sometimes atrophied. A contracted state and atrophy of the muscles are not incompatible with each other. There is a kind of paralytic loss of power in muscles which is combined with contraction;* we have seen the gastrocnemii both contracted and atrophied at the same time.

Curvatures of the vertebral column certainly in many cases arise from scrofulous inflammation of the intervertebral ligaments and vertebræ, producing softening, enlargement, suppuration, and loss of substance, but still more frequently they are owing to loss of balance in the action of the muscles of the trunk. That the curvature is of the latter kind may be known by the absence of the signs indicating rhachitis, and by the affection being benefited by gymnastic exercises. These spinal curvatures are, therefore, analogous to clubfoot and pes equinus. In tubercular suppuration of one lung, the thorax on that side is not elevated in respiration, because the lung is incapable of distension; the thoracic muscles of that side are not really paralysed.

4. *Movements arising from reflex nervous action.*

The nature of the reflected motions has been already fully investigated and explained at page 706 et seq. They include all muscular actions which arise from impressions on sensitive nerves exciting motor nerves to action through the intervention of the brain and spinal cord. They arrange themselves into two principal groups.

a. Reflected motions of the animal system.

These are the reflex motions of muscles which are under the influence of cerebro-spinal nerves; the impression which excites them may be made either on animal or on organic nerves; for example, in the skin or in the intestinal canal. Coughing from irritation of the mucous membrane of the lungs and larynx, vomiting from irritation of the mucous membrane of the pharynx, stomach, or intestine, and the contraction of the iris from irritation of the optic nerve, are examples of these reflex movements, of which we have described innumerable instances in the chapter on nervous reflexion, page 706. These reflected motions of the voluntary muscles consequent on sensitive impressions are for the most part momentary muscular actions, or else persistent long-continued contractions. A high degree of irritation of the spinal cord by violent impressions on sensitive nerves sometimes, however, gives rise to rapidly-repeated rhythmic contractions of the muscles; such as we observe in the trembling excited by the application of a moxa, or when, from long exposure to a cold bath, the teeth chatter. The rhythmic contractions of the perinæal muscles from venereal excitement of the genitals, and the rhythmic expulsion of the semen by these muscles, afford, however, the most remarkable example of rhythmic reflected

† See Ollivier, Traité de la Moëlle épinière et de ses Maladies, t. ii. p. 709.

motions. They are the more remarkable, since the vesiculæ seminales appear to have, not a rhythmic, but a vermicular motion. The vesiculæ by this motion pour their contents in an uninterrupted stream into the urethra, along which they are afterwards impelled by the rhythmic contractions of the ejaculator muscle.

b. Reflected motions of the organic system.

The movements of the organic involuntary muscles under the influence of impressions propagated to the brain and spinal cord, whether from parts supplied by cerebro-spinal nerves, or from organs under the influence of organic nerves, have been considered at page 736. The motion of the heart can be affected by impressions made at any part of the body, the spinal cord being the medium of transmission of the influence. The various symptoms of fever are probably due to the impression communicated from some one organ to the spinal cord, and perhaps the brain also, by organic nerves (see p. 808).

5. *The associate or consensual movements.*

These phenomena have already been considered generally, and their cause investigated (p. 683). Their peculiarity consists in the voluntary impulse to one motion giving rise to the production of other motions contrary to or independently of the will; thus, whenever the eye is voluntarily directed inwards, the iris contracts. The less perfect the action of the nervous system, the more frequently do associate motions occur. It is only by education that we acquire the power of confining the influence of volition in the production of voluntary motions to a certain number of nervous fibres issuing from the brain. An awkward person in performing one voluntary movement makes many others, which are produced involuntarily by consensual nervous action. In the pianoforte player we have an example, on the other hand, of the faculty of insulation of the nervous influence in its highest perfection. From the want of this faculty arises the absence of expression in the countenance of the uneducated; while on the perfection of this faculty depends in a great measure the defined character and expression of the features. The motions very prone to be associated involuntarily are those of the corresponding parts of the two sides of the body. The motions of the irides, of the muscles of the ear, of the eyelids, and of the extremities, in the attempt to effect opposed motions, are examples of such association (see p. 684).

Some of the most remarkable facts illustrating the association and antagonism of muscular actions are presented by the muscles which move the eyes. The corresponding branches of the third or motor oculi nerve of the two sides have a remarkable innate tendency to consensual action, a tendency which cannot be ascribed to habit. The two eyes, whether moved upwards, downwards, or inwards, must always move together; it is quite impossible to direct one eye upwards and the other downwards at the same time. This tendency to consensual motion is evidenced even from the time of birth; it must, therefore, be owing to some peculiarity of structure at the origins of the two nerves. This association in action of the corresponding branches of the two nervi motores oculi renders the absence of such tendency to consensual motion in the two external recti muscles and the sixth nerves the more striking. We do, it is true, in a certain measure cause the two external recti muscles to act together when we restore the two eyes, of which the axes are converging, to the parallel direction: but there the power of consensual action ends; the two eyes can never be made to diverge, however great the effort exerted to do so. The cause of this is not want of power in the external recti muscles; nor is it their mode of insertion, which is the same as that of the other recti muscles; nor does it arise from habit, for it is innate, like the tendency of the other recti to associate action,—the newly-born infant, though unable to fix the eyes on any object, can move them in any other direction, but is unable to make them diverge from each other. Moreover, the impossibility of directing the two eyes outwards at the same time cannot be owing to antagonistic action of the internal rectus, for either separately can perform that movement completely. In short, there is an innate tendency and irresistible impulse in the corresponding branches of the third nerve to associate action; while in the sixth nerves not only is this tendency absent, but the strong action of one of the nerves is incompatible with the action of the other. These innate tendencies in the third and sixth nerves are extremely important for the function of vision: for if, in place of the sixth nerves, the external recti muscles had received each a branch of the third nerve, it would have been impossible to make one of these muscles act without the other; one eye, for example, could not have been directed inwards while the other was directed outwards, so as to preserve the parallelism or convergence of their axes, but they would necessarily have diverged when one rectus externus had been made to act voluntarily. To render possible the motion of one eye inwards while the other is directed outwards, the external straight muscles have received nerves which have no tendency to consensual action. In consequence, however, of the tendency in the two internal straight muscles to associate motion, it is necessary, when one eye is directed inwards and the other outwards, that the contraction of the rectus externus of the latter should be so strong as to overcome the associate action of the rectus internus of the same eye; and in the effort to direct one eye completely outwards we actually feel this stronger contraction of the external rectus. These considerations enable us to understand perfectly the hitherto enigmatical fact that in all vertebrata the external rectus muscle receives a special nerve.*

In the same way we may explain why the superior oblique muscle has received a special nerve (the fourth nerve or n. trochlearis), which likewise has no tendency to consensual action with the nerve of the other eye. It is necessary, however, first to determine the action of the oblique muscles. The inferior oblique moves the pupil inwards and upwards; this can be very easily demonstrated by laying bare the muscle from the front, the eye and orbit being undisturbed, and by then drawing the muscle towards its point of origin. The superior oblique muscle rolls the eye downwards and somewhat outwards. Sir C. Bell† has proved this by experiments on animals and on the dead human subject. I have satisfied myself of the correctness of his statements; I laid bare the superior oblique muscle from above without disturbing the parts,—without moving the eye from its cushion of fat, and then exerted traction on the muscle; the eye each time moved in the segment of a circle downwards and a little outwards. The outward motion effected by the superior oblique is much less than the inward motion produced by the contraction of the obliquus inferior. When both oblique muscles act together, or when traction is exerted on both in the direction of their origins at the same time, the eye is drawn forwards and the pupil directed inwards. The two superior oblique muscles have no tendency to associate motion with each other; the fourth nerve in this respect resembles the nervus abducens of the external rectus. When one eye is directed downwards and outwards, the other eye is not also directed downwards and outwards, but downwards and inwards; this is the case from birth upwards; it proves that the motion of the superior oblique of one eye through the influence of the trochlearis nerve is incompatible with the action of the corresponding nerve and muscle of the other eye. It is not so with the inferior oblique; the branch of the third or motor oculi nerve, by which it moves the eye upwards and inwards, has a tendency to consensual action with its fellow nerve of the opposite side; the motion of the eye upwards and inwards takes place therefore simultaneously on the two sides; it does so indeed involuntarily during sleep. This position, which the eye takes during sleep, and also in hysterical paroxysms, may be regarded as the effect of the simultaneous action of all the branches of the nervus motor oculi. Muscles, we have seen (page 925), are slightly contracted even in the state of rest; and, if we suppose all the branches of the motor oculi nerve to be in a state of slight excitement, both eyes would necessarily be turned upwards and inwards. The superior and the inferior rectus would balance each other's action; the internal rectus would draw the eye inwards, and the inferior oblique upwards and inwards; the corresponding

* Compare Jessen, Beiträge z. Erkenntniss d. psychisch. Lebens. 1831, 183.

† Nervous System, 8vo. 1824, p. 312.

branches of the third nerve which supplies these muscles being consensual in their action, both eyes would be simultaneously directed upwards and inwards.

Let us consider another effect which would have resulted if the rectus externus muscle had, in place of the sixth nerve, received a branch of the third nerve: had such been the case, the simultaneous direction of one eye upwards and inwards, and of the other upwards and outwards, which so often happens, would have been impossible. While the inferior oblique, and the simultaneous action of the superior and internal straight muscles, directed the one eye upwards and inwards, the same muscles, owing to the association of action, would have given the other eye the same direction; it could not have been directed upwards and outwards. Hence it was necessary that there should be a special nerve having no tendency to associate action with its fellow nerve, but capable, by the stronger contraction of the external rectus which it supplies, not only of preventing the second eye from being carried upwards and inwards by the inferior oblique and superior and internal straight muscles acting consensually with the same muscles of the first eye, but also, with the aid of the superior straight muscle, of carrying it upwards and outwards. The same remarks apply in the case of the motion of the one eye downwards and inwards, and of the other eye downwards and outwards. If one eye be turned downwards and inwards by the rectus inferior and the rectus internus, the other eye is turned downwards and outwards by the rectus inferior and rectus externus, aided by the obliquus superior, which being also supplied by a special nerve,—the fourth,—no tendency to consensual movement in the corresponding muscle of the opposite eye is excited. The fourth nerve—nervus trochlearis—belongs also to the nerves of expression.

The associate motion of the iris, when the motor oculi nerve is thrown into action, has been described and explained at page 684.

The organic muscles also are, in some measure, subject to the laws of association. At page 740, reasons are given for believing that the increased frequency and force of the heart's action during muscular exertions of the body is owing to this cause. The action of the voluntary muscles has an influence on that of the intestinal canal; neglect of bodily exertion is often productive of torpidity of the bowels; every one is aware how beneficial muscular exercise is in preserving the regularity of the muscular action of the intestines and regularity of excretion.

6. *Movemens dependent on certain states of the mind.*

There are three classes of movements of this kind: 1, those dependent on mere ideas passing through the mind; 2, those arising from passions or the affections; and, 3, voluntary movements.

a. Movements excited by ideas.

Certain groups of muscles of the animal system are in a constant state of proneness to involuntary motion, owing to the susceptibility of their nerves, or rather the excitability of the parts of the brain from which they arise. This is the case with all the respiratory nerves, including the facial nerve. This excitability, this tendency to the discharge of nervous influence, is evidenced in the sneezing which occurs occasionally from internal causes; but the respiratory muscles may be excited to action merely by particular states of the mind. Any sudden change in the state of the mind is capable of causing these muscles to be excited to action. The sensorium acts here in the same way as an individual nerve in which any sudden change of condition of whatever kind sets the nervous principle in action. In this way we must explain the fact, that a sudden change of thoughts, such as occurs when the idea of the ridiculous arises in the mind, without any passion being excited, is capable of giving rise to an action of the nerves, which is evidenced in the muscles of the face and the respiratory muscles.

Yawning, inasmuch as it can be excited by the mere idea, or by seeing or hearing another yawn, belongs to the same class of movements. The disposition to the movements of the features and the respiratory muscles that constitute yawning, exists previously; and it becomes manifested when the idea gives to the nervous principle the determinate direction. The nerves engaged in the production of this movement also are the respiratory nerves and the facial nerve,—those branches of the facial which are distributed to the muscles of the face, as well as its branch to the digastric muscle. Ideas of fearful or detestable objects suddenly excited, even when called up by mere fictions, occasion in persons of excitable temperament the motion of shuddering; and the same occurs sometimes from the mere thought of a disgusting medicine : vomiting, indeed, may be produced by the mere recollection of a disagreeable taste.

b. Movements due to the passions of the mind.

It is principally the respiratory portion of the nervous system which is involuntarily excited to the production of muscular actions by passions of the mind. Here again we see that any sudden change in the state of the brain, propagated to the medulla oblongata, immediately causes a change of action in the respiratory muscles, through the medium of the respiratory nerves, including the respiratory nerve of the face. There are no data for either proving or refuting the hypothesis that the passions have their seat of action in a particular part of the brain, whence their effects might emanate. But these effects are observed to be transmitted in all directions by the motor nervous fibres, which, according to the nature of the passion, are either excited or weakened in action, or completely paralysed for the time.

The exciting passions give rise to spasms, and frequently even to convulsive motions affecting the muscles supplied by the respiratory and facial nerves. Not only are the features distorted, but the actions of the respiratory muscles are so changed as to produce the movements of crying, sighing, and sobbing. Any passion of whatever nature, if of sufficient intensity, may give rise to crying and sobbing. Weeping may be produced by joy, pain, anger, or rage. During the sway of depressing passions, such as anxiety, fear, or terror, all the muscles of the body become relaxed,—the motor influence of the brain and spinal cord being depressed. The feet will not support the body, the features hang as without life, the eye is fixed, the look is completely vacant, and void of expression, the voice feeble or extinct. Frequently the state of the feelings under the influence of passion is of a mixed character; the mind is unable to free itself from the depressing idea; yet the effort to conquer this, gives rise to an exciting action in the brain. In these mixed passions the expression of relaxation in certain muscles—in the face, for example,—may be combined with the active state of others; so that the features are distorted, whether in consequence merely of the antagonising action of the opposite muscles being paralysed, or by a really convulsive contraction. Frequently also, both in the mixed and the depressing passions, some muscles of the face are affected with tremors. The voluntary motion of a muscle half-paralysed by the influence of passion is necessarily of a tremulous character, in consequence of its being no longer completely under the influence of the will. We experience this particularly in the muscles of the face when, during the sway of a depressing or mixed passion, we endeavour to excite them to voluntary action; the muscles of the organ of voice also, under such circumstances, tremble in their action, and the words attempted to be uttered are tremulous.

The nerve most prone to indicate the state of the mind during passions is the facial; it is the nerve of physiognomic expression, and its sphere of action becomes more and more limited in different animals, in proportion as the features lose their mobility and expressive character. In birds it has no influence on the expression of the face; those only of its branches exist which are distributed to the muscles of the os hyoides and to the cutaneous muscle of the neck; and the erection of the skin of the neck, or, in some birds, of the ear feathers, are in them the only movements by which the facial nerve serves to indicate the passions. Next to the facial, the respiratory nerves,—those of the internal organs of respiration, the laryngeal and phrenic nerves, as well as those of the external thoracic and abdominal muscles, are most susceptible of the influence of the passions. But when the disturbance of the feelings is very intense, all the spinal nerves become affected to the extent of imperfect paralysis, or the excitement of trembling of the whole body.

The completely different expression of the features in different passions shows that, according to the kind of feeling excited, entirely different groups of the fibres of the facial nerve are acted on.* Of the cause of this we are quite ignorant.

[The disturbed action of the heart during mental emotions is a remarkable instance of the influence of the passions over the movements of organs supplied by the sympathetic nerve.]

c. Voluntary movements.

The cerebral and spinal nerves are alone capable of exciting voluntary motion. The history of cases of paralysis from disease of the spinal cord shows that the fibres of the spinal nerves are continued upwards to the medulla oblongata, and that the will has no direct action on them at any other part of their course than in the medulla oblongata, which is the source of all the voluntary movements. Again, the origin of the greater number of the cerebral nerves from that part of the nervous centres, and the possibility of tracing the roots of motor nerves apparently arising from other parts of the brain to the same point, as well as the history of lesions of the brain, prove that the cerebral motor nerves also receive their voluntary incitement to action from the medulla oblongata.

The fibres of all the motor, cerebral, and spinal nerves may be imagined as spread out in the medulla oblongata, and exposed to the influence of the will like the keys of a piano-forte. The will acts only on this part of the nervous fibres; but the influence is communicated along the fibres by their action, just as an elastic cord vibrates in its whole length when struck at any one point. It is in the present state of our knowledge—and perhaps always will be—impossible to determine how by an exertion of the will in the medulla oblongata the nervous fibres are excited to action. All that we can do is, to consider the fact in its greatest simplicity.

A voluntary movement might be supposed to result from the intensity of the conceived idea of its object, and of the necessity of its immediate performance; so that, when the idea had reached a certain intensity, the movement necessary for the attainment of the object would necessarily ensue. Such a view is easily refuted; for in that case the rapidity of the movement would become greater as the

* On the imitative movements, consult Huschke, Mimices et Physiognomices, Fragment. Physiol. Jena, 1821.

intensity of the idea increased. It might further be imagined that a voluntary movement would take place whenever the sensorium is completely occupied by the idea of the immediate necessity of the movement for the attainment of a proposed object, and when this idea is neutralised by no other; there being but this one idea present in the sensorium. When I say, I will now do this or that, and nevertheless do it not, either merely the idea of willing it, and not the consciousness of the immediate necessity of the movement, is in my mind, or the fulfilment of that idea is neutralised by some other. But if we have an absolute certainty of the immediate necessity of a movement, and no other idea neutralises this, then, it might be supposed, the current or oscillation of the nervous principle necessary for the voluntary motion must inevitably ensue. According to this view, volition would consist in the mental equilibrium being disturbed by an idea of the absolute necessity of a movement, and the consequent nervous action in the medulla oblongata would be comparable to the sinking of one scale of a balance when its equilibrium is disturbed. It admits readily of proof, however, that the voluntary movements do not merely occur when the idea of the necessity of the particular movement is alone present in the mind; for we are able to continue for a long time simultaneously three or four different movements which have not the least connection. We read, sing, and play; or dissect and sing, and even smoke in addition, all at the same time.

It is evident also that the ultimate source of voluntary motion cannot depend on any conscious conception of its object; for voluntary motions are performed by the fœtus before any object can occur to the mind, before an idea can be possibly conceived of what the voluntary motion effects; we must therefore view the question in a much simpler manner. On what do the first voluntary movements in the fœtus depend? All the complex conditions which give rise to voluntary motions in the adult are here absent. Its own body is the sole world from which the obscure conceptions of the fœtus that excite its actions can be derived. The fœtus moves its limbs at first not for the attainment of any object, but solely because it can move them. Since, however, on this supposition there can be no particular reason for the movement of any one part, and the fœtus would have equal cause to move all its muscles at the same time, there must be something which determines this or that voluntary movement to be performed,—which incites the retraction, first of this foot or arm, and then of the other.

The knowledge of the changes of position which are produced by given movements is gained gradually, and only by means of the movements themselves; the first play of the will on single groups of the radicle motor fibres of the nerves in the medulla oblongata must therefore be independent of any aim towards change of position; it is a mere play of volition, without any conception of the effects thereby produced in the limbs. This voluntary excitation of the origins of the nervous fibres without object gives rise to motions, changes of posture, and consequent sensations. The excitation of certain fibres produces constantly the same motions, the same changes of position, and the same sensations. Thus a connection is established in the yet void mind between certain sensations and certain motions. When subsequently a sensation is excited from without in any one part of the body, the mind will be already aware that the voluntary motion which is in consequence executed will manifest itself in the limb which was the seat of the sensation; the fœtus in utero will move the limb that is pressed upon, and not all the limbs simultaneously. The voluntary movements of animals must be developed in the same manner. The bird which begins to sing, is necessitated by an instinct to excite the nerves of its laryngeal muscles to action; tones are thus produced. By the repetition of this blind exertion of volition, the bird at length learns to connect the kind of cause with the character of the effect produced. The instinct of this dream-like and involuntarily-acting impulse in the sensorium has some share in the production of certain movements in the human infant, which are in themselves voluntary. In the sensorium of the newly-born child there is a necessitating impulse to the motions of sucking; but the different parts of the act of sucking are themselves voluntary movements.* Hence we perceive that the voluntary excitement of the radicle motor fibres to action is an original innate power connected with the developement of the animal, and not dependent on a conceived object, as in the adult.

We have learned already from many other facts that the nervous principle in the medulla oblongata is in a state of extraordinary tension, or proneness to action; that the slightest change in its condition excites a discharge of nervous influence, as manifested in laughing, sneezing, sobbing, &c. While the tension of the nervous principle is not disturbed, we are equally ready to excite voluntary movements in any

* [Anencephalous infants, in whom no part of the brain but the medulla oblongata is present, have been observed to suck when the lips were touched by the finger or nipple; and Mr. Grainger (Observations on the Spinal Cord, p. 80,) has shown that the same thing occurs when the brain has been artificially removed; a young puppy, deprived of its brain, "on touching the mamma, threw up its nose, moved the mouth, trying to get hold of the nipple," and afterwards sucked the finger introduced into the mouth; in one experiment, Mr. Grainger mentions, that "as the puppy lay on its side sucking the finger, it pushed out its feet in the same manner as young pigs exert theirs against the sow's dugs." These movements, as well as those of deglutition and respiration, also presented by anencephalous fœtuses, as well as the remarkable phenomena observed by M. Flourens in fowls after the removal of their brain (see pages 828 and 835), are evidently connected with an action of the medulla oblongata, and are considered by M. Müller as sufficient evidence of that part of the brain

part of the body, and such is the state of rest or inaction. Every mental impulse to motion disturbs the balance of this tension, and causes a discharge of nervous influence in a determinate direction,—that is, excites to action a certain number of the fibres of the motor nervous apparatus. The influence of the will on the fibres of the motor apparatus is not a solitary fact of its kind. There is in the central organs a power of voluntarily directing the mind to all the cerebral and spinal nerves, even to the nerves of common sensation, and the nerves of special sense. The phenomena showing this power are of importance with reference to the theory of the voluntary motions. The action of our organs of sense is usually accompanied by a constant concurrent action of the will. In regarding an object of complex figure, first one part is voluntarily impressed on our sensorium, then another; the effort of doing this is called "attention." We are looking, for example, at an architectural rosette,—a polygon, the angles of which are connected by lines; the figure remains the same, but still we see first one part, then another part of it more distinctly than the rest: at one moment the periphery is seen most distinctly; at another, separate triangles; again, at another, quadrangular figures, which are contained within the whole polygon. We do this not merely by moving the eyes so as to follow or describe, as it were, the outline of the figure with the axis of vision; but, the direction of the eyes remaining the same, the different parts of the figure are in succession impressed, by an effort of the attention, more distinctly on the sensorium, while the other parts are still perceived, but not attended to. In the organ of hearing it is still more evident that the modification of the impressions on the sense by attention does not depend on muscular motions. During the performance of an entire orchestra, we are seldom so passive as to perceive all the tones which strike the ear simultaneously, with a distinctness merely proportioned to their own intensity. On the contrary, by our faculty of attention we are able to follow the tones of a weaker instrument among the louder sounds of the others, which are disregarded for the time. If two persons are addressing different words to our opposite ears,

being the seat of volition; while other physiologists, as Mr. Grainger and Dr. Hall, regard all these phenomena, together with the movements of the fœtus in utero, as resulting from reflex nervous action. Some of the phenomena presented by the fowl deprived of its cerebrum can with difficulty be believed to result from reflex motor action independently of volition; but the argument which Professor Müller draws from pathology in favour of the medulla oblongata being the seat of the will appears to be imperfect. Lesions of the spinal cord below the medulla oblongata will, it is true, prevent the transmission of the influence of the will to parts supplied by nerves arising below the seat of the lesion, and disease of the medulla oblongata will affect also the action of cerebral nerves; but disease much higher in the brain, as in the optic thalamus or corpus striatum, is also productive of paralysis both of the cerebral and spinal nerves, when the medulla oblongata is apparently in a perfectly healthy condition.]

we can by attention follow what is said by the one, while we leave what the other says unnoticed. The same circumstance is observed in the case of simultaneous impressions on different senses. According to the direction we give our attention we cease to see distinctly, while we exert the power of hearing to a greater degree, and *vice versâ;* for only one object at a time can be taken cognizance of by the faculty of attention.

This analysis of the impressions made by objects on the senses is frequently performed quite involuntarily, in accordance with the laws of the association of ideas. But we have also the power of directing the attention according to our will. Thus, in the above examples, it depends entirely on our own choice what parts of the architectural rosette we should regard most accurately, of which instrument of an orchestra we should follow the tones, and to which of two persons speaking at the same time we should listen. In short, the will has here the same influence as in the production of voluntary motions. The only difference is, that in the latter case the motor nervous fibres previously in a state of repose are excited to action, while the action of the will in perceiving the impressions on the senses consists merely in rendering the sensation more intense or distinct.

The power of the will is not limited, however, to the motor and sensitive nerves; it also influences the mental operations. Our faculty of conceiving ideas, the imagination, acts, it is true, independently of the will, as in dreams; and, in the state of waking, we cannot produce with closed eyes illuminated images similar to those excited by the imagination in dreams; but still we have the power of voluntarily directing our thoughts. In short, we see that the voluntary effort of the sensorium can be directed upon motor or sensitive nerves, or made to affect the mental operations: an act of volition is nothing else than the voluntary and conscious direction of the nervous principle in the brain upon different cerebral apparatus; and on the part of the brain subjected to this voluntary action of the nervous principle depends, whether the effect shall be a muscular movement, a more distinct perception, or an idea.

The regulation of the quantity of nervous influence expended in voluntary motion, or the strength of the nervous action and of the muscular movement, are dependent on the same causes as the localization of the voluntary movement. Both the one and the other have determinate limits. Though the exertion of many muscles at the same time sooner exhausts the strength, yet it is most easy for the will to determine whole groups of muscles to action; and, as a general rule, it may be affirmed that a voluntary movement is more difficult the smaller the number of nervous fibres required to be excited, and the smaller the part to be moved. The nervous principle much more readily excites many than few nervous fibres to action; hence the tendency to the associate movements described at page 928. It is very doubtful whether distinct portions of a long muscle can be voluntarily excited to independent and separate action. The action of the nervous principle is here evidently shown to be less capable of localization when excited by volition than when determined by accidental involuntary stimuli. From internal causes independent of the will, very small parts of a muscle—for example, of the biceps of the arm,—are seen to contract separately. This never occurs from voluntary influence. The power of confining the voluntary excitement of the nervous principle to distinct groups of fibres is increased by much exercise, and the more frequently certain groups of fibres are excited to action by the influence of the will, the more capable do they become of isolated action; this is exemplified in performers on the piano-forte, &c. The movement of the same muscles when frequently repeated becomes difficult, however, after a time; this is intelligible on the principle that, although action alternating with rest increases power, yet any continued exertion of a vital property induces temporary exhaustion, in consequence of which the organ, whether a muscle and motor nerve, or an organ of sense, becomes for a time incapable of action (see page 52, et seq.)

The problem,—wherefore are the muscular parts supplied by the sympathetic nerve not subject to the will, except by association with voluntary muscles supplied by cerebro-spinal nerves? has been discussed at page 739.

Motions very frequently performed occur at last whenever the nervous influence in the brain receives in the slightest degree the direction necessary to produce them; hence frequently the mimic movements of the hands in speaking. This also shows that the conducting power of the nervous fibres increases with the frequency of their excitement. From this cause it is that obscure ideas, without any distinct consciousness, often give rise to perfectly determinate and appropriate motions, provided these motions have been previously many times excited in the same manner.

CHAPTER II.

OF THE COMPOUND VOLUNTARY MOVEMENTS.

By the compound voluntary movements we understand all combinations of movements in determinate groups, which the mind has a share in producing. The kinds of motion treated of in the preceding chapter may enter as elements into the composition of these combined movements. We have here to consider the simultaneous series of voluntary movements consequent on several series of ideas, the associations of movements, and of ideas with movements, the instinctive movements, and the movements of locomotion.

a. Simultaneous series of movements.

Not only can motion be determined voluntarily for a given object in very different parts of the body at the same time; but voluntary movements for very different objects can likewise be simultaneously performed. It is easy to write and smoke at the same time; a performer on a musical instrument reads the notes both of the song and the accompaniment, calling the muscles of the eyes into action for this purpose, and sings and plays simultaneously. How shall we explain the simultaneous occurrence of all these actions? Can we really follow at the same moment different series of ideas which have no connection with each other? or can but one idea be conceived at the same time; and is the complicated action of reading notes, singing, and playing, apparently at the same time, produced by a constant rapid transferring of the agency of the mind from one of those series of acts to another? The first thing to be ascertained is, whether the mind can in any case follow two series of ideas simultaneously. If this be possible, the appropriate movements corresponding to each series of ideas may also be produced. The voluntary motion of different motor apparatus,—for example, of the muscles of the voice and fingers,—at the same time, is not difficult of explanation; for it matters not whether several muscles moved simultaneously be situated in one and the same limb, or be very distant from each other: in both cases the action of the nervous principle is directed upon a certain sum of radicle nervous fibres. The difficulty consists in determining whether the two series of ideas which are the causes of the excitement of the nervous fibres can subsist at the same time. For the closer examination of this question we have a simple example in a person who, while walking, is engaged in an active train of reflection on some perfectly independent subject. We determine to visit some person; on our way we are so busied in other thoughts that we neither remark whom we meet, nor those who greet us; and, nevertheless, we arrive at the place that we had intended. During our immersion in a particular train of thought, we still followed the series of images excited in our sensorium by the houses and streets, through which we found our way almost unconscious of what house we were seeking.

The best example, however, for the solution of this problem, is afforded by persons learning particular movements. The motions are here so slow, and their combination so difficult and ill-executed, that we are able to watch the operations of nature in them. When a learner on the guitar or piano-forte attempts to sing and play at the same time, it is at once evident that he is unable to read the note of the song and those of the accompaniment simultaneously. The note for the voice is, perhaps, rightly conceived and would be sung; but the note for the piano is still wanting, and the instrument halts; and *vice versâ*. This arises, not so much from the difficulty of reading, as from the inability of converting what is read into ideas for exciting the movements. Each note is converted in our sensorium into an incitement to motion for the muscle of this or that finger, or for a muscle of the larynx; and in addition to these two simultaneous series of transpositions, by which notes of music being read are converted into incitements to motion, there is a third accompanying them, by which words read afford incitements for the motion of the organs of speech. In the last operation there is no difficulty, since we are exercised in it from youth upwards; but the incitement of certain muscles of the fingers, or certain muscles of the larynx, to action in accordance with the printed notes of music, requires practice. From the above example we learn clearly that the voluntary movements dependent on several different ideas can be executed simultaneously, but that they cannot be simultaneously conceived in the mind. Even the practised performer reads, although almost with the rapidity of lightning, first the notes for the voice, then those for the instrument; the idea of their proportional time is thus obtained, and the corresponding incitements to motion being formed from them in the sensorium, the movements are then executed simultaneously. It might be objected that, since for giving a different duration to the movements corresponding to two different notes a perfect recollection of their value is required, while at the same time the sensorium would be already occupied with the succeeding notes,—since, therefore, the sensorium is able to retain two different ideas in the memory, and at the same time conceive a third,—the simultaneous conception of several series of movements dependent on different ideas must also be possible. The validity of this objection is, however, only apparent; for the prolongation of a movement in accordance with the value of a note requires no action of the sensorium; for every movement is here continued until it is interrupted by the incitement of a new motion required by another note. The simultaneous performance of the most different movements is, we repeat, attended with no difficulty, for it is as easy to move the muscles of the larynx and those of the fingers at the same time, as to move several of the muscles of the arm simultaneously; but the conception of these different movements from different series of ideas can take place, it appears, only successively, though their succession may be as rapid as the lightning-flash. We now return to the consideration of the case before alluded to. We pass in deep thought through many winding streets to the house of a friend; we are so absorbed that on our way we observe nothing; we forget to greet friends, and do not notice those who greet us; and at last we arrive at the desired place without knowing how we came there. The voluntary locomotion, this constantly exercised alternation of flexion and extension of the limbs being a simple periodic repetition of two movements, can as easily as a single movement when once commenced be continued uninterruptedly at the same time with a constant succession of thoughts. It is more difficult to comprehend how we can find our way through the numerous windings of the streets, and at the same time follow an internal train of thought. It may, however, be very well explained, on the supposition of the attention being diverted at short intervals alternately from the one theme to the other. The laws of the association of ideas are in many ways engaged in this action. If two series of ideas of equally little interest present themselves to the mind, the attention can be directed alternately to the one or the other with the greatest facility, or may be diverted from these altogether by a third train of ideas. But if one series of ideas is predominant in the sensorium, as in a state of passionate excitement, any new idea excited through the medium of the senses may for a moment interrupt the ruling train of thought; but the sensorium always returns more readily to the original theme than it is diverted from it to remote associations.

b. Association of movements and ideas.

The rapidity and easy succession of movements is promoted by their frequent repetition. This is what we call practice. A person who is not practised cannot, in a constant rapid change, interrupt and again renew the same movement, or execute complex movements with regularity. The effect of practice shows that the more frequently the same fibres are thrown into action, the easier does their action become.*

We have to consider this kind of association in two points of view.

1. Association of movements with movements. Hitherto the involuntary consensual or associate movements have been frequently confounded with the voluntary associated movements. The former depend on the influence voluntarily directed in the sensorium to the excitement of one nerve extending involuntarily to another. Thus one eye cannot be voluntarily raised without the other being also raised involuntarily. Such phenomena are not the result of practice; their cause is innate. They are observed to the greatest extent in the persons least practised; and the object of practice, and the education of the muscular move-

* The laws of the association of voluntary movements have been so frequently explained, that they are now very generally recognised, even in writings on practical medicine. The phenomena of association have been studied more especially by Darwin, and are described in his Zoonomia, vol. i. Compare also Reil, Fieberlehre, iv. p. 609; Reil, von der Lebenskraft; Reil's Archiv. i.; and Brandis, Versuch über die Lebenskraft. Hannover, 1795.

ments, consist partly in learning to confine the action excited by the will to single groups of nervous fibres. The result of exercise or practice with respect to these movements is therefore the diminution of the tendency to the involuntary association. It is quite otherwise with the association of voluntary movements. Here practice developes in the muscles the capability for rapid succession or simultaneous execution of movements, when the muscles as yet have but little proneness to such association. The effect of practice is, therefore, in this case, the very reverse of its result in the case of the involuntary associate movements. Practice diminishes or annuls the innate tendency to involuntary association of movements, while it renders the voluntary association of several muscles in action more easy. Darwin and Reil have in some parts of their writings confounded these very different conditions of the nervous system. The law laid down by Darwin* is, that "all the fibrous motions, whether muscular or sensual, which are frequently brought into action together, either in combined tribes or in successive trains, become so connected by habit, that when one of them is reproduced the others have a tendency to succeed or accompany it." This may be granted generally; but the examples chosen by Darwin and Reil to illustrate this law are in part instances of the involuntary associate or consensual movements. Moreover, the law proposed by Darwin does not describe the facts quite correctly; for, were they as this expresses them, education and practice would only render us less expert in our movements. The associate movements taught us by practice would be frequently an inconvenience, a hinderance to our actions, instead of practice removing the innate tendency to involuntary association of movements, which is really the case. The example adduced by Darwin and Reil, that we cannot easily cut the air horizontally with one arm and move the other in a circle, does not illustrate the association of voluntary movements arising from practice; for this tendency to a similar movement of the two arms is innate, like that which regulates the movements of the eyes. On the contrary, practice gives us the power of executing the dissimilar movements of corresponding parts of the two sides. Another example mentioned by Darwin and Reil is a better illustration of the association of voluntary movements. A person learning to use the turning-lathe at first determines every new direction of his chisel by previous thought; after a time, his will seems to be seated at the point of his instrument. Here by practice the muscular movements are associated in quick voluntary succession; no one movement is the cause of the other occurring, their rapid combination merely is rendered more easy; and such is the case in all association of voluntary movements. When movements have been frequently associated in certain orders of succession, the difficulty of thus

* Zoonomia, p. 49.

associating them becomes constantly less, so that the will is then able to produce the whole series very rapidly, without, however, one of the movements composing the series taking place involuntarily. Facts, however, do not appear to me to warrant Reil's statement that the will, by determining one of the movements, can give rise to the whole series. There are, it is true, many movements due solely to habit, which are repeated on the least occasion, such as the unmeaning waving of the arms in actors and singers, and the movement of the hands in most persons of lively temperament; but these movements of habit do not belong to the association of voluntary movements with each other, but to the association of movements with ideas.

2. Association of ideas and movements.—The connection between ideas and movements is sometimes as close as that between different ideas; thus, when an idea and a movement have frequently occurred in connection with each other, the idea often excites the involuntary production of the movement. Hence it is that a threatening movement before the eyes, even the passing of another person's hand in front of them, causes the eyelids to be involuntarily closed; that we are accustomed always to accompany the expression of certain ideas with certain gestures, and that we involuntarily move our hands to catch a falling body. It is a general rule that the more frequently ideas and movements are voluntarily associated together, the more prone are the movements to be excited by those ideas rather than by the will, or to be withdrawn from the influence of the will. This kind of association plays as important a part as the association of movements with each other in the production of mechanical dexterity and perfection in the mechanical arts. The association of movements with each other can only be accounted for on the supposition of a more ready path being developed in the brain for the communication of nervous influence in a certain direction, and the concatenation of ideas and movements seems to indicate that every idea in the mind gives rise to a tendency to action in the nervous apparatus of the movement which expresses that idea, and that this tendency to action is by practice and habit so exaggerated that the mere disposition which exists in ordinary cases becomes, each time that the idea occurs, a real action. Yawning may serve as an example of this. If the disposition to yawn exists, the mere idea of yawning often excites the act. What connection subsists between the image in the sensorium of a person yawning and the involuntary movement thus induced? Whence arises it that among so many countless ideas formed in the sensorium this one only of the movements of a person yawning excites the act? The fact clearly proves that the idea of a movement alone suffices to produce a tendency to it in the apparatus by which it is effected. I have on another occasion remarked that the spectators of a fencing-match, or combat with swords, accompany

the blows of the combatants with slight involuntary movements of their body. A similar fact may be observed on a bowling-green. From the same cause, we experience, when in a dangerous situation on considerable eminences, a kind of propensity to precipitate ourselves down the height. The propensity to the imitation of movements is of the same nature. When we wish to look grave, and continue to think of laughing, we are obliged ultimately to laugh; like children, who look one another in the face to see which laughs first. Frequently, long after a ridiculous circumstance has occurred, an observer bursts into laughter from seeing others concealing or suppressing a laugh. Lastly, the occurrence of a paroxysm of convulsions in patients subject to them when they see others so affected, is another example of the association of movements with ideas. In hospitals, when several persons liable to convulsions lie in the same ward, the occurrence of a paroxysm in one sometimes excites the same in others.

M. Chevreul has explained the tendency to movements excited by the idea of the movement, and illustrated it by a complicated case, that, namely, of the vibrations of a pendulum held in the hand. The movement of the pendulum while the arm remains fixed is, according to his researches, effected by a slight muscular movement of which the individual is unconscious; this movement, he says, ensues involuntarily when the person looks at the pendulum which he is holding, but does not take place when the eyes are bound. The two principal facts here are, that a pendulum held in the hand can be set in motion by a muscular action so slight that the individual remains unconscious of it; and that looking at the motion once produced gives rise involuntarily to a series of muscular actions calculated to increase the motion, the mind remaining unconscious of this action of the muscles. M. Chevreul made application of this fact to the explanation of yawning also.* M. Behn† has, however, shown that one of the chief causes of the continued agitation of the pendulum held in the hand is the slight motion imparted to all parts of our body by the arterial pulse.

The association of movements with certain ideas is not an isolated fact of its kind, even if we do not take into account the frequent association of ideas with each other. Ideas do not act merely on the motor apparatus by which they are expressed; they as frequently affect the organs of sense, which then present sensorial impressions or images of the ideas. There is a great difference between the idea of a disgusting sensation and the sensation of disgust itself, and nevertheless the mere idea of a nauseous taste can excite the sensation even to the production of vomiting. The quality of the sensation is a property of the sensitive nerve, which is here excited without any external agent. The mere sight of a person about to pass a sharp instrument over glass or

* Froriep's Notiz. N. 831. † Müller's Archiv. 1835.

porcelain is sufficient, as Darwin remarks, to excite the well-known sensation in the teeth. The mere thinking of objects capable when present of exciting shuddering, is sufficient to produce that sensation in the surface in irritable habits. The special properties of the higher senses, sight and hearing, are rarely thus excited in the waking state, but very frequently in sleep and dreams; for, that the images of dreams are really seen, and not merely present in the imagination, any one may satisfy himself in his own person by accustoming himself regularly to open his eyes when waking after a dream. The images seen in the dream are then sometimes still visible, and can be observed to disappear gradually. This was remarked by Spinoza, and I have convinced myself of it in my own person.*

c. *Instinctive movements.*

The combined movements, of which the nature is most obscure, are incontestably the instinctive. All those acts of animals are instinctive which, though performed voluntarily, do not nevertheless depend primarily on the mere will of the animal, which have an object according with the wants of the organism but unknown to the animal, and of which the hidden cause, acting in accordance with the design of the system, incites the animal to the necessary acts by presenting to its sensorium the "theme" of the voluntary movements to be executed in detail by the influence of the will. We are ourselves conscious only of feelings and impulses to determinate acts. And these instinctive impulses in the human subject are few; the impulse to the movements of sucking in the infant is an instance of them. The acts which lead to the exercise of the sexual impulse are in animals generally excited by instinct; in man this is certainly only in part the case. Even admitting the embrace of forms which excite the feeling of love to be the result of an impulse implanted in us, the first of our race undoubtedly learnt the rest by experience. The number of the instinctive acts is great in animals in proportion to their incapability of accomplishing the design for which their species was created by their mental powers. It is not here the place to recount the great number of the instinctive acts connected with the migration of animals, the construction of nests and dwellings, the formation of webs, and the rearing of young.

The cause of instinct appears to be the same power as that on which the first production of the animal, and the perfection of its organisation in unison with an eternal law, depend.† The instinctive acts of animals

* See Gruithuisen, Beiträge zur Physiognosie u. Eautognosie. München, 1812; and J. Müller, über die phantastischen Gesichtserscheinungen. Coblenz, 1826. This subject will come under consideration again in the Sixth Book, on the mental faculties.

† The attributes of the creative organic force or power have been considered at pages 22 to 25.

show us that this power, which thus, independent of any organ, forms the whole organisation with reference to a determinate purpose and in accordance with an unchanging law, has moreover an action beyond this; they prove that it influences the voluntary movements. That which is effected by the instinctive movements is equally in accordance with a determinate purpose, and as necessary for the existence of the genus and species as the organisation itself; but while, in the case of the organisation of the being, the object attained formed part of the organism, in the case of the instinctive movement it is something in the exterior world; the mental power of the animal is incited by the organic creative force to the conception and attempt to attain some special object. The primary cause of instinct is therefore not seated in any one organ, but is identical with the creative force of the organisation, the operations of which are guided by an unvarying law and rational principle. The influence of this force in the production of instinct is, however, first manifested in the sensorium. The expression of Cuvier with reference to instinct is very correct. He says, that animals in their acts of instinct are impelled by an innate idea,—as it were, by a dream.

It is further to be remarked that the realisation of the ideas, images and impulses, thus developed in the sensorium, is admirably facilitated by the organisation of the animals. Both the internal impulse and the external organisation being dependent on the same original cause, the form of the animal appears in complete unison with its impulses to action; it wills to do nothing which its organs do not enable it to effect, and its organs are not such as to prompt to any act to which it is not impelled by an instinct. The mole, impelled by its internal instinct to a subterranean life, has an indistinct sight, (from the smallness of the eyes and from their being surrounded with thick hairs,) not fitted for other habits; and its fore-feet and legs are not only entirely formed for burrowing, but the way in which the fore-foot is articulated to the fore-arm is such that it can scarcely walk without burrowing. The extremities of the sloth again are constructed for climbing and living in trees, in which indeed they pass the night; and while on the ground their movements are extremely slow and awkward, their toes being turned inwards and the feet resting on the outer border, in trees they are very expert and powerful, though slow in their motions, like other climbing animals,—for example, the chameleon.

It is a subject full of wonder to observe how instinct imparts to animals faculties, capabilities, and intuitive perceptions, which we acquire only by the laborious process of experience and education. When we first see, we are unable to judge of the distance or nearness of objects, the images of which are formed in our eyes. All objects in the field of vision being depicted on a surface—as in painting, it requires long experience, and the aid of touch and voluntary movements, to enable us to attach to the image of an object in the field of vision ideas of its distance, size, and form. Animals appear, when born, as if they had been already submitted to this education. The calf soon after birth runs to the mother's teat. The human infant does not learn to go alone until after laborious practice, in which the laws of equilibrium and gravity, &c. must every moment be attended to, and until the degree of contraction of the muscles necessary for each movement has been learnt by experience and previous errors. The young of animals — at least, of the solidungula and ruminantia, — are born with the knowledge of these things. They soon after birth rise on their legs, and run to the mother to suck. This must be the result of the operation of the instinctive power which resolves all the problems of physics. In the sensorium of the newly-born animal there must be a power at work which directs the proper action of the levers of the locomotive members.

From the acts due to instinct, we must distinguish certain others which many animals are able to perform with great precision even during sleep after they have by previous practice gradually acquired the necessary ability. Many birds sleep standing upon one leg. They preserve their equilibrium with the greatest certainty, and there is no rest to the force exerted in these acts, though the sensorial operations of the sensorium be quite suspended. Sleep-walking is a similar phenomenon. It is not instinct that leads the somnambulist, but the faculty of walking safely acquired by experience, which faculty he continues to exercise even during sleep. All the knowledge acquired by education and experience with reference to maintaining his balance is put in practice; it is by the operation of his mind alone, and not by instinct, that he is prevented from falling: but his sensorium is active in one direction only, and in no others; and the circumstance of his being, in consequence of this limited action of his faculties, ignorant of danger, renders him secure, and carries him safely past precipices. These phenomena are indeed not so difficult of explanation as at first sight appears. The security with which a person walks over a moderately sloping surface depends entirely on his knowing that it is not at a great elevation. The same sloping surface on a steep hill appears dangerous and difficult to ascend; and provided a person does not see any danger in the last case, he will pass over the ascent as securely as if it were at a little distance only from the surface of the earth.

Since in animals there are evidently instinctive innate feelings and perceptions, which manifest themselves immediately after birth or at a later period, it becomes a question whether man also have not innate ideas which exert on him in a higher grade the same coercive power which the instinctive impulses and feelings of animals exercise over them. We shall return to this question in the part of the work which treats of the functions of the mind. Hopes have been indulged that the instinctive rational operation of the organising force might in certain states make us conscious of what we could not learn by our mental faculties. There is no ground for such hope; and I am not aware that the power of nature, which is quietly at work in the human system, ruling and creating the organisation independently of the mental consciousness, though in accordance truly with a rational and higher law, has ever communicated any knowledge to the mind, or that the divine reasoning spirit (of Spinoza), which has a creative power, has ever mingled itself with the images of objects conceived by our mind. The phenomena of this kind, reported to have occurred in the pretended magnetic states, are undeserving of the belief which credulous medical men have accorded to them; and they have in too many cases proved to be the result of deception or folly. The disclosures made in the magnetic state have been nothing more than products of the imagination, often indeed very confused, and of a nature appropriate to the capacity of the person affording them, and of the believing listeners.

d. Co-ordinate movements.

Although the movements of locomotion are dependent on the will, the appropriate combination of the separate muscular acts necessary for them appears, nevertheless, to be rendered more easy by some internal disposition of the nervous system, and there seems to subsist between the nervous centres, the groups of muscles and their nerves, a harmony of action dependent on original structure. This idea is suggested by the experiments on the functions of the cerebellum and the spinal cord. Decapitated birds are seen to make all kinds of attempts at locomotion. The same has been observed in frogs. Although they have not the character of voluntary movements directed by the influence of the brain, still there prevails a certain unison between the different acts of such tumultuous movements observed in geese after decapitation. They beat the ground with their wings, a movement for which the simultaneous and concordant action of many nervous fibres is necessary; and it appears, therefore, that there is some organic arrangement in the central organs which favours the co-ordinate action of certain nervous fibres. The movements of the decapitated bird are not mere spasmodic contractions of all the muscles subject to the influence of the spinal cord; for, were all the nervous fibres arising from the divided cord thrown into a state of irritation, all the muscles of the body would be equally excited to contraction; flapping of the wings would not be thus produced: at all events, it is not easy to conceive why the wings should not on the contrary be folded spasmodically close to the body. The twisting motion of eels, and the flapping of the tail in other fishes, after their head is cut off, are phenomena of the same kind. Invertebrate animals perform the movements of locomotion after decapitation, sometimes quite in the ordinary manner. The influence of the will, indeed, seems in them still to be exerted. (See page 793.)

The experiments of M. Flourens, moreover, show that there exists not merely in the spinal cord a provision for the performance of certain groups of movements in unison, but that the cerebellum more especially rules over the combination of the muscular actions required for locomotion (see pages 831—835). Injuries of the cerebral hemispheres, or their removal, did not deprive the animals of the power of executing combined movements. But the removal of the cerebellum produced not merely weakness, but loss of all harmony in the action of the groups of muscles. M. Flourens, however, observed that the bird, when laid on its back after the extirpation of the cerebellum, fluttered its wings; showing some slight remains of the power of co-ordination, which, as we see in geese after decapitation, may be derived from the spinal cord. This co-ordination of movements must be of great use to animals in the first employment of their extremities, which they are observed to move so aptly; the co-ordinate movements are indeed much engaged in the production of all the instinctive acts. In the act of sucking, an internal incitement to the necessary co-ordinate movements exists in the brain. Even the head of a decapitated kitten still performs the movements of sucking, as Professor Mayer has observed, when the finger is held in the mouth.*

CHAPTER III.

OF THE MOVEMENTS OF LOCOMOTION.†

Many animals are for the most part destitute of locomotion, and are only capable of a relative movement of particular parts with reference to the rest of the body. Some of these animals are fixed by one part of their body; others lie free.

The compound entozoa are in the first-mentioned condition; in the Cœnurus cerebralis, for example, the only motion of the separate animals united by a common vesicle consists in their elevating themselves above

* [Admitting that the act of sucking is, as was maintained by Sir G. Blane, and more recently by Mr. Grainger and Dr. Hall, (see note to page 936,) the result of reflex nervous action excited by the external stimulus of the nipple or finger, it would still afford the same evidence of the existence of a provision for the combination of certain movements in the nervous centres.]

† [Even the movements of locomotion are supposed by Mr. Grainger (on the spinal cord, p. 93—116) to be in some measure the result of reflex nervous action. He seems to think that the continuance of our movements of walking, for example, while the mind is abstracted, is owing to the propagation to the spinal cord of the impressions produced by the contact of the soles of our feet with the ground. His chief grounds

the surface of this vesicle, and their subsequent retraction. The compound polypes, again, are capable of no other locomotion than the protrusion of the head of the separate polype and its arms, and the retraction of them again into the polype-cell. Even the Pennatulæ, which were long believed to be free, and to move about in the sea, are fixed to the bottom like the Veretilla; the separate polypes only of these compound animals have motion. External influences excite the retraction of those polypes only on which they act directly.* Rapp, however, has observed a slow bending motion in the stem of the Veretillum. In what relation the independent movements of the separate polypes stand to these slow contortions of the stem in Veretillum, is not at present quite clear; indeed, the nature of the physiological connection between the polypes and their stem is a most difficult problem to solve. †

A part of the arm-polypes are capable of free locomotion, as the Hydra; a part are fixed, as the Coryne. There are some of the Annelida which have no free locomotion; for example, the Serpulæ, which inhabit calcareous tubes. The tubuli-branchiate gasteropods, as the Vermetus and Siliquaria, live in fixed tubes. The Ostracea (the oysters and allied bivalves) are in part fixed by their shell to rocks; others of them are free; but in either case they scarcely at all change their place, their movements being limited to the closing of their shell, which is opened by an elastic ligament: again, others of this family, as the Pinnæ, fix themselves to solid bodies by means of the byssus issuing from the rudiment of the foot, this byssus being their anchor, as Cuvier expresses it. The Mytilus, or sea-mussel, family, also employ

for this opinion are, that the motions excited by irritating the skin in decapitated animals resemble those performed in locomotion, and that the movements produced in paralysed limbs by irritating their surface (see note * p. 721), occur most readily, and are most energetic, when the sole of the foot, which in walking comes to the ground, is the part to which the irritation is applied. Mr. Grainger attributes great importance to the fact that the reflex movements of paralysed limbs are excited more readily and in a more marked degree through the medium of the sole, than by irritating any other part of the foot or leg where the skin is thinner; and remarks that the most sensitive parts are not the most excitable. But in the instance in question, the degree of excitability is directly in accordance with the sensibility of the parts; for on reference to page 701, it will be seen that according to the investigation of Professor E. H. Weber, the points of a pair of compasses applied to the skin of the dorsum of the foot or leg, cannot be felt as two distinct bodies until they are separated to the extent of eighteen lines, while, on the plantar surface of the metatarsal bone of the great toe, they can be distinguished at the distance of seven lines. Hence we see that the greater excitability of the sole of the foot than other parts of the limb will afford no argument for the existence of special excitomotory fibres distinct from the sensitive.]

* Rapp, über die Polypen, S. 8. On the structure of the stem of the polype, and on the currents observed in it, see Rapp, loc. cit. and Nov. Act. t. xiv. pt. 2. p. 650; Lister, Philos. Trans. 1835, pt. 2; and Meyen, Nov. Act. t. xvi. Suppl.

† See Ehrenberg, Die Corallenthiere des rothen Meeres. Berlin, 1834, p. 27.

their long foot more for the attachment of the byssus than for locomotion. Other allied conchifera, as the Anodon and Unio, (fresh-water mussels,) creep along the bottom by means of the foot. The Ascidiæ are attached to rocks, and are destitute of all locomotion. Their voluntary movements consist solely in the spirting of water from the mouth of the mantle, which is adapted for that act. Of the compound Ascidiæ, the Botrylli are fixed to foreign bodies, and are united, several in the form of a star; and Cuvier remarks that, if the oral orifice of a single animal be irritated, this one animal only contracts; but that if the common cavity in the centre of the star be touched, they all contract. The Pyrosoma, belonging to the same group of mollusca, is a compound animal, of which the individuals are so united as to form a hollow cylinder, into which the anal aperture of each opens. They are free, and are said to swim about by the combined contractions of all the individuals forming the compound animal.* The details of this phenomenon, which is so remarkable in a physiological point of view, are not known. The disappearance of the phosphorescence when any one part of the cylinder is injured, is certainly in favour of there being a community of action in these creatures. The compound polypes present us no instance of a condition so extraordinary.

Many animals belonging to very different classes are free during one part of their life, and fixed at another.—Some are first fixed, and afterwards free: of this, the Vorticellæ, according to Ehrenberg, afford us an example. Others are free during the earlier stage of their life, and afterwards become fixed, and destitute of all locomotion; of which remarkable circumstance, the interesting observations of Von Nordmann† respecting the Lernææ, of Dugès ‡ respecting the Hydrachnida, and of Burmeister § on the Cirrhopoda, present us with examples.

Animals endowed with locomotion.—The organs of motion in animals capable of changing their situation are sometimes cilia, bristles, laminæ, or fins, sometimes articulated members. In other cases the movement is effected by the expulsion of fluids previously taken in; by undulatory movements of the different parts of the body, which are in turn fixed, drawn after other parts, or stretched forwards; or by the alternate dilatation and contraction of the whole body.

Professor Ehrenberg|| has minutely described the organs of locomotion in the *infusory animalcules.* The more simple of the locomotive organs in these creatures are either processes capable of undergoing great changes, which can be protruded from different parts of the body, as in the genus Proteus, or Amæba of Ehrenberg; bristles, as on the

* Cuvier, Règne Animal.

† Micrographische Beiträge. ‡ Ann. d. Sc. Nat. 1834.

§ Beiträge zur Naturgeschichte der Rankenfüsser. Berlin, 1834.

|| Zur Erkenntniss der Organisation in der Richtung des kleinsten Raumes. Berlin, 1832, p. 28.

back of Chætonotus; cilia, which in the polygastric infusoria frequently occupy the whole surface; or, in other instances, hooks. The more complicated organs are the rotatory apparatus of the wheel-animalcules and some of the polygastrica. Ehrenberg has described several varieties in their forms; what he has discovered of their structure has been detailed at page 860. The vibrations of the cilia of the rotatory organs do not merely serve to produce currents in the water for the attraction of nutriment, but also to carry the animal through the fluid. The wheel-animalcule is, however, also able to creep over surfaces, by fixing alternately the anterior and posterior extremities of its body, the posterior extremity being drawn up towards the anterior, and this then stretched further forwards.

Acalephæ, that have a disc or bell-shape, change their place by the alternate contractions and expansions of their body, by which the water contained in the cavity of the bell is expelled. Others of the Acalephæ, the Beroe for example, move in part by means of vibrating laminæ arranged along the eight costæ of their globular body. Some other Acalephæ, as the Diphyida, have tubular swimming cavities, which act as the bell-shaped cavity of the Medusæ; in others there is an air-bladder, by means of which they keep themselves at the surface of the sea. In the Physalia there is, besides this great air-bladder, a part acting like a sail,— a membranous crest which can be filled with air, but which can also be emptied again. The air-vesicle has an opening at each end, closed by a sphincter.*

Echinodermata.—The Holothuria can propel itself by the expulsion of the water taken into its respiratory organs (fig. 18, p. 297); its whole body is capable of being shortened by strong longitudinal muscles. But the Holothuriæ, like the allied families of Asterias and Echinus, possess, moreover, the system of water-tubes discovered by Tiedemann; these tubes, communicating on the one hand with a contractile reservoir, terminate on the other hand in the hollow feet of the animals, which are protruded by being injected with the fluid, and are retracted by virtue of their own contractility.†

The *Annelida* which are not fixed swim through the water by undulatory movements of their body. The *Salpæ and allied Tunicata* move by taking in water by the posterior opening of the mantle, where there is a valve, and expelling it by the opening which is near the mouth. The creeping of worms (*terrestrial annelida*) and caterpillars (*larvæ of insects*) over solid bodies is thus effected: aliquot points of their body being fixed, others are drawn after them, when the extremity of the part last moved being fixed, the parts in front, which formed an arch, are stretched farther forwards. The means of attach-

* Eschscholtz, Syst. d. Acalephen. Berlin.

† Tiedemann, Anat. der Röhrenholothurie, &c.

ment are sometimes the parts about the mouth; sometimes feet, as in the caterpillars; sometimes suckers, as in leeches, &c. In other annelida, and in the mollusca generally, the movement of creeping results from the alternate contractions and dilatations of the body or of the foot. The earthworm does not creep like the leech by bringing its body into an arched form and then elongating it; but a certain number of segments of their ringed body are fixed, and the segments succeeding each one that is fixed is simply drawn towards it, diminishing the length, but increasing the breadth of this portion of the body; the posterior extremity of the part thus drawn together is then fixed, and the shortened part contracts transversely, so as to extend itself forwards; this kind of motion exists in the leeches also. In the *gasteropod mollusca* (snails, &c.) this movement takes place in so many separate points at the same time, that, when we observe a snail crawling on a plate of glass, the appearance presented is only that of a succession of very minute undulations, while the snail itself appears to move on uninterruptedly. A similar succession of undulations is seen in the foot of the Lymnææ (fresh-water snails) when they lie on their back, hanging, as it were, at the surface of the water. It is difficult to understand how separate points of a surface so smooth as the foot of the snail can in this way take fixed attachments.

Mechanism of locomotion.—The essential principle of locomotion in its most different forms, swimming, crawling, walking, or flying, and in almost all animals, is, that parts of their body form arches, which in straightening themselves act against a fixed point of resistance. In some cases the arches are formed by the whole worm-like body, as in the crawling and swimming of some animals; in other instances, in place of the arching and straightening of the body, the same is effected by the approximation and separation of the two sides of an angle; in which case one of the sides or branches of the angle, by the resistance it meets with from a solid or fluid substance, affords the fixed point which enables the separation of the two branches or opening of the angle to carry the other parts of the animal forwards. This is the principle of movement in animals with locomotive members, whether these be fins, wings, or legs, and whether they move in water, in the air, or on the ground: for even the air and the water afford resistance to bodies which strive to displace them; and the force exerted in displacing them reacts, in proportion to the resistance they give, on the body of the animal, and imparts to it a motor impulse in a determinate direction. In connection with this subject, the laws of the action of levers must necessarily be considered. Although many varieties of the lever are met with in the limbs of animals, yet they are for the most part so applied that power is lost; thus the muscles in many, indeed in most cases, act on them in an oblique direction, and are besides inserted very frequently near the fulcrum, and distant from the moving end of the lever. There are more important objects thus attained than mere beauty of form. Had nature in every limb adopted the arrangement of lever calculated to give the most power, such a complexity, angularity, and awkwardness of form would have resulted, that the increase of impediments to a harmonious co-operation of parts would have caused the expenditure of force to be in the end even greater than it now is. Extent of motion also required that the muscles should not be inserted far from the fulcrum of the lever: for had their insertion been placed nearer the moving extremity of the lever, power would, it is true, have been saved; but, on account of the slight degree of shortening of which muscles are capable, (according to M. Schwann's experiments, at most a third of their length,) extent of motion would have been lost,—the biceps, for example, would not have been able to bring the fore-arm close to the arm, which it can do in consequence of being inserted near the fulcrum. [Velocity of motion, also, as well as extent, is gained by this mode of insertion of muscles, for in the same time that the part of the lever immediately acted on passes through a small space, the other end, far removed from the fulcrum and moving force, traverses a much greater space, and moves with proportionate rapidity.]*

Swimming.†—Both in swimming and in flying, the medium which affords the resistance, is also that in which the animal moves. In walking and crawling, whether in the water or in the air, the water and air are passed through; but a solid body, the earth, affords the support for the propulsion of the centre of gravity. In swimming and flying, therefore, the medium which serves as the fulcrum for the motion is yielding; while in walking and springing it is solid. The greater the force with which the locomotive organs press upon the air or water in proportion to the mass of the body to be moved, and the resistance offered to its passage through the medium, so much the greater is the motion produced. By resistance is meant here the loss of motor power which a body forcing its way through a fluid medium experiences in displacing the particles of the fluid.

In swimming, the essential act consists in the straightening of an arch which in becoming straight exerts pressure on the water. If we suppose a flexible and elastic rod of the same size throughout lying in the water to become bent in the middle and then straightened, the two halves of the arch would strike the water in the oblique direction with equal force, and the straightened rod would not be impelled

* On the movements of locomotion, consult Borelli, de motu Animalium. Lugd Batav. 1685. 4.—Barthez, Neue Mechanik der willkührlichen Bewegungen des Menschen und der Thiere. Halle, 1800. 8.

† Borelli, loc. cit.—Muncke, in Gehler's Physikal. Wörterbuch.

forwards in the longitudinal direction. The result is the same when two levers of equal size united by a hinge are inclined towards each other and then extended, the mass of the two levers being the same; the power at their middle, which effects their approximation, will move each with equal force towards the other, and a force acting at the same part in such a manner as to extend the joint will move them with equal force from each other. But if the principal mass of the body form one of the levers, the force acting at the point of flexion will tend rather to move the smaller lever towards the larger one than this towards the smaller. While the larger lever will preserve its position in the water, the smaller one, both in flexion and extension, will alter its relative position to the larger mass. This is what takes place both in the boat propelled by a sculling-oar at the stern, and in the fish. In both, while lying in the water, the force exerted to change the relative position of the sculling-oar or tail, and the principal mass, to each other, moves primarily only the smaller part,—namely, the oar or tail, towards the body of the boat or fish. When, however, the oar is again brought to a straight line, it exerts a pressure upon the water behind it; and, were this water a solid body which could not be displaced, the boat would be impelled with the whole force with which the oar is moved, in the contrary direction,—namely, obliquely forwards. The pressure of the oar, however, imparts to the water a part of its own motor force, causing it to be displaced; the rest of the force with which the oar is moved tends to separate the water acted on, and the mass of the boat, from each other, and the latter is in consequence propelled obliquely forwards. The movement of the oar in the opposite direction gives to the boat an impulse obliquely forwards towards the contrary side; and a quick succession of such movements imparts to the vessel the middle straight direction. It is necessary, preparatory to each new stroke, that the oar be again brought from the straight line to an angle with the body of the boat, and since the water is thus acted on in the opposite direction, the propulsive force imparted to the boat would be neutralised, were this movement of the oar made with equal force with the former; for, in fact, an oar moved from side to side in the water with equal force in both directions gives no motion to the boat.

The motion of a fish in swimming is exactly similar to that of a boat propelled simply by the movement of the sculling-oar at the stern; the tail of the fish is the sculling-oar. Two strokes of the tail in quick succession are in many fishes with a short tail, as the carp, sufficient to give the fish the middle direction. It is frequently observable, however, that the fish, while swimming slowly, does not follow a straight course, but moves alternately from side to side in an oblique direction, in accordance with alternate strokes of the tail towards either side. Fishes with a long tail can form it into two arches looking in contrary directions, which they straighten at the same moment, thus impelling the body in a straight line forwards. The flat-fishes (plaice, turbot, and flounders,) and the cetacea strike the water with their tail in the perpendicular direction. The rays swim partly by means of their tail, which they use like most other fishes; their thoracic fins, however, are extended out on each side like wings, and they act in swimming in a similar manner to the wings of birds in flying. In all other fishes the fins have a very subordinate share in the production of the principal movements of swimming; this was proved by Borelli.* The fins serve like feet, by their pressure on the water, to preserve the position of the fish's body, and to steady its motion. Cuvier attributes to them the office, also, of producing the movements of the fishes to the side; but for this, as we see in the carp, the one-sided movement of the tail is much more effective.

Quadrupeds in swimming use their feet as oars, in the same way that boats are moved by oars. The resistance of the water displaced by the oar is the cause of the boat being propelled forwards, while the angle between the oars and boat enlarges. If the oar were moved backwards and forwards in the water with the same force and in the same position both ways, the boat would not be moved. The movement of the boat in one direction depends on the oar being brought back after each stroke through the air, or, if not, with the edge instead of the broad surface to the water. The same principle is observed in the swimming of animals by means of their feet. The hands and feet are brought back after each stroke in such a position as to press with a smaller surface on the water. A man in swimming brings his arms forward to the proper position with the cutting border of the fingers foremost, and then strikes the water with the flat surface of his hand. The quadrupeds which have not broad flat feet, as the horse, also propel themselves forwards by striking the water with a larger surface than they oppose to it in restoring their limbs to the position for the succeeding stroke; in the backward motion of their legs they act on the water with a much larger surface than when they bring them forwards again. Quadrupeds are for the most part swimmers by nature, since they use their limbs in the water nearly in the same manner as in moving on land; and the length of their nostrils, and smallness of their cranium, enable them to make the opening for respiration the highest part above the surface of the water. In man, the only position in which the opening into the respiratory organs is highest, is that in which he lies in the water on his back; man, too, before he can swim, must learn a particular movement of the limbs, to which he is previously unaccustomed,—such a movement, namely, that the legs and arms, in being brought forward for each new stroke, present a less surface to the water than in the back-

* Borelli, loc. cit. p. 257.

ward motion. The practised swimmer is able to float on the surface of the water with very little other movement than that of inspiration; he is supported at the surface as long as his lungs, distended with air, render him lighter than water. Like quadrupeds, man is naturally heavier than water; and he sinks in it, if he make no effort, as soon as he expires the air from his lungs. But while his chest is well filled with air, and his body extended on the back, he keeps at the surface. If we did not require to expire,—were we able to keep the chest constantly distended without changing the air,—we might remain quite motionless, without sinking; but, in consequence of the body sinking at each expiration, it is necessary to counteract this tendency by motion of the hands. Birds are kept at the surface of the water in consequence of the air being received into large cells in the abdomen and into the bones through communications with the lungs. Before diving, birds require to make a strong expiration. Swimming birds use their feet as oars; swans use also their extended wings as sails to move along the surface of the water.

The air-bladder of many fishes, which, according to Von Baer's observations,* is developed, like the lungs, from the pharynx, facilitates their movement in the upper regions of the water, and, by the compressibility of the air it contains, enables the fishes to move in different depths according to the degree of pressure exerted by the lateral muscles of the body upon it. By reason of its position at the upper part of the abdominal cavity, where, owing to the large size of the dorsal and lateral muscles, the centre of gravity would otherwise be situated, this organ also serves to keep the back of the fish uppermost in the water, although it is not indispensably necessary for this purpose. Fishes in which the air-bladder has been ruptured do not afterwards rise to the surface, and are liable to fall upon the side.

Flight.†—The flight of birds is effected by the action of the anterior extremities, spread out horizontally to their utmost extent, upon the air, which reacting by its resistance and elasticity, the body of the animal is raised. This movement requires great strength of the pectoral muscles, and a modified structure of the thorax; the dorsal vertebræ, namely, do not admit of motion; the central piece of the sternum is developed so as to give space for the attachment of the large pectoral muscles; while the articulation of the humerus is strengthened not merely by the strong clavicles, but also by the furculum uniting the two shoulder-joints. The wings are folded so as to offer less resistance to the air before they are raised for a new stroke; when raised, they are

* See Müller's Archiv. 1835, p. 234.

† Borelli, loc. cit. — Cuvier, Anat. Comp. t. i.—Fuss, Nov. Act. soc. sc. Petrop. xv. 1806.—Silberschlag, Schriften der Berlin, Gesellschaft Naturf. Freunde, 1784. 11.—Horner, in Gehler's Physikal. Wörterbuch, iv. p. 477.

again spread out. The carpal articulation in the wing of the bird is not capable of flexion and extension; the wing when expanded is on this account stiff, and better calculated to act against the resistance of the air; the only movement of the carpal joint is adduction and abduction, by which the carpus and metacarpus can be folded down to the fore-arm or separated from it. A succession of strokes of the wings when they are quite horizontal carries the bird perpendicularly upwards in the air, as we see larks ascend. When the wings are inclined so that their under surface looks backward, their action must cause the bird to ascend obliquely, whereupon it will descend in the same oblique direction; and a regularly repeated action of wings thus inclined will produce a horizontal flight in an undulating line. The motion of the wings themselves need not partake much of the horizontal direction; for, even when the stroke of the wing is perpendicular, the flexible feathers yielding to the resistance of the air must immediately render the surface of the wing oblique from the posterior border downwards towards the anterior fixed border. This circumstance was pointed out by Borelli. An alteration in the direction of the flight towards either side is effected by the unequal vibration of the two wings, and not by a lateral inclination of the tail; for pigeons deprived of the tail feathers can still wheel round in the air. By bending the tail, the posterior part of the body is raised, the anterior part depressed.

The immobility of the back in birds gives to the trunk, the lower part of which is the seat of the centre of gravity, the solidity required to support the vibratory motions of the wings; the tapering pointed head is well adapted to divide readily the air; and the long neck, by being retracted or extended, gives a means of altering the position of the centre of gravity. The large expanse of the wing is not formed solely by the feathers; for the skin itself extends as a fold between the anterior border of the arm and the fore-arm, and, when the wing is expanded, is stretched out by a special muscle—extensor plicæ alaris. In the anterior border of this fold there is an elastic band which in the intervals of flight draws the fore-arm towards the arm. The extensor plicæ alaris has a double tendon, of which one portion of a fibrous nature is connected with the musculus radialis externus longus, and the fascia antibrachii; the other is the elastic band in the anterior border of the fold, already mentioned, which goes to be attached to the carpus and metacarpus.* The birds of the ostrich family, Strutheonidæ, — the Struthio camelus (ostrich), Rhea Americana, Casuarius Indicus (cassowary), and Dromaius Novæ Hollandiæ (emeu),—and some water-birds, as the Aptenodytes and Alca (penguins and awks), are, on account of the small size of their wings, incapable of flying.

* Lauth, Mém. de la Soc. d'Hist. Nat. de Strasb. t. i.

The air in the bones of birds is evidently intended to render them lighter than they would be, were they filled with marrow. But the inflation of the air-sacs which communicate with the lungs cannot make the bird really specifically lighter, since the air in these sacs must have nearly the same density as the atmosphere. [The great heat of the bird's body must, however, in some measure rarefy the air within it.]

In many insects the injection of air into the tracheæ ramifying in the wings, which at other times are folded together, appears to contribute to maintain them extended and stiff.

In other classes besides birds, there are animals which can fly, or at least keep themselves suspended some little time in the air by means either of wing-like membranes or long fins. The order "Cheiroptera" (the bats), among mammalia, have their anterior extremities perfectly adapted for flying. The surface destined to strike the air is here formed by a membrane which extends between the elongated phalanges of the four fingers and metacarpal bones, stretches across the angle between the arm and fore-arm, and is continued from the elongated bones of the arm along the side of the body to the hind-feet, and from these even to the tail. This membrane of the bat also contains elastic tissue. The extinct reptile, Pterodactylus, was a true volant; the outer finger only, however, was in this animal much elongated for the purpose of flight; the other four were short, and armed with claws, like the thumb of the bat.

Other animals belonging to different classes have a membrane extending between their digits, which are short and all furnished with claws, between the arm and fore-arm, and between the arms and legs; but this membrane serves merely as a "parachute," as, for example, in the flying-cat (Galeopithecus). The cutaneous expansion between the anterior and posterior extremities of the flying-squirrel (Pteromys), and of the flying phalangers (Petaurus), and the fold of skin expanded between the lengthened posterior ribs of the reptiles with parachute (Draco volans), are of similar nature and purpose.

Some fishes (Dactylopterus and Exocætus) are enabled, by means of their elongated pectoral fins, to raise themselves above the surface of the water for a short space.

Crawling or creeping. — Both in crawling and in walking, a solid body affords the point of resistance. There is no essential difference between these movements, except that in walking special extremities are used both to support and to propel onwards the weight of the body; while, in crawling, the same objects are effected by aliquot parts of the vermiform body itself. In walking, angles formed by the legs are widened and contracted; in crawling, the vermiform body of the animal is alternately arched and straightened. Both movements can be performed in the water as well as in the air, a solid body always giving the points of resistance. Crawling can be performed in very different modes. The kind of crawling most similar to walking is that in which two points of the body only are applied to the resisting surface, while the rest of it is raised in an arched form; this mode of crawling is observed in the leech. In others of the annelida, the same movement takes place in many different parts of the body simultaneously, as in the earthworm and caterpillars, and sometimes in the leech. This last kind of crawling is most remarkable in the snail (see page 953); and since, though able to crawl over very smooth surfaces — such as glass, it has no other instruments for attachment and support which are necessary to enable the animal to move in a particular direction, it is probable that the foot takes points of attachment by elevating and thus exhausting different points along its surface in succession; this action of the sucker being transmitted from one part to another during the movement of crawling.

The crawling of snakes is very peculiar; the body moving forward constantly and rapidly in a horizontal undulating line, which line every point of the body follows. The points of support and resistance against the ground are taken by the extremities of the ribs aided by the abdominal plates; while the parts situated behind each point of support are drawn towards it, and others pushed forwards.

Walking and running.—In swimming, the body is borne up wholly or in part by the water, and its motor power is nearly entirely expended in the act of propulsion. In flying, the body is not supported by the medium in which it moves, and a certain additional amount of force is required to neutralise the tendency to fall after each act of propulsion. In walking, the body is both supported and moved forwards by its own strength; and there is this peculiarity, that the body in this movement is alternately supported on each extremity which is fixed on the ground, while by the other it is propelled forwards. One half of this movement is represented in a boat moved on the water by a pole pushed against the bottom; but what the water effects in supporting the boat is done by the other extremity in the act of walking in the air. In leaping, in which the body for a short space of time is kept suspended in the air by the propulsive force imparted to it, the second act of the movement—that of supporting the weight of the body—does not take place till the spring is completed. In this case, as in flying, the body is kept up by the same movement that propels it forwards; the medium serving for the point of resistance is, however, different, namely a solid body. After the influence of one movement of the wings in flying has ceased, the bird is prevented from falling by a new movement of propulsion; at the end of the movement of leaping, the body is prevented from falling by supporting itself on a solid surface.

The means by which these movements are performed in the human subject, is the extension of two joints flexed in opposite directions, namely the ankle and knee-joints. By this act of one extremity the centre of gravity is carried forwards, while the weight of the body is supported towards the end of the movement by the second extremity. The two extremities alternately support and move the body. The movement of propulsion being exerted, not in the middle line, but by both extremities at the side, the extension of the joints gives an impulse not merely forwards, but towards the opposite side. The arm of the side on which the extremity is being extended is each time thrown forwards.

The researches of Dr. Eduard Weber concerning the articulations,* and those of MM. E. and W. Weber respecting the movements of walking and running, have made us acquainted with many remarkable facts of a physical nature relating to these movements of locomotion, and with their laws. The physiology of these movements has first received a scientific accuracy from their discoveries. The most important facts which they have established are the following, which I extract from their work.† In the first place, and as a key to many other remarkable facts, we must mention the discovery of Dr. Eduard Weber, that the head of the thigh-bone cannot be separated by the mere weight of the limb from the surface of the articular cavity to which it is accurately adapted; but that, in all its motions, it is retained close to the articular surface by the pressure of the atmosphere. All the muscles which surround the hip-joint may be divided, but the weight of the limb does not remove the head of the bone from its cavity. If, however, the pressure of the atmosphere be allowed to act from the cavity of the joint on the head of the bone, by a hole being bored from the cavity of the pelvis into the acetabulum, the head of the femur immediately falls out of its socket.

The three physiologists named above have confirmed this discovery by means of the air-pump. The experiments were performed in the presence of Professor Magnus and myself. The hip-joint of a subject was dissected clean from the surrounding parts, the thigh-bone was sawn across below the trochanters, and the capsular ligament then carefully laid open all round; a weight of two pounds was attached to the remaining portion of the femur, and the whole hip-joint then placed in the bell of an air-pump. By the time the air in the bell had been so far rarefied that its pressure was equal to one inch only of the mercurial column, the head descended pretty rapidly seven lines from the articular cavity, without, however, escaping from the cartilaginous rim; when the air was again admitted to the bell of the air-pump, the head of the bone rapidly ascended again. Even when the head of the bone had

* Müller's Archiv. 1836, p. 54.

† Mechanik der menschlichen Gehewerkzeuge, mit 17 taf. Gött. 1836–8.

been forcibly removed from the articular cavity, if it were replaced so as to expel all the air from the cavity of the joint, it retained its position firmly, and could be with difficulty removed by traction in the perpendicular direction. The joint being again exposed to the vacuum of the air-pump, the same phenomena occurred as before; but now the bone fell entirely out of the articular cavity, when the pressure of the air was reduced to one inch. The influence of the atmosphere appears to be the same in all joints of this kind. It results from this important discovery of M. Weber, that the extremity freely suspended is maintained in its relation to the joint, in all the movements of rotation, by the atmospheric pressure; and, therefore, that the mere relaxation of the muscles cannot give rise to a separation of the head of the bone from the articular cavity. In ascending very high mountains, where the air is greatly rarefied, the muscular force must on that account become more necessary to maintain the articular heads of bones in their proper cavities, and the peculiar kind of fatigue which has been experienced by persons passing over high mountains is probably attributable to this cause.

MM. E. and W. Weber have further pointed out the importance of the pendulum-like oscillations of the legs in walking. If the body be supported on one leg upon a raised pediment, the other leg, being set in motion, will vibrate backwards and forwards like a pendulum. These vibrations may also be produced if, while standing with one leg upon a level surface, the other leg be bent to such a degree as not to strike the ground in its vibrations. The time of these vibrations, like that of the vibrations of a pendulum, depends on the length of the limb and on the mode of distribution of its weight. Thus, in persons with short legs, the vibrations are quicker than in those with long legs; but, in the same person, the number of oscillations within a certain period are always the same. This property of the legs, and the circumstance that each step of the foot previously extended behind the body commences with a pendulum-like oscillation, give to our steps the greatest regularity, even at times when our attention is not directed to the movements of our limbs. The leg, while moving with the pendulum-like oscillation, is somewhat flexed, that it may not strike the ground.

The general mechanism of walking is as follows:—The body is supported by the two legs alternately, and the moment in which each forms the support is immediately succeeded by that in which the heel of the same limb is elevated and the body impelled forward by it. At the time that the foot A gives this movement of impulsion, the body is supported by the leg B, which, however, during the movement of the body forwards in an oblique direction, and while the leg A makes the pendulum-like movement forwards for the new step, proceeds to elongate itself by raising the sole of the foot from the ground, in order to give the body a fresh impulse. The extremity A now becomes the support for the body. The MM. Weber compare the gradual raising of the soles of the feet from the ground to a wheel rolling along the surface. By this movement the step is lengthened by the whole length of the foot. In every step we may distinguish two periods; one in which the body is supported by one leg only, and a shorter period in which both legs rest on the ground. It is only in very quick walking, which nearly amounts to running, that the feet only touch the ground alternately, one ceasing to support the body when the other begins to receive its weight. In ordinary walking there is between the periods in which the body rests on one leg only, a state of transition, which lasts from the moment when the front foot is put to the ground, and that at which the hind foot is quite raised from it. According to the MM. Weber, this period is in slow walking about half as long as that during which the body rests on one leg. The quicker the walk, the shorter is this period.

The trunk is inclined forwards in walking. This position is necessary for walking easily; it is impossible to move forwards a rod balanced perpendicularly on the fingers, without its falling. To walk with the body perpendicular, it would be necessary to exert a constant muscular effort to restore the balance disturbed by the resistance of the atmosphere. In quick walking the trunk is more inclined forwards, while there is only a very short, if any period, at which both feet rest simultaneously upon the ground; and the steps are both longer and quicker. The condition on which all these circumstances in quick walking depend is, as MM. Weber show, the less height at which the two heads of the thigh-bones are moved above the surface of the ground. When the level at which the hip-joints are carried is low, the steps are longer, because the leg with which the step is to be made can be moved farther from the vertical position when its upper extremity is low than when it is high. The step, moreover, is quicker under these circumstances; for, the lower the level at which the head of the femur is carried in walking, the greater is the inclination of the leg which gives the impulse to the body, and hence the greater also is the force and velocity of the movement it imparts. With regard to the number of steps made in a given time, this depends partly on the length of the leg which swings from behind forwards, and partly on the time at which this motion of the limb is interrupted by the foot being put to the ground. The longer the leg, the slower are its oscillations,—that is, if the movement of the limb be not accelerated by muscular effort. Hence, abstraction being made of this power of voluntarily accelerating the movement, there is in every individual a certain maximum of the number of the steps taken in a given time, which cannot with ease be exceeded. This maximum rate of walking without great effort is attained when the limb moving from behind forwards is brought to the ground, after it has already passed through half the extent of its natural oscillation. But the succession of the steps can be rendered slower by allowing the leg to pass through more than half its arc of oscillation before putting it to the ground.

It necessarily follows, from the nature of the movements of walking, that the body must, at each impulse forwards, rise somewhat and then sink again. These vertical undulations are, however, on account of the legs being capable of elongation and shortening, very slight, amounting, according to MM. Weber, to only 32 millimetres (about 1 inch $3\frac{1}{4}$ lines). The movement of the arms backwards and forwards always takes place in the opposite direction to that of the leg of the same side. The leg, by acting against the ground so as to propel the body forwards, gives an impulse to the whole trunk, which might be expected to cause the opposite leg and both arms to fall forwards. But while the leg of the opposite side, and the arm on the same side with the limb which gives the impulse, move forward, the other arm is thrown backwards. This order of the movements of the limbs, which is maintained so habitually that it is practised without our consciousness, contributes not a little to the preservation of the good carriage and equilibrium of the body. On each side, namely, one limb is thrown forward at the same time; on one side an arm, and on the other a leg; and in this way the defects of movement in the trunk which might be produced by the swinging of the leg from behind forward are corrected.

The circumstance characteristic of running is, that only one leg comes to the ground at a time, while in walking there is a period at which both feet rest on the ground. In quick running, indeed, the body is at one moment of each act supported by neither leg, but is moved through the air for a short space of time by the impulse communicated to it.

The locomotion of quadrupeds on the surface of the ground is performed, generally, on the same principles as the walking and running of man; but it presents a greater number of modifications, which have reference either to the part of the extremity which is put to the ground, or to the order of succession or simultaneous occurrence of the actions of the different limbs. Many animals, as the quadrumana (monkeys), and plantigrade carnivora (bear, racoon, and coati), rest upon the whole sole of the foot. In the marsupial animals (kangaroo, opossum, &c.) the carpus is raised from the ground; the digitigrade carnivora and the rodentia tread wholly on the toes; the feline family of digitigrade carnivora rest upon the first two phalanges, the last phalanx which supports the claw being retracted by an elastic ligament. The hog, the solidungula, and the ruminantia rest only on the last phalanx of two toes, while the rudiments of two other toes do not reach the ground; and in the horse there is only one toe remaining, of which the last phalanx only comes to the ground.

But the order of action of the four extremities varies very much in quadrupeds. The main impulse to locomotion is given by the posterior extremities. The anterior extremities serve principally for support; in some rare instances, where the hinder extremities are ill adapted for locomotion, the anterior extremities drag the body after them, which is the case in the sloth.

1. *Walking pace.*—There are here four different acts; the fore-feet are advanced in a determinate order: first one of the fore-feet, then the hind-foot of the opposite side; then the other fore-foot, and lastly the other hind-foot. The two diagonal limbs, therefore, follow each other, and in the next moment they become the supports of the body; while by the extension of the joints of the other hind-leg on which the body as yet rests, and which is situated most posteriorly, the trunk is impelled forwards. While the body is thus moving forwards upon the support of the fore-leg just before advanced, the other fore-leg, which is the diagonal of the hind-leg which has given the impulse, is in its turn moved forwards, and the hind-leg just mentioned immediately follows it. The other hind-leg is now the hindermost, and the movements are repeated as before. These are the usual movements of walking both in mammalia and in reptiles.

2. *The amble.*—In the amble the body of the animal is propelled forwards, first on the two legs of one side, and then on those of the other; it staggers or rolls consequently from side to side. This kind of movement is seen sometimes in young and weak horses,—also in the giraffe.

3. *The trot.*—There are here only two successive acts; two extremities, the fore and hind legs of opposite sides, being in each put to the ground simultaneously. The trot is the ordinary mode of rapid locomotion in mammalia and in some reptiles,—for example, in the salamanders.

4. *The canter.*—There are here three successive acts. The whole body is raised and impelled forwards by the hind-legs. The fore-feet come to the ground, one after the other,—either the right-foot first and then the left, or the left first; the hinder part of the body is then raised from the ground by the extension of the joints of the hind-legs, which are immediately afterwards advanced. The longer the hind-legs of the animal are, the higher must the fore part of the body be raised when the whole trunk is propelled forwards by the action of the hind-legs, which otherwise would tend to throw the hind part of the body over the fore part. This raising of the fore part of the body is necessary, for example, in hares and mice. The movement of these animals resembles leaping. The rodentia, in moving over a plane surface, step

forward with their fore-feet, and then bring the hind-feet after them. This kind of movement is likewise observed in frogs.

5. *The gallop* differs from the canter in the fore-feet being both put to the ground at the same time.

It was remarked by Cuvier, that the flexion and extension of the joints of the extremities in mammalia are performed in vertical planes, nearly parallel to the line of the vertebral column; while in oviparous quadrupeds, as the lizards, the articulation of the humerus and ulna, and that of the femur and tibia, are more frequently directed very much outwards,—a circumstance which influences the position in which the foot is put to the ground; and hence it is, that the trace of such animals can be distinguished by the position of the foot from that of a mammiferous animal.

*Leaping.**—The peculiarity of the movement of leaping consists in the body being raised completely from the ground for a longer period than in the other movements of locomotion. When the spring or leap is carried to the utmost, it is effected by the sudden extension of three joints, the hip, knee, and ankle joints, previously flexed in opposite directions. The foot, before the leap, may be applied to the ground by the entire sole, or only by the toes; in the former case, the foot is gradually raised from the ground, from the heel towards the toes, during the movement; if the toes only touch the ground, and the ankle therefore be already in a state of extension, this joint is still more strongly extended. The body is always inclined forwards towards the thighs. When, in a leap made with sufficient force to raise the body to a considerable height from the ground, the three joints of the lower extremities are extended, if no resistance were opposed to it, the length of the body would merely be simultaneously increased at each extremity; but the resistance offered by the ground causes the impulse to be imparted to the centre of gravity of the body, which is thus propelled, in the manner of a projectile, in the mean direction of the joints which are thus extended. The direction which the body takes in leaping does not depend on the inclination of one portion of the extremities only; for instance, it is not necessary for springing in the perpendicular direction that the leg should be nearly perpendicular to the floor, as Treviranus and others have asserted. Whatever inclination the leg may have with reference to the floor, the leap can nevertheless be made either forwards or backwards. The conditions which essentially facilitate the spring backwards are more evident when this movement is made in the most simple manner. Thus, the leap backwards may be made quite independently of any action of the ankle-joint, if, while standing on the edge of the heels of the shoes, the knee

* Tiedemann's Zeitschrift für Physiol. t. iv. pt. i. p. 87.

previously bent be forcibly extended without any perceptible movement of the hip-joint. In this case the body receives an impulse in the direction of a line drawn between the heel and the hip-joint; and, inasmuch as this line passes behind a perpendicular line falling from the centre of gravity to the heels before the movement was made, the motion given to the body is obliquely upwards and backwards.

A spring may be made in the same direction when the whole sole of the foot rests on the ground, also without extending the ankle, merely by the extension of the knee-joint. So also, when we spring backwards while standing on our toes, the only difference in the case is, that the point of support is changed; the impulse is still given by the extension of the knee-joint. As soon, however, as the hip-joint is brought within the line of the centre of gravity, it becomes impossible to spring backwards.

It is possible also to leap forwards while standing upon the heels, when the raising of the sole of the foot from the ground can have nothing to do with the movement. We may observe, that in making the spring thus the knee maintains its flexed position nearly unaltered, but that the angle between the trunk and thigh is forcibly straightened, and that the whole trunk has a share in the action. The two branches of the arch which here straightens itself are, on the one hand the entire extremity which is held stiff from the heel to the hip, and on the other the trunk of the body; the line of direction in which this arch strives to straighten itself lies in front of the line of the centre of gravity.

Again, while the knees are kept bent and stiff, we may jump forwards by merely extending the ankle, if the line, towards which the two branches of the arch of the straightening ankle-joint tend, lies in front of the perpendicular of the points of support. Lastly, all the joints being made to act, the leap may be made either forwards or backwards, according as the mean direction which the different joints give to the body is forwards or backwards, or the direction of the line which they tend to in straightening themselves is in front of or behind the line of the centre of gravity or point of support. A spring in the perpendicular direction can take place with any inclination of the different joints, whether the direction of one or of another be forwards or backwards, if the different impulses which they tend to give compensate each other, so that the mean direction may be upwards.

There are two different modes in which quadrupeds leap. In one, the body, being projected upwards and forwards by the hind-legs, is received upon the fore-legs, and the hind-legs are drawn after. In the second kind of leap, the fore-legs are not called into action to receive the weight of the body: this is the case in many quadrupeds with very long hind-legs, namely, in some rodentia, as the jerboas (the genera Dipus and Pedetes); in some insectivora, as Macroscelides; and in some marsupialia, as the kangaroo; this movement is presented also by many birds, as the passerine family, and by frogs.

Climbing.—The mechanism of climbing is sufficiently well known. Some climbing animals, as those of the feline tribe, the squirrels, opossums, and Phalangistæ, take their attachment by means of claws; the climbing birds (scansores) by means of their toes, one or two of which are directed backwards; some few animals, as the opossums and Phalangistæ, have a prehensile tail, and a distinct opposible thumb on the hind-foot. Some animals are specially organised for prehension by the length and freedom of motion of their digits, as the apes, in which there is an opposible thumb on both hind and fore feet. The howling monkeys (Mycetus) and the tribe Cebus have in addition a prehensile tail. The monkeys destitute of thumbs, the Ateles of Geoffroy, are equally adapted for climbing by the length of their fingers and toes, and by their prehensile tail. Among the edentata, some anteaters, and the sloths, are fitted for climbing by their long claws, with which they can embrace objects; the climbing anteaters have also a long prehensile tail. Both the anteaters and sloths walk with difficulty on the surface of the ground on account of the length of their claws; they both tread principally on the outer border of their feet. The arm and fore-arm are so disproportionately long in the sloths that they are obliged in walking to support themselves on their elbow-joints. It is, however, an error to suppose that Nature has neglected these animals, for their limbs are perfectly adapted for climbing and moving about on trees. The chameleon, amongst reptiles, may be compared to the sloth amongst mammalia; the toes of the chameleon, like the toes of climbing birds, are arranged in an anterior and posterior pair for facility of climbing; they have also a tail which they can wind round branches of trees.

The more minute details of the modifications which the extremities of vertebrate animals present in accordance with their destined use in flight, swimming, prehension, climbing, and burrowing, is the province of comparative anatomy. How different are the hand of the ray and that of the horse! in the former the fingers and their phalanges which compose the fin, are in extraordinary number, while the arm and fore-arm are wanting; in the fish-like mammalia, the cetacea, we again find an excessive number of phalanges, but a short arm and fore-arm are present; the solidungula, as the horse, present the other extreme,—the hand and foot are reduced to a single finger and toe.*

The movements of the articulata, particularly those of locomotion, in the last place demand our attention for a moment. While many insects (as the Hydrophilus, &c.) employ feet organised for

* On the adaptation of the hand to its uses in the different orders of animals, consult Sir C. Bell's Bridgewater Treatise on the Hand. London, 1834.

walking on solid bodies as oars, and others (the Dytiscus, Notonecta, &c.) move in the same way in the water by means of ciliated oar-like extremities; the Hydrometer, on the contrary, presents to our observation the remarkable phenomenon of a light animal body springing from spot to spot on the surface of the water, its feet supporting it on that fluid. The progression of insects on land appears agile and regular to a degree that we should not at first expect from seeing the great number of their feet. The movements are rendered easy by the numerous limbs engaged in their moving in a determinate order; thus the movement of progression in insects, though they have six legs, is quite simple. In watching insects which moved slowly, I perceived distinctly that three of their legs were always moved at a time; they were advanced and put to the ground, while the other three propelled forwards the body of the insect. The feet which moved simultaneously were the fore and hindermost foot of one side, and the middle foot of the opposite side; then the fore and hind foot of this side, and the middle one of the other side; so that in two steps all the six feet were set in action. In spiders, which have eight feet, four seem to be put to the ground while the four others are raised; the movements are here more difficult to observe than in insects; but it appears as if between two feet, which transmit the weight of the body to the ground, there is always one which is being raised. Indeed, even in the Scolopendra with fourteen feet, there seems to be a very regular order observed in the action of the feet, a certain number of which move simultaneously, while the appearance produced by the movement of all is that of an undulating motion.

In many light animals, and particularly insects, the feet are furnished with organs which enable them to attach themselves to perpendicular surfaces, even when such surfaces are quite smooth, or to the ceiling itself.* Thus flies have the soles of their feet furnished with organs which probably can be retracted in the centre, and leave an exhausted cavity, so as to act as suckers; and many similar apparatus exist in other insects, by which either close contact and adhesion are obtained, or really attachment by sucking. We have a similar example among the reptiles in the Gecko, which has the under surface of the toes both of the fore and hind feet furnished with regular transverse plicæ, (like the sucker on the head of the Echeneis remora,) by the erection of which vacua are probably produced, and a firm attachment obtained. The Gecko is said to be able to run along perpendicular surfaces, and even on the ceiling.

This is the proper place to make mention also of a mechanism by which many animals are enabled to preserve with ease a position which appears to require great muscular effort. The standing posture of animals generally, as well as of man, is maintained by a long-continued action of

* Sir E. Home, Phil. Transact. 1824; and Lectures on Compar. Anat. iv. 81.

the extensor muscles; but in some animals there is a mechanical provision facilitating the act of standing, which is in them continued without fatigue day and night. The storks and several other birds frequently stand for a long time without intermission upon one leg, and even sleep in that position. The peculiar structure of the ankle-joint in the stork which enables it to do this, was mentioned by Cuvier. In the middle of the anterior surface of the lower end of the tibia there is a fossa, into which a prominence of the metatarsal bone must be received before flexion of the joint can take place. In the extended state this prominence lies below the fossa, between the projections of the pulley of the tibia. The passage of the prominence into the hollow in question, so as to allow flexion, is opposed by the lower edge of the hollow which is prominent, and by ligaments which act like springs.* This mechanism, which enables the long-legged birds to stand with little muscular effort, is not, however, found in all cases in which animals are capable of standing for a long period on one leg. Ducks, for example, sleep standing upon one leg, though destitute of this mechanical provision; a convincing proof that even in sleep that part of the nervous centres which is the source of all the movements of locomotion, can regulate the action of the extensor muscles for the maintenance of the equilibrium of the body.

In birds which sleep sitting, there is a provision for keeping firm the hold of the body on which they perch. It was first pointed out by Borelli, the correctness of whose explanation was questioned by Vicq d'Azyr, but has been admitted, and with good reason, by Cuvier. The tendons of the flexor muscles of the toes not only pass behind the tarsal joint, and therefore flex the toes when this joint is bent; but they can be acted on by an accessory muscle which lies at the inner side of the thigh, and of which the tendon passes in front of the knee-joint. The flexion of both these joints under the weight of the body must, in consequence of this structure, flex the toes, and thus keep the attachment of the feet firm; this effect may indeed be produced by flexing the knee and ankle joints after death.

A similar result is produced by the particular disposition of other muscles in the dog. Extension of the knee-joint in the dog makes the gastrocnemius tense, and consequently extends the heel. Hence a dog is still able, in some measure, to use the foot in walking, after the division of the ischiadic nerve, in consequence of the extensor muscles of the leg, which are not paralysed by division of that nerve, straightening the knee-joint, and acting on the heel, as we have described.

* Dr. Macartney, in the Transactions of the Royal Irish Academy, vol. xiii. p. 20.

SECTION III.

Of Voice and Speech.

CHAPTER I.

OF THE GENERAL CONDITIONS FOR THE PRODUCTION OF SOUND.

The sounds of the voice and speech are not, it is true, the immediate result of muscular action, but of the vibrations of a peculiar apparatus which may be compared to a musical instrument: the tension of the instrument necessary for the production of sound, and the height and succession of the tones, are, however, determined by the contraction of muscles; hence the physiology of the voice and speech will be properly considered in this place. Before, however, entering on the consideration of the human voice itself, we must become acquainted with the general conditions on which the production of sound depends.

A sudden mechanical impulse upon the organ of hearing gives rise to the sensation of sound, which resembles a report if the impulse be violent, or is less intense if the impression be more feeble. The rapid escape of compressed air, or the rapid entrance of air into an imperfect vacuum, produces the sensation of sound, if the concussion of the air be communicated to the organ of hearing. But to produce sounds of uniform character which may be compared with each other, it is necessary that the impulse communicated to the ear should be of a particular kind, namely, a frequent repetition of the same impulse. The difference of sounds as to pitch or sharpness depends on the number of these impulses which occur during a certain time. The cause of the sensation of sound, in most cases, is the communication of the vibrations of sonorous bodies to the interior of the organ of hearing and the auditory nerve. The facts that sonorous bodies have elasticity either from their attraction of cohesion, as the solid sonorous bodies,—or from their tendency to expansion, as the gases,—or from tension, as the sonorous cords,—and that all these bodies vibrate while in the act of emitting sound, naturally lead to the supposition that the vibrations alone are the essential cause of the sound. It would, however, be very incorrect to imagine that the oscillating motion or vibration must be imparted to the auditory nerve itself for the sensation of sound to be produced. On the contrary, it appears that the immediate cause of the sensation of sound, even when this is excited by the vibrations of sonorous bodies, is really the regular succession of impulses which the auditory nerve receives. This is proved by the investigation of those sounds which are produced, not by the vibrations of an elastic body, but by a series of mere impulses quickly succeeding each other. If a piece of wood be held against the teeth of a rapidly revolving wheel, every stroke of the teeth of the wheel will be communicated as an impulse to the ear, and produce the sensation of sound. If, however, the wheel be now made to revolve more rapidly, so that the separate strokes on the wheel cannot be distinguished, in place of a succession of shocks, a continuous sound will be perceived; the pitch of which will be higher as the rapidity of the wheel's motion is increased. Still greater interest, in reference to the theory of the essential cause of sound being a quick succession of impulses, attaches to the tones which may be produced by a current of a gas, or liquid such as water or quicksilver, interrupted at regular and very short intervals, particularly since liquids are not elastic, and therefore not capable of producing sound by vibration. Thus, in the siren, an instrument invented by M. Cagniard la Tour, a rapidly revolving wheel interrupts momentarily, and at successive intervals of very short duration, the escape of a fluid from the opening in the body of the instrument. Even when the revolving wheel is under water, and interrupts at regular and frequent intervals the current of water supplied by pressure from below, the impulses produced by the periodic escape of the fluid, if they follow each other in sufficiently rapid succession, give rise to a clear sound, of which the pitch is higher in proportion to the rapidity of the succession of the impulses, or moments of interruption of the current.

With reference to the human organ of voice, it is important to examine further the action of those sonorous bodies which produce the necessary number of impulses by vibration. The elastic bodies only are capable of producing sound in this manner. An impulse given to any part of such bodies is communicated to the whole mass, which is thrown into a state of vibration; the impulses produced by the vibrations are imparted to surrounding bodies, and in this way are transmitted to the ear.

The height or sharpness of the tones produced increases with the frequency of the vibrations. For the deepest tone ordinarily employed in music, the C of the open organ pipe, 32 feet in length, 32 vibrations of the air in the pipe take place in a second; for the octave higher than this there are 64 vibrations; for the next octave 128; and for the next there are 256 vibrations in a second. It being a matter of indifference whether impulses are produced by the teeth of a revolving wheel or by the vibrations of a sonorous body, we have now in an instrument invented by M. Savart, in which the sounds are produced by the successive strokes of the teeth of a wheel, an easy means of ascertaining with precision the number of vibrations necessary for the production of each tone.

The vibrations of a sonorous body may extend throughout its whole mass; or separate segments of the body may vibrate in opposite directions, these vibrating segments being separated by points (nodes or nodal points) which remain motionless. Small fragments of paper laid upon the nodal points are not moved.

The direction in which bodies vibrate is also various; it may be transverse, longitudinal, or rotatory. A cord stretched between two points, and vibrating from side to side, and a bar of metal fixed at one extremity, present good examples of transverse vibrations. Longitudinal vibrations occur in the air, in cords, or in bars of metal; they are excited in the last two kinds of sonorous bodies by friction in the longitudinal direction. In longitudinal vibrations a state of alternate compression and expansion is transmitted from one particle to another to the extremity of the body, or to a nodal point, and then takes the opposite direction. Chladni has observed the rotatory vibrations only in bars. The bodies which produce sound by vibrations are either gaseous bodies, such as the air, or bodies made elastic by tension, such as stretched cords or strings, or solid bodies elastic in themselves, as metallic bars, and metallic or glass plates. The laws which regulate the production of sonorous vibrations in these different classes of soniferous bodies are of great importance in relation to the theory of the human voice. We will take a cursory view of them, that we may perceive to which class the organ for the production of sound in man belongs.*

1. *Solid elastic bodies.*

Some of these bodies, as the strings of stringed instruments and the parchment of a drum, are rendered elastic by tension; in others, as metallic bars and plates, elasticity is a property of their substance. Either of these kinds of elastic bodies may influence the sound by their length and thickness only, when they have the shape of cords; or by their expansion in several directions, when they have an extended membrane-like form.†

a. Bodies elastic from tension.

Vibrating strings.—The frequency of the vibrations of stretched cords or strings increases proportionally to the shortness of the arc of vibration, just as a pendulum vibrates more frequently the shorter it is;

* In our account of the different means of producing sounds, we shall follow principally Chladni, Biot, Savart, and W. Weber. With respect to those kinds of instruments which have the nearest affinity to the human organ of voice, we shall adduce original observations of our own.

† Chladni, Akustik, Leipz. 1802, p. 64.

the height of the tone is proportionate to the number of the vibrations.

A tense string gives out its deepest tone or fundamental note when it vibrates in its entire length: if, while its tension remains the same, it be divided into two equal parts by a bridge passed beneath it, the sound emitted by either half when made to vibrate, will be the octave of the lowest note, the vibrations of the string becoming twice as frequent. If one fourth of the string be isolated and struck, its degree of tension remaining the same, the sound produced will be the second octave, which is the result of vibrations four times as frequent as those of the fundamental note. It is a general law that in strings of the same substance, thickness, and degree of tension, the number of the vibrations is in the inverse ratio of the length of the string. When the length of strings is equal, but their degree of tension different, the relative frequency of the vibrations is in the proportion of the square-roots of the forces exerted in rendering them tense.*

The number of vibrations for the different notes intervening between the lowest or fundamental note of the string and the first octave will be in the inverse ratio of the different fractional lengths of the string corresponding to the notes. Thus the number of vibrations for the fundamental note being taken as 1, and the number for the octave, in which the length of the string is one half, as 2, the number of vibrations corresponding to the different notes in the scale of music universally adopted will be as follows:

	Fundl. tone.		Third.		Fifth.			Octave.
Number of vibrations	1	$\frac{9}{8}$	$\frac{5}{4}$	$\frac{4}{3}$	$\frac{3}{2}$	$\frac{5}{3}$	$\frac{15}{8}$	2
Names of notes	C	D	E	F	G	A	B	C

While a cord or string is giving out the sound corresponding to the vibrations of its whole length, it may also make more rapid vibrations in aliquot parts of its length, giving rise to other tones. If we strike a single isolated string or a monochord where there are no other cords which can be thrown into vibration at the same time, we shall perceive by a little attention other sounds mingling with the lowest or fundamental note of the string, and particularly those which stand in a simple numerical relation to the fundamental note with respect to the number of vibrations of each,—for example, the fifth note of the octave, and the third of the second octave [of which the number of vibrations are three and five, those of the fundamental note being one].

If a stretched cord be slightly touched at one-third, one-fourth, or one-fifth of its length, a nodal point is formed at the place of contact; and if the bow of the violin be then carried across the string, nodal

* Biot, Precis élément de physique expérimentale. t. i. p. 361.—Lehrbuch d. Experimental-physik. ubers. v. Fechner, b. ii. p. 30.

points are developed between the other thirds, fourths, or fifths of its length, and, instead of the lowest or fundamental note of the string, sounds corresponding to the different lengths separated by these nodal points are given out; such sounds are called harmonic notes.

It being possible to obtain low notes from cords by diminishing their tension, when their length is otherwise not such as to vibrate sufficiently slowly for the production of such notes, we ought theoretically to be able to produce all the notes, high or low, on very short cords by mere variation of their tension. However, when the tension is much reduced, the vibrations become too irregular, on account of the diminished elasticity, to allow us to obtain a very deep tone from a very short cord by greatly lessening its tension. Nevertheless, very short cords, if they retain some elasticity when relaxed, as is the case with cords of caoutchouc, are still capable of yielding deep notes; and elastic laminæ, made tense in one direction, will, though very short, yield tones of great clearness if they form the boundary of a narrow cleft through which air is pressed, this current of air keeping the laminæ in a state of vibration. To this subject we shall return in speaking of the "tongued" or "reed" instruments.

Bodies of membranous form made elastic by tension.—In membranes stretched in one direction only, the tones yielded vary in accordance with the laws of cords or strings. When the extension is made in all directions, as in the drum, the height of the tones increases in the mean, as the tension is greater; but the laws which regulate the number of the vibrations in these kinds of sonorous bodies are not known, and a perfect knowledge of them would be of no importance in relation to the theory of the human voice.

b. Bodies elastic by the property of their substance.

Straight or bent rods.—The vibrations of these bodies are similar to those of strings or cords; their elasticity supplies what the tension of the cords effected; hence they vibrate as well when one end only, as when two are fixed. Metal bars or plates of this kind sound when struck; if the plates, whether of metal or wood, be sufficiently thin, they may be thrown into vibration by a current of air, as in the tongued or reed instruments, in which air is forced between a vibratory plate and the frame in which it is fixed. The mouth-harmonicon is an example of a simple-tongued instrument of this kind.

The pitch of the tones or the frequency of the vibrations in the elastic rods or bars is regulated by a different law from that which governs the vibrations of strings. The height of the tones, or number of vibrations within a given period, is here in direct ratio with the thickness of the bar, and in an inverse ratio with the square of its length.

Inflexible elastic bodies of membranous form, bent or plane. Disks and bells.—The organ of voice has no similarity to either the rod-like or expanded membrane-like forms of these solid elastic bodies. It is unnecessary, therefore, to dwell upon them.

2. *Elastic fluids. The air.*

The vibrations of the air, which produce sound, consist of successive condensations and expansions, which are propagated in wind instruments of the flute kind in a longitudinal direction through the tube. In most wind instruments the contained air is the seat of the sonorous vibrations, which pass as waves, backwards and forwards, from one end of the column of air to the other. The rapidity of the undulations is generally the same, whatever the width of the tube; and depends, principally at least, on the length of the wave or of the space which it traverses. Organ-builders, however, have learnt by experience that, to produce the same note, pipes must be made somewhat shorter if their diameter be increased; and M. Savart has discovered that a column of air yields tones of much lower pitch in flexible elastic tubes than in solid pipes of the same length. The relaxation of the walls of a flexible tube by impregnation with the vapour of water may have the effect of lowering the pitch of its fundamental note as much as two octaves.

Flutes or mouth-pipes.—The sounds produced by these instruments result from a column of air contained within a tube being thrown into vibrations by blowing upon it at some one point. This method of producing sounds is exemplified in the most simple manner by blowing over the mouth of a tube,—for instance, the bore of a key. The vibrations are excited in the same manner in the German flute, except that in it the column of air is acted on, not from its extremity, but from its side. In the common English flute and flageolette the air blown through the mouth-piece, and escaping by a side aperture, sets the column of air contained in the tube of the instrument in vibratory motion; one class of the organ-pipes, the flute-, or mouth-pipes, have a similar construction. It is the air only which sounds in these instruments. Pipes of the same length, whether they be made of wood, metal, or pasteboard, yield notes of the same pitch, though of different timbre. The vibrations of the column of air necessary for the production of sound continue so long only as the current of air which excites them is maintained. Since there is no current of air through the tube itself in these instruments, but merely a vibratory motion of the column of air contained in it, the extremity of the tube may be either closed or open.

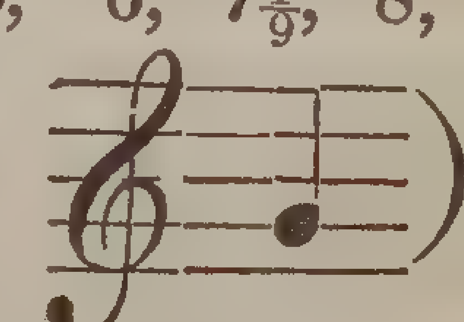
The simplest mode of vibration of the air in the pipes with closed extremity is that in which the undulations pass through the whole length of the tube without any nodal points arising in the column of air. The only nodal point is here the closed extremity of the pipe. A tube of the same length, but open at its extremity, yields a fundamental note one octave higher, a nodal point being formed in the middle of the column of air.* The pitch of the tones given out by a closed or open pipe becomes, *cæteris paribus*, lower in a direct ratio with the increased length of the tube; but the same column of air yields higher notes according to the force of the impulse, nodal points being developed by blowing strongly. The notes which MM. Biot and Hamel produced by blowing into a tube closed at one extremity stood with relation to each other, in regard to the number of vibrations producing them, in the same ratio as the series of uneven numbers. They were:

Names of notes . .	C,	G^1,	E^2,	$A\sharp^2+$,	D^3,	$F\sharp^3-$,	$A\flat^3+$,	B^3.
Relative number of sonorous vibrations in each . . .	1,	3,	5,	7,	9,	11,	13,	15.

(The fundamental note C being )

The series of notes which were elicited from an open tube, on the contrary, by the same procedure of blowing more strongly so as to increase the number of nodal points, corresponded to the natural series of numbers, namely:

Names of notes . . .	G,	G^1,	D^1,	G^2,	B^2,	D^2,	F^2,	G^3,	C^3,	D^3.
Relative number of sonorous vibrations in them . . .	1,	2,	3,	4,	5,	6,	$7\frac{1}{9}$,	8,	$10\frac{2}{3}$,	12.

(The fundamental note G being the fiddle G )

It was only by blowing feebly that they could obtain the fundamental note (G of the treble clef) from a glass tube one inch in diameter and thirty-seven inches long. The notes produced by blowing with different degrees of force into the end of an open tube, are, as the above series shows, more distant from each other the nearer they are to the fundamental note; and, the higher the pitch of the notes, the nearer do the notes approach each other in the musical scale. Thus, between the fundamental note G and the first octave, for which the vibrations are twice as frequent, there is no intervening note; between the first octave and the second octave, G^2, for which the vibrations are four times as frequent, there is one note, D^1; between the second and the third

* On the theory of the open and stopped pipes of organs, consult Biot, loc. cit. t. i. p. 407. Fechner's translation, B. ii. p. 100.

octave, G^3, for which the vibrations are eight times as frequent, three notes.

These laws are generally applicable, not merely with regard to the vibrations of atmospheric air, but also for all gases. It must be remarked, however, that the fundamental note varies according to the specific gravity and density of the gas, for organ-builders have found that the fundamental note of a pipe is a little altered even by holding it long in the hands. According to theoretical calculation, the tones of tubes of equal length should be in the inverse ratio of the square roots of the density of the gases, pressure and temperature being equal. The observed results do not exactly correspond with this theory.*

The embouchure of the tube has also some influence on the pitch of the fundamental note. This has been demonstrated by MM. Biot and Hamel. They employed a quadrangular pipe four feet long and four inches in diameter, the mouth of which, when open, was of the full size of the tube, but could be diminished by a sliding plate. The sounds produced according to the different size of the embouchure were as follows:

Size of the embouchure . .	66·0,	36·5,	26·0,	20·5,	16·5,	14·0,
Sounds	C,	G^1,	E^2,	B^2,	D^3,	F^3,
Proportional numbers of vibrations . . .	1,	3,	5,	7,	9,	11.

The size of the opening indicated by 66·0 parts was one square inch. The proportional number of the vibrations for the different notes of the series thus produced was the same as in the series of notes produced by blowing with varied force into a tube closed at one extremity; the effect of diminishing the aperture is therefore the same in a tube closed at one extremity, as that of varying the force of blowing. In neither case can octaves be obtained.

The influence of the embouchure upon the pitch of the pipe appears to me not to be at present satisfactorily explained. There is a mode of covering the mouth of the tube by which the pitch of the pipe can be considerably lowered. I find that by laying a card firmly upon the upper lip of a cylindrical mouth-pipe of brass, so as to cover a part of the orifice, I can lower the fundamental note more than a tone; but if I place the card pressed against the upper lip of the tube over the opening in such a way that it covers the orifice like the roof of a house (dachförmig), the pitch of the pipe becomes still lower, and the more so the closer the roof-like card is depressed towards the opening. In this manner any notes, to the extent of some entire tones below the proper fundamental note of the tube, may be produced at

* Biot, loc. cit. p. 423. Fechner's translat. p. 107.

will; and by no means the notes corresponding to the numbers 1, 3, 5, 7. After forcing the plug or "tompion" (Stempel) of the pipe so far in as to reduce the length of the tube to two inches, I was able, by covering the embouchure in the roof-like manner already mentioned, to lower the fundamental tone from D to the G# below it, that is, nearly the interval of a fifth; and the intervening tones were easily produced by varying the degree in which the card was depressed over the opening. In a square pipe, one foot in length, also, the pitch could be lowered by this procedure of covering the mouth of the tube with a card inclined like a roof over the opening.

The preceding remarks refer to pipes in which the tube is destitute of side apertures; they are also applicable to the proper flutes, which are open tubes capable of yielding, when all the lateral apertures are closed, the different tones corresponding as to the number of their vibrations with the series of numbers 1, 2, 3, 4, and 5, according as they are blown more or less strongly. By the successive opening of the side apertures the intervening tones can also be produced. The opening of each hole causes a sharpening of the fundamental note, and the degree in which the note is made sharper depends on the size of the hole left open, and its distance from the upper part of the instrument.*

We have lastly to inquire whether, by the use of the different means calculated to lower the fundamental tone of a pipe of given length, a very short tube can be made to yield low notes on submitting the column of air to a very feeble blast. A tube partially closed approaches the condition of one entirely shut at one extremity, in which the fundamental tone is a whole octave lower than that of an open tube of the same length; and the tone may be lowered nearly a fifth, as we have stated, by covering the embouchure with a card placed in an inclined position like a roof. Feebleness of the blast is not capable of lowering the tone below the fundamental note; there may, however, be means of enabling us to produce still slower vibrations, of sufficient regularity to constitute musical tones, by the application of a still weaker blast. A kind of pipe or whistle much in use among hunters, which is blown while held between the lips, and serves to imitate the different notes of birds, appears to possess this desideratum: although the conditions in it are very different from those which produce a lower pitch of the tones in the common pipes. This whistle, or bird-call, is made of ivory or brass, and is broader than it is long; measuring four lines in length, and from eight to nine lines in breadth. Each end is covered with a thin plate perforated in the middle by a hole, through which the air passes, so

* Further information respecting the mode of action of the flute and other pipes without reeds, must be sought in Biot's Precis element. de Physique experimentale. p. 402 to p. 429. Lehrb. d. Experimental-physik. p. 87—112., and in Muncke's article "Schall," in Gehler's Physik. Wörterbuch, 8 bd. p. 349—369.

that the current of air traverses the axis of the instrument. The principle of this kind of pipe has been investigated by M. Savart.* He supposes that the current of air, passing through both openings, carries with it a small portion of the air contained in the cavity of the pipe; and, thus diminishing its density, renders it incapable of resisting the pressure of the atmospheric air without, which consequently repels it and compresses it until a new rarefication ensues; a repetition of this action he imagines to be the cause of the sound. By varying the force of the blast the tones of this instrument may be varied to the extent of half an octave or two octaves: and, by practice in regulating the current of air, the tones may be carried to a much greater extent, both higher and lower. The size of the instrument may be double or quadruple the size of that above indicated, or it may be less, without the results being in any remarkable degree altered. The deeper tones are more easily obtained when the instrument is large, and its parietes thin; but every instrument has a note which is produced more readily than others. The direction of the margins of the opening has an influence on the pitch; when they are directed obliquely inwards towards the cavity of the instrument, its tones are generally lower. The tones have also a lower pitch when the size of the openings is more considerable. We have at present no calculated theory of the vibrations of this instrument; it is not yet determined whether the air be really the seat of the primary sonorous vibrations, or whether this pipe should not rather be referred to the class of reed or tongued instruments, which we have next to consider. In the common reeds the mode of action of the tongue depends on its length and thickness only; but if one of the perforated plates in this pipe or whistle act as a vibrating tongue, the breadth as well as the length and thickness would have to be taken into account. However this may be, the instrument in question can be combined with a tube just as the common reeds can, and the sounds then produced resemble those obtained by the combination of a common "reed" with a tube. The fundamental tone, namely, is not that of the vibrating tongue, but one of the notes of the tube which is very near the fundamental note of the tongue. The notes of the "hunter's whistle," or "bird-call," combined with a tube of any dimensions, correspond like those of an open pipe in the number of their vibrations to the series of numbers, 1, 2, 3, 4, 5, &c.

3. *Musical instruments in which the properties both of solid and of fluid elastic bodies come into play. Reed, or tongued instruments.*

These are musical instruments consisting merely of a simple vibrating tongue, which is set in motion by means of a current of compressed air; such are the jew's-harp and mouth-harmonicon. Experience has shown

* Magendie's Journal de Physiol. t. v. p. 367.

that such vibrating tongues may be formed not merely of bodies elastic by virtue of their property of cohesive attraction, as metal and wood, but also of laminæ or membranes made elastic by tension. From the combination of vibrating tongues of either kind with a tube or pipe, compound instruments result; constituting, when the tongue is formed of solid elastic substances, what are known by the name of "reed-instruments." The theory of the action of these instruments is of the greatest importance in connection with the inquiry into the mode of production of the human voice.

First class of tongued instruments.

a. Tongues without superadded tube.

The simplest-tongued instrument of this kind is the jew's-harp, which consists of a lamina of steel lying between two parallel bars of steel, and fixed at one end. The ordinary mode of producing the sonorous vibrations in this instrument, is by striking the thin lamina with the finger while the bars are held between the teeth; but the tongue may be thrown into vibrations by merely drawing a current of air into the mouth. The mouth-harmonicon consists of several tongues fixed in one frame. Into the oblong rectangular openings in a small metal plate are fitted thin laminæ of metal, which are fixed by one extremity, but can vibrate in their frame without coming in contact with it. These laminæ are thrown into sonorous vibrations by holding the common frame between the lips and forcing air against the tongues.

The mouth-pieces or reeds of reed-instruments, and of one class of organ-pipes, have the same mechanism. A half-cylindrical tube of steel or brass, open at one end, has its flat side towards the other end, which is closed, formed by an elastic plate which does not completely close the tube at this part, being able to vibrate within its cavity; air forced into the open end of the tube passes out at the sides of the elastic lamina and causes it to vibrate. The tongue can also be made to vibrate by forcing air upon it from the outside; the end of the tube at which the tongue is situated being held free in the mouth, a blast of the breath passes into the tube at the side of the tongue, and throws it into vibrations; and it is thus that the air acts on the reeds in organ-pipes. It is evident, therefore, that the only essential part of the reed is the tongue itself and the frame, as in the jew's-harp.

The mode in which the vibrations of sonorous tongues are produced appears to me not to have been hitherto satisfactorily explained; Fechner has expressed the same opinion. I believe the true theory to be this :—The tongue is forced by the blast of air out of the opening in which it is fixed, receding from the impelling force with gradually diminishing velocity in accordance with the law of inertia, until its elasticity, which increases in power in proportion as the tongue is bent, counteracts the force of its motion. The current of air still continuing, the tongue would remain in the position thus given it, were it not that, when removed from the opening, it is much less exposed to the pressure of the air, and therefore is carried back by its elasticity like a pendulum, and would indeed return to its straight position with increasing velocity, did not the continued current of air in some measure retard it. When thus restored by its elasticity to its former place in the opening of the frame, the tongue is again forced out by the air, which now acts with greater power upon it. If the pressure of the air upon it were constantly the same, the tongue would be kept continually in one position, that, namely, in which its resistance balances the force exerted upon it.

Not merely a confined current of air will throw a tongue into sonorous vibration; even a current of air blown free upon the surface of a thin tongue, such as those of the mouth-harmonicon, will, if sufficiently strong, set the tongue in motion. A very thin tongue, and the longest in the harmonicon, may, even when removed from its frame, if fixed at one end, be made to emit a feeble sound by blowing a strong current of air upon it from a tube with a small orifice. The current of air must, in this case, be directed upon the edge of the tongue, and perpendicularly to its surface. The theory of the vibrations thus produced seems to be the same as that just given for those of the tongue set in motion by a confined current of air. The fact that a sound can be obtained from a tongue free from all surrounding framework, shows clearly that too much importance should not be attributed to the ordinary mode of forming the reeds and tongued instruments, and to the passage of the air between the tongue and its frame.

The law regulating the variations in the notes yielded by the tongue of a "mouth-piece" or "reed," has been shown by M. W. Weber* to be the same when the tongue is thrown into vibrations by a current of air,—as when the vibrations are produced by striking or bending the tongue. It is the same law which regulates the vibrations of vibrating rods; namely, that the frequency of the vibrations of two rods of equal thickness and same material is in the inverse ratio of the squares of their length. The same experimenter has found that the note given out by a reed without a tube is the same as to pitch, whether it be produced by a current of air or by striking the tongue. The pitch or sharpness of the note is, for the most part, independent of the strength

* The nature of the sounds produced by reeds has been investigated by W. Weber, Leges oscillationis oriundæ si duo corpora diversa celeritate oscillantia, &c.—Abstracts of his researches are given by Chladni in Kastner's Archiv. t. x. p. 443; by Muncke in the art. "Schall," Gehler's Physik. Wörterb.; and by Fechner in his translation of Biot's Experimental-physik. bd. ii. p. 112. Compare Weber in Poggendorf's Annal. t. xvii. p. 193.

of the blast;* but the strength of the tones can be increased by blowing with increased force. It was shown by M. Biot that the chemical properties of the gas used for exciting the sonorous vibrations of elastic tongues have no influence on the pitch of the tone. The dimensions of the fissure left between the tongue and the frame within which it vibrates, are also, according to M. W. Weber, of little importance. A large size of the opening increases the difficulty of eliciting the tone, but does not alter its pitch.

Theory of the production of sounds by vibrating tongues. — The vibrations of tongues obey, it appears, exactly the same laws as the sonorous vibrations of metallic rods; but it is generally supposed that there is this difference, that in the latter case the sound is produced really by the vibrations of the rods, while in the case of tongues and reeds, the air itself is the source of the sound. The same difference is supposed by many to subsist between the sounds produced by striking a tongue, and that obtained when the tongue is thrown into vibration by a current of air. In the first case, the tongue alone is the source of the sound: in the second, the tongue will also necessarily produce a sound; but the air itself is supposed to be the main source of the peculiar tones. The grounds of this view are the following:

The sound produced by a tongue thrown into vibration by striking it is feeble; that emitted when a current of air is forced upon the tongue is strong; the timbre of the two sounds is also quite different. Hence it is concluded that, although a difference of size of the cleft at the side of the tongue does not modify the sound, the air must nevertheless have an essential share in the production of the sound; the air receiving, under the conditions in which tongues vibrate, a regular succession of impulses, though nodal points are not developed. We know that, for the production of a sound, it is only necessary that a certain number of impulses should be propagated to the auditory nerve, and we know that vibrations produce sound merely by giving rise to these impulses. The manner in which the tongue vibrates in its frame is supposed to give rise to the production of impulses of the air, and consequently of sound, in the same way as the action of the instrument called the siren; namely, by each vibration of the tongue interrupting for a moment the current of air through the opening. The pitch of the note would, as in the siren, depend on the frequency of the interruptions to the current of air; and, as according to this theory the interruptions to the current of air are produced by the vibrations, the frequency of the interruptions will be equal to that of the vibrations. This theory of the

* This is the more remarkable, since we shall find that notes obtained from membranous tongues may be raised several semi-tones by increasing the force of the blast.

sounds produced by vibrating tongues must be by no means regarded as proved. Even the sounds which can be produced by directing a strong current of air from a small tube against a thin and sufficiently long tongue of a mouth-harmonicon merely fixed at one extremity, and not surrounded by any frame, are alone sufficient to prove that the sounds produced by vibrating tongues do not depend solely on the impulses of the air; although in such an experiment the current of air must be somewhat arrested by the return of the vibrating tongue, while it would have a free course at the moment of the vibration, in which the tongue is carried out of the line of the current. We shall consider this subject more fully hereafter [in Appendix to the section on the voice].

b. Vibrating tongues, or reeds, combined with a tube which modifies their pitch.

The sound yielded by a reed or tongue is much altered in pitch when a tube or pipe is supperadded to it,—as in the oboe, clarionet, and bassoon. Here the air which sets the tongue in vibration has to traverse the whole length of the tube before escaping into the atmosphere; and the instrument is a compound of two, of which the sonorous vibrations are regulated by different laws. The pitch of the reed and that of the tube, sounded separately, may be quite different; but combined they react on each other, or accommodate themselves to each other in such a way that only one note is heard, which is neither always the fundamental note of the reed alone, nor that of the column of the air in the tube sounded without the reed. Hence not only does the frequency of the vibrations of the reed and column of air become the same, but they must reciprocally accommodate themselves to each other.

We owe the knowledge of a trustworthy theory of the action of these compound reed-instruments entirely to the labours of M. W. Weber.* We cannot here give all the results which he has obtained; but those which form a basis for an inquiry into the action of reed-instruments with membranous tongues — the instruments which most resemble the organ of voice—must be detailed.

1. The pitch of a reed may be lowered, but cannot be raised, by joining to it a tube.

2. The sinking of the pitch of the reed thus produced is at the utmost not more than an octave.

3. The fundamental note of the reed thus lowered may be raised again to its original pitch by lengthening the tube; and, by increasing

* Poggendorf's Annal. xvi. and xvii.; and an account of his experiments by Fechner in his Repertorium der Experimental-physik, i. p. 314 to 334.

the length of the tube after this, the fundamental note can be again lowered, but only to a certain extent.

4. The length of tube necessary to lower the pitch of the instrument to any given point depends on the relation which exists between the frequency of the vibrations of the tongue of the reed and those of the column of air in the tube, each taken separately.

5. Thus: the fundamental note of the reed-instrument sinks gradually as the tube is lengthened, until the tube acquires such a length that it would separately yield the same fundamental note as the reed of the instrument without the tube; the pitch of the instrument then suddenly rises to the pitch of the reed. By increasing still further the length of the tube, the pitch of the instrument may be again lowered to the "fourth" of the descending scale; and when the length of the tube has reached the double of that which would give the same note as the fundamental note of the reed, the pitch of the instrument again rises to that note. By still increasing the length of the tube, the pitch may be again lowered to the minor third, after which it again rises to the original note. During the transition, two different notes can be produced by varying the force of the blast. (These facts are, as we shall presently see, capable of useful application in explaining the action of reed-instruments with membranous tongues.)

6. If the note yielded by the reed alone corresponds with any one of the series of harmonic tones of the tube, the pitch of the two united does not necessarily differ from that of the reed alone, if they be sounded by a gentle blast; but, by blowing more strongly, the octave below the original note, or the fourth, minor third, or other intervals of the descending scale corresponding to the numerical series $\frac{7}{8}\ \frac{9}{10}\ \frac{11}{12}$, may be produced.

These facts furnish certain data for determining whether the organ of voice, or other musical instruments, should be regarded as simple flute or mouth-pipes, or as reed-pipes; for if a wind instrument can by the addition of a tube be made to yield tones of any depth in proportion to the length of the tube, it must certainly be regarded as a flute-pipe, the column of air within being alone the cause of the sound: but if, on the contrary, the pitch of the instrument can be lowered only an octave or less, by lengthening the tube, the embouchure remaining the same, then we may be certain that it is a reed-instrument.

In the clarionet, oboe, and bassoon, the different notes are produced by closing or opening a series of holes, the proper position of which has been determined by experiment: in the reed-pipes of the organ, which are tubes with a reed inserted into them through a plug, each note has a separate pipe.

Disk-shaped or metallic tongues.—It has been shown by the experiments of Clement and Hachette, confirmed by M. Savart, that a thin plate held before an opening in a plane surface, through which a current of air is forced, is thrown into vibrations, and gives rise to very deep dull sounds. And I have found that sonorous vibrations may be produced by forcing air between the edge of a circular disk of brass, fixed by a central rod, and the sharp border of a surrounding frame. We might, hence, expect that a circular disk would act as a vibrating tongue when air is forced through an opening in its centre; and, at first sight, the hunter's whistle, described by Savart, would seem to present us with an example of an instrument on that principle. But the opening in the centre of the disk in this "whistle" is proportionally much larger than the cleft between the tongue and its frame can be to allow of sound being produced; though it is true, that a very delicate metallic tongue can be made to vibrate by forcing a strong current of air against its edge even when there is no frame to confine the air. The whistle or bird-call has, however, more analogy with a pipe or flute in which the air only vibrates, than with a reed-instrument. I can produce sounds by drawing in air through the central opening of a disk of ivory so thick that its borders cannot vibrate, and therefore cannot act as a tongue.

Second class of tongued or reed instruments.

Instruments with membranous tongues rendered elastic by tension.

The tongues of this kind have hitherto been little studied, which is the more to be regretted, since a knowledge of their action would be a key to the theory of the organ of voice in men and birds. MM. Biot and Cagniard la Tour have sought to imitate the membranous tongues of the larynx,—namely, the vocal cords,—by stretching elastic bands of caoutchouc over the end of a tube. Henle also has formed an artificial larynx by means of animal membrane. Hitherto, however, the subject has not been sufficiently investigated to afford data for a perfect comparison between these artificial instruments and the organ of voice. I have therefore made the action of vibrating bands and membranes my study, and beg the reader's attention to the following results of my observations, a knowledge of which is necessary for the understanding of the experiments on the human voice and larynx to be afterwards detailed. The reader should also peruse the foregoing account of the principal facts regarding the action of musical instruments; otherwise what follows will not be intelligible.

The sonorous tongues which we have hitherto considered were solid plates of metal or wood, which vibrate according to the same laws as vibrating rods or bars. We saw that on account of being so short they give no sound, or only a very feeble one, when struck; but that the continued impulse of a current of air causes them to yield a sound which corresponds in pitch to the elasticity and length of the tongue. Bodies made elastic by tension, also, if much shortened, do not emit sound when struck, but are capable of being thrown into sonorous vibrations by a continuous current of air; such are the membranous tongues, the properties of which we are about to examine. These tongues may be rendered tense by stretching in one direction only, like the musical strings; or they may be extended in all directions, like the parchment of the drum.

Here, again, we shall consider separately the simple tongues, and the tongues combined with a tube modifying their tone.

A. *Simple membranous tongues without a tube.*

a. Tongues extended like vibrating cords.

A strip of thin membranous caoutchouc, one or two lines in breadth, stretched over a ring of wood or a four-sided frame, gives, when struck as a musical cord, a feeble sound only, as harsh as that of a metallic tongue when struck. But if a plate of pasteboard or wood be fixed to the ring on either side of the strip of caoutchouc, and so near it as to leave merely a narrow cleft between, a musical instrument is formed, which, when blown in the same way as the mouth-harmonicon, yields a clear, strong, and musical note.

We showed that sound could be elicited by forcing air from a tube upon a metal tongue, even though it were not fixed in a frame. The same experiment succeeds much more easily with a narrow tongue of caoutchouc stretched over a frame of eight lines, or one inch in diameter. Such a tongue, when a current of air is directed perpendicularly upon it at one of its edges, vibrates from side to side, and emits a musical sound; or if the current of air be thrown from the side over one surface of the elastic band, which is the better method of making the experiment, it immediately vibrates upwards and downwards, and a clear, strong sound, of the same character as when the air is forced through a cleft on each side of the tongue between it and solid plates of card or wood, is heard. When the current of air from a small tube is directed transversely across the elastic band at its middle, or between its middle and one end, the fundamental note of the band may in either case be produced; but sometimes, if the current strikes the surface of the strip of caoutchouc further from the middle, and the blast be strong, a different note is the result. The force of the blast, however, influences in some measure the pitch of the note produced. By laying a spatula perpendicularly across a caoutchouc tongue tied across a ring, in such a way that the edge of the spatula touches the middle of the tongue and the ring at two points, and then directing a current of air against one half of the band of caoutchouc, the octave of its proper fundamental note is produced. By increasing the tension of the band of caoutchouc, sounds of higher pitch can be obtained, and very high notes thus produced are still clear and full. On the other hand, the fundamental note of the band may be raised half a tone or more by increasing the force of the blast. The general law, however, regulating the vibrations of these membranous tongues, as of the common vibrating strings, is, that their number is in the inverse ratio of the length of the tongue, and probably also, as in the case of the strings, in the direct ratio of the square roots of the forces producing their tension. The tongues of metal and wood vibrate, we have seen, according to a different law, namely, in the inverse ratio of the squares of their length. The membranous tongues differ from the common vibrating strings merely in the circumstance of the pitch of their note varying with the mode in which the current of air acts upon them. The tongue being tied over the mouth of a tube, with a plate of pasteboard or wood on either side, the sound produced is half a tone or a whole tone lower, when air is drawn through the intervening clefts into the tube, than when it is forced out, though the force of the current be as much as possible the same in both directions. The force of the current of air influences the pitch of the note produced, as well when the air is drawn into the tube as when it is forced out. The size of the cleft at each side of the membranous tongue has no very perceptible influence on the pitch of the note, but the sound is more easily produced when the cleft is narrow. If any point of the tongue strike an inequality of the lateral bounding plates during its vibrations, a nodal point is developed, and a much higher note than the fundamental note of the tongue is heard.

The membranous tongues, made elastic by tension, may have either of three different forms, namely,—

1. That of a band, extended like a cord, and included between two firm plates, so that there is a cleft for the passage of air on each side of the tongue. This is the form which we have already considered.

2. The elastic membrane may be stretched over the half or any portion of the end of a short tube, the other part being occupied by a solid plate, between which and the elastic membrane a cleft merely is left.

3. Two elastic membranes may be extended across the mouth of a short tube, each covering a portion of the opening, and having a chink left open between them.

The laws of the action of the second form of tongue are exactly the same as those which we found to regulate the action of the first form. The only circumstances to be noticed are, that the note produced when the tongue was made to vibrate by blowing through the tube was from half a tone to a tone higher than when the sonorous vibrations were excited by forcing a small current of air upon the edge of the membrane itself. When the air was drawn into the tube through the cleft between the tongue and solid plate, a higher note was produced, unless the solid plate was placed somewhat within the tube, and its border behind that of the membranous tongue, when the sound produced was lower in pitch than the fundamental note. The position of the solid plate is of importance. If, when the air is forced from within the tube outwards, the border of the plate be directly opposed to that of the membranous tongue, the note produced may be the interval from C to F higher than when the plate of pasteboard is placed somewhat more forward than the vibrating tongue.

The third form of tongue, that in which two elastic membranes alone form the borders of a cleft, as at the glottis, is the most interesting. The two membranes may have either the same or different degrees of tension. To ascertain that they have the same degree of tension it is only necessary to sound each separately, which may be done by directing a current of air from a fine tube upon the edge of one while the other is depressed, or covered with a thin lamina of pasteboard; their tension may then be altered, until they each yield separately the same note. The sound emitted by the two tongues conjointly, when both have the same tension, is of a deeper pitch than the fundamental note of each separately; in three experiments the difference was a semitone. If the two elastic tongues have different degrees of tension, so that the pitch of the sounds they yield separately is different, they frequently appear not to accommodate their vibrations to each other, as the metal tongue of the reeds and the column of air in the tube of reed-instruments do. It is seldom that the sounds of both tongues are heard when the tube to which they are fixed is blown. Usually we hear the note of one only, as if the tongue which is more tense or more lax than the other was not sounding, or as when one tongue is covered and fixed by a plate of pasteboard. Frequently the tongue, which on account of not being sufficiently tense yields sound with difficulty, vibrates but feebly, and is somewhat protruded by the current of air. Sometimes the vibrations of the two tongues seem really to influence each other reciprocally. That such may be the case, has been noticed by Cagniard la Tour: he observed, that if the relative tension of the two tongues was, for example, such that there was an interval of a "fifth" between the notes they gave separately, the note which the two emitted when sounded conjointly was the intervening "third." That this is sometimes the case I have no doubt, but I must point out a source of error in such experiments. Frequently the tongues appear to be accommodating their vibrations to each other when such is not really the case. Thus, in one of my experiments, the two tongues differed from each other in their pitch about an octave: the tongue of the highest pitch gave, when the other was covered with a solid plate, the note F; but, when both were sounded, the note heard was the B below this F.

Here, then, a membranous tongue giving the note F, and another tongue with the pitch of an octave lower, seemed to influence each other reciprocally so as to produce the intermediate note B. But this reciprocal influence or accommodation of the vibrations was not real; for on pressing back the tongue of the lower pitch, and putting in its place a solid plate of pasteboard, the edge of which was made to project somewhat in front of the edge of the opposite elastic tongue, this tongue did not give out the F as when the edge of the solid plate was on the same level with it, but the lower B. The position given to the pasteboard plate to cause the tongue to yield this note, was exactly that which the tongue of lower pitch had assumed when protruded by the blast of air, and vibrating feebly. The law regulating the action of two tongues of unequal tension fixed over the mouth of a tube, with a narrow cleft between them, is the following. When one tongue is most readily thrown into vibrations by the current of air, the sound is emitted by it alone; but, if the blast be such as to throw them both into motion, they may both vibrate together, and by reciprocation produce a simple sound intermediate between the fundamental notes of the two separately: they may also, however, emit two different sounds; or, the blast being modified, the two sounds may be produced in succession. The metallic tongues of the mouth-harmonicon do not accommodate their vibrations to each other when they are sounded together by forcing air into the instrument from one general reservoir, the mouth.

The elastic membranous tongues, fixed to the end of a tube, may be so placed that their edges overlay each other, and clear tones will still be produced.

The sound elicited from membranous tongues may be much modified by arresting the vibrations of the tongue at different points by the finger. By touching the outer part of one of the caoutchouc bands tied to the end of a tube, I cause the note produced to be somewhat sharper; and the nearer the pressure of my finger approaches the cleft through which the air passes, the sharper become the sounds.

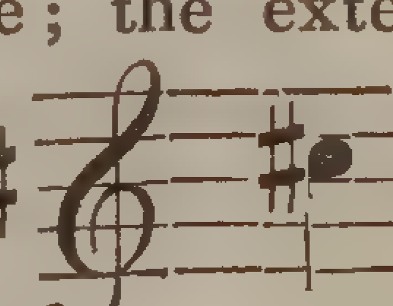
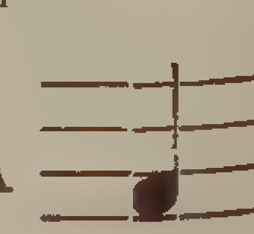
The membranous tongues differ from the metallic with respect to the effect of increased force of the current of air on the pitch of the notes they produce. When vibrations of a soniferous body are longitudinal, as in a column of air, the fundamental note is somewhat raised by increasing the force of the blast; but in bodies which vibrate transversely, as strings and metallic tongues, an increase of the moving force, while it causes the sphere of the vibrations to be more extensive, lowers in some degree the note given out. Hence the tone of a reed with metallic tongue becomes somewhat deeper when it is blown strongly. The cause of this, perhaps, may be, that when the blast is more gentle, the base of the tongue is not made to vibrate. The membranous tongues differ from other bodies which vibrate transversely in yielding constantly a higher note when thrown into action by a stronger blast of air. (It appears to me, however, that the tone of a mouth-harmonicon with a very delicate vibrating tongue also rises somewhat when the instrument is very strongly blown; and the very delicate vibrating tongue of a child's trumpet, whether the mouth-piece which contains the tongue be alone sounded, or the whole pipe, can by successive blasts of increasing strength be made to rise through the whole extent of an octave and a half without intervals.)

b. Tongues stretched in several directions, like the parchment of drums.

Hitherto we have considered merely the membranous tongues stretched in one direction only; but two membranes extended over the end of a tube, with a cleft between them, may be stretched in several directions, or one membrane may be stretched in all directions with merely a round opening in the middle for the passage of the air: both these cases would present some analogy to the parchment of the drum, but the tongues of the form last mentioned are generally insusceptible of sonorous vibrations, and, in the rare cases where they do yield a sound, it is a very feeble one.

B. *Membranous tongues combined with a tube.*

The addition of a tube below the tongue influences the notes yielded by a membranous tongue in much the same way as, we have seen from M. Weber's researches, it does those of the metallic tongues.

The note does not become uniformly higher or lower in a direct ratio with the length of the tube; the experiments which I have performed by means of a reed furnished with a tongue of caoutchouc, and a tube capable of being lengthened by small degrees to the length of four feet, show that the effect of the addition of a tube on the note given out by the membranous tongue depends on the relation which the proper fundamental note of the tongue bears to the fundamental note of the tube. Usually the note becomes lower and lower by semitones, in proportion as the tube is lengthened, until the tube becomes nearly of the length proper to give the same fundamental note as the tongue; there is then a sudden rise to that note. But the lowering of the note ceases before the tube has reached such a length as to be in unison with the tongue, for the pitch is not easily lowered an entire octave; the extent to which the note sinks is, for example, only from C♯  to A  from D♯  to G♯  or from E  to A 

When the note has risen to the pitch of the tongue, or to a note near the fundamental note of the tongue, the further increase of the length of the tube again lowers it, until the tube has attained about the double of the length which it had when the note rose before to the pitch of the tongue, to which pitch it then again rises. Further lengthening of the tube again lowers the note produced. In several instances I found that the pitch of the instrument continued to fall for a longer period, namely, till it was nearly as low as the lower octave; in such cases the rise to the fundamental note of the tongue did not occur when the tube was of about such a length that its fundamental note was that of the tongue, but not until the tube had double this length. The cause of this difference I could not determine. Experiments of this kind with membranous tongues do not admit of the same degree of precision as can be attained in experiments with metallic tongues,* on account of the proneness of the note yielded by membranous tongues to vary as much as a tone or semitone, according to the force of the blast of air, while the note given out by metallic tongues is very little affected by this cause. This source of inaccuracy might be avoided by using bellows compressed by a certain weight to give the blast; but there are advantages attending the blowing with the mouth in such a manner as to produce the slightest current of air which will excite sound,

* The following are the results given by W. Weber (in Poggendorf's Annal. xvi. 425. & xvii.) as afforded by his researches on the influence of a tube on the sounds yielded by reeds with metallic tongues :

(Let *a* designate one-fourth of the length of the tube, the column of air in which yields the same fundamental note as the metallic tongue without the tube; the length of tube designated by *a* will, of course, be longer or shorter in proportion as the fundamental note of the tongue is deeper or higher.)

1. A tube gradually lengthened, until it equals *a*, deepens the note in an imperceptible degree.

2. While the tube is gradually lengthened from *a* to 2 *a*, the deepening of the note becomes marked; but still increase of the length of the sonorous vibrations is not proportionate to the increase in length of the column of air.

3. While the tube is lengthened from 2 *a* to 3 *a*, the pitch of the note falls rapidly, and nearly in the ratio of the increase in length of the column of air.

4. During the elongation of the tube from 3 *a* to 4 *a*, the pitch of the fundamental note falls still more rapidly, quite as rapidly as the length of the tube increases, till at length it is an octave lower than the fundamental note of the tongue alone. Further lengthening of the tube causes the sound produced to rise suddenly to the pitch of the original fundamental note of the isolated metallic tongue. If the elongation of the tube be continued after this, the fundamental note falls in pitch in the same way as before; and, when the tube has reached the length of 8 *a*, is an interval of a "fourth" deeper than the proper fundamental note of the isolated tongue. Further lengthening of the tube causes the note to rise again suddenly to its original pitch, from which it again falls as the tube is lengthened, until, at the length of 12 *a*, the note produced is the "minor third" of the fundamental note of the tongue. It then rises again to this fundamental note. [See also page 985 supra.]

and any other mode of effecting the blast is scarcely admissible, since frequently a note cannot be obtained from the instrument except by a particular mode of blowing and position of the lips (without any alteration in the force of the blast). [The experiments from which the above results are deduced are given in the Appendix.] Besides the variation of the length of the tube, there are two means by which the note yielded by a membranous tongue combined with a tube may be altered; namely, change in the force of the blast, and partial occlusion of the end of the tube.

The note produced by blowing through a reed with membranous tongue furnished with a tube of some length,—for example, four feet,—can be raised in pitch almost an octave in successive semitones by altering the force and manner of blowing. Notes which cannot be produced by blowing with increased force can be obtained by making the opening of the lips narrower while the blast is given. The fundamental note of a membranous tongue combined with a pipe four feet in length was C , by increasing the force of the blast, and contracting the opening of the lips at the same time, or without this, I could produce the sound of C#, D, D#, and E, with ease; F with great difficulty; then again, F#, G, G#, A, and A#, readily; but B was difficult to produce, and was not a perfect tone.

It has been stated by the MM. Weber,* that reed-instruments with metallic tongues are capable of yielding harmonic tones, the octave or the fifth of their fundamental note, by the developement of nodal points, just as is the case with pipes without vibrating tongues, which are closed at one extremity. But it is peculiar to the instruments constructed with membranous tongues, that the note yielded by the tongue, whether this be combined or not with a tube, can be raised by semitones to a certain extent by gradually increasing the force of the blast. If in place of dry elastic tongues of caoutchouc, moist elastic membranes—for example, arterial tissue,—be used, the note can be raised by semitones nearly the extent of a " fifth," when no tube is superadded.

The size and condition of the lower opening of the tube has an influence on the note emitted by the membranous tongue. The length of the tube being three inches, I could, by gradually covering a larger and larger portion of the lower opening, cause the note to sink the extent of a " fifth." The tube being six inches in length, covering half the orifice caused a lowering of the note the extent of a semitone; the introduction of the finger lowered the pitch from C to the F below. In many instances, however, the introduction of the finger had directly the

* Wellenlehre, 526.

opposite effect, namely, the production of a higher note. The cause of this apparently contradictory result was for a time an enigma. At length, however, I found that as long as the note is sinking with the increasing length of the tube, covering its extremity lowers the note still more; but that, when the length of the tube has reached the point where the pitch of the instrument is about to rise again to the fundamental note of the tongue, covering the orifice of the tube may induce a higher note, and even cause the note to rise at once to the pitch of the tongue alone.

A considerable constriction or obstruction of the tube at the other extremity, namely, close to the tongue, generally causes the note to be higher.

If the ordinary reed of a clarionet be replaced by a reed with a tongue of caoutchouc, it is found that the influence of the side-holes of the tube of the clarionet on the notes elicited is much less than when the instrument is furnished with its ordinary reed. In a clarionet with the usual construction the successive opening of the side-holes and keys from below upwards raises the notes by successive semitones; but, when the clarionet has a membranous tongue, the rise of the notes thus produced is very slight, not being perceptible, except when the highest holes are opened, and at last amounting to no more than a tone.

C. *Influence of a tube prefixed to vibrating membranous tongues upon the sound they produce.*

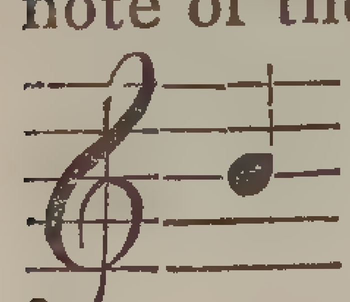
The influence exerted by the prefixed tube or "porte-vent" upon the pitch of a reed-instrument with metallic tongue was, it appears, first observed by M. Grenié.* The nature of this influence has not been hitherto satisfactorily elucidated. I find that the length of the tube which conveys the current of air to a membranous tongue has as powerful an effect in lowering the pitch of the sound produced as that of the tube beyond the tongue. This is a point of very great importance in relation to the organ of voice, and must be here fully investigated.

There are five principal conditions in which a vibrating tongue may be sounded. 1. The tongue may be destitute of any bounding frame, and have no pipe or tube either above or below it; and it may be thrown into vibrations by a free current of air blown upon it from a small tube. 2. The tongue may be bounded by a frame without any tube, and the air may be forced upon it directly from the mouth, the frame being embraced by the lips. 3. The tongue may be sounded in the same manner as in the last case; but to the tongue and frame is

* See Muncke in Gehler's Physik. Wörterb. bd. viii. p. 376.

superadded a tube or pipe, through which the air passes after acting on the tongue. 4. The tongue has no tube beyond it, but the current of air before reaching it passes through a tube, to the lower end of which the tongue with its frame is fixed. 5. The tongue has both a tube prefixed, and one attached to it below.

The simplest form in which the influence of a tube prefixed to the membranous tongue upon the sound which it emits can be examined, is that where the tongue is stretched over the lower end of the tube which conducts the current of air, and has no other tube or pipe beyond it. Changes in the length of the prefixed tube have exactly the same effect on the sounds given out as we have seen to arise from alterations in the length of a tube placed below the tongue. In proportion as the prefixed tube is lengthened, the notes given out become deeper and deeper, but not to the extent of an octave. When the lengthening of the tube has reached a certain point, the tone suddenly rises to the original pitch; a further increase of the length of the tube is attended with a fresh deepening of the tones, till again they rise to the same pitch as before; and this alternate sinking and sudden rising of the tones to the original pitch is renewed while the tube is gradually lengthened. There is not, however, a perfect accordance between the length of a tube prefixed to a membranous tongue and that of a tube placed below it, necessary for the production of a given note. In the experiments by which I ascertained these facts, the tongue used was a single lamina of caoutchouc stretched over a tube half an inch in length, with its edge opposed to that of a solid plate of wood, as in the experiments also on the effect of variations in the length of the tube or pipe below the tongue upon the pitch of the sounds. In these experiments a tube which could be lengthened at will was prefixed to the tongue thus arranged, and the tongue was sounded through the medium of this tube. The following table illustrates the comparative effect of variations of length of the tube prefixed to the tongue, and of that placed below it; in the first case there was no tube below the tongue, in the last the air was forced upon the tongue directly from the mouth; in both cases the fundamental note of the tongue alone was the same, the middle B of the treble clef

.

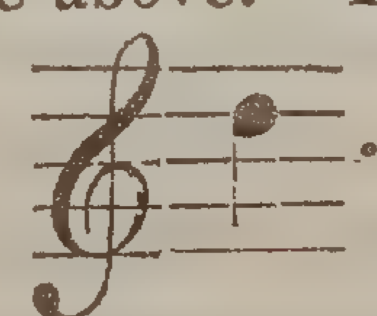
Sounds with prefixed tube or "wind-pipe."		Sounds with tube attached below the tongue.	
Notes.	*Length of tube.* *inch. lines.*	*Notes.*	*Length of tube.* *inch. lines.*
A♯	4 6.	A♯	1 2.
A	9 10.	A	2 0.
G♯	13 0.	G♯	3 0 to 5 inches 6 lines.
G	15 6.	G	7 6.
F♯	17 6.	F♯	9 0.
F	19 0.	F	10 0.

Sounds with prefixed tube or "wind-pipe."

Notes.	*Length of tube.* inch.	lines.	
F and A♯	20	0	(sudden rise of the sound.)
A	24	6.	
G♯	27	6.	
G	29	0.	
F♯	32	0.	
F and A♯	35	0	(sudden rise of the sound.)
A	37	0.	
G♯	42	0.	
G	46	0.	

Sounds with tube attached below the tongue.

Notes.	*Length of tube.* inch.	lines.	
E	13	0.	
D♯	17	0.	
A♯	22	4	(sudden rise of the sound.)
G	23	0.	
F♯	25	6.	
F	27	6.	
E	32	0.	
D♯	39	6.	
G	40	0	(sudden rise from D♯ to G.)
F♯	42	0.	
F	45	0.	

The following were the results of a second experiment, which I detail for sake of comparison with the above. The fundamental note of the tongues without either tube was E 

With prefixed tube.

Notes.	*Length of tube.* inch.	lines.	
D	4	9.	
C♯	6	0.	
C	7	6.	
B	9	6.	
A	10	0.	
D	15	9	(sudden rise of the sound.)
C♯	18	9.	
B	22	0.	
D	24	9	(rise.)
C	30	6.	

No further sound could be produced.

With tube attached below the tongue.

Notes.	*Length of tube.* inch.	lines.	
E	1	0.	
D♯	3	0.	
D	3	9.	
C♯	4	9.	
C	5	6.	
B	6	2.	
A♯	7	4.	
A	10	0.	
E to D♯	13	6	(sudden rise of the sound.)
D	15	0.	
C♯	15	8.	
C	17	6.	
B	20	0.	
A	24	0.	
D♯	28	0	(sudden rise of the sound.)
D	29	6.	
C	30	0.	
B	30	6.	
A♯	34	0.	
A	35	0.	
D♯ to E	41	6	(rise.)
C	42	0.	
B	43	6.	

We must lastly mention the changes produced in the sounds by contracting the calibre of the tube prefixed to the tongue at either extremity. A plug perforated in the middle for the passage of the air being introduced into that end of a short tube which is nearest to the tongue, a higher note was produced. The effect being the same as that of shortening the tube.

If, on the contrary, the tube was diminished in calibre at the upper extremity, — that most removed from the tongue, — which was done by contracting the lips while blowing, a deeper note was the result, provided the pitch of the instrument had not previously been lowered by lengthening the tube; when the tone had been already rendered much deeper by an increase of the length of the tube, contracting the orifice of the lips either had no effect, or caused even a slight rise of the note.

D. *Membranous tongues with both a tube prefixed and one added below the tongue.*

The tube prefixed to the tongue, and the tube or pipe placed below it, not only require different lengths for the depression of the pitch of the notes to the same degree; there exists also no relation of compensation between them. In other words, their relative influence is not such, that when a certain length (n) of pipe below the tongue, without any tube above, produces the note x, a smaller length of the pipe ($n—a$), with a prefixed tube of compensating length (a), produces the same note (x). With a pipe below the tongue of $12\frac{1}{2}$ inches in length, for example, the note F♯ was produced; but with a pipe of $6\frac{1}{4}$ inches, and a tube prefixed to the tongue of $6\frac{1}{4}$ inches, the note was G♯.

If the two tubes are made respectively of such length that the one with the tongue at its upper extremity (in which the blast is directed from the mouth immediately upon the tongue), and the other with the tongue at its lower extremity (in which the air passes through the tube before striking the tongue), give the same note; the union of both with the same tongue, one above and the other below, will also give the same note. This experiment I have repeated frequently, and constantly with the same result. It would, from this fact taken conjointly with that previously mentioned, (the absence of a compensating relation between the upper and lower tubes,) appear that each tube exerts a special influence on the vibration of the tongue; and that hence, when the tube above the tongue and that below it would, separately combined with the tongue, give rise to different notes, they will also exert distinct influences upon it when both are conjoined with it. The tongued instrument is therefore rendered still more complicated by the addition of the tube above the tongue; and since, whether the instrument be sounded by means of the mouth or by bellows, the cavity conveying the column of air is to be regarded as a prefixed tube, the note produced in the most simple experiment in which a tongue with merely the lower tube is sounded by the mouth, must be modified by the air passing through the cavity of the mouth, &c. It would be of the greatest importance to know the respective influences of the tube prefixed to the tongue, and of that below it; for, in the organ of voice, the larynx and bronchi represent a tube prefixed to the membranous tongue, — and the cavity in front of the inferior ligaments of the larynx, a tube placed below the tongue. This is, however, one of the most difficult problems in the science of acoustics, and I have not succeeded in arriving at any result which approximates to a law. All I can attain to is a constant confirmation of the observation that the elongation of the prefixed tube, while the lower tube or pipe remains the same, causes a continued change of the note produced, until the two tubes have such comparative length that their respective influence on the sound of the instrument is the same. If the upper tube have a fixed length, the lengthening of the tube below the tongue causes a lowering of the notes to a certain point, when they again rise to the original pitch; a further lengthening of the tube induces a second fall of the notes, till at a certain point they again rise as before; and this gradual falling and sudden rising of the notes is repeated at regular intervals. Thus: in one experiment the tube above the tongue was 6 inches in length, and the fundamental note was D on the fourth line of the treble clef: on a tube 4 inches in length being added below the tongue, the note fell to C♯; this tube being lengthened to $4\frac{1}{2}$ inches, it rose again to D♯: when the lower tube was 5 inches in length, the note became again lower; and before the length of the tube was 6 inches, it was D♯. While the length of the tube increased to $8\frac{1}{2}$ inches, there was a gradual fall until the note was C♯, at which it remained until the tube measured $16\frac{1}{2}$ inches, when it again rose to D. While the tube was lengthened from 18 to 24 inches, the pitch of the instrument fell again to C♯; at $27\frac{1}{2}$ inches, it rose to D; at $32\frac{1}{2}$, it had fallen to C♯, at which it remained until the tube below the tongue was 4 feet in length.

E. *Musical instruments with membranous tongues.*

The artificial contrivances, the action of which we have been considering, constitute a peculiar class of reed-instruments, of which no use has hitherto been made in music. The human organ of voice, and the organ of voice in birds, belong, as we shall see, to the same category; the vocal cords being the membranous vibrating tongues.

But the lips also may act as tongues when rendered tense by the contraction of the sphincter oris, which thus compensates for the want of elasticity in the lips themselves. If the breath be forced through the contracted orifice of the lips made tense by the contraction of the sphincter, sounds are produced which belong to the class of sounds emitted by reed-instruments. The cavity of the mouth and respiratory organs form the "porte-vent" or prefixed tube, and the instrument consists of a reed or tongue with a prefixed tube, but without the lower tube or pipe. If a pipe of pasteboard or metal be added in front of the lips, the sounds produced not only become more sonorous, but may be modified in pitch.

The sphincter ani is capable of acting in the same way as the sphincter oris: rendering the skin of the margin of the anus tense, it enables it to vibrate as a tongue, while the rectum filled with gas constitutes a prefixed tube; the pipe below the tongue is wanting.

Allied to the reed-instruments constructed with membranous tongues are the trumpets and horns, in which the lips thrown into vibration by the blast of air act as tongues. In other reed-instruments the reed is a distinct portion of the instrument which yields sounds when separated from the tube. In horns and trumpets, the part called the mouth-piece is incapable of yielding any tone when a current of air is merely blown through it; the lips are necessary to convert the mouth-piece of these instruments into a musical reed. The lips rendered tense by the contraction of the sphincter are thrown into sonorous vibrations of definite value by the current of air forced between them; and the notes produced are higher, the more strongly the lips are contracted by the sphincter. In whistling, the notes become deeper as the opening of the lips is widened; and it at first sight appears that in sounding trumpets also the size of the opening of the lips has an influence on the pitch of the notes; but it is the stronger or weaker contraction of the sphincter muscle, attending the diminution or increase of the size of the opening of the lips, which in this case alters the pitch of the notes, acting in the same way as the increased or diminished tension of the elastic membranous tongues.

The mouth-piece of the trumpet is at its commencement cup-shaped. In sounding the trumpet, the border of the cup-shaped opening is applied to the lips, and the air is forced through the narrow orifice of the lips, the edges of which, rendered tense by the contraction of the sphincter, vibrate like a tongue in the free space afforded by the cup-shaped cavity just mentioned. Hence the necessity of this cavity at the opening of the mouth-piece; if it be filled up so as to leave merely a narrow central passage, the lips firmly pressed upon cease to give any sound. That this is the essential cause of the sound produced in blowing the trumpet, is evident from the fact that a similar sound is heard when the breath is forced merely through the orifice of the contracted lips. One lip is indeed sufficient for the production of such sonorous vibrations; a sound may, for example, be produced by drawing down the upper lip over the surface of the lower lip, and forcing air between them, when the upper lip alone vibrates. The opening of the mouth-piece of the horn is not cup-shaped, but conical; its use is the same, namely, to allow the edges of the lips to vibrate freely.

The trumpets and horns are classed by M. Biot among the pipes of the flute kind; and the different notes emitted by them are supposed by him to be produced, as in the flutes and mouth-pipes, by variations of the force of the blast. But the pitch of the notes depends really on the degree of tension of the lips, and is little influenced by the force of the blast, which merely affects the loudness of the sound. The trumpets and horns are by M. Muncke classed more correctly among reed-instruments; they are, as we have shown, reed-instruments with membranous tongues, the tone of which is altered in timbre by the metal, and in pitch by the vibrating column of air of the tube. The pitch of the notes, however, does not regularly rise in the inverse ratio with the length of the tube, as in flute-pipes: on the contrary, the effect of the length of the tube in varying the notes is, as in reed-instruments, generally only slight and subordinate. The tube is lengthened to produce this effect in trumpets and horns by the addition of different pieces, crooks, (Einschiebsel); in the trombone (Posaune) by drawing out the sliding tube. The horns and trumpets have nearly as many supernumerary tubes or crooks as there are "keys" in music. The different notes are produced in these instruments by two other methods: first, by altering the degree of tension of the lips; and secondly, by closing or partially closing the lower extremity of the tube, which in reed-instruments with membranous tongues has, as we have already seen, the effect of lowering the notes. The principal means, however, is the increased tension of the lips by muscular contraction: hence, after long blowing, the player is for a time disabled; and the exertion required is greatest in producing the high notes, not on account of a stronger blast being required for them, but because they are the result of greater contraction of the lips.

The finger-keys closing side-openings in the tube, which have recently been added to the trumpets and horns, have the same influence on the sounds as they have in the clarionet, oboe, and bassoon.

CHAPTER II.

OF THE VOICE, OF THE ORGAN OF VOICE, AND OTHER MEANS FOR THE PRODUCTION OF SOUND IN MAN AND ANIMALS.

The facts made known in the preceding chapter afford us data for correctly estimating the means which contribute to the production of voice and other sounds in man and animals. We have three principal classes of musical sounds to consider: 1, the voice of man and quadrupeds; 2, sounds formed in the mouth; 3, the voice of birds. These three classes of sound are produced by different instruments and in different parts. The different sounds of the voice in man and mammalia are generated in the larynx, and are somewhat modified in quality by the parts in front of the larynx through which the air passes. In whistling, we give rise to an entirely different series of sounds, which have their source in the lips and cavity of the mouth. The voice of birds again has another seat; it is produced not in the superior, but in the inferior larynx, which occupies the lower extremity of the trachea at its point of division into the bronchi. In the few other vertebrata below birds which have voice, as the frogs and toads, the sound is generated in the proper larynx, as in man and mammalia. Besides the organs of voice which prevail extensively through entire classes of animals, there are other special instruments of sound in some animals, even among the lower classes; the examination of these, however, would lead us too far from our proper object.*

1. *Of the human voice.*

A. *Of the human organ of voice.* — If any question relating to the human voice have been determined with certainty, it is that regarding the part of the air-passages in which the voice is formed.

* The authors who have written concerning the human voice are: Dodart, Mém. de l'Acad. de Paris, 1700, 1706, 1707.— Ferrein, ibid. 1741. — Magendie, Précis élément. de Physiol. — Physiology translated by Milligan, Biot, Précis Element. de Physique experiment, Paris, 1824, t. i. p. 457.—Fechner, in his translation of Biot's Experimental-physik. ii. p. 149. — Savart, in Magendie's Journ. de Physiol. v. Liscovius, Theorie der Stimme. Leipz. 1814. — Chladni, in Gilbert's Ann. lxxvi. p. 187. — Mayer, in Meckel's Archiv. 1826. — Bennati, Recherches sur le Méchanisme de la voix Humaine. Paris, 1832. — Muncke, in Gehler's Physik. Wörterbuch, viii. 373. — Mayo, Outlines of Human Physiology. —Sir C. Bell, Philos. Transact. 1832, pt. ii.—Malgaigne, Arch. Gén. de Méd. 25. — Willis, Transact. of Philos. Soc. of Cambridge, 1832. — Bishop, in Lond. and Edinb. Philos. Magaz. 1836. — Lehfeldt, Diss. de Vocis Formatione, Berol. 1835. On the voice of birds, see Cuvier, Anat. Comparée; and Savart, Froriep's Not. 331, 332.

Observations on living subjects, as well as experiments on the larynx taken from the dead body, prove that the sound of the voice is generated at the glottis, and neither above nor below this point. If an opening exist in the trachea in the human subject, or if an opening be made in this situation in an animal, the sound of the voice ceases, but returns on the opening being closed. This experiment has been often made, and its accuracy is beyond a doubt. An opening into the air-passages above the glottis, on the contrary, does not prevent the voice being formed. M. Magendie, moreover, has convinced himself that the voice is not lost, though the epiglottis, the superior ligaments of the larynx, and the upper part of the arytenoid cartilages be injured. He has also seen in living animals, whose glottis he had laid bare, that during the emission of sound the inferior ligaments of the larynx, which bound the fissure of the glottis, were thrown into vibration. We know also that injury of the laryngeal nerves supplying the small muscles, which alter the states of the aperture of the glottis and make tense the vocal cords, puts an end to the formation of vocal sounds; and that, when these nerves are divided on both sides, the loss of voice is complete. Again, if we attempt to produce sounds by forcing a current of air from the trachea through the larynx in the dead human subject,—an experiment in which a person the most unpractised may succeed, provided the vocal cords be in some degree tense and the aperture of the glottis narrowed, — we shall find that the sounds are produced, whether the part of the trachea which serves to convey the current of air to the larynx be long or short; and even though it be entirely wanting, and the air forced immediately through the glottis from the lower extremity of the larynx. Again, a larynx thus cut from the body may be freed from all the parts lying in front of the glottis; the epiglottis, the upper ligaments of the larynx, the ventricles of the larynx between the superior and inferior, or vocal ligaments, the greater part of the arytenoid cartilages, their upper part namely, may be all removed: if the inferior ligaments or vocal cords only remain, and be approximated so that the fissure of the glottis be narrow, clear tones will be produced by forcing air through it from the trachea. All these facts establish the correctness of the view which regards the glottis and the inferior laryngeal ligaments or vocal cords which form the immediate boundaries of the glottis as the essential source of the voice: the trachea as the "wind-chest"* of the wind-instrument; and the vocal tube in front of the glottis, comprehending the upper part of the cavity of the larynx, and the air-passages thence upwards to the openings of the mouth and nostrils, as the tube of a musical instrument by which the sound may be modified, but not generated.

* "Wind-chests" are the reservoirs of air in the organ, whence the wind in distributed to the pipes, when the keys or pedals are pressed down.

The parts forming the boundaries of the glottis, namely, the vocal cords, (fig. 58, 3,) first claim our attention. They are elastic, and can be made tense by the depression of the thyroid cartilage (figs. 57 and 58, 8),

Fig. 57.*

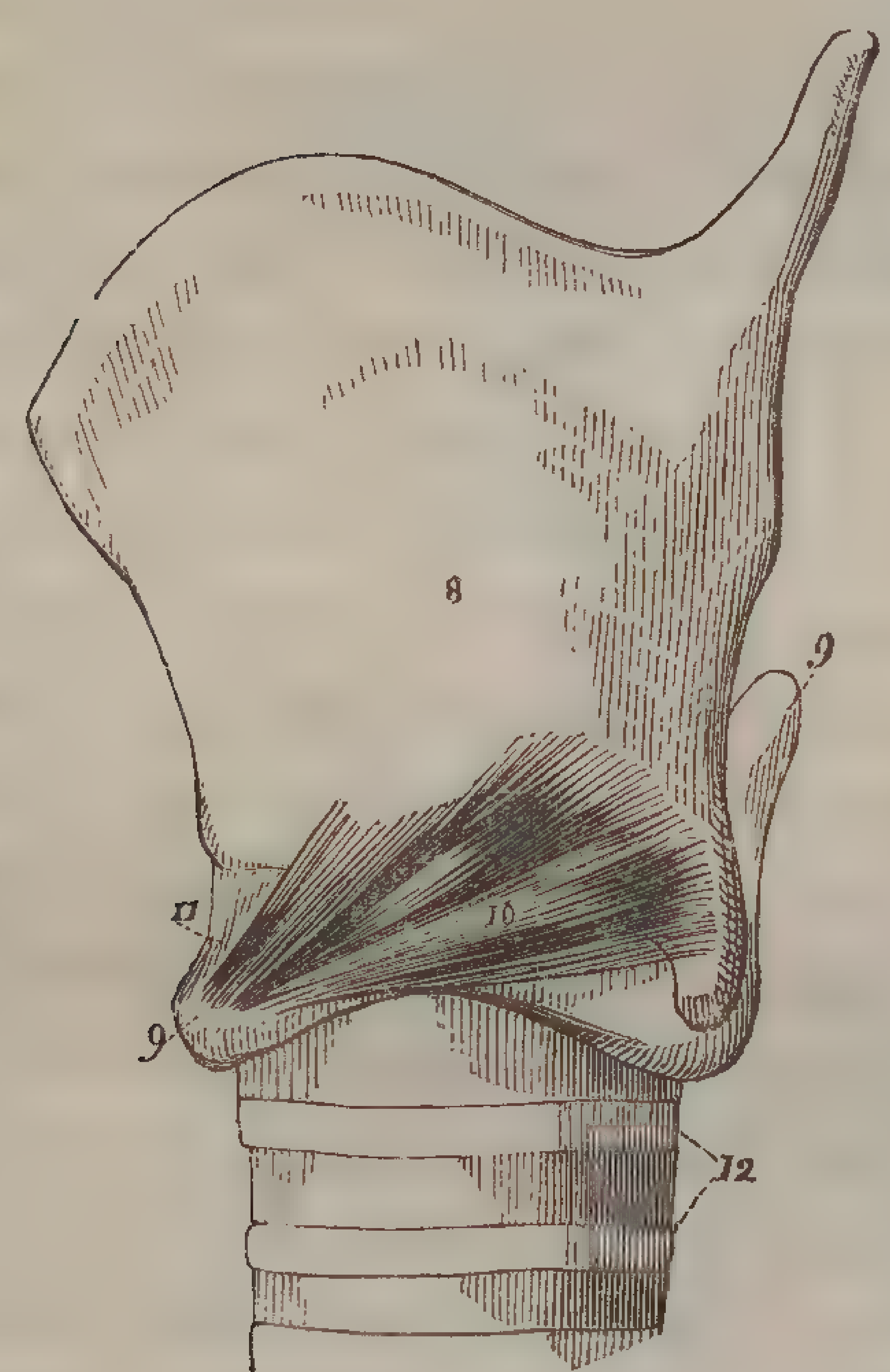


Fig. 58.†

towards the cricoid cartilage (figs. 57 and 58, 9), by means of the crico-thyroid muscles (fig. 57, 10), as well as by the retraction of the arytenoid cartilages (fig. 58, 2), which are moved backwards by the posterior crico-arytenoid muscles (fig. 58, 4), at the same time that they are approximated to each other by the musculi arytenoidei (6). The effect of these movements of the thyroid and arytenoid cartilages is, as we have said, to make tense the vocal cords, either by the depression of the thyroid cartilage, the arytenoid cartilages having been previously fixed by their muscles, or by the retraction of the latter, after a fixed point has been obtained by the movement of the former. The length of the fissure of the glottis depends on the degree to which the cords are thus stretched. The aperture of the glottis is narrowed by the approximation of the arytenoid cartilages, which is effected by the musculi

* [Fig. 57. Lateral view of exterior of larynx, after Mr. Willis.—8. Thyroid cartilage. 9. Cricoid cartilage. 10. Crico-thyroid muscle. 11. Crico-thyroid ligament. 12. First rings of trachea.]

† [Fig. 58. Bird's-eye view of interior of larynx.—1. Aperture of glottis. 2. Arytenoid cartilages. 3. Vocal cords. 4. Posterior crico-arytenoid muscles. 5. Lateral crico-arytenoid muscle of right side, that of left side removed. 6. Arytenoid muscle. 7. Thyro-arytenoid muscle of left side, that of right side removed. 8. Thyroid cartilage. 9. Cricoid cartilage. 13. Posterior crico-arytenoid ligament. With the exception of the arytenoid muscle, this diagram is a copy from Mr. Willis's figure.]

arytenoidei; it is dilated by means of the musculi crico-arytenoidei postici, which draw the arytenoid cartilages asunder. The vocal cords, by virtue of their elasticity, are capable of being thrown into regular vibrations, after the manner of membranes extended longitudinally from two extremities (see page 988). Their elasticity is due to the elastic tissue which composes them, and which is also found in many other parts of the body (see page 875).

The vocal cords are not, however, the only parts of the larynx composed of elastic tissue. The ligamentum hyo-thyroideum and the ligamentum crico-thyroideum medium have been long known as yellow elastic ligaments. The last-named ligament must by its elasticity, and quite independently of any action of the crico-thyroid muscle, keep the corresponding borders of the cricoid and thyroid cartilages approximated to each other, and will therefore offer some resistance to the movement of the arytenoid cartilages backwards in the act of producing tension of the vocal cords, a certain degree of which will be produced by the elasticity of this ligament alone when the arytenoid cartilages are fixed by their muscles. A much wider distribution still of the elastic tissue in the larynx has been pointed out by M. Lauth.* The principal portion of the elastic tissue arises, according to M. Lauth, from the lower half of the angle of the thyroid cartilage between the insertions of the thyro-arytenoidei muscles. Thence the fibres radiate downwards, obliquely backwards, and even somewhat upwards, forming a continuous membrane, which is attached to the entire upper border of the cricoid cartilage, except at the situation of the arytenoid cartilages, where the fibres become connected with the anterior angle of the basis of those cartilages and with their anterior border. This radiating elastic membrane has three accessory fasciculi; one, which passes downwards, is the crico-thyroid ligament; the other two are the inferior thyro-arytenoid ligaments, or vocal cords. This elastic membrane forms also the superior ligaments of the glottis, which are connected with the inferior or true vocal cords by an extremely thin expansion of elastic tissue covering the ventricle of the larynx. The hyo-thyroid ligament also is elastic; and the same tissue exists likewise in the thyro-epiglottic, hyo-epiglottic, and glosso-epiglottic ligaments. If we add to these parts the elastic longitudinal fibres in the membranous part of the trachea and bronchi, we shall have an idea of the great extent of the tissues susceptible of consensual vibration and resonance in the parts surrounding the organ of voice.

The next point to be considered is the variety of forms which the aperture of the glottis (fig. 58, 1) is capable of assuming, and which it

* Mém. de l'Acad. Roy. de Méd. 1835.—Müller's Arch. 1836.—Jahresbericht, p. clvii.

really assumes at the time of emitting sound. According to M. Lauth's researches, the glottis is able to take the following different forms. In the passive state, when emitting no sound, the aperture of the glottis is lance-shaped; it dilates somewhat, as is already known, during inspiration, and becomes narrowed again during expiration. The lateral boundaries of the aperture are, posteriorly, the inner surface and anterior process of the base of the arytenoid cartilages (fig. 58, 2); anteriorly, and in the greater extent, the vocal cords (3), which are connected posteriorly to the above-mentioned anterior process of the basis of the arytenoid cartilages. The whole length of the aperture of the glottis when open is eleven lines, of which the posterior part between the arytenoid cartilages and their anterior process measures four, the anterior part between the vocal cords seven lines. When dilated to its full extent (by the musc. crico-arytenoidei postici) (4), the aperture of the glottis has the form of a lozenge, of which the posterior angle is truncated. The lateral angles correspond to the anterior processes of the base of the arytenoid cartilages, which may be separated from each other to the distance of $5\frac{3}{4}$ lines. In the contracted state, the rima glottidis may have either of three forms. The anterior processes of the base of the arytenoid cartilages may be approximated to each other through the agency of the lateral crico-arytenoid muscles (5), and by coming into contact may divide the fissure of the glottis into two parts; or the rima, though narrowed, may remain open in its whole length; or, lastly, the posterior part of the rima may be quite closed by the approximation of the arytenoid cartilages themselves, together with their anterior processes, to which the chordæ vocales are attached. The movement of the arytenoid cartilages, which produces this last form, is effected by the united action of the proper arytenoid muscles (6) and of the lateral crico-arytenoid (5). The rima glottidis is here confined to the space between the sharp borders formed by the elastic vocal cords; it comes to a point both anteriorly and posteriorly; its length and breadth vary here very much, according as the vocal cords are stretched or not. The relaxation and shortening of the vocal cords are effected by the thyro-arytenoid muscles (7), which also are able to diminish the transverse diameter of the space above and below the vocal cords.

The form of the rima glottidis in the human subject during life, at the moment of the emission of sound, is not at present very accurately known; but that it becomes narrowed is certain. The anterior portion of the aperture,—that bounded by elastic and sharp borders,—being alone susceptible of sonorous vibration from the action of the current of air, the posterior part of the opening, which cannot contribute to the original production of sound, can only by considerably increasing the area of the opening disturb the action of the air on the other part.

Mr. Mayo* has made some observations on the movements of the glottis in the human subject during life. A man in an attempt to commit suicide divided the larynx immediately above the chordæ vocales; in consequence of the oblique direction of the wound the vocal cord and arytenoid cartilage of one side were wounded. During undisturbed respiration, the form of the aperture of the glottis was triangular. As soon as a sound was uttered, the chordæ vocales became almost parallel, and the rima glottidis took a linear form. It would appear from the figure that the posterior part of the aperture was not closed. In another patient the incision passed into the pharynx above the thyroid cartilage, rendering the upper part of the arytenoid cartilages visible. During the emission of sound the arytenoid cartilages kept the same position as when the glottis was closed. Kempelen † has stated, that the glottis, to produce sound, must be approximated to within $\frac{1}{12}$th, or at most $\frac{1}{10}$th, of its diameter; and Rudolphi ‡ confirms this statement, from the observation of the parts in a man whose pharynx was by the absence of the nose laid so open to view that the opening and closing of the glottis could be readily seen.

M. Magendie excludes from the glottis the space between the arytenoid cartilages, which he has found in experiments on animals to be closely applied to each other during the emission of sound. Malgaigne has made the same observation. This may possibly be generally the case; and sounds cannot be readily elicited from the human larynx removed from the body, when the posterior portion of the glottis is not closed. Nevertheless it is not, according to my experiments, absolutely necessary; I have, in some rare cases, been able to produce a sound artificially, when the chordæ vocales were made somewhat tense and the aperture of the glottis narrowed, though open in its whole length.

B. *Of the modulation of the voice, and the causes on which it depends.*—Experiments on living animals have hitherto afforded few results calculated to elucidate the physiology of the human voice, notwithstanding the labours of MM. Magendie and Malgaigne, which are in a certain measure valuable. M. Magendie laid bare the glottis in a dog by means of an incision between the thyroid cartilage and os hyoides; he then observed that the vocal cords, during the utterance of deep notes, vibrated in their entire length, but that the portion of the rima glottidis which lies between the arytenoid cartilages was closed. During the utterance of very high notes, the vibrations were perceptible only in the most posterior part of the vocal cords, and the air

* Outlines of Physiol. 1837, p. 371.

† Mechanismus d. Menschlich. Sprache. Wien. 1791, p. 81.

‡ Physiologie. ii. I. 370.

escaped only through that part of the rima glottidis. It is difficult to understand how the closing of the anterior part of the glottis could be effected. Such a change in the glottis, causing the air to be transmitted only through the posterior part, cannot be imitated in the human larynx; while, on the contrary, it is not difficult to shorten the fissure of the glottis at its posterior part by approximating the anterior processes of the arytenoid cartilages to which the vocal cords are attached, the tension of these cords still remaining the same. Careful experiments on the human larynx itself, after its removal from the body, offer the best prospect of useful results.

Experiments on the separated larynx are in first attempts attended with extreme difficulty; all the parts are moveable, and it is not at first apparent how the uniform tension and the uniform fixed position of the cartilages, so necessary for attaining any degree of accuracy in the experiments, can be given; and at the same time how the position once given can be made capable of alteration as the experiment may require. With a little contrivance, however, these objects can be accomplished. The first thing to be done is to obtain a fixed point in the larynx. The anterior wall is naturally mobile in the greater part of its extent, and the posterior wall at its upper part. The thyroid cartilage can be moved towards the cricoid cartilage, and the arytenoid cartilages also; and by either movement the vocal cords are rendered tense. The arytenoid cartilages being the most moveable parts, and those by the wrong position of which an error in the experiments might most easily be caused, my first aim is to fix them. With this view I pass an awl or pin transversely through their base; doing this with very great care, in order that, when afterwards extended, the two vocal ligaments may have an equal degree of tension; and also making the transfixion in such a manner that, when the two cartilages are approximated on the pin, the anterior processes at their base may touch each other. The larynx, with a small portion of the trachea attached, being thus prepared, is fixed, with its posterior wall downwards, to a board by means of the cricoid cartilage; and the pin which transfixed the arytenoid cartilages (these being put into any position or degree of approximation that may be wished) is also firmly tied down to the board. The posterior wall of the larynx being thus fixed, any degree of tension required may be given to the vocal cords by exerting traction on the anterior wall formed by the thyroid cartilage. To avoid the resistance which might be offered by the attachment of the thyroid to the cricoid cartilage, it is well carefully to separate their connections. As a means of drawing away the thyroid cartilage from the posterior wall of the larynx, and thus of making tense the vocal ligaments, I fix a thin cord to the angle of the thyroid cartilage immediately above the attachment of the ligaments, and passing it over a pulley connect with it a scale;

by putting different weights into this scale I can accurately regulate the tension exerted. The epiglottis, superior ligaments of the glottis, the ventricles of the larynx, the capitula laryngis of Santorini, the ligamenta aryteno-epiglottica, and even the upper portion of the thyroid cartilages, not being essential to the production of the vocal sounds, are all cut away to render the vocal cords and aperture of the glottis more easily visible. Besides, it is necessary to determine first what can be effected by the vocal cords alone, before investigating the influence of the superior part of the cavity of the larynx. A wooden tube for the experimentor to blow through is inserted into the portion of trachea left attached to the larynx.

The *results of experiments* performed by means of the contrivance above described and frequently repeated are as follows:

By blowing from the trachea through the aperture of the glottis narrowed by the approximation of the vocal cords, clear and full tones, which come very near to those of the human voice, are produced.* These tones emitted by the lower ligaments of the glottis alone differ from those heard when the upper ligaments and the epiglottis are not removed, merely in the latter being louder; the parts of the larynx last mentioned being, when present, as well as the posterior wall of the trachea, thrown into strong vibrations whenever the vocal cords vibrate. The sonorous vibrations of the vocal cords are produced most readily and certainly when the posterior part of the glottis—that part between the arytenoid cartilages—is closed: this disposition is, however, not absolutely necessary; for, although Magendie and Malgaigne have asserted the contrary, sounds may frequently be produced when the glottis is open in its whole length: still these sounds are feeble, and produced with difficulty. If the arytenoid cartilages be approximated in such a manner that their anterior processes touch each other, but yet leave an opening behind them as well as in front, no second vocal tone is produced by the passage of the air through the posterior opening, but merely a rustling or bubbling sound.

The height or pitch of the note produced is the same whether the

* Very similar sounds may be produced also by blowing through a tube, on the end of which there are two bands of moist elastic arterial tissue stretched by their extremities only, but closing the whole end of the tube with the exception of a slight fissure between them. The best kind of artificial larynx is, in fact, thus formed: moist bands of the middle arterial coat being composed of the same tissue as the vocal ligaments, and having the same physical properties. Other materials, as caoutchouc, may be substituted for the moist arterial tissue, and the sounds will not be very different The moist elastic bands have the advantage, however, of yielding good sounds, even when reduced to a very small size; in which respect they bear a stronger resemblance to the true vocal ligaments, and are not subject to the objection made by Cagniard la Tour, who observed that the laminæ of caoutchouc were not comparable to the natural vocal cords in that respect. (Magendie's Physiologie.)

posterior part of the glottis be open or not, provided the vocal cords maintain the same degree of tension; the closing of the posterior part of the glottis must not, however, extend at all further forwards than the point of attachment of the vocal cords to the base of the arytenoid cartilages. The width of the aperture of the glottis also, as Ferrein observed, has no essential influence on the height of the note as long as the vocal cords have the same tension; the tone is merely, as in the case of caoutchouc tongues (see p. 989), more difficult to produce, and is less perfect, the rushing of the air through the aperture being heard at the same time.

When the tension of the two vocal cords is unequal, there is generally produced but one sound; in some rare instances, however, as in the case of the caoutchouc tongues, two notes are heard. Frequently, also, as we observed with regard to the tongues of caoutchouc, one vocal cord is seen to vibrate alone; this is particularly the case when the two cords are not on the same level. Sometimes, when the tension of the two cords is quite equal, instead of the proper fundamental note, a much sharper sound is heard; this happens especially when the cords come into contact with each other at some point during their vibrations, and is to be attributed to the production of nodal points. The same thing occurs sometimes in experiments with caoutchouc tongues.

Vocal sounds can be produced not only when the lips of the glottis are separated by a narrow interval, but even when they are quite in contact, especially if the chordæ vocales are much relaxed; in which case the vibrations of the lips of the glottis are very strong. The same thing is observed in experiments with tongues of caoutchouc.* The notes emitted in such a condition of the glottis,—namely, when the vocal cords are in contact, and their tension at the time slight,—are stronger and fuller; but provided the length of the cords be the same, and the tension in both cases equally slight, the height of the note is not influenced by the cords being in contact, or by their being separated by a narrow interval.

The vocal cords can without difficulty be made to sound even when quite relaxed, provided the glottis be much shortened; for example, by pressing together the lips at their posterior part by means of forceps. Even when the length of the glottis is thus diminished to two lines, notes can still be obtained from it; but then the vocal cords must be relaxed and their edges in contact. This production of sound by very relaxed and shortened cords cannot be imitated with caoutchouc tongues; but it may with moist bands of elastic tissue, such as that of the middle coat of arteries. Elastic tissue, even when much

* The caoutchouc tongues often produce sounds when quite in contact with each other, and even still more readily when the border of one overlaps that of the other; or when the border of a single caoutchouc lamina lies upon the border of a thin plate of wood.

relaxed and destitute of tension, is still capable of reacting by virtue of its elasticity against the current of air; the air distends the lax lips of the glottis, when this is very short, to such a degree as to enable them to react, and the vibrations thus produced have so extensive a sphere that the glottis is alternately opened and shut. It is not, however, necessary that the chordæ vocales should be rendered so elastic by distension that in their vibrations they should periodically close the glottis; they may vibrate while they are still kept distended by the current of air, without being restored by their elasticity to the straight line.

The height of the notes is regulated by the length and tension of the vocal cords. The notes are, *cæteris paribus*, lower in pitch in proportion to the length of the glottis; but deep notes may be obtained from a glottis much shortened by its lips being pressed together with forceps, if the vocal cords be at the time relaxed; and a very long glottis will yield high notes, if the chordæ vocales have a great degree of tension. The effect of increasing tension of the chordæ vocales on the sound emitted from the glottis while open in its entire extent from the angle of the thyroid cartilage to the attachment of the cords to the anterior process of the arytenoid cartilages, which are in contact, does not altogether accord with the effects of increasing tension on the sounds obtained from strings and membranous tongues extended from two opposite points. The increase in the height of the notes, or in the number of vibrations produced in strings of uniform length, takes place, we have seen (p. 975), in a direct ratio with the square roots of the extending forces. For example, if a string extended by a force equal to the weight of four loth* give the note C, it will, when the force is increased to sixteen loth, yield the octave of C; and when the extending force equals sixty-four loth, the note produced will be the second octave of C. But, on repeating similar experiments with the human larynx, it is found that the notes obtained, when the extending force is increased in the ratio of four, sixteen, sixty-four, are not the octaves of the original note, but generally a semitone or a tone, three semitones or two or three tones, lower than the octaves. Still the series of notes correspond sufficiently in the number of vibrations to the numbers one, two, four, to prove the analogy between the laws regulating the notes of the human organ of voice and those of strings and membranous tongues (see Appendix). The experiments by which this result is obtained are extremely difficult to perform, from the necessity of giving the two vocal cords as nearly as possible the same degree of tension, and of preventing the two cords from coming in contact at aliquot parts of their length, by which harmonic notes would be produced. A single vocal cord separated from the larynx with merely portions of the

* [A loth is about half an ounce.]

thyroid and arytenoid cartilages attached, being fixed to a board by one extremity, while by the other it is extended by a cord passed over a pulley and suspending a scale with weights, can also be made to emit a sound by blowing upon it through a fine tube, as in the experiment on caoutchouc tongues (see p. 988); and the notes thus produced also follow nearly, but not exactly, the law regulating the notes of strings extended by varying forces. The notes are somewhat lower than they should be according to that law.

The compass of the notes which may be produced by varying the longitudinal tension of the vocal cords is about two octaves; when the tension is carried further than this, the notes become disagreeable, shrill, and whistling or shrieking. If the different degrees of tension of the ligaments cannot be produced by extending them in a line with their own direction by means of a cord passed over pulleys, it may be done very easily by drawing down the thyroid cartilage towards the cricoid, which is the mode adopted by nature: while a person singing is gradually raising his voice from low to high notes, the space between the thyroid and cricoid cartilages in front can be felt with the finger to be diminished (by the agency of the crico-thyroid muscles). In the experiments which I performed in this manner (see Appendix), the weight required to raise the lower notes a semitone was about half a loth; but as the tension became greater, and the notes higher, it required more and more, and at last three loths, to raise the notes the same extent. The effect of the same weight is of course different according to the change in the position of the thyroid cartilage; and the elasticity of the vocal cords will by long tension be diminished, but the effect thus produced is slight. The weight of about one pound, and a corresponding degree of muscular power, is required to raise the notes through the compass of two octaves.

If, while the posterior part of the glottis is closed, and the arytenoid cartilages fixed, a more complete relaxation of the vocal cords be induced by approximating the thyroid to the arytenoid cartilages (by means of a scale with weights suspended by a cord passing over a pulley behind the larynx, which is placed perpendicularly, the crico-thyroid ligament having previously been divided to remove all tension which it might produce), still deeper notes can be obtained. We in fact imitate by such a mechanism the action of the thyro-arytenoid muscles. By blowing upwards through the glottis thus arranged, by means of a curved tube, while the weight which diminished the tension of the cords was gradually increased, I was able to produce the deepest bass notes (see Appendix).

Two perfectly distinct series of tones can be produced in a larynx separated from the body, when the tension of the vocal cords is very slight: one of these series of tones has the most perfect resemblance to the tones of ordinary voice; the notes of the other series are generally higher than those of the former, and are the highest that can be produced; they are in every respect similar to the falsetto notes. When the vocal cords have a certain degree of tension, both these kinds of tones may be produced; sometimes one kind, and sometimes the other is heard. A certain tension of the cords is always productive of notes with the falsetto tone, whether the air be blown through the glottis forcibly or feebly. When the vocal ligaments are much relaxed, the tones are always those of ordinary voice, however feebly or forcibly we blow. If a slight tension of the ligaments is maintained, it depends on the manner of blowing whether the note be of the ordinary tone or falsetto; (the falsetto note being most easily produced by blowing very gently:) and the two different notes thus produced may be very distant from each other in the musical scale, even as much as an octave. For experiments on the two registers of vocal sounds, the ordinary notes and the falsetto, it is better to take the male larynx. The posterior part of the glottis should be closed as before, and the whole larynx fixed perpendicularly as in the last-mentioned experiments. The degree of tension necessary for producing either kind of note is given by the mere elasticity of the crico-thyroid ligament; if greater force be applied to render tense the vocal cords, the ordinary vocal sounds can no longer be produced. It was first observed by Liscovius that the vocal cords are lax while the ordinary sounds are produced, and tense during the emission of the falsetto notes: but the mere tension of the vocal cords is not the cause of the difference of these notes, for there is a certain state of the cords in which, by varying the mode of blowing, either the one or the other kind of note may be produced; and the different height of the notes of the natural voice is owing to the different degrees of relaxation of the vocal cords, and not, as he supposed, to the degree of width of the rima glottidis. The real cause of the difference between the falsetto and the notes of the natural voice is, that for the former merely the thin border of the lips of the glottis vibrate, while for the latter the whole breadth of the vocal cords are thrown into strong vibrations which traverse a larger sphere. This fact was first observed by Lehfeldt. The falsetto notes have been compared by Gottfr. Weber* to the harmonic notes of strings, and supposed, like them, to be produced by the vibration of the vocal cords in segments separated by nodal points; but it is evident that they are not thus produced, for when the vocal cords have that very slight degree of tension which permits either the notes of the natural voice or falsetto notes to be produced by different modes of blowing, it can be seen that the vocal cords, as well when the falsetto notes as when the others are heard, vibrate in their whole length; and the real difference is perceived to be, that for the falsetto notes the vocal ligaments vibrate only at their border, and the

* Cœcilia, i. p. 81.

fissure of the glottis is then generally defined and distinctly visible, while for the other notes the whole vocal bands vibrate in their entire breadth, and the arc of the vibrations is so extensive that the appearance produced by the motion of the two lips becomes confused, and obscures the fissure of the glottis: indeed, not only the vocal cords themselves vibrate, but also the adjoining membrane immediately below them, as well as the lower and stronger part of the thyro-arytenoid muscle, which lies external to the lining membrane of the larynx at that part.

The deeper notes of the natural voice are produced, as we have already seen, by approximating the thyroid to the arytenoid cartilages; but, when the relaxation of the vocal cords thus effected passes a certain point, vocal sounds cease to be heard. By gradually drawing away the thyroid again from the arytenoid cartilages in a good male larynx, series of bass notes from the deepest upwards to the extent of an octave are produced; but, when the vocal cords have acquired a certain degree of tension, the notes assume the falsetto character. There are, however, two other modes of producing high notes, without increasing the tension of the vocal ligaments so much as to cause them to give out falsetto tones. One is to blow with greater force, by which means the notes may without difficulty be raised through a series of semitones the extent of a "fifth;" but the higher notes thus produced are unpleasant to the ear, shrieking and harsh (see Appendix). The other mode of raising the notes consists in narrowing the diameter of the larynx immediately below the inferior ligaments, or vocal cords.

The great importance of this part of the larynx, which gradually contracts until it terminates superiorly in the glottis, has not hitherto been recognised; though the mere circumstance of its being invested externally at each side, to the extent of some lines, by the thick portion of the thyro-arytenoid muscle, ought to have directed attention to it. If the thyro-arytenoid muscles be dissected away in a male larynx, prepared as already described, and the membrane of the larynx pressed inwards on each side by means of the flat handles of two scalpels, so as to narrow the part of the cavity of which we are speaking without pressing on the vocal cords themselves, the notes produced by blowing will, *cæteris paribus*, be higher, and at the same time be prevented more than by any other method from assuming the falsetto character. The lower portion of the thyro-arytenoid muscles must during life have a similar action; and the influence of the narrowing of the larynx at this part on the height or acuteness of the notes is analogous to the effect of diminishing the calibre of the tube prefixed to a tongue of caoutchouc at the part nearest to the tongue (see p. 997).

The thyro-arytenoid muscle has, however, other uses. It extends upwards at the side of the vocal cords, with the exterior fibres of which it is intimately connected, as far as the side of the ventricles of the larynx, and can act as a damper upon the vibrations of the membranes at that part, and indeed upon the outer part of the vocal ligaments themselves; the effect of which would be, as we have seen in experiments on the caoutchouc tongues (see page 991), a sharpening of the tones. A third action of these muscles will be to modify the tension of the vocal ligaments by virtue of the connection with their fibres pointed out by Lauth, which I have verified. The vocal cords, when relaxed as for the production of deep notes, will be rendered tense by the contraction of the thyro-arytenoid muscles, in the same way that the lips in horn-blowing are affected by the action of the sphincter oris.

The action of the thyro-arytenoid muscle may be imitated by compressing laterally the thyroid cartilage (which for this experiment must not be ossified). By so doing, the artificial notes may be raised to as high a pitch as the human voice is generally capable of reaching with ease; and, if the vocal cords be not tense, falsetto tones are not produced. The deepest note which I could produce in one of my experiments by relaxing the vocal cords was the middle C of the bass clef

 ; by producing slight tension of the cords, and blowing with

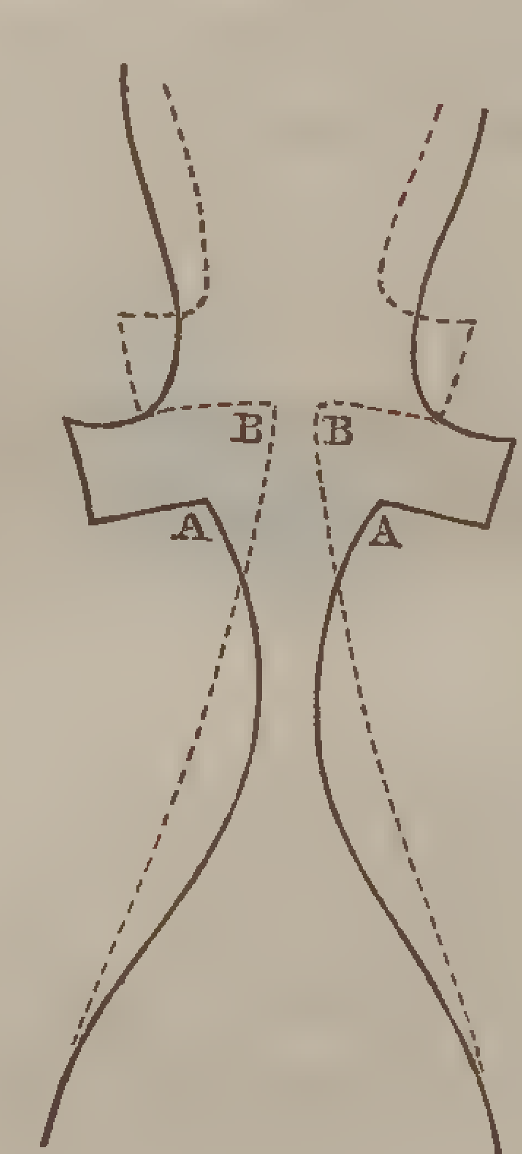
greater force, I could produce the octave above this (C^1), but I could in that way raise the notes no higher; by compressing the larynx laterally, however, about the situation of the vocal cords and below them, I was able to produce a series of higher notes to the extent of another octave (C^2) without any falsetto tone, although under other conditions falsetto notes could be produced from the A♯ below the second C (C^1) upwards. The prevention of the falsetto notes, which was here attained by the lateral compression of the larynx, seems during life to be effected by the action of the thyro-arytenoid muscles.

According to the foregoing observations, the following will be the mode of production of the notes of the natural voice:—The vocal ligaments vibrate in their entire breadth, and with them the surrounding membranes and the thyro-arytenoid muscles. For the deepest notes, the vocal ligaments are much relaxed by the approximation of the thyroid to the arytenoid cartilages. The lips of the glottis are, in this state of the larynx, not only quite devoid of tension; they are, when at rest, even wrinkled and plicated; but they become stretched by the current of air, and thus acquire the degree of tension necessary for vibration. From the deepest note thus produced the vocal sounds may be raised about an octave by allowing the vocal cords to have the slight degree of tension which the elastic crico-thyroid ligament can give them by drawing the thyroid cartilage towards the cricoid. The medium state, in which the cords are neither relaxed and wrinkled nor stretched, is the condition for the middle notes of the natural register, those which are most easily produced. (The ordinary tones of the voice in speaking are intermediate between these and the deep bass notes.) The higher notes are produced, and the corresponding falsetto tones avoided, by the lateral compression of the vocal cords, and by the narrowing of the space beneath them (the aditus glottidis inferior) by means of the thyro-arytenoid muscles, and further by increasing the force of the current of air. The muscular tension given to the lips of the glottis by the muscles above-mentioned must also be taken into account as contributing to the production of the notes of the natural register.

The falsetto notes are produced by the vibration of the inner portion or border of the vocal ligaments; their variation as to height or sharpness being effected by variation of the tension of the ligaments.*

* [To the above account of the conditions of the glottis and vocal cords necessary for the production of the different sounds of the voice, we may here append some observations on the same subject by several English physiologists. A very interesting paper by Mr. Willis, in the Transactions of the Cambridge Philosophical Society, 1832, (read May 1829,) contains some original views as to the position of the lips of the glottis during the production of voice. Mr. Willis compares the vibrating lips of the glottis to elastic membranes (of leather or caoutchouc) of which the upper edge is free and the other edges confined, and of which the planes have the same direction as the tube through which the current of air causing their vibration passes. (Professor Müller regards the vocal ligaments as analogous to membranous plates placed transversely to the direction of the tube, with their edges opposed.) Mr. Willis shows, that elastic membranes, such as we have described, do not vibrate or give rise to sound when inclined either inwards or outwards from the direction of a current of air passing between them; but that when placed parallel, or nearly so, to each other and to the current of air, they vibrate, and emit a loud musical sound. These facts he applies to the explanation of the production of voice by the vocal cords. In the ordinary position of the glottis, during respiration without vocalization, he supposes that the lips of the glottis are inclined from each other, (as at A, fig. 59, which is an imaginary transverse perpendicular section of the vocal tube,) and that to produce voice they must assume the parallel state (as at B, fig. 59). He attributes the different notes of the human voice to different degrees of tension of the vocal ligaments, since laminæ of leather, and, still better, caoutchouc, will, he shows, yield a variety of notes according to the degree of tension given them. But it is not tension alone, he argues, which enables the lips of the glottis to produce sounds. For as size of the space between the thyroid and cricoid cartilages, felt externally, indicates the tension of the vocal ligaments,—being small when they are tense and high notes produced, and large when the ligaments are

Fig. 59.



The observations which we have detailed also prove clearly that neither the epiglottis, the superior ligaments of the glottis, the ventricles of the larynx, nor, in fact, any of the parts in front of the vocal cords, are necessary for the production either of the notes of the natural voice or of the falsetto notes.

The notes which are easily elicited from the *female larynx* are generally higher than those from the *male larynx,* though by complete relaxation and approximation of the vocal cords the female larynx can be made to yield deep tones. The principal cause of this is, that the vocal cords are in general much shorter in the female larynx; although the smaller size of the cavity of the larynx, and the less thickness of its walls, affording less means of resonance necessary for the low notes, have also a great influence. On the same principles we must explain different kinds of male voices, the bass and tenor; and of female voices,

relaxed for the production of bass notes,—and as the medium size of this space, proper for the production of intermediate notes, does not differ from that which it has in the state of rest, when no voice is uttered, he infers that in that state the ligaments possess the tension required for the average pitch of speech, but have not the necessary parallel position. That the production of voice does not depend on diminishing the size of the aperture of the glottis he thinks certain, "because we can make the aperture of the passage pass through all degrees of contraction up to absolute closing during the expiration of the breath, without producing any sound, except the usual rushing noise of a forcible current of air passing through a narrow aperture." Mr. Willis attributes to the thyro-arytenoid muscles the office of placing the arytenoid cartilages and the lips of the glottis in the vocalizing position.

Mr. Mayo has observed, in cases of wound of the pharynx, (as is stated in the text at page 1007,) that the edges of the glottis are in contact during the utterance of vocal sounds; and this state of the glottis, together with a certain degree of tension, he believes to be the condition for vocalization. The vocalizing position pointed out by Mr. Willis, he conceives to be the necessary result of the vocal ligaments being on the stretch.—Mayo's Physiology, Ed. 4th, p. 370.

Mr. Bishop states, as the result of experiments on the larynx after death, "that, in order to produce any sounds whatever, it was requisite to close the chink of the glottis by bringing the edges of the vocal ligaments into immediate contact, when, by straining them tolerably tight, the sounds became loud and distinct." He also remarked, "that when the gravest tones were uttered, the ligaments vibrated throughout their whole length; and that, as the tones became more acute, a proportionally smaller extent of the ligaments was thrown into vibration." This observation accords with those of M. Magendie in experiments on living dogs (see page 1007). "During the production of the most acute tones," Mr. Bishop says, "the tension of the vocal ligaments was but slightly increased, and the greatest possible tension was insufficient to produce acute tones, whilst these ligaments vibrated throughout their whole length." The latter observation is opposed to the results of Professor Müller's experiments. Mr. Bishop ascribes to the thyro-arytenoid muscle the power, not only of rotating the lips of the glottis into the vocalizing position described by Mr. Willis, but also of forcing them into contact with each other during its contraction; and to the thyro-arytenoid and crico-thyroid muscles the power of so affecting the vocal cords "that a portion of them only is rendered susceptible of vibration."—London and Edinb. Philos. Mag. 1836.]

the alto and soprano. The male voice is, it is true, capable of being raised to high notes by great tension of the cords, but the tones thus produced are of the falsetto character; notes of the same height can be produced with ease by the shorter vocal cords of the female larynx with less tension. Moreover, there must be a limit to the tension of the male chordæ vocales, on account of muscles being able to shorten themselves by contraction only to a certain extent; the maximum of shortening of which they are susceptible is, according to M. Schwann, only about one-third of their length. The means of rendering tense the vocal ligaments are somewhat greater than this calculation would indicate, since the vocal cords can be acted on by muscles both before and behind; and the cartilages to which the cords are attached are capable of a lever-like movement. Still there must be a limit to the raising of the pitch of the voice attained in this way. A still higher but feeble note may be accidentally produced, while the vocal cords are tense, by their coming into contact with each other at some point, causing a division of them into their aliquot parts.

I have endeavoured to ascertain by measurement the relative length of the vocal cords in the male and female larynx. The following table shows the results which I have obtained in several experiments:

	Men past puberty.						*Women past puberty.*			*Boy of 14 years.*
Length of the vocal cords at the greatest degree of tension . . .	21	21	25	26	23	23	16	15	16	14·5
Length of the vocal cords in the state of repose .	18	16	- -	21	19	- -	12	12	14	10·5

—	*Male larynx.*	*Female larynx.*
Mean length of the vocal cords in the state of repose .	$18\frac{1}{4}$	$12\frac{2}{3}$
Mean length of the vocal cords in the state of greatest tension	$23\frac{1}{6}$	$15\frac{2}{3}$

The cyphers indicate the number of millimetres.* The relative length of the vocal cords in the male and in the female larynx would appear from these measurements to be as three to two, both in the extended and the unextended state. The degree to which the cords can be extended beyond their ordinary length is, in the male larynx, somewhat less than five millim.; in the female, three millim. The vocal cords alone, and not the whole length of the aperture of the glottis, extending posteriorly between the arytenoid cartilages, were measured. A small part of the vocal ligament extends farther back than the extreme point of the anterior process of the arytenoid cartilage, being attached to the

* [A millimetre is 0·03937, or about $\frac{1}{25}$ of an English inch.]

upper border of this process towards the anterior edge of the cartilage; this portion of the ligament was included in the measurements.*

If the air be drawn in through the glottis instead of forced out, the tension of the vocal cords remaining the same, no vocal sound is generally produced, but sometimes a deeper rustling sound was heard. (Compare the experiments on the tongues of caoutchouc at page 989.) Touching the outer part of the ligaments of the glottis, so as to stop the vibrations at that part, raises the pitch of the sounds, as in the case of caoutchouc tongues (see page 991).

Influence of the vocal tube.—The length of the tube prefixed to the vibrating tongues, which has so marked an influence in modifying the height of the notes produced by tongues of caoutchouc or even of arterial tissue, appears from my experiments to have, contrary to M. Magendie's opinion, founded on the analogy of the organ of voice with the reed-pipes of M. Grenié, no perceptible effect on the pitch of the notes yielded by the human larynx. In many cases the variation of the length of the prefixed tube seemed to have no influence at all on the note produced; in other instances the elongation of the tube lowered the note a semitone, very rarely an entire tone, when the force of the blast was perfectly uniform. I am inclined, therefore, to deny any power of modifying the height of the notes to the slight variation of length which the trachea can undergo.

The superaddition of a tube in front of the vocal cords, which were already furnished with a prefixed tube or "porte-vent" of given length,†

* Admeasurements of the vocal cords of the larynx in the tense and lax condition, in bass, tenor, contr'alto, and soprano singers, and also in eunuchs, after death, would be of great interest in a physiological point of view; but the same parts should be measured in other individuals at the same time, that the grounds of the comparison may be the same: for if the vocal cords be measured from their anterior extremity only, as far as the point of the anterior process of the arytenoid cartilage, the length indicated will be less than when they are measured in the manner above described.

† The performance of these experiments is attended with great difficulty. In the first place, it is not easy to fix a tube to the larynx in front of the vocal ligaments; and, when this is done, it is difficult to give the vocal cords a determinate degree of tension. These objects are attained in the following manner:—The posterior extremities of the vocal cords are tied together, by means of a ligature, close to the anterior or vocal processes of the arytenoid cartilages, the ends of the ligature being brought out backwards over the membrane between those cartilages. The epiglottis, aryteno-epiglottic ligaments, the capitula laryngis of Santorini, and the membrane and muscles uniting the arytenoid cartilages, are left to facilitate the attachment of the tube; and, for the same purpose, the upper border of the thyroid cartilage is cut away. A short tube, six or eight lines in diameter, being fixed in front of the larynx, other portions of the same size can be added to it as required. The larynx being fixed, and the arytenoid cartilages approximated by a ligature from behind, any degree of tension required can be given to the vocal cords by means of the ligature by which they are bound together at their posterior extremity. The opening by which this ligature is brought out of the cavity of the larynx at its posterior wall is closed during the production of the sounds produced by blowing.

had likewise either no influence on the pitch of the notes, or caused the difference of only a semitone, or very rarely a tone.

I have instituted many experiments, with the view of ascertaining the cause of this want of agreement between the natural and artificial larynx.* The most probable explanation appears to me to be, that in the human larynx the vocal cords, at a certain degree of tension, are for the most part alone engaged in sonorous vibrations, the membrane which connects them with the walls of the larynx not being made tense; while in the artificial larynx, constructed with laminæ of caoutchouc or arterial tissue, the vibrations are effected not merely by their longitudinal extension at their free border, but also by the more lax portion, as is evident from the effect of slightly touching them at their outer part so as to damp its vibrations (see page 991). On account of the greater breadth of these elastic membranes, and from the connection of their tense with their unextended portion, they are capable of many more modifications of vibrations and sounds required by the varying length of the prefixed or superadded tubes (the "porte-vent" and "pipe") than is the glottis, in which the vibrations are principally confined to the vocal cords themselves.

I imagined that the extensile nature of the trachea might have some share in diminishing the influence of the length of the superadded tubes in front of the glottis on the height of the notes given out by it; but, on substituting for the trachea a wooden tube, I found no difference in the result. It is possible, however, that the extensile property of the membrane connecting the different cartilages of the larynx, while the walls of the artificial larynx with caoutchouc tongues are quite solid and inextensile, may be in some measure the cause of this peculiarity of the natural larynx.

In my experiments on the influence of tubes of different length on the height of the note produced by the vibrations of the vocal cords, it sometimes appeared that the note was not so perfect when the prefixed tube had a certain length as when its length was different, owing to the column of air not being of such length as to accommodate itself to the vibrating tongues. Mr. Wheatstone† had previously made the same remark with reference to other reed-instruments, and Mr. Bishop attributes great importance to the reciprocal adaptation of the columns of air above and below the vocal cords to each other during life. The circumstance to which I have alluded occurred, however, but very few

* This want of agreement is not however absolute; for sometimes, particularly when the sounds are produced with difficulty, the bands of caoutchouc being too tense or too lax, these artificial vocal cords yielded sounds which were not at all, or only in a very inconsiderable degree, lowered in pitch by the elongation either of the tube placed below the vibrating tongues or of that prefixed to them (see Appendix to page 994.)

† Mayo's Physiology, Ed. 4th, p. 373.

times in my experiments; I cannot, consequently, ascribe the great importance to this accommodation of the columns of air in the human organ of voice which Mr. Bishop does. On the contrary, it is evident that the shortening and elongation of the trachea, and the shortening and elongation of the vocal tube in front of the glottis, by the elevation or depression of the larynx, can have but very little influence on the acuteness of the vocal sounds. At most, we can merely admit that the elongation of the vocal tube in front of the glottis by the descent of the larynx, *cæteris paribus*, facilitates the formation of the deep notes, and the shortening of the tube by the ascent of the larynx that of the high notes; thus much is, in fact, confirmed by what takes place in the formation of high and low notes during life.

The partly membranous nature of the trachea has no perceptible influence on the sounds produced by the vocal cords; the note produced by blowing through the trachea was the same as when a wooden tube of the same diameter was used. In this respect reed-instruments with membranous tongues differ remarkably from flute-pipes with merely a vibrating column of air. In the latter instruments the reciprocal vibrations of the membranous walls of the tube influence so much the primary vibrations of the column of air, that, according to the observation of M. Savart,* who discovered this circumstance, a pipe of moist thin paper walls will lower the note an entire octave below that which a tube of solid parietes of the same length would yield. In very short cubic pipes the difference may be as much as two octaves (see page 981). I formed a tube, 7½ inches in length, partly of human trachea, which measured 3 inches, and in the rest of its extent (4½ inches) of a wooden pipe. The note produced by blowing through this tube upon a vibrating tongue of caoutchouc at its lower extremity was the same as when the tube used was of equal length but of solid materials. The contact of the hand with the membranous part of the trachea had no perceptible influence on the note.†

* Froriep's Not. 332, p. 21.

† [Mr. Wheatstone had observed, that columns of air reciprocate the sonorous vibrations of other columns of air, or of vibrating bars or reeds in their neighbourhood, rendering the sound much louder, when their length is such that they would alone yield the same note; but that, if not thus in unison, they will not reciprocate the vibrations of other bodies.—(Quarterly Journal of Science, vol. iii.) He applied this law to the human organ of voice, supposing that the trachea undergoes changes in length in accordance with the notes produced by the vibrating vocal cords; its length being diminished as the sounds become sharper. But since the larynx ascends during the production of high notes, it would appear that the trachea is lengthened when it ought to be shortened: Mr. Bishop states, however, that the trachea is not really lengthened by this movement of the larynx, he finds that it is raised out of the thorax nearly to the same extent as the larynx is elevated; he therefore concludes, that an absolute shortening of the entire vocal tube, including the trachea and the

The circumstance of the vocal tube in front of the vocal cords being double, consisting of the oral and nasal canals, seems to have no other effect on the height of the notes than a simple tube; but it causes their character to be altered by the resonance. I attached to the short anterior tube of an artificial larynx with caoutchouc tongues a bifurcated tube; the result was no raising of the notes, but they were rendered more sonorous.

The *epiglottis*, by being pressed down so as to cover the superior cavity of the larynx, serves to render the notes deeper in tone, and at the same time somewhat duller, just as covering the end of a short tube placed in front of caoutchouc tongues lowers the tone (see page 994). In uttering very deep notes during life, we evidently employ the epiglottis in this way; at least, such seems to be the object of the retraction and depression of the tongue while we press down the head in front, in endeavouring to produce very deep notes. In no other respect does the epiglottis appear to have any effect in modifying the vocal sounds. Direct experiments which I have performed do not confirm the opinion of MM. Biot and Magendie, that the epiglottis has the same office as the vibrating plate which M. Grenié, an organ-builder, placed in front of the metallic tongue of a reed-instrument with a view of facilitating the elevation of the notes by a more forcible current of air. An epiglottis placed in the pipe in front of the vibrating tongues of an artificial larynx in about the same situation as in the natural organ, and with such a disposition that it could vibrate freely, had no effect on the height of the note; if the epiglottis was so placed as to act as a fixed impediment to the current of air, the result was the same as when the tube in front of the vibrating tongues was narrowed in any other way. By gradually increasing the force of the blast, the height of the note can, *cæteris paribus*, be raised the extent of a "fifth," whether

cavities above the glottis, is produced by the elevation of the larynx towards the base of the skull. But the variation in the length of the tube being insufficient to render it capable of adjusting itself to the whole range of vocal tones, Mr. Wheatstone (Mayo's Physiology, Ed. 4th, p. 373,) and Mr. Bishop suppose that the defect is supplied by the varying tension of the walls of the trachea; on the principle determined by M. Savart, that a tube of constant length may yield an extensive range of sounds if its elastic parietes are made to vary in tension. The diminished diameter of the trachea during the ascent of the larynx would, Mr. Bishop remarks, favour the production of higher notes. A still further influence on the voice is attributed to the trachea by Mr. Wheatstone. He has observed, that a column of air may not only vibrate by reciprocation with another body whose vibrations are isochronous with its own, but also when the number of its own vibrations are any multiple of those of the sounding body. Such would be the vibrations of the column of air in the trachea divided into harmonic lengths, with relation to the vibrations of the vocal cords. The falsetto notes, he suggests, may be the result of the vibrations of the harmonic subdivisions of the column of air in the trachea. Mr. Bishop adopts this view.]

the epiglottis be present or not. The epiglottis can be felt, by the finger passed in at the side of the mouth, to maintain the same position during the utterance of musical notes, whether they be of the falsetto character or those of the natural voice.

The *arches of the palate and the uvula* become contracted during the formation of the higher notes, as was first observed by Fabricius ab Aquapendente, and more recently by Mayer, Bennati, and Dzondi. But the contraction of the isthmus of the fauces is the same for a note of given height, whether it be falsetto or not; and in either case the arches of the palate may be touched with the finger, without the note being altered. This completely refutes the opinion of Bennati, that the falsetto tone is wholly or in part due to the action of the palatine arches.

The approximation of the palatine arches, and retraction of the uvula, in the production of the higher notes, seems to be merely the result of involuntary associate nervous action, caused by the voluntarily increased exertion of the muscles of the larynx. If the palatine arches contribute at all to the production of the higher notes of the natural voice and the falsetto register, it can only be by their increased tension strengthening the resonance.

According to the theory of reed-instruments, narrowing of the *upper part of the larynx* immediately in front of the vibrating tongues or vocal cords ought to raise the notes in some degree: but this cannot be proved experimentally; for, in a larynx removed from the body, the upper part of the cavity cannot be compressed without, in some measure, acting on the vocal cords. Simple narrowing has no perceptible influence. The office of the *ventricles of the larynx* is evidently, as M. Malgaigne, Sir C. Bell, and others have remarked, merely to afford a free space for the vibrations of the lips of the glottis. M. Malgaigne compares them to the cavity at the commencement of the mouth-piece of trumpets, which allows the free vibration of the lips.

C. *Theories of the voice.*

The general conclusion which we must draw from the results of the experiments on the artificial larynx with membranous tongues, as well as from those afforded by the experiments on the natural larynx removed from the body, which, in all essential points, agree with the former, is that *the human organ of voice is a reed-instrument with a double membranous tongue.* This opinion has been previously held by several cultivators of natural philosophy, as MM. Biot, Cagniard la Tour, and Muncke; by writers on the theory of music, as Gottfr. Weber; and by some physiologists, as MM. Magendie, Malgaigne, and others.

The experiments of Ferrein on the sounds to be obtained from the larynx in the dead body, by which he showed that the note varied according to the length and tension of the vocal cords, have, as early as the year 1741,* afforded a sound basis for this theory. Even M. Savart,† who denied the analogy of the larynx with a reed-instrument, admitted that when air is blown into the trachea after the removal of the upper part of the larynx, as low as the inferior ligaments or vocal cords, notes can be produced in the same way as by means of vibrating tongues: it is true, he stated that the sounds thus produced were different from those of the human voice; to me, however, they appear, when the experiment is performed as I have directed, to differ in no essential respect from the vocal sounds: I obtain, by the methods I have described, notes of the natural scale, and falsetto notes with all their characteristic tones; any difference between them and the vocal sounds of the living larynx may be attributed to the influence of the vocal tube in front of the larynx.

According to M. Savart, the air in the ventricles of the larynx between the superior or false, and inferior or true ligaments, is really the source of the sound; the organ of voice being compared by this philosopher to the bird-call or hunter's whistle, described at page 980. The elastic structure of the inferior ligaments of the larynx or vocal cords, and the contrivances adopted for rendering them tense, characterise the larynx, however, too evidently as an instrument with vibrating tongues, to permit us to attribute much importance to M. Savart's objection respecting the difference of tone; and, moreover, the notes may be modified by varying the tension of the vocal cords, as well when the ventricles of the larynx and superior ligaments are preserved as when they are removed, leaving merely the true vocal cords. The theory of M. Savart is rendered quite untenable by the fact of the superior ligaments of the glottis being entirely absent in some mammalia, namely, in the ruminantia.

The apparatus in front of the true vocal cords may probably, like the pipe of reed-instruments, have some influence in modifying the vocal sounds, particularly by undergoing contraction in the upper cavity of the larynx, at which part changes can be produced that cannot be imitated in artificial reed-instruments; changes in the length of the tube in front of the glottis are less influential. The principal cause of the vocal sounds, however, is still the vibration of the vocal cords.

Fechner ‡ objects to the theory of the organ of voice being a reed instrument, that in that case no sound could be produced while the glottis is open, since the sound emitted by reeds is supposed to be

* Mém. de l'Acad. d. Sc. † Magendie's Journal de Physiol. t. v.

‡ In his translation of Biot's Précis de Physique.

owing to the periodic interruption of the current of air by the alternate opening and closing of the passage; whereas the vocal cords can vibrate and produce sounds without the glottis being periodically closed. We have, however, shown that the theory of the sounds emitted by reed-instruments, on which this objection of Fechner is based, is not so accurate as is generally supposed; for, by merely directing a current of air across the edge of delicate tongues without surrounding frame, the same notes with the same "timbre" may be produced as by blowing through an opening closed by a tongue acting as a valve: again, the current of air which throws the tongue of a reed-instrument, whether metal or membranous, into sonorous vibrations, may be so strong as to prevent its returning to close the opening periodically; and lastly, notes may often be elicited from an artificial larynx with caoutchouc tongues when a space of considerable width intervenes between the lips of the tongues.

The vocal cords were likened by Ferrein to vibrating strings, and to a certain extent correctly; but the comparison is in other points inaccurate. Ferrein's experiments, by which he demonstrated the resemblance of the vocal cords to vibrating strings, are among the best that have ever been instituted. He showed that the vocal cords sound, according to analogous laws with those of strings which are thrown into sonorous vibrations by currents of air, and that the notes produced are in no respect altered by difference in width of the aperture of the glottis. From half the length of the vocal cords he obtained the octave of the fundamental note; from two-thirds, the fifth. Lastly, he found that a change in the length of the vocal cords to the extent of from two to three lines was sufficient to produce all the notes of various pitch; (the change in tension here supplying what is effected by change in the length of the cords when the tension remains the same.) M. Bertin attempted to controvert these experiments; but they were confirmed by Montagnat, Runge, and Nollet.* My experiments on caoutchouc tongues, already detailed, (page 988,) afforded completely parallel results; and the experiments on the effect of graduated extension on the notes of the vocal cords also prove that their vibrations obey the general laws of vibrating strings. I cannot assent to M. Biot's remark, when he says,† "What is there in the larynx that resembles a vibrating string? where is the space for such a string of sufficient length to yield the lower notes of the voice? How could sounds of the compass which the human voice presents, be produced by a string which the larynx would contain? The simplest prin-

* See Haller's Element. Physiol. t. iii. libr. ix. § 8, 9, and 10.

† Précis de Physique, t. i. p. 458.—Lehrbuch der Experimental-phys. ii. p. 143.

ciples of acoustics are sufficient to refute this strange notion." M. Biot's objection can be easily controverted. A string, however much shortened, would still be able to yield deep notes, if, at the proper degree of relaxation, it retained the necessary elasticity for vibration. The elastic membranes and the laminæ of caoutchouc retain this elasticity when greatly relaxed. Small bands of caoutchouc indeed, if made tense, give out clear sounds when struck, although these sounds are not of long duration as when produced by long strings. The continuous influence of the current of air in blowing renders these sounds continuous; and converts a lamella, which vibrates as a string when simply struck, into a tongue. In this respect, therefore, the vocal cords agree perfectly with vibrating strings, and the only difference in their action arises from the body by which their vibrations are excited. Thus far Ferrein's comparison of the vocal cords to strings is completely accurate.

In one respect, however, the vocal cords differ from strings; and this point of distinction is important enough to give to them, with other membranous tongues, a special place among musical instruments. When strings are more strongly struck, deeper notes are produced; the note given out by a membranous tongue is, on the contrary, raised by a stronger blast the extent of one, two, or more semitones; and if the tongues be of moist nature, as are the vocal cords and bands of arterial tissue, even many semitones. The sound emitted by the metal tongue of a child's trumpet also always rises, according to my observation, the extent of an octave and a half without intervals, when blown with increased force; and the reason that this is not the case with other metal tongues is, that they are too strong to be affected by the current of air. The note emitted by a tongue depends, therefore, not only on the tongue itself, but also on the air giving the impulse. A string, on the contrary, being once struck, its vibrations undergo no further modification by the continued impulse; the vibrations, once excited, are regulated only by the length and tension of the string.—(See Appendix, p. 11. —*Theory of the action of Tongues.*)

There are several physiologists, and among them Dodart and Liscovius, who ascribe the modulation of the voice to the varying size of the fissure between the lips of the glottis, and to the vibration of the air produced at that part. Dodart* was acquainted with the influence of the tension of the vocal cords upon the notes produced; but he supposed that the variation of the tension of these cords acted by altering the size of the opening through which the air, vibrating in its passage, is transmitted. The difference of $\frac{1}{54}$ of a fibre of silk, or $\frac{1}{384}$ of a hair, in the size of the rima glottidis, was sufficient, he supposed, to produce a dif-

* Mém. de l'Acad. d. Sc. 1700.

ferent note. This is quite erroneous; for even a considerable difference in the width of the rima glottidis, if the tension of the vocal cords remain the same, has no effect on the pitch of the notes produced. Liscovius * supposes that the air driven with some force and rapidity through the opening of the glottis experiences such compression and impulses that its smallest particles are moved to and fro, as in other cases, where air is propelled through any narrow orifice; and that the larger the opening of the glottis is, the deeper will be the note produced, in consequence of the undulations of the air being then larger, and therefore slower.

The arguments which Liscovius adduces in opposition to the opinion that the vocal cords are the source of the sound are,—First, That the vocal cords are stretched during the production of deep notes, and relaxed while high notes are being uttered; for the glottis, he says, is dilated, and the vocal cords are separated from each other, during the production of deep notes. The dilatation of an opening is necessarily attended with extension of its borders, if their continuity be perfect; hence, he says, dilatation of the glottis cannot take place without its lips becoming extended; and for deep notes the vocal cords must be tense, for high notes relaxed. This is evidently an error. When a certain degree of tension has been given to the vocal cords by the contrivance described at page 1008, the width of the aperture of the glottis may be varied at will, without the tension of the cords being altered. The aperture of the glottis can, in fact, be either wide or narrow, whether the cords be tense or relaxed. Moreover, the fact that the posterior part of the aperture of the glottis, that part which lies between the arytenoid cartilages, may be either closed or open (see page 1009), without the pitch of the notes being thereby modified, proves that the air cannot be the primary source of the sound; otherwise the notes would be much lower when the glottis is open in its entire length, than when that part merely is open, which is included between the vocal cords themselves. Next, Liscovius remarks that dry strings only can be elastic, and that the vocal cords are always moist. The string, however, is only one kind of cord-like body made elastic by tension; and this kind loses its elasticity when made moist. The elastic tissue of the human body, on the contrary, is elastic only when it is moist, and loses its elasticity as it becomes dry. These are differences which do not alter the fixed laws regulating the action of cord-like bodies made elastic by tension. We have already refuted the objection that the vocal cords cannot possibly give rise to so many and such deep notes. In comparing the vocal cords with strings, the attention has been confined too much to the properties of one kind of cord-shaped body elastic by tension, and hence have arisen erroneous views. If, for

* Theorie der Stimme. Leipzic, 1814.

the strings of gut, more elastic cords, or bands of caoutchouc or animal elastic tissue, be substituted, much that belongs only to the strings, and is not essentially the property of elastic tense cords, is got rid of. Liscovius remarks, that no string can receive sufficient impulse from a mere current of air to produce sounds of any intensity. But bands of caoutchouc, or of moist animal elastic tissue, when a fine current of air from a small tube is directed free upon them, emit very loud sounds. To the assertion of Liscovius that the tension and relaxation of the ligaments of the glottis have no influence on the pitch of the notes, except inasmuch as the aperture of the glottis is thereby dilated or contracted, I must oppose the constant result of my experiments,—namely, that notes to the extent of two octaves may be produced by the mere variation of the tension of the vocal cords, the width of the rima glottidis remaining the same.

Liscovius observed that if, while air was blown into the glottis, one of the vocal cords was very tense and the other very lax, two notes were not produced, but one only, the height of which was proportionate to the width of the aperture between the vocal cords. The first part of this observation is perfectly correct. In this respect the vocal cords exactly resemble the tongues of caoutchouc, of which, as we have seen, only one gives sound, while the other acts as a fixed boundary of the opening, if their degree of tension be unequal. On some rare occasions, however, each caoutchouc tongue gives utterance to its fundamental note, and the same is the case with the vocal cords.

Liscovius found that when he touched the vocal cords with the finger, without affecting the size of the aperture of the glottis, the pitch of the note remained unaltered; while, if the vocal cords were subject to the laws of vibrating strings, the note ought to have been raised. According to my experiments on laminæ of caoutchouc, as well as my observations on the vocal cords, touching them so as to damp their vibrations modifies very much the height of the note they yield, even though the size of the aperture remain the same.

It is supposed that mere diminution of the size of the glottis, without any change in the tension of the vocal cords, will render the pitch of the note higher, and that mere dilatation of the opening will render them lower; the pitch of the notes being regulated, however, not by the mere width of the aperture, but by its whole area,—the length and breadth together. My experiments have taught me that low notes may be obtained from a much shortened rima glottidis, provided the vocal cords are quite relaxed; and that, though the notes rise in proportion as the glottis is shortened from before backwards, yet this only takes place when the tension of the cords remains the same. The width of the aperture of the glottis has no essential influence upon the pitch of the notes, except inasmuch as it is difficult to elicit sounds from the larynx by blowing through the trachea when the aperture of the glottis is wide; the sound is then not only devoid of musical tone, but the note can be raised by increased force of the blast a trifling degree only above the fundamental note; while, when the aperture of the glottis is narrow, it may be raised by this means a succession of semitones up to the "fifth," or beyond it.

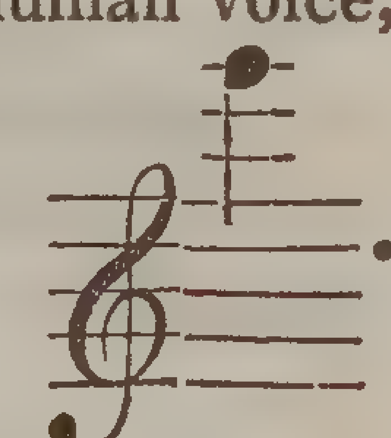
The influence of increasing the force of the blast in raising the pitch of the notes was correctly observed by Liscovius and Lehfeldt. A point of especial importance in reference to the theory of the production of the notes of the natural register and the falsetto notes,—namely, that for the former the entire vocal cord vibrates, and for the latter only its border, as well as the fact that the falsetto note is, *cæteris paribus*, higher,—was first discovered by Lehfeldt.*

D. *Of singing.*

There are three different kinds of sequence of the notes which the organ of voice is capable of producing. The first is the monotonous, in which the notes succeeding each other have all nearly the same pitch, as in ordinary speaking; the variety of the sounds of speech being owing to articulation in the mouth; in speaking, however, occasional syllables generally receive a higher intonation for the sake of accent. In poetry there is rhythm in addition to the accent, but the modulation of music is wanting. The second mode of sequence is the successive transition from high to low notes, and *vice versâ*, without intervals; such as is heard in the sounds, which, as expressions of passion, accompany crying in men, and also in the howling and whining of dogs. This succession of dissonant sounds, in which the musical intervals are not observed, often occurs in nature, as in the howling of the wind; and may be produced on instruments,—for instance, by diminishing or increasing the tension of a string while it is being sounded, or by blowing with gradually increased force into a short pipe closed at one extremity. A membranous tongue is capable of the same succession of notes, and the same is the case with the vocal cords. The dissonant succession of rising and falling notes in howling must be produced partly by increase and diminution of the force of the current of breath, and partly by gradual alteration of the degree of tension of the vocal cords. The third mode of sequence of the vocal sounds is the musical, in which each

* Of previous writers, Ferrein, Liscovius, and Lehfeldt, have contributed most to the elucidation of the theory of the voice. A very good account of the opinion of the older writers, with original reflections, is contained in Lehfeldt's dissertation, "De vocis formatione." Berol. 1835. A complete review of later theories and observations will be found in Heusinger's edition of Magendie's Physiology.

sound has the requisite number of vibrations, and the number of vibrations in the successive sounds have that relative proportion which characterises the notes of the musical scale. Music has a rhythm in common with poetry.

1. *Compass of the voice.*—The compass of the voice in different individuals comprehends one, two, or three octaves; in singers,—that is, in persons capable of singing,—it extends to two or three octaves. But the male and female voices commence and end at different points of the scale. If we commence the scale at the C of the eight-feet organ-pipe , the male bass voice will take its beginning from the first E, the barytone at A, the tenor at C^1; and these male voices will reach, the bass to A^1, or higher, the barytone to F^2, and the tenor to C^3. The female voice is as deep as the male only in masculine women. The voices of women, boys, and eunuchs begin between F^1 for the alto, and C^2 for the soprano, and reach as high as F^3 for the alto voice, or A^3 for the mezzo-soprano, or C^4 for the soprano, at the furthest as high as F^4. The lowest note of the female voice is therefore about an octave higher than the lowest of the male voice; the highest note of the female voice about an octave higher than the highest of the male. The first four notes of all voices are generally weak. The compass of the male and female voices taken together, or the entire scale of the human voice, includes four octaves,—namely, from E  to E^4 .

For the convenience of readily comparing the extent of the different voices, we subjoin a table of the whole scale of the human voice, showing the mean compass of its different varieties.

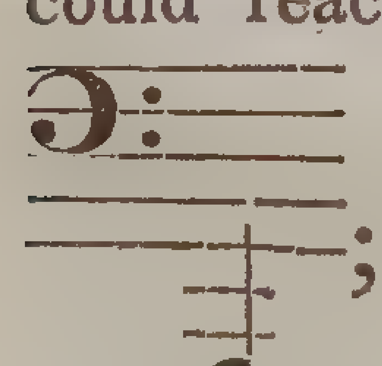
Soprano

Alto

C D E F G A B C^1 D^1 E^1 F^1 G^1 A^1 B^1 C^2 D^2 E^2 F^2 G^2 A^2 B^2 C^3 D^3 E^3 F^3 G^3 A^3 B^3 C^4

Bass

Tenor

Fischer, the father of the singers who afterwards became celebrated, could reach to the F of the octave below the above scale,—namely, ; the youngest of the female singers, named Sessi, had a compass of voice of three octaves and three notes,—namely, from C^1 to

F^4.* Zelter's voice included three; Catalani's, three and a half octaves.†

2. *Varieties of voice in different individuals.* The principal difference between the male and the female voice is in their pitch; but they are also distinguished by their tone,—the male voice is not so soft. But the voice presents other varieties besides the male and female; there are two kinds of male voice, the bass and tenor, and two kinds of female voice, the contr'alto and soprano, all differing from each other in tone. The bass voice usually reaches lower than the tenor, and its strength lies in the low notes; while the tenor voice extends higher than the bass. The contr'alto voice has generally lower notes than the soprano, and is strongest in the lower notes of the female voice; while the soprano voice reaches higher in the scale. But this is not the essential distinction between the different voices; for bass singers can sometimes go very high, and the contr'alto frequently sings the high notes like soprano singers. The essential difference between the bass and tenor voices, and between the contr'alto and soprano, consists in their tone or "timbre," which distinguishes them even when they are singing the same note. The qualities of the barytone and mezzo-soprano voice are less marked; the barytone being intermediate between the bass and tenor, the mezzo-soprano between the contr'alto and soprano. They have also a middle position as to pitch in the scale of the male and female voices.

The different pitch of the male and the female voice depends on the different length of the vocal cords in the two sexes; their relative length in men and women being as three to two (see page 1018). The difference of the two voices in tone or "timbre" is owing to the different nature and form of the resounding walls, which in the male larynx are much more extensive, and form a much more acute angle anteriorly. The different qualities of the tenor and bass, and of the alto and soprano voices, probably depend on some peculiarities of the ligaments and the membranous and cartilaginous parietes of the laryngeal cavity, which are not at present understood, but which might be determined by the examination of the larynx in different tenor, bass, soprano, and contr'alto singers after death. We may form an idea of the cause of these differences of timbre from recollecting that musical instruments made of different materials, as metallic and gut strings, metallic, wooden, and membranous tongues, metallic, wooden, and paper pipes or flutes, may be tuned to the same note, but that each will give it with a peculiar tone or timbre.

The larynx of boys resembles the female larynx; their vocal cords before puberty have not two-thirds the length which they acquire at that period. The angle of the thyroid cartilage is as little prominent

* Muncke in Gehler's Physik. Wörterbuch, t. viii. p. 386.

† Rudolphi, Physiologie.

as in the female larynx. Boys' voices are alto and soprano; but, after the larynx has undergone the change produced during the period of developement at puberty (between the fourteenth and the fifteenth year), they become immediately bass or tenor. While the change of form is taking place, the voice is imperfect, frequently hoarse and crowing, and is unfitted for singing until the new tones are brought under command by practice. In eunuchs, who have been deprived of the testes before puberty, the voice does not undergo the ordinary change. The contr'-alto and soprano voices of boys and eunuchs resemble in pitch those of women; but differ somewhat from them in timbre, and are louder. Liscovius remarks that the eunuch's voice differs in tone from the boy's, and attributes this difference to the circumstances of the resounding walls of the cavities of the mouth and nares becoming as extensive in the eunuch as in other men, though the larynx remains in the condition of youth. But those cavities are also spacious in women; and the greater firmness of the cartilages and ligaments of the larynx in the eunuch than in the boy may have a greater influence.

3. *Varieties of voice in one and the same individual.—The natural and falsetto voices.*—Most persons, particularly men, besides that their voice belongs more or less to one of the varieties already described, have the power, if at all capable of singing, of modulating through a double series of notes of different character. These are the notes of the natural voice, or chest-notes (note di pettó), and the falsetto notes (note di testa). The natural voice is fuller, and excites a distinct sensation of much stronger vibration and resonance, than the falsetto voice, which has more a humming character. The deeper notes of the male voice can be produced only with the natural voice,—the highest with the falsetto only; the notes of middle pitch can be produced either with the natural or falsetto voice; the two registers of the voice are therefore not limited in such manner that one ends when the other begins, but they run in part side by side. The tenor voice generally follows the falsetto register, from A^2 of the scale given at page 1030, while the notes below A^2 can be uttered either with the natural or falsetto character. The bass voice becomes falsetto lower in the scale than the tenor. The female voice seldom presents a sufficiently marked distinction between the natural and falsetto registers.

The mode of production of the natural register of vocal sounds and the falsetto register has been already explained (see page 1013). Since the note of the natural register is much deeper than the falsetto note produced by vocal cords in the same state of relaxation, and by blowing with as much as possible the same force; and since a note of the natural register can be raised to the same pitch as the falsetto note only by compressing the cavity of the larynx below the vocal cords, or by increasing the force of the current of breath; we may understand why, in passing from the natural to the falsetto register, it is often difficult to hit upon the right falsetto note.

4. *Differences of the voice as to tone.*—Each individual has a peculiar tone of voice dependent on the form of the air-passages and of their lining membranes, and on their resonance; hence, many persons, by altering the form of their vocal organs, can imitate the various tones of voice of other individuals. The *nasal "timbre"* is a peculiar quality of voice dependent on a similar cause. M. Biot supposes that the ordinary character of the voice is due to the soft palate applying itself to the posterior nares and closing them, so that the air can escape only through the mouth. But I cannot subscribe to this opinion; for ordinarily, while the voice has its natural character, the posterior nares are open, and the voice resounds through both the oral and the nasal tube simultaneously. The nasal tone may be given to the voice in two ways. 1. When the external openings of the nares are closed the voice may retain its natural sound, or it may become nasal: in the former case the arches of the fauces remain open; in the latter they approach each other, and the larynx ascends much higher than when the voice has its natural character. Obstruction of the nostrils by mucus has the same effect as closing the anterior openings of the nares; but neither the one nor the other can alone give the nasal tone to the voice. When the nasal tone is produced in this first way, the cavity of the nostrils becomes a separate resounding chamber. 2. The nasal twang may also be given when the nostrils are open, the mouth being either open or closed. In this case likewise the larynx ascends considerably; the arches of the fauces contract; the dorsum of the tongue is approximated to the palate, or brought into contact with it; and the air merely passes between the narrowed arches of the fauces, and receives the resonance of the nasal cavities without that of the cavity of the mouth.

The voice of old people is deficient in tone, is unsteady, and more restricted in extent: the first defect is owing to the ossification of the cartilages of the larynx and altered condition of the vocal cords; the want of steadiness arises from the loss of nervous command over the muscles; the result of which is here, as in other parts, a tremulous motion. These two causes combined render the voice of old people void of tone, unsteady, bleating, and weak.

5. *Strength of the voice.*—This depends partly on the degree of capability of vibration of the vocal cords; and partly on the fitness of the membranes and cartilages of the larynx, of the parietes of the thorax, lungs, and cavities of the mouth, nostrils, and communicating sinuses, for resonance. The capability of vibration of the vocal cords is diminished or destroyed by inflammation and suppuration of the mucous membrane of the larynx, by profuse secretion of mucus, by œdema glottidis, &c. The resonance of the pulmonary membrane is diminished,

and the voice consequently rendered weaker, by phthisical disease. The strength of the male voice is also in part attributable to the greater capacity of the chest. In many genera of apes there are other accessory resounding membranous sacs communicating with the throat, or indeed saclike expansions of the thyroid cartilages and os hyoides, as in the howling apes, Mycetes.

6. *Increase and diminution of the intensity of the vocal sounds.*—The intensity or loudness of a given note emitted by the larynx cannot be rendered greater by merely increasing the force of the current of air through the glottis; for increase of the force of the current of air, *cæteris paribus*, raises the pitch both of the natural and the falsetto notes. Increased strength of the blast has the same effect on the notes produced by some musical instruments, namely, flute-pipes and reed-instruments with delicate metal tongues or membranous tongues (see pages 991 and 992); strong metal tongues, on the contrary, emit a lower note when the force of the current of air is increased. This defect, which prevents the harmony from remaining perfect when notes are swelled or sounded more faintly, can be remedied, according to the observation of W. Weber, in the case of the stronger metallic tongues, by combining with them a tube accurately measured, so as to be in unison with the fundamental note of the tongue; the tongue lowering the note while the column of air in the tube raises it, a compensation is established which enables the player to increase or diminish the intensity of the note without altering its pitch. This principle of compensation cannot, however, be applied in the case of the membranous tongues, since their notes are raised like those of the column of air in pipes by increased force of blast; we cannot, therefore, expect to find a relation of compensation between the vocal cords and column of air in the vocal tube in the human organ of voice: moreover, a very different length of tube would have been required for different notes, and the vocal tube can be altered in length at most but an inch, by the ascent and descent of the larynx.

Since the human organ of voice possesses the power of increasing the intensity of a note from the faintest "piano" to "fortissimo" without its pitch being altered, there must be some other means of compensating the tendency of the vocal cords to emit a higher note when the force of the current of air is increased. This means evidently consists in modifying the tension of the vocal cords. When a note is rendered more intense, the vocal cords must be relaxed by remission of the muscular action in proportion as the force of the current of the breath through the glottis is increased. When a note is rendered fainter, the reverse of this must occur. The analogy of the reed-instruments constructed with membranous tongues, and the experiments on the production of the higher notes of the musical scale, (page 1014,) teach us also that the contraction of the cavity of the larynx immediately below the glottis by the action of the thyro-arytenoid muscles may assist in compensating for the effect of diminishing the force of the current of air in passing from "forte" to "piano," for contraction of the cavity at that part raises the pitch of the note; and, if the note be raised in pitch by the increased force of the current of air, the dilatation of the same part of the larynx may lower it.

For such actions of compensation an accurate balancing of the opposed actions is necessary; and hence we can understand why the raising and lowering the voice without altering the musical pitch of the note is so difficult, even for practised singers, and cannot be at all effected by the unpractised without dissonance being produced in one way or other.

7. *Perfectness of the notes.*—The dissonance of the voice after long singing may easily be accounted for in part by the slight changes which the vocal cords have undergone in consequence of repeated tension; and in a greater degree by the fatigue of the muscles, which at length cease to obey the will perfectly, and execute inappropriate movements. An habitual dissonance of the voice, or inability to sing in tune, depends partly on defect of the sense of hearing, and partly on the difficulty of observing the uniform "temperament" of our musical scales. Temperament is usually already obtained in musical instruments by tuning; the singer must attend to it at each note.

Man, like the singing-bird, learns unconsciously the different internal changes in the state of the larynx, and the different muscular actions necessary for each note. Sounds accidentally uttered, and the muscular actions which accompanied them, become associated in the sensorium, and afterwards readily excite each other when a melody is to be imitated. When singing is learnt methodically, the signs of the different notes are also associated with them, and with the muscular motions producing them. In addition to all this, however, a good ear is necessary; without which, a voice of good quality and great compass may be useless in singing.

We must conclude our observations on the human voice with some remarks on the artificial construction of a vocal organ. No musical instrument can be in all respects compared to the organ of voice; for even the organs and pianos, of which the compass is so great, are defective in other respects. Some musical instruments, as the simple flute-pipes, are not susceptible of an increase of the intensity of the notes from piano to forte; in others the notes cannot be prolonged, namely, in all those instruments in which the sounds are produced by striking strings. The organ has two registers of notes,—those of the flute-pipes and the reed-pipes; and in this respect it resembles the human voice, which has the natural register and the falsetto: but no instrument combines like the human organ of voice all these advantages. Although the organ of voice belongs to the class of reed-instruments; and though these reeds, when combined with a system of compensating pipes, are (with the violin) the most perfect of all instruments; yet still the vocal organ is more perfect in being capable of giving with one tube all the notes and all the possible variations of the scale, while in the most complete instrument constructed of reed-pipes each note requires a special pipe. The artificial construction of a vocal organ would, in some measure, be attained, if with a reed-pipe an apparatus, of not too difficult management, for regulating the tension of elastic tongues in the reed, could be combined; but the tones of such an instrument, in which dry elastic bands only could be permanently used, would not resemble the soft full tones given out by the moist, animal, elastic tissue, and there would always be great difficulty in managing such an instrument.

2. *Of musical sounds formed in the mouth.*

We do not speak here of all the noises which may be produced in the mouth, but only of those which have a musical quality or tone. Both at the anterior and at the posterior part of the oral cavity musical sounds may be produced on the principle of the sounds of reed-instruments; such are the snoring and other sounds given out by the arches of the fauces in vibrating, and the sounds produced by pressing air between the lips which are thrown into distinct vibrations; the notes thus produced being higher in pitch, the greater the tension of the lips.

Another kind of musical sound produced in the mouth is "*whistling*,"* in which the air is the source of the sound. It is easy to convince one's-self that the sound in whistling is not owing to vibration of the lips; for they may be touched, covered, or even a disk of cork with a central hole held between them, as Cagniard la Tour showed, and yet the same sounds will be produced. Cagniard la Tour's theory of the cause of the sound appears to me to be quite correct. The air is thrown into sonorous vibration by friction against the borders of the opening. How the friction produces the sonorous vibrations in this case is not evident, for the sounds produced by the friction of other bodies evidently arises from the periodic adhesion of the body exerting the friction, as when the border of a glass is rubbed by the finger. How this intermission of adhesion or friction can take place between the air and the solid borders of an opening which do not themselves vibrate, is difficult to explain. That the motion of the air traversing the opening is periodically arrested

* See Muncke in Gehler's Physikal. Wörterb. viii. p. 383; and Cagniard la Tour, in Magendie's Journal de Physiol. t. x.

by the friction can be more easily imagined than proved. The possibility of the adhesion of air to water is evident, however, from the ripple (gekräuselten Wellen) which wind produces on the surface of water.*

It appears to me that Cagniard la Tour attributes too little importance to the oral cavity in his explanation of whistling. The analogy of whistling with the sound of flute-pipes, which he endeavours to disprove, appears to me to be very great. Savart has shown that musical sounds can be obtained from the mere mouth-piece of a pipe; so that in reality the sound is excited and the air thrown into vibrations in the mouth-piece of the instrument, and the vibrations are merely modified by the column of air in the tube of the pipe. The same seems to be the case in whistling; the cause of the vibration is the friction of the air against the borders of the opening, but the vibration there excited throws the whole column of air in the mouth into vibrations, and the vibrations of this column of air, by a reciprocal influence, determine the rapidity of the vibrations of the air at the orifice. The only difference between whistling and the sounds of a pipe is, that in whistling the whole column of air is in constant progressive motion through the tube and orifice; while in a pipe the air in the tube merely vibrates, and does not move as a current.

The analogy between whistling and the sounds of a pipe or flute is proved by the following facts. 1. The pitch of the note is raised by increasing the force of the current of air, the size of the orifice of the lips and the position of the tongue remaining the same; this is exactly in accordance with the effect of blowing with increased force into small pipes (see Appendix, page 18). 2. The pitch of the note may be modified by altering the size of the orifice of the lips in the same manner as the notes of pipes, by diminishing or increasing the size of the embouchure (see page 979). 3. The notes of whistling are rendered lower by retracting the point of the tongue,—higher by advancing it. The same changes are produced in the pitch of the notes of pipes by increasing or diminishing the length and diameter of the tube.

The notes produced by the jew's-harp, like those of whistling, vary, *cæteris paribus*, according to the form of the cavity of the mouth and position of the tongue. The vibrations which, in whistling, are produced by the friction of the air passing through the opening of the lips are, in the case of the jew's-harp, excited by striking the steel tongue, or by drawing the air forcibly into the mouth between the tongue and lateral bars of the instrument.†

* Weber, Wellenlehre, p. 33.

† [The variation of the tones of the jew's-harp, produced by altering the size of the cavity of the mouth, is thought by Mr. Wheatstone to be the result of the law pointed out by him,—that a column of air will vibrate, and produce sounds, whenever it is of such length that its vibrations are a multiple of those of the body originally vibrating.]

3. *Of the voice of mammalia and reptiles.*

The mode of production of the voice in *mammalia* is exactly the same as in man. The *chordæ vocales* can be seen vibrating in experiments on the larynx of the ox, and by relaxing them the notes become deep and loud. The superior ligaments of the glottis and the ventricles are wanting in the ruminantia; hence they cannot be essential to the production of deep notes.* The solidungula have a superior ligament of the glottis; in the horse the mucous membrane forms a semilunar fold also below the epiglottis, which passes across from one vocal cord to the other; this fold does not exist in the ass and mule.† Below the semilunar fold in the horse there is a funnel-shaped cavity; and above it, beneath the epiglottis, a second cavity, which in the ass and mule is more capacious: in the latter animals also the ventricles of the larynx are larger, and their openings narrow and situated nearer the epiglottis. The hog also has below the epiglottis a spacious membranous sac.‡

In the apes the essential form of the organ of voice does not vary, but the resounding walls frequently present peculiarities; such is the sac which exists in the orang-outang between the thyroid cartilage and os hyoides, and the membranous sacs which Cuvier found in the Mandrill, Pavian, and Macacos, below the os hyoides. The apparatus for the resonance of the voice is greatest, however, in the howling apes of the New World, the Mycetes; the os hyoides and thyroid cartilage are expanded so as to contain large cavities, which open into the ventricles of the larynx. Brandt has discovered, moreover, laryngo-pharyngeal sacs. The epiglottis in these apes has a very large size and peculiar form. In the Sapajous (Ateles and Cebus) a curved tube is formed by the increased size and altered forms of the cartilago Wrisbergi and epiglottis. The voice of these animals has a whistling character.§

The sounds produced by *reptiles and amphibia*, like the voice of mammalia, have their source in the larynx. Frogs, as well as the crocodile, have vocal cords. The small size of the organ of voice in the frog cannot make us wonder at the deepness of the tones it utters, since we know that membranous bands in a relaxed state and merely distended by the air will emit deep notes. In the male frog membranous sacs at

* See Lehfeldt's experiments on the larynx of different mammiferous animals, loc. cit.

† Cuvier, Anat. Comparée.—Gurlt. Vergl. Anat. der Haussäugethiere, ii. p. 167.

‡ The anatomy of the larynx of other orders of mammalia has been accurately described by Brandt in his Diss. de Mammal. quorund. præsertim quadruman. vocis instrumento. Berol. 1826-4, to which we refer for further information.

§ The use of the cartilagines cuneiformes in mammalia, where they are frequently very large, and of peculiar cartilages found in the larynx of mammiferous animals, has been explained by Brandt.

the sides of the neck become distended during the emission of the sound, and serve to increase its intensity. In the Rana Pipa, the larynx, in which, as in the other frogs, the bronchi terminate directly without the intervention of a trachea, forms a large cartilaginous box, in the interior of which are two solid rodlike bodies,* almost as long as the larynx itself: the anterior extremity of these bodies is fixed; their posterior extremity is free, and projects on each side towards the opening of the bronchus. The vocal sound is produced here by the vibration of rod-shaped tongues, which act like a tuning-fork; while in other animals of the same class the parts which emit the sound are membranous. If a small piece of cartilage, some lines in length, be fixed by one extremity, and a current of air directed from a small tube upon its edge at the other extremity, a humming sound is heard.

4. *Of the voice of birds.*

The *organ of voice in birds*† is the inferior larynx, which is formed by the union of several of the rings of the trachea. A process from the lowest of these rings projects downwards before and behind, and in most birds endued with voice a bony bar passes across from one process to the other, dividing the lower part of the trachea into two lateral halves, which form the openings into the bronchi. In the goose, and many other birds, there is a fold of membrane on the outer side only of each lateral compartment of the larynx; the mode in which this fold is formed is as follows:—Between the lower end of the larynx and the first ring of the trachea on each side, the tube is membranous, and the membrane which forms it is lax; but at the lower extremity and outer border of the larynx it is rendered tense by being attached to the anterior and posterior processes of the larynx above-mentioned: the tense fold thus formed—named by Cuvier the vocal ligament—does not, however, project far into the interior of the organ. In singing-birds there is also another membranous fold, called by Savart ‡ *membrana semilunaris*, at the inner border of each lateral compartment of the larynx; this fold is of greatest size in birds which can be taught to speak. M. Savart has described two other vocal cords at the commencement of each bronchus. The rings of the bronchi form only segments of a circle. The three first of these arches have a peculiar form, described and represented by Savart. Along the inner surface of the third arch runs a cord formed of a peculiar tissue, apparently elastic; this is the external lip of the glottis of singing-birds. The lip at the inner surface of the glottis is in these birds formed by a small cartilage, called by Savart cartilago

* Described by Mayer, Nova Acta. Nat. cur. xii. 2. 541.

† In the anatomical description we follow Cuvier and Savart, the researches of whom, particularly those of Savart, on this subject, have been so complete.

‡ Froriep's Not. 331.

arytenoidea, and by bands of the same substance as that which forms the external lip. These parts forming the internal lip of the bronchial glottis are contained in the membrane—*membrana tympaniformis* of Cuvier—which stretches from the cartilages of the bronchi to the transverse bony portion of the larynx. The membrana tympaniformis is continuous with the membrana semilunaris of the larynx, which can consequently be made tense through its medium; it is very small in some birds, as the ducks and geese, and the rings of the bronchi are then nearly complete: in singing-birds it extends, according to Savart's observation, as low as the fourth or fifth cartilage of the bronchus; but it is of greatest extent in birds which are capable of speaking. The larynx has special muscles, by which the first cartilage of the bronchi can be drawn up towards the larynx, or the distance between the vocal cords increased or diminished. In singing-birds there are five pairs of these muscles; parrots have three pairs, two to close and one to open the glottis, which in them is single, there being no transverse bony bar at the lower part of the larynx, but the first half-ring of the bronchus has such a form that it resembles a valve articulated before and behind to the larynx, into the cavity of which it can project considerably. In other birds, which have little power of modulating the voice,—as birds of prey, water-hens and water-rails, snipes, lapwings, gulls, the cormorant, kingfisher, goatsucker, heron, bittern, and cuckoo,—there is only one muscle approximating the half-ring of the bronchus to the trachea. Other birds, again, have no special muscle of the larynx, the trachea merely is capable of being considerably shortened by the musculi sterno-tracheales and ypsilo-tracheales; this is the condition of the gallinæ, and of ducks and geese among the palmipedæ. In the ducks and goosanders (mergus) the inferior larynx presents dilatations of its walls, and in the male bird is extended into a large unsymmetrical cavity, partly bony and partly membranous, which is evidently the source of the peculiar sound of the voice in the male sex.

The trachea in birds, which with the cavity of the mouth forms the tube or pipe placed in front of the organ of sound, is capable of great shortening by the space between the different rings being diminished, or even by the rings being received one within the other. In some birds, as the cock of the wood, Penelope crane, stork and crane, and particularly in the male of these birds, the trachea is longer than the neck, being thrown into convolutions; in the wild swan, indeed, a convolution of the trachea is lodged within the sternum. The forms of the trachea are various; sometimes it is cylindrical; at other times conical, becoming gradually wider towards the mouth, as in herons and cormorants. The trachea presents a sudden dilatation in the Anas clangula and fusca, and also in Palamedea bispinosa, according to Humboldt's observation ; gradual dilatations in the Mergus and male of the duck family.

*Theory of the voice in birds.**—The voice was proved to have its source in the inferior larynx by Cuvier, who observed that a blackbird, a magpie, and a duck were still able to utter cries when the trachea was divided ; he stopped the upper portion of the divided trachea and kept the beak closed,—the cry was heard as before; even after the head of the duck was cut off, several sounds were uttered. These experiments, which constantly afford the same result, are confirmed by observations made on the larynx removed from the body of the bird. If air is blown into the bronchi of a duck, a sound exactly similar to the natural cry of the bird is produced; the same result is obtained by blowing into the trachea of the duck or goose, even when the bronchi have been cut away; as long as the very tense portion of the bronchial membrane which is situated at the lower border of the inferior larynx remains, (and it is not removed in tearing away the bronchi,) I never fail to produce sounds.

According to Cuvier's theory, the sounds issuing from the larynx of birds are rendered deeper by elongation and relaxation of the vocal folds or ligaments, and higher by shortening and tension ; these means being aided by variations of the size of the opening, and the consequent alteration of the rapidity of the current of air. But Cuvier believed that merely the harmonics of the fundamental note, namely, the octave, fifth of the octave, the second octave, and the third and fifth of this octave, and so on, could be produced by alterations of the tension of the vocal ligaments. Here, however, Cuvier was in error ; for since the notes emitted by membranous tongues become higher in the inverse ratio of the length of the tongues, and in the direct ratio of the square roots of the extending forces, and since the degree of tension may be varied to any fraction between 1, 4, and 16, all sounds between the harmonics, the vibrations of which stand in the ratio of 1, 2, and 3, may of course be produced by such tongues. Cuvier confounded the properties of a reed with those of the mouth-piece of a flute-pipe, from which the harmonic intervals are obtained by blasts of increasing intensity. The sounds which are not harmonics of the fundamental note are produced, Cuvier supposed, by shortening of the trachea; the tone above the fundamental note, for example, by the trachea being shortened $\frac{1}{9}$th of its entire length, the harmonics of the notes thus obtained being produced by changes in the larynx without further alteration of the length of the trachea. To ascend, however, in this way through the intervals of an octave, the trachea would require to be shortened one half, which can scarcely be effected; but the defect is supplied by the size of the aperture of the upper larynx being varied, by which means the notes

* Cuvier, Anat Comparée.—Savart, Froriep's Not. 331, 332.

may be raised nearly an octave, just as in a covered pipe the tones are raised in pitch in proportion as the occlusion of the lower opening is diminished. In comparing on this account the organ of voice to trumpets, the great naturalist again confounded flute-pipes with reed-pipes, to which class of instruments trumpets belong (see page 1000). In a reed-pipe, however, the sounds are not, as in flute-pipes, modified in pitch in an uniform ratio with the length of the tube, but in accordance with perfectly different laws. By M. Savart the organ of voice of birds, like that of man, is compared to a pipe in which the air alone is the seat of sonorous vibrations; and he regards the lower larynx as analogous to the mouth-piece of such a pipe, and not to the mouth-piece or reed of a reed-instrument. M. Savart has, however, himself showed, by his experiments on pipes of equal dimensions but different materials, that the walls of the trachea must have a great influence on the notes produced by the column of air (see page 1021).

It appears to me to be a question very difficult, and at present almost impossible to determine, whether the sounds of the voice in birds are produced, as in man, by the vibrations of a reed or tongue; or, as in mere flute-pipes, by vibrations of a column of air excited by friction against the lips of an opening. The simple organ of voice of many birds —the duck, goose, and others—is undoubtedly a reed-instrument. Not only can the vocal cord or band forming the outer margin of the opening in the larynx be seen to vibrate strongly, but the sound produced has also the greatest resemblance to a sound arising from the vibrations of membranes. (The same remark applies to all birds which utter notes of the same character, as ravens, which however belong to the class of singing-birds.) The length of the trachea of the goose has moreover a very subordinate influence on the note produced by blowing through the bronchi; and the same characteristic sound is heard as well when the trachea is very much shortened as when it is long. But whether the piping, whistling sounds of other birds are produced in the same way, and not in the manner of whistling by the mouth, is another question. To me it appears much more probable that these sounds also are produced by the vibration of tongues: for, in the first place, the vocal folds cannot during a certain action of the muscles escape being thrown into vibration, and even though the friction of the air have some share in the production of the sound, a compensation must ensue between the vibrations of the air and those of the vocal ligaments; and in that case the organ of voice in birds would not be completely analogous to a whistle or pipe, but would be in part constituted as a reed-instrument. Then, again, by blowing by means of a tube inserted into a bronchus through the lower larynx of some birds (the raven and starling), after separating it from the trachea, I can produce sounds which are not perceptibly altered (as in the human organ of voice) by holding a tube in front of the larynx, the current of breath being uniformly gentle. The length of the trachea has, at all events in the goose, a very slight influence on the note produced by the lower larynx, just as the length of a tube placed in the front of the human larynx has but a very slight influence on the pitch of the notes obtained. The greater number of the notes of birds may evidently be elicited from the inferior larynx by varying the force of the blast, as Savart pointed out, which certainly agrees with the effect of blowing with varying force upon the notes of flute-pipes of the same size as the trachea of small singing-birds; but the same variation of the notes by varying the strength of the blast may be produced in reed-instruments with membranous tongues, and even in reeds with very delicate metallic tongues (see page 991).

The effect of the trachea on the notes may either be the same as that of the tubes of flute-pipes, or it may merely influence the notes in the manner of the tube of reed-instruments. Contraction of the superior opening of the trachea at the superior larynx may, as in pipes and reed-instruments, lower the note.

The membrana tympaniformis, which vibrates strongly during the production of sounds in the lower larynx, must have an influence on them; a relation of compensation must subsist between the internal vocal cord, the membrana semilunaris, and the membrana tympaniformis. This latter membrane is analogous to the vibrating membrane of a pipe formed of a reed-stalk.

V. *Sounds produced by fishes.*

Very few fishes, as the Trigla, Cottus, and Pogonias, are known to utter sounds. The anatomy of these fishes is sufficiently well known; but it is at present quite impossible to offer a satisfactory theory of the mode of generation of the sounds they produce. I must, therefore, confine myself to a short statement of the facts.

The Triglæ emit a grunting sound when they are taken out of the water; no organ has been discovered in these animals to which the production of this noise can with certainty be attributed. Is it possible that the peculiar muscle of the air-bladder in these animals has a share in causing the sound? The Cottus, from which a sound is heard to proceed when pressure is made upon its body, has no air-bladder. In the Sciænoid family there are several fishes which emit sounds; but those most known are the Corvina ronchus and the Pogonias. The Pogonias has on this account acquired the name of Tambour. These fishes produce continued sounds under the water.* Their air-bladder is very large, as in most of the Sciænoid family which emit a sound; is

* The observations of Mitchell, White, Schoepf, and others, concerning these fishes, have been collected by Cuvier and Valenciennes.

covered by strong muscles; and has appendages which, according to Cuvier, pass between the ribs, and become imbedded in the muscles. In a Pogonias fasciatus which I examined, the viscera and air-bladder had unfortunately been removed: band-like filets were attached to the ribs internally, and had probably been torn from the air-bladder; they were not, however, hollow. The pavement-like teeth of the upper and lower palate-bones of these fishes are of extraordinary size.*

CHAPTER III.

OF SPEECH.†

BESIDES the musical tones formed in the larynx, a great number of other sounds can be produced in the vocal tube between the glottis and the external apertures of the air-passages, the combination of which into different groups to designate objects, properties, actions, &c. constitutes language. The languages do not employ all the sounds which can be produced in this manner, the combination of some with others being often difficult. Those sounds which are easy of combination enter for the most part into the formation of the greater number of languages. Each language contains a certain number of such sounds, but in no one are all brought together. On the contrary, different languages are characterised by the prevalence in them of certain classes of these sounds, while others are less frequent or altogether absent. It comes within the province of physiology to investigate the natural classification of the sounds of language. The attempts to form a natural system of the articulate sounds, instituted by grammarians, have been quite inadequate to the object, the principle of classification having been derived from properties which are not essential. The classification of the sounds of articulate speech, according to the organs by which they are formed,—for example, into the labial, dental, guttural, and lingual,—is faulty when

* The sounds produced by the Sphinx atropos, and the humming sounds of dipterous insects, will be found explained by R. Wagner, in Müller's Archiv. 1836, and by Burmeister, in Poggendorf's Annal. xxxviii. The Acheta domestica and locustæ also emit sounds. See Cuvier's Règne Animal, t. v. p. 184.

† The authors who may be consulted on the subject of speech are: J. Wallis, De loquelâ s. sonorum formatione, in C. Amman, Surdus loquens. Lugd. Bat. 1727.—Kratzenstein, Tentamen resolvendi problema ab Acad. Sc. Petrop. 1780; propos. Petrop. 4.—Kempelen, Mechanismus der menschlichen Sprache, nebst der Beschreibung seiner sprechenden Maschine. Wien, 1791, 8.—Reitter, Methodenbuch zum Unterricht für Taubstumme. Wien, 1828.—Rudolphi, Physiologie.—Chladni, in Gilbert's Ann. 1824, st. 2.—C. Mayer, in Meckel's Archiv. für Anat. u. Physiol. 1826.—R. Willis, in Poggendorf's Annal. xxiv. and Transact. of Philos. Soc. of Cambridge, vol. iii.—Heusinger, in his edition of Magendie's Physiology.—Purkinje, Badania w przedmiocie fizyologii mowy Ludzkiéj. Kraków. 1836, 8. (Forschungen über die Physiologie der Menschlichen Sprache. Krakaw, 1836.)

carried farther than the distinction of the oral and nasal sounds; for sounds which are, according to physiological principles, in part quite different from each other, are thus classed together, and, moreover, for the formation of most sounds several parts of the mouth co-operate. The distinction of the mutes and liquids is in part founded on correct principles; but the application of these principles has been imperfect. Even the properties of the vowels, as contra-distinguished from the consonants, have not been properly estimated. Their essential character is usually considered to be that they are independent sounds, originally formed in the larynx, though modified in the mouth; while consonants are not formed in the larynx, and cannot be sounded perfectly unless conjoined with a vowel. The difference between vowels and consonants is, however, much less considerable than this; for all vowels, as well as the consonants, can be produced without a vocal tone, as in whispering; and, moreover, one whole class of consonants can, as we shall presently see, be uttered with a vocal sound as well as without this sound. The essential difference between vowels and consonants is of a very different nature. A main error in many of the attempts at classification of the articulate sounds has been the failing to pay sufficient attention to the circumstance of it being possible to form them without vocal tone, as in whispering; while to recognise the essential properties of the articulate sounds we must first examine them as they are produced in whispering, and then investigate which of them can also be uttered in a modified character conjoined with vocal tone. By this procedure we find two series of sounds: in one the sounds are mute, and cannot be uttered with a vocal tone; the sounds of the other series can be formed independently of voice, but are also capable of being uttered in conjunction with it. Another important character of some of the articulate sounds is that they are only of momentary duration, taking place during a sudden change in the conformation of the mouth, and are not capable of prolongation by a continued effusion of the breath ("strepitus incontinuus explosivus"); while others can be prolonged, *ad libitum*, as long as a particular disposition of the mouth and a constant expiration are maintained ("strepitus continuus").* All sounds of the first kind are insusceptible of combination with vocal tone ("intonation"), and are absolutely mute; nearly all the consonants of the second kind may be attended with "intonation." Peculiar modifications of the sounds are thus produced, but the absolutely mute consonants with "strepitus explosivus" may by aspiration be completely changed to other sounds.

* [Kempelen, in his experiments on the artificial production of articulate sounds, observed, that the vowel sounds were distinct only when contrasted with each other; and even in the natural voice, as Mr. Willis observes, "if any given vowel be prolonged by singing, it soon becomes impossible to distinguish what vowel it is." This is more remarkably the case with many of the continuous consonants than with the vowels.]

A. *Mute sounds of the whisper.*

I. *Mute vowels.*

All the vowels with their nasal modifications can be expressed in a whisper without vocal tone. These mute vowel sounds differ, however, in some measure as to their mode of production from the consonants. All the mute consonants are formed in the vocal tube above the glottis, or in the cavity of the mouth or nose, by the mere rushing of the air between surfaces differently modified in disposition. But the sound of the vowels, even when mute, has its source in the glottis, though the vocal cords are not thrown into the vibrations necessary for the production of voice; and seems to be produced by the passage of the current of air between the relaxed vocal cords. That the whispered vowels are formed at the glottis, and not in the mouth, any one may satisfy himself by experiments in his own person. The same sound can be produced in the larynx when the mouth is closed, the nostrils being open, and the utterance of all vocal tone avoided. This sound, when the mouth is open, is so modified by varied form of the oral cavity as to assume the character of the vowels *a*, *e*, *i*, *o*, *u*.

The oral canal or cavity of the mouth assumes the same form for the articulation of each of the mute vowels as for the corresponding vowel when vocalized; the only difference in the two cases lies in the kind of sound emitted by the larynx. Kratzenstein and Kempelen have pointed out that the conditions necessary for changing one and the same sound into the different vowels are differences in the size of two parts—the oral canal and the oral opening; and the same is the case with regard to the mute vowels. By oral canal, Kempelen means here the space between the tongue and palate: for the pronunciation of certain vowels both the opening of the mouth and the space just mentioned are wide; for the pronunciation of other vowels both are contracted; and for others one is wide, the other contracted. Admitting five degrees of size, both of the opening of the mouth and of the space between the tongue and palate, Kempelen states the dimensions of these parts for the different vowels as follows:

Vowel.	*Sound.*	*Size of oral opening.*	*Size of oral canal.*
a	[English *a* in far]	5	3
e	[English *a* in name]	4	2
i	[English *e* in theme]	3	1
o	[as in English]	2	4
u	[like *oo* in cool]	1	5

The relation in which other vowel sounds stand to the above as to the size of these parts is easily ascertained.

It has been remarked by Purkinje that the conditions for the formation of some of the vowels, particularly of *a* and *e* [the two sounds of the English *a* in *far* and *name*] have not been quite correctly stated by Kempelen. The production of both these sounds depends principally on the form of the cavity of the throat between the root of the tongue and the pharynx; in both cases this space is large, but largest in the pronunciation of *e* [long *a*]: the size of the opening of the mouth is the same in the two cases; not different, as Kempelen states. The position which he ascribes to the lips in pronouncing *o* is also unnecessary.

The nasal "timbre" of the vowels *a, i, o,* and *œ*, as in the French words *sang, singulier, ombre,* and *œuvre*, is given by merely contracting the isthmus of the fauces and elevating the larynx.

II. *Mute consonants with "strepitus æqualis s. continuus." Continuous sounds.*

All consonants of this class can be pronounced with an uninterrupted sound, which continues as long as the expiration can be prolonged; the disposition of the parts within the mouth remaining throughout as at the commencement of the formation of the sound. The consonants of this kind are *h, m, n, ng, f, ch* [as in the Scotch word "loch," or like the *gh* in the word "light," as pronounced by the Scotch], *sch* [equivalent to the English *sh*], *s, r,* and *l.* They may be arranged in three orders.

1. Continuous oral sounds uttered with the whole oral canal open.—The only sound of this kind is the aspirate, *h.* This sound does not depend on any opposition offered by the walls of the oral cavity to the passage of the air; it is the most simple result of the resonance of the parietes of that cavity during expiration. The *h* does not exist in the Italian language except in a few words, as "ho," "hai," "ha," "hanno."

2. Continuous sounds produced by expiration through the nasal canal, which is quite open.—Such are *m, n,* and *ng.* During the pronunciation of these consonants the air passes simply through the nasal canal, the aperture of the mouth being closed either by the lips, or by the tongue being pressed against the palate. Here also there is no opposition offered to the passage of the air. In the pronunciation of all the three consonants of this order the cavity of the mouth forms a blind diverticulum of greater or less length from the throat and nasal canal. This diverticulum is largest during the utterance of *m*, smallest when *ng* is being pronounced. The mouth is closed by the lips while *m* is spoken, which has misled Rudolphi and others into the belief that it is a labial consonant,—but such it is not: the lips merely close the mouth; the sound of the letter is not produced by this act of closing the lips, but, after they are closed, by the simple passage of the air through the

nasal cavity, together with the resonance of the diverticulum formed by the cavity of the closed mouth. In forming *n*, the mouth is closed by the extremity of the tongue being pressed against the fore part of the palate.

Ng, or *ñ*, exists as a well-marked consonant, and not a mere combination of the sounds of two consonants, in many languages. It is as clearly a simple sound as *m* and *n*; for example, in the words "sing" and "bang." In pronouncing it the passage of the mouth is closed more posteriorly than for *m* and *n*, namely, by the application of the dorsum of the tongue to the posterior part of the palate. The *ng* of the French language is formed still deeper in the throat.

3. Continuous oral sounds developed by the valve-like application of different parts of the mouth to each other.—Such are the consonants *f*, the German [and Scotch] *ch*, *sch* [or *sh*], *s*, *r*, and *l*.

The parts which are thus pressed in a valve-like manner one against the other, so as to oppose the passage of the air, may be the lips, the teeth, or the tongue and palate. For the pronunciation of *f* the lips are kept in the position of blowing. There are two modifications of this puffing or blowing sound, namely, the true *f* and the German *w* [resembling most nearly the English *v*].

For *f* the opening of the lips is more nearly round.

For the German *w* the lips are very nearly approximated, but leave a long cleft between each other.

[The *f* in English pronunciation is produced rather by the application of the lower lip to the upper teeth than of the two lips to each other; and the *v* differs from the *f* only in being less aspirated.]

Ch, the Greek χ. The sound which this consonant has in the German language does not exist in the French [nor in the English, but some of its modifications are met with in the Scotch and Irish dialects]. For its production the tongue is applied closely to the palate, and the air is pressed through the small space left between them. There are three modifications of the sound, according to the part of the palate to which the tongue is applied. In the first modification the fore part of the tongue is applied to the fore part of the palate, as in pronouncing the German words "lieblich" and "selig." (The sound of the Greek χ is expressed in German sometimes by the *ch*, and sometimes by *g*). In the second, the dorsum of the tongue is approximated to the middle of the palate; this sound is very different from the preceding, it is heard in the German words "tag," "suchen," "ach," &c. The third modification of this sound of *ch* is used by the Swiss, Tyrolese, and Dutch; to produce it, the dorsum of the tongue approaches the back part of the palate or the soft palate: the sound exists as "chet," Hebr., "cha," Arab.; and, according to Purkinje, in the Bohemian language. [The sounds of the *ch* in the Scotch word "loch," and of the *gh* in the Irish word "lough," are perhaps identical with the second variety of the sound of the *ch*, here spoken of.]

The German *sch* [the English *sh*, and the French *ch*] is a very well-marked and simple sound; during the utterance of which the teeth are closely applied to each other, while the tip of the tongue lies behind them without touching them.

S. For this sound the teeth approach, or are in contact with each other, while the point of the tongue touches the lower teeth. The English *th* is a modification of this sound.

For the sound of *r* the tongue vibrates against the palate.

In the pronunciation of *l* the point of the tongue is applied closely to the palate, and the air escapes on either side between the tongue and cheeks, or it may escape only on one side.

III. *Mute consonants with "strepitus explosivus." Explosive sounds.*

These are the Greek β, γ, δ, and their modifications, π, κ, τ. They are the explosive sounds of Amman.

The organs of speech engaged in the formation of these sounds undergo a sudden change of position during their production; the sound commences with the closing of the mouth, and terminates with the opening of it. Hence these consonants cannot be prolonged *ad libitum.* The sound ceases as soon as the mouth is opened.

1. Simple explosive sounds, *b*, *d*, *g* (the hard *g* or gamma).

B. β. The lips are brought together so as to close the mouth, and separate at the moment that the air is expired.

D. δ. The mouth is closed by the tongue being applied to the anterior part of the palate or to the upper teeth, and opens with the escape of the breath.

G. γ. The momentary occlusion of the passage through the mouth takes place more posteriorly by the application of the back part of the dorsum of the tongue to the palate. It is only the hard *g* [as in "gold," "gag," "gun,"] corresponding to the Greek γ, that is thus pronounced. The palatal sound of the German *ch*, which is often written *g*, [and the English *g* soft, as in "gentle," "gin,"] are produced in a different manner.

The mute or whispered sounds of *b*, *d*, *g*, are usually formed by the sudden opening of the vocal tube previously closed in the way we have described. They may, however, be produced likewise by the sudden occlusion.

2. Aspirate explosive sounds, *p*, *t*, *k*.

These are merely modifications of *b*, *d*, *g*, produced by a stronger aspiration during the opening of the previously closed passage of the mouth.*

* This explanation was given in my "Grundriss der Physiologie," in 1827.

All the principal sounds of articulate language are, as we have seen, capable of being pronounced in the manner of the mute or whispering speech. There are only a few modifications of the consonants which require for their formation an accompanying vocal tone; such are the German *j* [or English *y*], the French *j* and *ge*, the French [and English] *z*, and the vocalised *l* and *r*. In place of these vocalised consonants, corresponding mute consonants are produced when the former are attempted to be uttered in a whisper. Thus,

For the	German *j* or English *y*,	the German *ch* is produced.
—	French *j* or *ge* . .	the English *sh* (the German *sch*).
—	French or English *z* .	the English *s*.
—	vocalised *l* . . .	the mute *l*.
—	vocalised *r* . . .	the mute *r*.

B. *The sounds of vocalised speech.*

In the vocalised speech some few consonants have still merely the character of whispered sounds, being incapable of combination with any vocal tone. Other consonants are in vocalised speech susceptible of two modes of pronunciation, the mute and the vocalised. The vowels have the vocal tone.

I. *Vowels.*—The disposition of the organs of speech is the same for the vocalised as for the mute pronunciation of the vowels; the vocal tone produced in the larynx by the vibrations of the vocal cords is modified in the throat, mouth, and oral opening into the different vowels. The proper diphthongs are combinations of two vowels. [The English *i* in its long sound is the equivalent of the German diphthong *ei*, and seems to be really a combination of two sounds. The sound of *i* cannot, like a true vowel, be prolonged *ad libitum;* but appears rather to result from the transition from a peculiar murmur to the sound of *e*, just as the diphthong *oy* or *oi* results from the transition from broad *a* to *e*].*

A peculiar murmuring sound accompanies several consonants, which does not resemble any of the vowels. This kind of intonation can be produced either with the mouth open or with it closed, the nasal passage being in the latter case open.

* The so-called mute *e*, the Hebraic scheva, which occurs in the German words "habe" and "sage," at least in some dialects, is a peculiar vowel, approaching very near the sound of the whispered vowels. The vowels do not commonly occur as mute or whispered sounds in the open vocalised speech. There is, however, a trace of such sounds in the Sclavonian dialects, for example, in the Polish language. In the word "wab'" the *b* is followed by the sound of a mute or whispered *i* [or English *e*]. The same sign after other consonants indicates the mute sound of the same vowel: but from the mute *i* [*e* English] there is an easy transition to the sound of the German *ch*, which is produced by such a similar disposition of the oral tube. [The English *y* also, which, when pronounced in a whisper, is replaced by the German *ch*, seems to result from the transition from an aspirated *e* to the succeeding vowel.]

II. *Consonants which, in vocalised speech, are not accompanied with a vocal sound.*

1. The explosive *b, d, g* (γ), and their modifications *p, t, k*. It is quite impossible to combine the sounds of these consonants with an intonation of the voice. If it be attempted to pronounce them aloud, the intonation only follows them, and the result is the combination of the mute consonant with a vowel.

2. The only continuous consonant which cannot be pronounced in combination with a vocal sound is the aspirate *h*. The aspiration of the *h* ceases immediately that the vocal cords are thrown into sonorous vibrations.

III. *Consonants which, in vocalised language, can be pronounced either as mute sounds or with vocal intonation.*—These are all of the class of continuous consonants; namely, *f*, the German *ch, sch* [the English *sh*, and French *che*], *s, r, l, m, n, ng*. The vocalised sounds of these consonants are wanting in many languages; they exist in greatest number in the French language, in which they are sometimes expressed by special letters; for example, the vocalised *s* is written *z*, thus "zone" in a whisper is "sone;" the German *sch* [or English *sh*], vocalised, is written *j*, as in "jamais;" or else the vocal intonation of the consonant is expressed by the mute *e* being placed after it, as in words ending with *le, me, ne*, and *re*. The *e* in these words is not really pronounced as such, but merely expresses the intonation of the preceding consonant. The mute *e* after other consonants has no signification, unless to indicate that their pronunciation is to be changed; the French *ge* and *che*, for example, are the German *sch* [the English *sh*], while *g* before *a* is the real gamma.* The German language distinguishes in one case only a consonant with a vocal sound from its corresponding mute; the German *j* is the vocalised *ch*, as in "ja." Kempelen observed that the German *j* was produced by the vocalisation of the *ch*; that the French *z* is a vocalised *s*, and that the French *j* is the German *sch*, with a vocal intonation.† [The mute *e* in the English language does not change the pronunciation of the preceding consonant, as in French words; the English *z*, which in the middle of a word has the sound of the French *z*, is in whispering also pronounced

* The sound of the German *ch* occurs in the French language only in combination with the "*l* mouillé," for example in the word "mouillé," where the *le* has the sound of *lyé* [written in German *ljé*], or, when pronounced in a whisper, of *lché* [the German *ch*].

† We gave the same statement of the parallel sounds of mute and intonated speech in our "Grundriss der Physiologie," Bonn. 1827. Kempelen classes the consonants *l, m, n*, and *r* among the vocalised sounds, but they are certainly not always so; they are heard distinctly as true mute sounds in the vocalised speech. The consonants *b, d*, and *g*, which he also reckons amongst the intonated sounds, are as mute as the *p, t, k*, which he correctly classes among the mute consonants.

as *s*; the English *y*, which is equivalent to the German *j*, has the sound of the German *ch* when pronounced in a whisper, for example, in the word " yes."]

The consonant *ng* can be vocalised *ad libitum*. The German *f* and *w* when vocalised have both the sound of *w* [or English *v*.]

The French language is especially characterised by the prevalence of consonants accompanied by vocal intonations. It is the prevalence of the soft consonants with vocal intonation that gives the French language its beauty. It has, however, a degree of nasal monotony from the frequent use of the nasal consonants *m*, *n*, and *ng*, and particularly of the last-named, in constant combination with vowel sounds of nasal timbre to the exclusion of other vowels not of nasal character, with which the *ng* is associated in the English and German languages. Even where such combinations as *em* and *ing* occur in French words other nasal vowels are substituted in pronunciation, as in " empereur," " singulier."

[The following table contains Professor Müller's classification of articulate sounds.]

			Mute.	*Corresponding sounds with vocal intonation.*
Vowels.			a	a.
			e	e.
			i	i.
			o	o.
			u	u.
Consonants.	Continuous.	Aspirate	h.	
		Nasal.	m	m.
			n	n.
			ng	ng.
		Oral.	f	v (in German, w).
			v (the German w)	v (in German, w).
			ch χ, (the Scotch and German ch)	y English (in German, j).
			sh	j French, as in " jamais."
			s	z French, as in " zone."
			r	r.
			l	l.
	Explosive.	Simple.	b.	
			g, γ.	
			d.	
		Aspirate.	p.	
			k.	
			t.	

The sounds which we have hitherto considered are the essential elements of all perfect languages; they have different signs in different languages, but that is a circumstance which it does not come within our purpose to consider. *Q*, *X*, and Z are not independent consonants, but compound sounds. [The *j*, soft *g* and *ch* of the English language are also compound sounds. The *j* and *g* being pronounced like the French *j* in " jamais" preceded by *d*; the *ch* like *t* followed by *sh*.] *

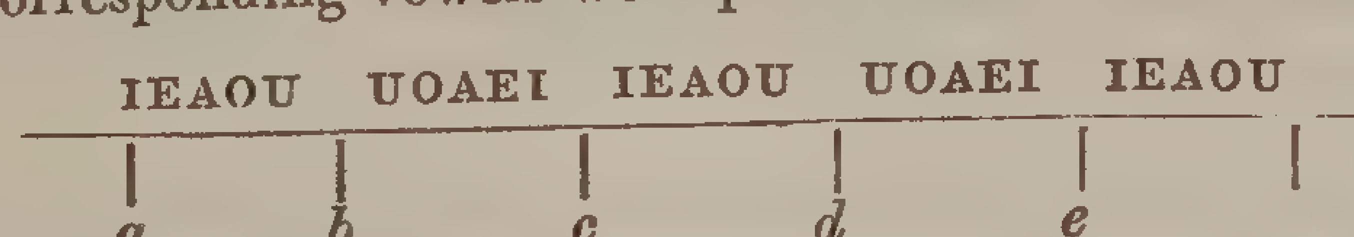
Besides the sounds of consonants which ordinarily enter into the

* On the comparative prevalence of the different sounds in different languages, consult Purkinje, loc. cit.

formation of languages, there are a number of other sounds capable of being formed in the mouth and throat. The smacking sounds which can be produced in separating the tongue from the teeth or palate, are said by Lichtenstein and Salt to occur in the language of the Hottentots and other African tribes.

The different sounds and tones of language being dependent on certain physical conditions, are of course capable of imitation by artificial contrivances. Some are produced very easily in this manner, as *b*, which is heard when the sound of the voice is made to pass into a cylindrical tube, before which the hand is held and then withdrawn; the German *w* [*v*] may be formed in the same way if the tube be a pipe with membranous tongue. Experiments relative to the artificial production of the articulate sounds have been made by Kratzenstein, Kempelen, and Mr. R. Willis.* They have succeeded in imitating a great part of the sounds used in speech. But these speaking-machines are always to a certain extent imperfect, since every simple and independent sound and consonant requires a special apparatus; and the combination of the different apparatus with a common tube for the supply of air, so as to form words, is exceedingly difficult. We cannot be surprised also at some birds, as the parrot and raven, being capable

* [Kratzenstein produced the vowel sounds by means of reed-tubes of curious forms. Kempelen employed a conical funnel-like tube, with a reed at its upper narrow extremity, and obtained the sounds of the different vowels by covering the lower wide opening to a greater or less extent. Repeating these experiments, Mr. Willis found that, with an instrument of the form Kempelen used, the vowels *u*, *o*, and *a* only could be produced, but that with a much shallower funnel the whole series, *u*, *o*, *a*, *e*, *i*, could be obtained. This induced him to try the effect of tubes of different length. The result he arrived at was, that the different vowel sounds may be produced by merely varying the length of the tube affixed to a reed. Let *a b*, *b c*, *c d*, &c. in the diagram represent the lengths of a stopped pipe in unison with the reed. The letters above the line will indicate the length of the tube measured from *a*, by which the corresponding vowels were produced.



As the tube was lengthened from *a* to *b* the note of the reed assumed the characters of IEAOU; between *b* and *c* the series were heard again in the inverse order; and between *c* and *d* in the direct order again; and so on in cycles, which were a repetition of that between *b* and *d*.

The respective vowels in these cycles (u o a e i, i e a o u) stand in all cases at the same distance from the points *a*, *c*, and *e*, whatever the length of the wave of the reed, or of the portion of pipe in unison with the reed. Hence, if the pitch of the reed be high, and the length of pipe and column of air in unison with it consequently short, the vowels furthest distant from the points *a*, *c*, and *e* cannot be formed. And this, Mr. Willis remarks, is exactly the case in the human voice; female singers are unable to pronounce U and O on the higher notes of their voice. According to Mr. Willis, the peculiar vowel character of any sound is owing to that sound being accompanied by the musical note appropriate to the production of the vowel.]

of uttering articulate sounds, since their mouth has the same general conformation with parts which can act as valves. The mode of articulating sounds is, without doubt, learnt by these birds in the same way as by the human infant. The different sounds are first produced without any order or proposed end; but, while thus produced, the movements necessary for the formation of each become impressed on the sensorium, and are therefore readily associated again when the sound which they are calculated to give rise to is heard.

C. *Ventriloquism.*

The peculiarity of the particular mode of speaking which is so called, has been supposed by some physiologists, as M. Magendie, to consist merely in the varied modification of the sounds produced in the larynx, in imitation of the modifications which voice ordinarily suffers from distance, &c.; by others it is imagined to depend on some common cause, which modifies all the tones uttered, for example, on the articulation taking place during inspiration. This last is the view generally taken of the cause of ventriloquism. It is certainly possible to articulate during inspiration, though with difficulty; and the sounds thus produced have some similarity with the tones of the voice of the ventriloquist. But, nevertheless, I regard the opinion in question as erroneous; for the sounds uttered by the ventriloquist can be perfectly imitated much more easily by another method, which I am convinced must be adopted by the ventriloquists themselves. The method to which I allude consists in inspiring deeply, so as to protrude the abdominal viscera by the descent of the diaphragm, and then speaking while the expiration is performed very slowly through a very narrow glottis by means of the lateral parietes of the thorax alone, the diaphragm maintaining its depressed position. The timbre which the voice has in speaking during an expiration thus performed is that peculiar to ventriloquism. Sounds may be thus uttered which resemble the voice of a person calling from a distance.

A great part of the art of the ventriloquist, for example, in imitating the voices, coming from particular directions, consists merely in deceiving other senses than hearing. We never distinguish very readily the direction in which sounds reach our ear; and, when our attention is directed to a particular point, our imagination is very apt to refer to that point whatever sounds we may hear.

D. *Defective speech.*

The proper exercise of the faculty of speech presupposes the possession of a normally-formed oral cavity as well as a good sense of hearing. Imperfections of speech arise from a want of either of these requisites. An opening in the palate renders the formation of some sounds impossible, and gives to the voice a nasal timbre; want of teeth also renders the speech imperfect.*

By want of command, or loss of power of the tongue, speech is rendered indistinct and unintelligible. This is observed as a temporary consequence of intoxication, and as a permanent result of paralysis of the ninth nerve.

The speech may, however, be imperfect also from the sounds not following each other as they ought to do, though the individual sounds be pronounced perfectly; such is stammering. It consists in a momentary inability to pronounce a consonant or vowel, or to connect it with the preceding sounds. This impediment may occur either at the commencement or in the middle of a word. In the latter case, the commencement of the word is often several times repeated; the part of the word thus repeated may end with a vowel, and the difficulty then consists in connecting with this the following consonant; or it may be merely the commencing consonant which is repeated, and with which the succeeding vowel cannot be combined. The repetition of the commencement of the word, as Schulthess rightly remarks, is not the essential condition of stammering; it is merely a new attempt at overcoming the impediment. If the consonant preceding the impediment be one of the explosive class, (*b, d, g* and *p, t, k*), which do not admit of a continuous pronunciation until the formation of the vowel is attained, it is more prone to be frequently repeated; thus, a person who stammers, says for "bitter," b-b-b-bitter. But if it be a continuous consonant as *m, n, ng, f*, χ [the German and Scotch *ch*], *sh, r, l*, or *s*, it is not necessarily repeated, because the sound of a continuous consonant can be prolonged *ad libitum*, until the vowel follows it; for example, in the word "laughing." It does, however, sometimes happen that the continuous consonant is repeated in such a case, and the word is pronounced l-l-l-l-laughing. Sometimes letters which do not belong to the word are involuntarily introduced.

Schulthess maintains that the stammering does not arise from any difficulty in the pronunciation of the consonants, but that the impediment attends the utterance of the vowels. This view is founded on good observations; but, though an improvement on the previous erroneous opinions, it goes further than facts justify, for the vowel is often formed while the following consonant cannot be combined with it. I knew a young man of distinguished mathematical attainments, who had previously stammered very badly, and, in pronouncing his own name, was apt to say Te-tessot instead of Tessot. In many cases also the impediment attaches to the first consonant of a word; and here likewise the difficulty does not so much depend on the parts of the mouth which are engaged in articulation, as on the arrest of the passage of the air necessary for the pronunciation of a particular consonant, by the momentary closure of the glottis. This closure

* On defects in the formation of particular letters, see Kempelen and Schulthess, loc. cit.

of the glottis, the importance of which has been particularly pointed out by Dr. Arnott,* occurs only in the attempt to articulate particular sounds, by involuntary association, the supply of air for the articulation of other sounds not being impeded ; the syllable preceding the arrest of speech can, for example, be frequently repeated. The essential cause of the impediment is always situated in the glottis, whether it be that the vocal cords do not give the requisite sound when it is a vowel which is attempted to be formed, or that the passage of air is arrested during the attempt at articulation in the mouth. In persons who stammer very badly there are evident signs of the struggle at the glottis, afforded by the impediment to expiration and by the congestion of blood in the head and veins of the neck. The essential cause of stammering is, therefore, clearly an unnatural associate movement in the larynx by consent with the movements of the mouth, or articulate movements. When the struggles of stammering are violent, associate movements are observed also in the face. It is the same condition as that of a person who wishes to move one particular muscle of his face, but on account of association of nervous action, or defect of the power of insulating the nervous influence, cannot do it without distorting all his features.†

I agree entirely with Dr. Arnott and Schulthess in considering the immediate cause of stammering to be a spasmodic affection of the glottis. This affection consists in a momentary closure of the aperture, partly by the approximation of the arytenoid cartilages and partly by the pressure of the musculi thyreo-arytenoidei, which are capable of pressing the ligaments of the glottis into contact with each other. It must be remembered as a principle that this momentary spasm depends entirely on a morbid association of the muscles of the larynx with the movements of the organs of articulation. The position of the mouth for the pronunciation of *b* is assumed, and the lips can be separated in the manner proper for the utterance of the sound; but when this is done, or ought to be done, the breath is wanting,—it is arrested at the larynx. The natural indication, therefore, for the prevention of stammering is to attempt to bring more under the command of the will the associations between the movements of articulation and the movements of the larynx. One method of fulfilling this indication is the singing of the words, in which the attention is directed more to the action of the larynx than in ordinary speaking. Persons who stammer pronounce better in singing than in mere speaking.

A too low position of the tongue in the mouth appears to favour stammering. The method of treatment practised by Mad. Leigh consisted in preventing this position of the tongue, and in raising its point

* Elements of Physics, vol. i.

† See the remarks on associate nervous action and associate movements, at pages 683 and 928.

towards the palate. The practice of placing bodies under the tongue, which was known to the ancients, tended to the same object.

The method proposed by Dr. Arnott for the cure of stammering, whatever be the result of its practice, is, at all events, founded on a sound physiological view of the nature of the affection. "Had the edges of the glottis," says Dr. Arnott, "been visible, like the external lips of the mouth, the nature of stuttering would not so long have remained a mystery." The glottis is repeatedly closed in persons who stammer, and the cure of the affection must therefore be effected by conquering this morbid tendency to closure by voluntarily keeping it open as much as possible. For this purpose Dr. Arnott advises that the patient should connect all his words by an intonation of the voice continued between the different words, as is done by persons who speak with hesitation. This plan may afford some benefit, but cannot do everything; since the main impediment occurs in the middle of words themselves, and depends on the abnormal association of the movement of the larynx with certain movements of articulation. Were I called upon to advise a method of treatment in a case of stammering, I would recommend, in addition to Dr. Arnott's plan, the following procedure. I would let the patient practise himself in reading sentences in which all letters which cannot be pronounced with a vocal sound, namely the explosive consonants *b*, *d*, *g*, *p*, *t*, and *k*, were omitted, and only those consonants included which are susceptible of an accompanying intonation of the voice; and I would direct that all these letters should be pronounced with such a sound of the voice, and that their sound should be very much prolonged. By this means a mode of pronunciation would be attained in which the articulation would be constantly combined with vocalisation, and the glottis consequently never closed. When the stammerer had long practised himself in keeping the glottis open without intermission, even between the words by Dr. Arnott's method, and in maintaining the glottis open during and after the pronunciation of every consonant capable of vocalisation and of the vowels, he might proceed to the mute and continuous consonant *h*, and the explosive sounds *g*, *d*, *b*, *k*, *t*, *p*. In such a plan of treatment the patient himself would perceive the principle; while the ordinary method—that of Mad. Leigh—is mere groping in the dark, neither teacher nor pupil knowing the principle of the procedures.*

There is a kind of defect of speech essentially different from stammering, consisting in a protracted intonation of the voice between words, or the introduction of a more or less prolonged *a* or *au*,—nasal vowel sounds, or peculiar vocal sounds modified by a jingling character between the words, which themselves are correctly pronounced; for example, I . . . a . . . have. It is like the prolonged vibration of a musical

* See Schulthess, loc. cit. p. 166.

instrument beyond the required duration. These sounds form and facilitate the transition from one word to another, and they may frequently be produced as a means of transition; although they, in many instances, also arise from hesitation or want of readiness of the ideas. This mode of speaking sometimes attends stammering, probably because the impediment to the commencement of the next word is avoided by this transition of sounds.

The formation of perfect vocal tones presupposes the possession of the sense of hearing. It is only with the greatest labour that individuals born deaf can learn to utter a series of harsh sounds. The deaf and dumb owe their want of speech to their deafness: they can by great labour learn the movements of articulation by means of their sight; but their speech is never more than a series of harsh sounds, not adapted for human society, for they want the sense of hearing to regulate their articulation.

There is no neaerr medium of connection between the faculties of speech and hearing than the brain, and it is not evident how nervous communications could be of service to either organ. The connection of the facial nerve with the lingual branch of the fifth can have no influence on speech or hearing; for the facial nerve has nothing to do with hearing; the lingual branch of the fifth nothing to do with speech. The nerve on which the movements of speech principally depend is the ninth nerve, which supplies all the muscles of the tongue; the facial also has some share in articulation, at all events as regards the movements of the lips. Both the last-named nerves are engaged in physiognomical expression, since the automatic movements of the features as well as speech disclose in different ways what is passing in the mind. Both nerves appear to arise from the same nervous centre,—the olivary body.*

* See Retzius, Müller's Archiv. 1836.

BOOK THE FIFTH.

Of the Senses.

PRELIMINARY CONSIDERATIONS.

The senses, by virtue of the peculiar properties of their several nerves, make us acquainted with the states of our own body, and they also inform us of the qualities and changes of external nature, as far as these give rise to changes in the condition of the nerves. Sensation is a property common to all the senses; but the kind, ("*modus*,") of sensation is different in each: thus we have the sensations of light, of sound, of taste, of smell, and of feeling or touch. By feeling, or touch, we understand the peculiar kind of sensation of which the ordinary sensitive nerves generally — as, the nervus trigeminus, vagus, glosso-pharyngeus, and the spinal nerves,—are susceptible; the sensations of itching, of pleasure and pain, of heat and cold, and those excited by the act of touch in its more limited sense, are varieties of this mode of sensation. That which through the medium of our senses is actually perceived by the sensorium, is indeed merely a property or change of condition of our nerves; but the imagination and reason are ready to interpret the modifications in the state of the nerves produced by external influences as properties of the external bodies themselves. This mode of regarding sensations has become so habitual in the case of the senses which are more rarely affected by internal causes, that it is only on reflection that we perceive it to be erroneous. In the case of the sense of feeling or touch, on the contrary, where the peculiar sensations of the nerves perceived by the sensorium are excited as frequently by internal as by external causes, it is easily conceived that the feeling of pain or pleasure, for example, is a condition of the nerves, and not a property of the things which excite it. This leads us to the consideration of some general laws, a knowledge of which is necessary before entering on the physiology of the separate senses.

I. In the first place, it must be kept in mind that *external agencies can give rise to no kind of sensation which cannot also be produced by internal causes, exciting changes in the condition of our nerves.*

In the case of the sense of touch, this is at once evident. The sensations of the nerves of touch (or common sensibility) are those of cold and heat, pain and pleasure, and innumerable modifications of these, which are neither painful nor pleasurable, but yet have the same kind of sensation as their element, though not in an extrême degree. All these sensations are constantly being produced by internal causes in all parts of our body endowed with sensitive nerves; they may also be excited by causes acting from without, but external agencies are not capable of adding any new element to their nature. The sensations of the nerves of touch are therefore states or qualities proper to themselves, and merely rendered manifest by exciting causes external or internal. The sensation of smell also may be perceived independently of the application of any odorous substance from without, the nerve of smell being thrown by an internal cause into the condition requisite for the production of the sensation. This perception of the sensation of odours without an external exciting cause, though not of frequent occurrence, has been many times observed in persons of an irritable nervous system; and the sense of taste is probably subject to the same affection, although it would always be difficult to determine whether the taste might not be owing to a change in the qualities of the saliva or mucus of the mouth; the sensation of nausea, however, which belongs to the sensations of taste, is certainly very often perceived as the result of a merely internal affection of the nerves. The sensations of the sense of vision, namely colour, light, and darkness, are also perceived independently of all external exciting cause. In the state of the most perfect freedom from excitement, the optic nerve has no other sensation than that of darkness. The excited condition of the nerve is manifested, even while the eyes are closed, by the appearance of light, or luminous flashes, which are mere sensations of the nerve, and not owing to the presence of any matter of light, and consequently are not capable of illuminating any surrounding objects. Every one is aware how common it is to see bright colours while the eyes are closed, particularly in the morning when the irritability of the nerves is still considerable. These phenomena are very frequent in children after waking from sleep. Through the sense of vision, therefore, we receive from external nature no impressions which we may not also experience from internal excitement of our nerves; and it is evident that a person blind from infancy in consequence of opacity of the transparent media of the eye, must have a perfect internal conception of light and colours, provided the retina and optic nerve be free from lesion. The prevalent notions with regard to the wonderful sensations supposed to be experienced by persons blind from birth when their sight is restored by operation, are exaggerated and incorrect. The elements of the sensation of vision, namely the sensations of light, colour, and darkness, must have been previously as well known to such persons as to those of whom the sight has always been perfect. If, moreover, we imagine a man to be from his birth surrounded merely by external objects destitute of all variety of colours, so that he could never receive the impressions of colours from without, it is evident that the sense of vision might nevertheless have been no less perfect in him than in other men; for light and colours are innate endowments of his nature, and require merely a stimulus to render them manifest.

The sensations of hearing also are excited as well by internal as by external causes; for, whenever the auditory nerve is in a state of excitement, the sensations peculiar to it, as the sounds of ringing, humming, &c. are perceived. It is by such sensations that the diseases of the auditory nerve manifest themselves; and, even in less grave transient affections of the nervous system, the sensations of humming and ringing in the ears afford evidence that the sense of hearing participates in the disturbance.

No further proof is wanting to show, that external influences give rise in our senses to no other sensations, than those which may be excited in the corresponding nerves by internal causes.

II. *The same internal cause excites in the different senses different sensations ;—in each sense the sensations peculiar to it.*

One uniform internal cause acting on all the nerves of the senses in the same manner, is the accumulation of blood in the capillary vessels of the nerve, as in congestion and inflammation. This uniform cause excites in the retina, while the eyes are closed, the sensation of light and luminous flashes; in the auditory nerve, humming and ringing sounds; and in the nerves of feeling, the sensation of pain. In the same way, also, a narcotic substance introduced into the blood excites in the nerves of each sense peculiar symptoms; in the optic nerves the appearance of luminous sparks before the eyes; in the auditory nerves, "tinnitus aurium;" and in the common sensitive nerves the sensation of ants creeping over the surface.

III. *The same external cause also gives rise to different sensations in each sense, according to the special endowments of its nerve.*

The mechanical influence of a blow, concussion, or pressure excites, for example, in the eye the sensation of light and colours. It is well known that by exerting pressure upon the eye, when the eyelids are closed, we can give rise to the appearance of a luminous circle; by more gentle pressure the appearance of colours may be produced, and one colour may be made to change to another. Children, waking from sleep before daylight, frequently amuse themselves with these phenomena. The light thus produced has no existence external to the optic nerve, it is merely a sensation excited in it. However strongly we press upon the eye in the dark, so as to give rise to the appearance of luminous flashes, these flashes, being merely sensations, are incapable of illuminating external objects. Of this any one may easily convince himself by experiment. I have in repeated trials never been able, by means of these luminous flashes in the eye, to recognise in the dark the nearest objects, or to see them better than before; nor could another person, while I produced by pressure on my eye the appearance of brilliant flashes, perceive in it the slightest trace of real light. (See page 93.)

The supposed emission of light by the eyes of animals has been already discussed in the Prolegomena, page 93. It is not, *à priori*, contrary to known laws, to suppose that the nerves of animals may develope luminous matter; and since we have in the retina of the eye an opportunity which we have nowhere else, of observing a nerve through transparent media without inflicting any injury on the animal, it would be here that such a phenomenon would be best observed. The fact of light being developed by the retina and nerves, even were it proved by experiment, would not, however, influence the explanation of the appearance of light produced in the eye by internal causes.

A mechanical influence excites also peculiar sensations of the auditory nerve; at all events, it has become a common saying, "to give a person what will make his ears ring," or "what will make his eyes flash fire," or "what will make him feel;" so that the same cause, a blow, produces in the nerves of hearing, sight, and feeling, the different sensations proper to these senses. It has not become a part of common language that a blow shall be given which will excite the sense of smell, or of taste; nor would such sayings be correct;* yet mechanical irritation of the soft palate, of the epiglottis and root of the tongue, excites the sensation of nausea. The action of sonorous bodies on the organ of hearing is entirely mechanical. A sudden mechanical impulse of the air upon the organ of hearing produces the sensation of a report of different degrees of intensity according to the violence of the impulse, just as an impulse upon the organ of vision gives rise to the sensation of light. If the action of the mechanical cause on the organ of hearing be of continued duration, the sound is also continued; and when caused by a rapid succession of uniform impulses, or vibrations, it has a musical character (see page 972). If we admit that the matter of light acts on bodies by mechanical oscillation, (the undulation theory,) we shall have another example of a mechanical influence, producing different effects on different senses. These undulations, which produce in the eye the

* [The influence of mechanical agency in exciting the nerve of taste to its peculiar reaction may be made quite perceptible; but the stimulus must be applied in a particular manner. If the end of the finger be made to strike quickly, but lightly, the surface of the tongue at its tip, or its edge near the tip, so as to affect not the substance of the organ, but merely the papillæ, a taste sometimes acid, sometimes saline, like the taste produced by electricity, will be distinctly perceived. The sensation of taste thus induced will sometimes continue several seconds after the application of the mechanical stimulus.]

sensation of light, have no such effect on other senses; but in the nerves of feeling they produce the sensation of warmth.*

The stimulus of electricity may serve as a second example, of a uniform cause giving rise in different nerves of sense to different sensations. A single pair of plates of different metals applied so as to include the eye within the circle, excites the sensation of a bright flash of light when the person experimented upon is in a dark room; and, even though the eye do not lie within the circle, if it be not distant from it,—as, for example, when one of the plates is applied to one of the eyelids, and the other to the interior of the mouth,—the same effect will be produced, owing to a part of the current of electricity being diverted to the eye. A more intense electric stimulus gives rise to more intense sensations of light. In the organ of hearing, electricity excites the sensation of sound. Volta states that, while his ears were included between the poles of a battery of forty pairs of plates, he heard a hissing and pulsatory sound, which continued as long as the circle was closed.† Ritter perceived a sound like that of the fiddle G at the moment of the closure of the galvanic circle.

The electricity of friction, developed by the electrical machine, excites in the olfactory nerves the odour of phosphorus. The application of plates of different metals to the tongue, gives rise to an acid or a saline taste, according to the length of the plates which are applied one above, and the other beneath the tongue. The facts detailed with regard to the other senses are sufficient to show that these latter phenomena cannot be attributed to decomposition of the salts of the saliva.

The effects of the action of electricity on the nerves of common sensation or feeling, are neither the sensation of light, of sound, of smell, nor of taste, but those proper to the nerves of feeling, namely, the sensations of pricking, of a blow, &c.

Chemical influences also probably produce different effects on different nerves of sense. We have, of course, but few facts illustrating their action on these nerves; but we know that in the sensitive nerves of the skin they excite the different kinds of common sensation,—as the sensations of burning, pain, and heat; in the organ of taste, sensations of taste; and, when volatile, in the nerves of smell, the sensations of odours. Without the infliction of great injury on the textures, it is impossible to apply chemical agents to the nerves of the higher senses, sight and hearing, except through the medium of the blood. Chemical substances introduced into the blood act on every nerve of sense, and excite in each a manifestation of its properties. Hence the internal

* [According to the generally received doctrines of physics, the heating power of light is due to calorific rays distinct from those which produce the sensations of light and colours in the eye.]

† Philos. Transact. 1800, p. 427.

sensations of light and sound, which are well known to result from the action of narcotics.

IV. *The peculiar sensations of each nerve of sense can be excited by several distinct causes internal and external.*

The facts on which this statement is founded, have been already mentioned; for we have seen that the sensation of light in the eye is excited:

1. By the undulations or emanations which from their action on the eye are called light, although they have many other actions than this; for instance, they effect chemical changes, and are the means of maintaining the organic processes in plants.
2. By mechanical influences; as concussion, or a blow.
3. By electricity.
4. By chemical agents, such as narcotics, digitalis, &c. which, being absorbed into the blood, give rise to the appearance of luminous sparks, &c. before the eyes independently of any external cause.
5. By the stimulus of the blood in the state of congestion.

The sensation of sound may be excited in the auditory nerve:

1. By mechanical influences, namely, by the vibrations of sonorous bodies imparted to the organ of hearing through the intervention of media capable of propagating them.
2. By electricity.
3. By chemical influences taken into the circulation; such as the narcotics, or alterantia nervina.
4. By the stimulus of the blood.

The sensation of odours may be excited in the olfactory nerves:

1. By chemical influences of a volatile nature,—odorous substances.
2. By electricity.

The sensation of taste may be produced:

1. By chemical influences acting on the gustatory nerves either from without or through the medium of the blood; for, according to Magendie, dogs taste milk injected into their blood-vessels, and begin to lap with their tongue.
2. By electricity.
3. By mechanical influences; for we must refer to taste the sensation of nausea produced by mechanically irritating the velum palati, epiglottis, and root of the tongue.*

The sensations of the nerves of touch or feeling are excited:

1. By mechanical influences; as sonorous vibrations, and contact of any kind.
2. By chemical influences.
3. By heat.
4. By electricity.
5. By the stimulus of the blood.

* See note to page 1062.

V. *Sensation consists in the sensorium receiving through the medium of the nerves, and as the result of the action of an external cause, a knowledge of certain qualities or conditions, not of external bodies, but of the nerves of sense themselves ; and these qualities of the nerves of sense are in all different, the nerve of each sense having its own peculiar quality or energy.*

The special susceptibility of the different nerves of sense for certain influences,—as of the optic nerve for light, of the auditory nerve for vibrations, and so on,—was formerly attributed to these nerves having each a specific irritability. But this hypothesis is evidently insufficient to explain all the facts. The nerves of the senses have assuredly a specific irritability for certain influences; for many stimuli, which exert a violent action upon one organ of sense, have little or no effect upon another: for example, light, or vibrations so infinitely rapid as those of light, act only on the nerves of vision and common sensation; slower vibrations, on the nerves of hearing and common sensation, but not upon those of vision; odorous substances only upon the olfactory nerves. The external stimuli must therefore be adapted to the organ of sense—must be "homogeneous:" thus light is the stimulus adapted to the nerve of vision; while vibrations of less rapidity, which act upon the auditory nerve, are not adapted to the optic nerve, or are indifferent to it; for, if the eye be touched with a tuning-fork while vibrating, a sensation of tremours is excited in the conjunctiva, but no sensation of light. We have seen, however, that one and the same stimulus, as electricity, will produce different sensations in the different nerves of the senses; all the nerves are susceptible of its action, but the sensations in all are different. The same is the case with other stimuli, as chemical and mechanical influences. The hypothesis of a specific irritability of the nerves of the senses for certain stimuli, is therefore insufficient; and we are compelled to ascribe, with Aristotle, peculiar energies to each nerve, — energies which are vital qualities of the nerve, just as contractility is the vital property of muscle. The truth of this has been rendered more and more evident in recent times by the investigation of the so-called "subjective" phenomena of the senses by Elliot, Darwin, Ritter, Goethe, Purkinje, and Hjort. Those phenomena of the senses, namely, are now styled "subjective," which are produced, not by the usual stimulus adapted to the particular nerve of sense, but by others which do not usually act upon it. These important phenomena were long spoken of as "illusions of the senses," and have been regarded in an erroneous point of view; while they are really true actions of the senses, and must be studied as fundamental phenomena in investigations into their nature.

The sensation of sound, therefore, is the peculiar "energy" or "quality" of the auditory nerve; the sensation of light and colours that of the optic nerve; and so of the other nerves of sense. An exact analysis of what takes place in the production of a sensation would of itself have led to this conclusion. The sensations of heat and cold, for example, make us acquainted with the existence of the imponderable matter of caloric, or of peculiar vibrations in the vicinity of our nerves of feeling. But the nature of this caloric cannot be elucidated by sensation, which is in reality merely a particular state of our nerves; it must be learnt by the study of the physical properties of this agent, namely, of the laws of its radiation, its developement from the latent state, its property of combining with and producing expansion of other bodies, &c. All this again, however, does not explain the peculiarity of the sensation of warmth as a condition of the nerves. The simple fact devoid of all theory is this, that warmth, as a sensation, is produced whenever the matter of caloric acts upon the nerves of feeling; and that cold, as a sensation, results from this matter of caloric being abstracted from a nerve of feeling.

So, also, the sensation of sound is produced when a certain number of impulses or vibrations are imparted, within a certain time, to the auditory nerve: but sound, as we perceive it, is a very different thing from a succession of vibrations. The vibrations of a tuning-fork, which to the ear give the impression of sound, produce in a nerve of feeling or touch the sensation of tickling; something besides the vibrations must consequently be necessary for the production of the sensation of sound, and that something is possessed by the auditory nerve alone. Vision is to be regarded in the same manner. A difference in the intensity of the action of the imponderable agent, light, causes an inequality of sensation at different parts of the retina: whether this action consists in impulses or undulations, (the undulation theory,) or in an infinitely rapid current of imponderable matter, (the emanation theory,) is a question here of no importance. The sensation of moderate light is produced where the action of the imponderable agent on the retina is not intense; of bright light where its action is stronger, and of darkness or shade where the imponderable agent does not fall; and thus results a luminous image of determinate form according to the distribution of the parts of the retina differently acted on. Colour is also a property of the optic nerve; and, when excited by external light, arises from the peculiarity of the so-called coloured rays, or of the oscillations necessary for the production of the impression of colour,—a peculiarity, the nature of which is not at present known. The nerves of taste and smell are capable of being excited to an infinite variety of sensations by external causes; but each taste is due to a determinate condition of the nerve excited by the external cause; and it is ridiculous to say that the property of acidity is communicated to the sensorium by the nerve of taste, while the acid acts equally upon the nerves of feeling, though it excites there no sensation of taste.

The essential nature of these conditions of the nerves, by virtue of which they see light and hear sound,—the essential nature of sound as a property of the auditory nerve, and of light as a property of the optic nerve, of taste, of smell, and of feeling,—remains, like the ultimate causes of natural phenomena generally, a problem incapable of solution. Respecting the nature of the sensation of the colour "blue," for example, we can reason no farther; it is one of the many facts which mark the limits of our powers of mind. It would not advance the question to suppose, the peculiar sensations of the different senses excited by one and the same cause, to result from the propagation of vibrations of the nervous principle of different rapidity to the sensorium. Such an hypothesis, if at all tenable, would find its first application in accounting for the different sensations of which a single sense is susceptible; for example, in explaining how the sensorium receives the different impressions of blue, red, and yellow, or of an acute and a grave tone, or of painful and pleasurable sensations, or of the sensations of heat and cold, or of the tastes of bitter, sweet, and acid. It is only with this application that the hypothesis is worthy of regard: tones of different degrees of acuteness are certainly produced by vibrations of sonorous bodies of different degrees of rapidity; and a slight contact of a solid body, which singly excites in a nerve of common sensation merely the simple sensation of touch, produces in the same nerve when repeated rapidly, as the vibrations of a sonorous body, the feeling of tickling; so that possibly a pleasurable sensation, even when it arises from internal causes independently of external influences, is due to the rapidity of the vibrations of the nervous principle in the nerves of feeling.

It was perhaps from an obscure acquaintance with the phenomena of the sensation of light from internal causes, that even the older philosophers derived their imperfect idea of the essential part which the eye itself plays in the sensations of light and colour. Such an idea can evidently be traced in Plato's doctrine of vision in the Timæus. He says,—"Illorum tamen instrumentorum primum ædificarunt (dii) ipsos oculos, luciferos quidem illos: quibus tantum ignis illigarunt quantum quidem comburere non valeret, lumen tamen proprium posset præbere: ut quidem perfectum quoddam diei corpus ita sit machinatus. Nam quod in nostris oculis est, germanâ quâdam et cognatâ cum die naturâ est: et quidem ita ut dii purum ejus ignem effecerint, illumque per oculos lævem densumque fluere, universo quidem, at medio potius oculo ita impleto, ut aliud quidem, quantum nimirum crassius est, omne contineat: illud autem quod purum perspicuumque sit, tantum percolet. Quum autem diurna erit lux in ipso visus fluxu, tunc excidens simile ad simile compactum atque concretum, unum corpus conciliatum atque necessitudine quâdam devinctum constitutum est ad rectam oculorum inspectionem, quocunque contrarium fulciatur id quod intus incidit, ad id quod extra evenit. Quum autem oculus ad noctem accedit, a cognato igne deciditur, nam quum ad rem sibi dissimilem venit, et ipsam naturam quodammodo mutat atque extinguitur: nec amplius proximo aeri adnascitur: quippe qui ignem minimè habeat."

Aristotle's treatise on dreams* contains views in themselves more correct, and stated in a more scientific form. His explanation of spectral appearances as the result of internal actions of the sense of vision, is quite on a level with the present state of science. He adduces indeed the observation since made by Spinoza, that images seen during sleep can still be perceived in the organs of vision after waking (cap. 3.); and the varying colours of the ocular spectra produced by gazing at the sun were well known to him. (cap. 2.)

In the present more perfect state of the different branches of natural science, which are studied separately, and in part independently of each other, it still remains a task, well deserving the labour it would cost, to test the theories of fundamental phenomena, more especially of those which interest different sciences, such as the actions of light upon organic beings. But this would be a task of extreme difficulty, requiring for its proper performance a critical examination of the various facts.

During recent years, philosophy has done little in this field of inquiry. The manifestation of different objects to each other cannot express the nature of light; that it renders objects visible to us depends merely on our having an organ of vision with vital properties. And in this way many other agents have the same power of rendering objects manifest: were we endowed with as delicate an organic re-agent for electricity as for light, electricity would have the same influence as light in rendering manifest the corporeal world.

From the foregoing considerations we have learnt most clearly that the nerves of the senses are not mere conductors of the properties of bodies to our sensorium, and that we are made acquainted with external objects merely by virtue of certain properties of our nerves, and of their faculty of being affected in a greater or less degree by external bodies. Even the sensation of touch in our hands makes us acquainted, not absolutely with the state of the surfaces of the body touched, but with changes produced in the parts of our body affected by the act of touch. By imagination and reason a mere sensation is interpreted as something quite different.

The accuracy of our discrimination by means of the senses depends on the different manner in which the conditions of our nerves are affected by different bodies; but the preceding considerations show us the impossibility that our senses can ever reveal to us the true nature and essence of the material world. In our intercourse with external

* Of which I have given a translation in my paper Über die phantastischen Gesichts-erscheinungen.

nature it is always our own sensations that we become acquainted with, and from them we form conceptions of the properties of external objects, which may be relatively correct; but we can never submit the nature of the objects themselves to that immediate perception to which the states of the different parts of our own body are subjected in the sensorium.

VI. *The nerve of each sense seems to be capable of one determinate kind of sensation only, and not of those proper to the other organs of sense; hence one nerve of sense cannot take the place and perform the function of the nerve of another sense.*

The sensation of each organ of sense may be increased in intensity till it becomes pleasurable, or till it becomes disagreeable, without the specific nature of the sensation being altered, or converted into that of another organ of sense. The sensation of dazzling light is an unpleasant sensation of the organ of vision; harmony of colours, an agreeable one. Harmonious and discordant sounds are agreeable and disagreeable sensations of the organ of hearing. The organs of taste and smell have their pleasant and unpleasant tastes and odours; the organ of touch, its pleasurable and painful feelings. It appears, therefore, that, even in the most excited condition of an organ of sense, the sensation preserves its specific character. It is an admitted fact that the sensations of light, sound, taste, and odours, can be experienced only in their respective nerves; but in the case of common sensation this is not so evidently the case, for it is a question whether the sensation of pain may not be felt in the nerves of the higher senses,—whether, for example, violent irritation of the optic nerve may not give rise to the sensation of pain. This question is difficult of solution. There are filaments of the nerves of common sensation distributed in the nerves of the other organs of sense: the nostrils are supplied with nerves of common sensation from the second division of the nervus trigeminus in addition to the olfactory nerves; the tongue has common sensibility as well as taste, and may retain the one while it loses the other; the eye and organ of hearing likewise are similarly endowed.

To determine this question, it is necessary to institute experiments on the isolated nerves of special sense themselves. As far as such experiments have hitherto gone, they favour the view that the nerves of sense are susceptible of no other kind of sensation than that peculiar to each, and are not endowed with the faculty of common sensibility.

The olfactory nerves laid bare in the dog evince, when pricked, as Magendie observed, no sign of common sensibility; and the retina and optic nerve were also in Magendie's experiments* insusceptible of pain from mechanical injury. On the other hand, it has been observed that the division of the optic nerve in extirpation of the eye was attended

* Journal de Physiol. t. iv. p. 180.

with the perception of a great light, a fact of which my friend M. Tourtual assured me from his own observation. The luminous rings seen when the eyes are suddenly turned to one side are facts of the same kind; they are the result of the mechanical stretching of the optic nerve. In many of the cases in which extirpation of the eye is indicated, the optic nerve is itself so changed in structure as to be no longer capable of sensation; consequently, the above phenomenon must not be expected to be constant in its occurrence. In two cases of extirpation of the eye, performed in Berlin, it was not perceived. I am not aware, however, that the division of the optic nerve was in these instances attended with more pain than the other parts of the operation; while the division of a common sensitive nerve of the same thickness is productive of the most rightful pain, and in animals calls forth a sudden and loud cry.

An impression upon one nerve of sense may, it is true, give rise by reflection through the intervention of the brain to other sensations; for example, the sound of scratching glass excited in the auditory nerve, produces the feeling of cold creeping over the surface, "horripilatio," in the nerves of common sensation. And in the same way a dazzling sensation of light in the optic nerve, may possibly give rise by reflection to a painful impression on the sensitive nerves of the orbit and ball of the eye; in this way we may, at all events, explain the painful sensations in the eye which follow the impression of a very bright light.

With respect to the sense of smell, it is evident that Magendie was deceived in ascribing the power of distinguishing odours to the nasal branches of the fifth nerve, after the destruction of the olfactory nerves; since the stimuli which he applied — for instance, acetic acid, liquor ammoniæ, oil of lavender, and oil of dippel, — are themselves strong excitants of the common sensibility of the mucous membrane.* In all accurately observed cases of absence of the olfactory nerves, the true sense of smell has been wanting.†

No one can deny the possibility of the optic nerves influencing the nerves of the other senses, to the extent in which one nerve can act on another, through the medium of the brain. What an extensive affection of the nerves is seen in neuralgia! what manifold disturbances of the organs of sense result from a nervous condition which has its source in the viscera of the abdomen! How common in such cases are imperfection of vision, noises in the ears, &c.! although it is certain that much which is laid to the score of the abdomen has a much deeper source, namely, irritation of the spinal cord.

It is thus, also, that we must regard the sympathy of the optic nerve with the frontal branch of the fifth, and those cases of amaurosis ob-

* Eschricht, Magendie's Journal de Physiol. t. vi. p. 339.

† Eschricht, loc. cit.

served to follow injury of the frontal nerve; though it would perhaps be more correct to explain such affections, which according to my experience are now but rarely seen, as the result of concussion of the eye and optic nerve produced by a blow on the forehead.

The arguments adduced from anatomy in favour of the view that the function of one nerve of sense may be performed by another, have a very weak foundation. The optic nerve of the mole was supposed to be the orbitar branch of the fifth nerve; Koch and Henle have, however, shown that the mole has a special optic nerve, uncommonly small, it is true, but corresponding in size to the eye itself; and the same may be the case in the Proteus anguinus. Treviranus and E. H. Weber have demonstrated the independence of the acoustic nerve from the fifth nerve in fishes. Even the circumstance of fibres of different function being included in one sheath, is by no means an argument for the possibility of different sensations being transmitted by one conductor. It is on the supposition of such a union of different fibres in one sheath, that we may explain the existence in fishes of a nervus accessorius nervi acoustici, which arises sometimes separately from the brain, sometimes from the fifth nerve, and sometimes from the vagus;* and also the fact stated by Treviranus,† that in some birds the nervus vestibuli is a branch of the facial. The olfactory nerves were supposed to be absent in the dolphin, but rudiments of them have been found by Blainville, Mayer, and Treviranus;‡ so that it is not necessary to attribute the sense of smell in these animals to other nerves, and it is, moreover, by no means ascertained that they have any sense of smell.

Among the well-attested facts of physiology, again, there is not one to support the belief that one nerve of sense can assume the functions of another. The exaggeration of the sense of touch in the blind will not in these days be called seeing with the fingers; the accounts of the power of vision by the fingers and epigastrium, said to be possessed in the so-called magnetic state, appear to be mere fables, and the instances in which it has been pretended to practise it, cases of deception. The nerves of touch are capable of no other sensation than that of touch or feeling. Hence, also, no sounds can be heard except by the auditory nerve; the vibrations of bodies are perceived by the nerves of touch as mere tremours, a sensation wholly different in its nature from sound; though it is indeed even now not rare for the different modes of action of the vibrations of bodies upon the sense of hearing, and upon that of feeling, to be confounded. Without the organ of hearing with its vital endowments, there would be no such a thing as sound in the world, but merely vibrations; without the organ of sight, there would be no light, colour, nor darkness, but merely a correspond-

* E. H. Weber, de Aure et Auditu. Lip. 1820, pp. 33. 101.

† Zeitschrift für Physiol. v.

‡ Biologie, v. 342.

ing presence or absence of the oscillations of the imponderable matter of light.

VII. *It is not known whether the essential cause of the peculiar "energy" of each nerve of sense is seated in the nerve itself, or in the parts of the brain and spinal cord with which it is connected; but it is certain that the central portions of the nerves included in the encephalon are susceptible of their peculiar sensations, independently of the more peripheral portion of the nervous cords which form the means of communication with the external organs of sense.*

The specific sensibility of the individual senses to particular stimuli, —owing to which vibrations of such rapidity or length as to produce sound are perceived, only by the senses of hearing and touch, and mere mechanical influences, scarcely at all by the sense of taste, — must be a property of the nerves themselves; but the peculiar mode of reaction of each sense, after the excitement of its nerve, may be due to either of two conditions. Either the nerves themselves may communicate impressions different in quality to the sensorium, which in every instance remains the same; or the vibrations of the nervous principle may in every nerve be the same and yet give rise to the perception of different sensations in the sensorium, owing to the parts of the latter with which the nerves are connected having different properties. The proof of either of these propositions I regard as at present impossible. Closely connected with this subject is the question of the existence of a difference in properties between the sensitive, motor, and organic nervous fibres. Do these fibres differ from each other by the nervous principle in each having a peculiar mode of oscillation? or are their different actions due to the parts with which they are connected as conductors? All that can be advanced with regard to this problem in the present state of our knowledge will be found at page 723.

It is, however, ascertained, beyond a doubt, that certain parts of the brain participate, at least, in the peculiar energies of the senses; for pressure on the brain has been frequently observed to cause the sensation of light. Luminous spectra may still be excited by internal causes after complete amaurosis of the retina.* Alex. von Humboldt† states that, in a man who had lost one eye, he produced, by means of galvanism, luminous appearances on the blind side. And Luicke‡ relates the case of a patient who, after the extirpation of the eye for fungoid disease, perceived all kinds of luminous appearances independently of external objects, and was so teased by them as to imagine he really saw them with his eyes. When he closed the remaining sound eye, he per-

* See the examples given in my treatise, Über die phantastischen Gesichtserscheinungen. Cobl. 1826.

† Die gereizte Muskel-und Nerven-faser, t. ii. 444.

‡ De Fungo medullari. Lips. 1834.

ceived different images—such as lights, circles of fire, many dancing figures, &c.—floating before the orbit whence the eye had been removed. These sensations (which are analogous to those referred to a limb lost by amputation) continued for several days.

Sometimes, also, sensations and violent pains are felt in limbs quite devoid of sensibility to external impressions (see page 692). It is probable that here also the central organs are the source of the sensations. Since, therefore, the peculiar energies of the senses are possessed by certain portions of the sensorium, the question really requiring solution is, Whether the nerves, which are the conductors of the external impressions, participate or not in these properties or "energies." This question cannot at present be answered; for the facts that are known may be explained on either supposition. That sensations arising from internal causes are often felt in peripheral parts, cannot be regarded as an argument for the nerves possessing the special sensitive energies; since it is known that affections even of the central organs of the nervous system are often manifested in peripheral parts of the body.

VIII. *The immediate objects of the perception of our senses are merely particular states induced in the nerves, and felt as sensations either by the nerves themselves or by the sensorium; but inasmuch as the nerves of the senses are material bodies, and therefore participate in the properties of matter generally, occupying space, being susceptible of vibratory motion, and capable of being changed chemically as well as by the action of heat and electricity, they make known to the sensorium, by virtue of the changes thus produced in them by external causes, not merely their own condition, but also properties and changes of condition of external bodies. The information thus obtained by the senses concerning external nature, varies in each sense, having a relation to the qualities or energies of the nerve.*

Qualities which are to be regarded rather as sensations or modes of reaction of the nerves of sense, are light, colour, the bitter and sweet tastes, pleasant and unpleasant odours, painful and pleasant impressions on the nerves of touch, cold and warmth: properties which may belong wholly to external nature are "extension," progressive and tremulous motion, and chemical change.

All the senses are not equally adapted to impart the idea of "extension" to the sensorium. The nerve of vision and the nerve of touch, being capable of an exact perception of this property in themselves, make us acquainted with it in external bodies. In the nerves of taste, the sensation of extension is less distinct, but is not altogether deficient; thus we are capable of distinguishing whether the seat of a bitter or sweet taste be the tongue, the palate, or the fauces. In the sense of touch and sight, however, the perception of space is most acute. The retina of the optic nerve has a structure especially adapted for this perception; for the ends of the nervous fibres in the retina are, as Treviranus discovered, so arranged as to be at last perpendicular to its inner surface, and by their papillar extremities form a pavement-like composite membrane. On the great number of these terminal fibrils depends the delicate power of discriminating the position of bodies in space possessed by the sense of vision; for each fibre represents a greater or less field of the visible world, and imparts the impression of it to the sensorium.

The sense of touch has a much more extended sphere of action for the perception of space than has the sense of vision; but its perception of this quality of external bodies is much less accurate, and considerable portions of the surface of the body or skin are in many instances represented in the sensorium by very few nervous fibres; hence, in many parts of the surface, impressions on two points considerably removed from each other are, as E. H. Weber has shown, felt as one impression. Although the senses of vision, touch, and taste are all capable of perceiving the property of extension in space, yet the quality of the sensations which give the conception of extension is different in each of these senses; the sensation in one is an image of which the essential quality is light; in another, a perception of extension with any of the modifications of the quality of touch, between pain, cold, heat, and pleasure; in the third, a perception of extension with the quality of taste.

The external cause which excites in the organ of sense the sensation which conveys also the notion of extension, may be various. In the organ of vision it is usually the external light, but a concussion given to the eye by an external body may also be the cause; for example, if a determinate portion of the retina is pressed upon, a luminous spectrum is produced at that part, which will occupy a definite portion of the field of vision. Even electricity applied to the eyes can give rise to images of definite extent and form, such as lines of fire, the position of which varies according to the position of the poles of the galvanic battery: to the consideration of these phenomena we shall return. Light also may excite in the organ of touch a sensation with definite extent; for instance, the sensation of the parts warmed by the light of the sun has its limits as to extent. But ordinarily the impressions which inform us of the qualities and conditions of external bodies through the medium of the sense of touch, are mechanical contact, friction, concussion, pressure, or the communication of the vibrations of bodies, which we feel as tremours. By means of mechanical impressions on the sense of touch we obtain the first and most important information regarding the form and density of bodies, of which information reason afterwards makes use to interpret the perceptions of the other senses.

The distribution of nerves of common sensation throughout the entire mass of the limbs, indeed throughout most parts of our body, gives to our sense of touch the faculty of distinguishing the extension of our own body in all its dimensions; for each point in which a nervous fibre terminates is represented in the sensorium. Collision with other bodies also, if forcible enough, may excite sensation to a certain depth in the mass of our body, and produce the perception of contusion in all the dimensions of the "cube." Usually, however, the three senses which make us acquainted with the space occupied by bodies, submit to our perception the property of superficial extension only, owing to the exciting causes acting only on the sentient surfaces. The sense of touch has, however, here this advantage over the sense of vision, that the parts endowed with it can be made to embrace a body in several directions; and although the sensation even then affords essentially only a perception of superficial extension, namely, of that of the surface of our body corresponding to the surfaces of the object, yet the mind, by taking into account the movements required for the embrace of the object, obtains from a sensation of superficial extent an idea of a body with a certain cubic capacity.

There exists in this respect less real difference between the sense of vision and that of touch than is generally supposed. To place them on an equality, it is only requisite that the eye should be able to change its position so as to look towards the different surfaces of an object; and this defect can be supplied by changing the relative position of our body and the object.*

The sense of hearing is almost totally incapable of perceiving the quality of extension; and for this reason, that the organ of hearing has no perception of its own extension. The cause of this difference between the senses is not known. The retina, even when the subject of no excitement from without, perceives its own extension and locality as darkness before the eyes. The organ of smell is sensible at least of the organ in which the odours are perceived, and is conscious of the whole cavity of the nostrils being occupied by a penetrating odour; we cannot make the odorous substance act on less than the entire nasal cavity. With respect to the sense of hearing, on the contrary, we have no perception at all of the part at which the sound is heard.

The sensation of motion is, like motion itself, of two kinds,—progressive and vibratory. The faculty of the perception of progressive motion is enjoyed in different manners by the three senses of vision, touch, and taste,—by those senses, therefore, which are capable of recognising extension in space generally, on which capability the former faculty is indeed dependent, and of which it is the mere result. An impression is perceived travelling from one part of the retina to another, and the movement of the image is interpreted by the imagination as motion of the object; the same is the case in the sense of touch. The

* [See the remarks on the estimation of the form of objects by vision in the third chapter of the section on vision.]

movement of a sensation of taste over the surface of the organ of taste can also be recognised.

The motion of tremors, or vibrations, is perceived by several senses. This faculty is most evident in the cases of hearing and touch; but even the retina and optic nerve appear to be capable of distinguishing such impressions. In the first place, with regard to the sense of hearing, it is known that vibrations communicated through the conducting apparatus of the ear, and lastly through the fluid of the labyrinth to the auditory nerve, are, if rapid, perceived merely as a continuous tone, the acuteness of which varies with the rapidity of succession of the vibrations; but, if they succeed each other slowly, the auditory nerve becomes to a certain degree sensible of the successive vibrations as an intermittent sound, and not merely of the general impression as a continued tone.

The vibrations which in the organ of hearing give rise to the sensation of sound, are perceived by nerves of touch in the skin as tremors frequently attended with the general impression of tickling; for instance, when a vibrating body, such as a tuning fork, is approximated to a very sensible part of the surface. These are completely parallel phenomena to those produced by vibrations in the organ of hearing. Just as the latter organ perceives the impulses of a vibrating body separately as a series of unmusical sounds, and their rapid succession as a continuous tone, so the nerve of touch is sensible of distinct tremors, and if the vibrations succeed each other with sufficient rapidity, becomes the seat of the itching or tickling sensation peculiar to the sense of touch.

The experiments of Savart with the toothed wheel, and those of Cagniard la Tour with the siren, (see page 973,) have proved that the undulatory motion of vibrations is not necessary for the production of the sensation of sound in the organ of hearing, and that a rapid succession of mere impulses has the same effect, producing a musical note. In this respect, also, the action of the impulses of a body upon the nerves of touch forms a parallel to the phenomena produced in the organ of hearing; for the nerves of touch, brought into contact with a vibrating tuning-fork, receives a succession of impulses, of which each singly would not produce the sensation of tickling or itching.

The faculty of discerning the rate of succession of impressions is possessed by all the senses, though in a high degree only by the auditory nerves, in which its delicacy is very remarkable.

The instrument invented by M. Savart, in which tones are produced by the friction of the teeth of a revolving wheel against a hard body, has afforded the means of determining more accurately than was before possible the deepest and most acute notes perceptible by the ear. Savart has shown that tones which correspond to 24,000 impulses, or 48,000 simple vibrations, in a second, if of proper intensity, may still be heard.

Two impulses succeeding each other, or four successive vibrations, are sufficient to form a tone of which the pitch can be compared with that of other tones; that is to say, a tone which, if continued a second, would require 1000 impulses to produce it, will be recognisable if only two of the impulses are heard, and will be distinguishable from another sound which in a second would have 2000, or more or less impulses. From this it results that the sense of hearing can discriminate the interval of $\frac{1}{12000}$ of a second, since 24,000 impulses in a second upon Savart's instrument produced the most acute sound which could be perceived by the ear.

The eye can communicate to the sensorium the image of a vibrating body, and can distinguish the vibrations when they are very slow; but here the vibrations are not communicated to the optic nerve in such a manner that the latter repeats them, or that it receives their impulses; while in the ear the vibrations can be imparted directly to the auditory nerve, in consequence of this nerve being spread out on parts which contain the "fluid of the labyrinth." The optic nerve is not in the condition either to propagate or to receive vibrations, such as those of a sonorous body; to adapt it for such a purpose, it would require to be spread out, like the auditory nerves, upon sac-like membranes, filled and surrounded externally with fluid, and to have connected with it an apparatus for conducting the vibrations from without. If the optic nerve were, like the nerves of hearing and touch, capable of the perception of vibrations, the effect of the propagation of the vibration of an external body through the air to the retina would be a general appearance of light, just as sound is the result in the auditory nerve. I have already mentioned that the impulses of a vibrating tuning-fork brought into contact with the eye, are not adequate to excite the peculiar sensibility of the optic nerve. The cause of this may be either that the impulses are too feeble, or that they succeed each other too slowly. The feebleness of the impulses which do not strike immediately upon the retina, is probably a principal cause; for a stronger impulse upon those parts of the eye where the retina exists, produces the sensation of light. It is possible, also, that very feeble impulses, if repeated with much greater rapidity, and acting on the retina itself, would excite its peculiar sensation — light. Such is the mode of action of external light upon the eye according to the "undulation theory," which has gained increased probability during the later steps of the science of physics. Newton* applied the theory of the undulations of light to the explanation of vision. According to the "undulatory theory," colours are the result of the different rapidity of the vibration and length of the undulations. The undulations which excite in the eye the sensation of violet, are the shortest; according to

* Optics. London, 1704, p. 135. Query 12.

Herschell's calculation, their length is 0·0000167 of an inch, and their number in a second is 727,000000,000000. The undulations of the red ray are the longest; their length being 0·0000266, and their number in a second 458,000000,000000. The vibrations of bodies which excite the sensation of sound in our sense of hearing are much slower. The column of air of the thirty-two feet organ-pipe vibrates thirty-two times in a second; and, according to M. Savart, tones are perceptible which result from seven or eight impulses only during a second, each impulse having a duration of $\frac{1}{16}$ of a second.

We are made acquainted with chemical actions by several senses, but principally by taste, smell, and touch, and by each of these senses in the mode proper to it. Volatile bodies disturbing the conditions of the nerves by a chemical action, exert the greatest influence upon the organ of smell; and many matters act on that sense which produce no impression upon the organs of taste and touch,—for example, many odorous substances, as the vapours of metals, of lead for instance, and of many minerals, &c.

It cannot, however, be stated as a general rule that volatile substances are perceived only by the sense of smell; for the same substances are also capable of impressing the senses of touch and taste, provided they are of a nature adapted to disturb chemically the condition of those organs, and in the case of the organ of taste are dissolved by the fluids covering it. Some volatile substances — as, the vapours of horse-radish and mustard, and acrid suffocating gases, — act very powerfully upon the common sensitive nerves of certain tracts of mucous membrane, as the conjunctiva and the mucous membrane of the lungs, exciting merely modifications of common feeling; many volatile matters also excite the sensations of burning, pain, &c. in the organ of touch when the skin is denuded of its epidermis.

It is not known whether fluid bodies are capable of exciting the peculiar energy of the organ of smell [in man]; and, owing to the position of the organ, we have little opportunity of deciding the question by experiment. Although nothing of the kind has ever hitherto been observed in man, it is not *à priori* to be regarded as impossible, since even volatile substances must be dissolved by the fluids of the mucous surface of the organ of smell before they can act on the olfactory nerves. Fishes, however, afford us a direct example of smell being excited by substances in the fluid state; and I cannot conceive why the nerves of smell in any animal should not be excited to their peculiar sensation by a fluid which excites in the nerves of taste the sensation of taste. The perception of odours in the air and water bear the same relation to each other as respiration in the air and water.

Fluid bodies, applied to the organs of touch and taste, produce chemical disturbances in their nerves, which excite in each a different sensation; mustard, alkalies, acids, and salts, produce upon the skin, and upon the tongue, totally different effects. Their chemical action must primarily be the same; but the reaction excited differs according to the property of the nerves. On the tongue, however, both results are most probably produced in different nervous fibres at the same time, and by the same substance. Of all the nerves of sense, that of taste is most exposed to chemical influences, and is most affected by very slight modifications of the chemical constitution of bodies. The different conditions as to sensation, into which the nerves of touch can be thrown by chemical agents, are not by any means so numerous; moreover, these nerves are, at least upon the skin, (not on the mucous membranes,) protected from chemical influences by the epidermis.

In consequence of their contact with and reaction against external chemical influences, the three senses, smell, taste, and touch, become important instruments for the distinction and recognition of different substances, although neither of them reveals to us anything of their internal properties. The impressions produced on the senses by bodies similarly constituted are not always the same, and those produced by bodies of different chemical constitution are not constantly different.

The senses of sight and hearing are not exposed to the action of chemical influences from without; but it must not thence be concluded that they are insusceptible of excitement by such influences.

An important difference between the senses has reference to the proximity or distance of the bodies concerning which they give us information. Strictly speaking, the senses make us conscious only of that which is immediately present in them. By the eye we do not really perceive the luminous body; but the ends of the rays emitted from it strike the retina, and the parts of that membrane thus acted on become the seat of sensation. By the ear we do not feel the vibrating body, but merely the impulses transmitted to it from that body. Our imagination influences and modifies so powerfully the idea communicated to our sensorium by the act of vision, that this sense appears to us to have an action exterior to our body, and, in place of the images depicted on the surface of the retina, the imagination conceives the idea of real objects; the image of a country, which occupies the space of a window, seems to the imagination an immediate perception of the different near and distant objects. In the senses of smell, taste, and touch, the imagination cannot have so great an influence: we refer, it is true, the sensations in the nerves to the objects themselves; but, since the objects excite the sensations of taste and touch by immediate contact, we become on reflection immediately conscious that our notions concerning the properties of the bodies are derived with only a relative degree of certainty from the affections which they induce in our organs of sense.

IX. *That sensations are referred from their proper seat towards the exterior, is owing, not to anything in the nature of the nerves themselves, but to the accompanying idea derived from experience.*

To know the first independent action of our senses distinct from the results of their education, it would be necessary that we had a full recollection of the first impressions made upon them independently of the ideas obtained through their means. This is impossible. Obscure ideas arise even from the first impressions on the senses of the child. It only remains for us then to analyse the act of sensation and the idea with reference to their real import. Doing this, we find in the act of the mind which accompanies sensation, opposed to each other, *the percipient conscious subject*, or self, of the sentient body whose conditions, whether internal or determined from without, are objects for this "conscious self," and the *external world*, with which the sentient body is brought into collision. To the mental consciousness,—to the "self" of the animal being,—every sensation, every motive from without, every "passion" in the logical sense, is something external. The "self" of the individual opposes itself as a free "subject" to the most intense sensations,—to the most tormenting pains. The limb which gives us pain can be removed without the integrity of the individual spirit being diminished; the "self" of the being may be deprived of most of the limbs (parts) of the organic body, and yet be itself as perfect as before; but we have thus far made no distinction between the "exterior" which the organised limbs of our body form in relation to the consciousness of our "self," and the "exterior" which the external world itself forms with regard to our body. The origin of this distinction can be recognised most easily in the sense of touch, which is the first to come into collision with the external world. If we imagine a human being, in which—as in the fœtus in utero, for example,—the sense of vision has never received any impressions, and in which sensations of touch merely have been excited by impressions made upon its body from without, it is evident that the first obscure idea excited could be no other than that of a sentient passive "self" in contradistinction to something acting upon it. The uterus, which compels the child to assume a determined position, and gives rise to sensations in it, is also the means of exciting in the sensorium of the child the consciousness of something thus distinct from itself and external to it. But how is the idea of two "exteriors,"—of that which the limbs of the child's body forms in relation to its internal self, and of the true exterior world,—developed? In a twofold manner. In the first place, the child governs the movements of its limbs, and thus perceives that they are instruments subject to the use and government of its internal "self;" while the resistance which it meets with around is not subject to its will, and therefore gives it the idea of an absolute exterior. Secondly, the child will perceive a difference in the sensations produced, according as two parts of its own body touch each other, or as one part of its body only meets with resistance from without. In the first instance, where one arm, for example, touches the other, the resistance is afforded by a part of the child's own body, and the limb thus giving the resistance becomes the subject of sensation as well as the other. The two limbs are in this case external objects of perception, and percipient at the same time. In the second instance, the resisting body will be represented to the mind as something external and foreign to the living body, and not subject to the internal "self." Thus will arise in the mind of the child the idea of a resistance which one part of its own body can offer to other parts of its body, and at the same time the idea of a resistance offered to its body by an absolute "exterior." In this way is gained the idea of an external world as the cause of sensations. Though the sensations of the being actually inform him only of the states of himself, of his nerves, and of his skin, acted on by external impressions, yet, henceforth, the idea of the perception of the external cause becomes inseparably associated with the sensation of touch; and such the condition of sensation in the adult. If we lay our hand upon a table, we become conscious, on a little reflection, that we do not feel the table, but merely that part of our skin which the table touches; but, without this reflection, we confound the sensation of the part of the skin which has received the impression with the idea of the resistance, and we maintain boldly that we feel the table itself, which is not the case. If the hand be now moved over a greater extent of the table's surface, the idea of a larger object than the hand can cover is obtained. If, to encompass the resisting object, the hand require to be moved in different directions and planes, the idea of surfaces applied to each other in different directions is conceived, and thus the notion of an external solid body occupying space obtained.

Our perception by sensation of the muscular movements necessary for thus passing our hand over the different surfaces of an object, is the immediate source of our idea of the external body; for the first idea of a body having extension and occupying space arises in our mind from the sensation of our own corporeal extension. This consciousness of our own corporeal existence is the standard by which we estimate in our sense of touch the extension of all resisting bodies. The question, whether the idea of space is originally innate in our sensorium, and influences all our perceptions, or whether it is the result of experience, may be here passed over: we shall return to it in discussing the physiology of the mental faculties. Thus much only is certain, that even though the idea of space did not originally exist as an obscure faculty in the sensorium, which is afterwards called into action and applied when sensations begin to be perceived, it would assuredly be obtained by experience in the first acts of the sense of touch.

The obscure conceptions of a percipient body opposed to the external world, and itself occupying space, concerning the attribute of extension, or corporeal existence of external things, already exist, therefore, and have acquired some degree of lucidity and certainty before birth, at which time the sense of vision comes into action. The sensations of vision, in consequence of this, become soon intelligible; and the ideas already obtained through the means of the sense of touch are readily applied to their interpretation.

It is exceedingly difficult, if not quite impossible, to form a conception in any degree probable of the mode in which the child judges of the first impressions made upon the retina, and to decide whether it regards the image in its eye as a part of its own body, or as something external. The image cannot at all events be regarded as identical with the percipient "subject," or "self;" for, like pain and everything that is felt, it is an object opposed to this "self" of the child; but whether, as an object, it be looked upon as a part of the living body, or as something external and removed from it, is not so easily decided. It has been frequently asserted to be a peculiar property of the sense of vision that the sensation perceived by it does not, as in the sense of touch, appear to occupy the seat of its production,—that the retina does not perceive any sensations in itself; and that the sensation becomes an object of perception, not in the retina, but far distant from it. This cannot, however, be asserted thus absolutely; for the appearance of darkness before the eyes when closed, which is the sensation of the repose and unexcited state of the retina, seems to us to exist only in front of the eyes,—that is, in the situation of the sentient organ,—and neither behind us, nor at the sides, nor in the distance. And this dark field of vision of the closed eyes is the same frame, the same *tabula rasa*, in which, when the eyes are opened, all the images of visible forms appear as the results of the affection of determinate parts of the retina.

If the ideas of external objects, as the causes of sensation, had not already been gained by means of the sense of touch, the first use of the sense of vision would be attended with the same process as we have described to accompany the first acts of touch. The affections of the retina would be objects to the "conscious self" of the child; but whether they belonged to the living body, or were external to it, would not be evident. The child is, however, born already furnished with obscure ideas of objects external to its own body,—with ideas of their real existence as causes of sensations; and sensation and the idea of the external object of perception are already confounded in its sensorium. The next steps of the process, as far as they can be imagined with probability, will be these:

The images of objects are formed in the retina in one surface, just as the retina is extended in that form. They will appear to the mind as depicted on a surface, and will excite no idea of proximity or distance, or of the actual occupation of space. However soon the child may recognise the images as things exterior to itself, they still appear to it to occupy one plane, to be all at the same distance from it: it catches at the most distant, as at the nearest object,—it grasps at the moon. The boy born blind, to whom Cheselden restored sight by operation, saw all objects as if they lay in one plane, although in him the ideas of the corporeal world obtained through the sense of touch were completely developed. It seemed to him as if the objects "touched his eyes as what he felt did his skin."

The images of external bodies will be distinguished from the image of one's own body, which presents itself with them in the field of vision in the following manner. A part of our body throws an image, like external bodies, upon our retina. The part of our body thus visible with external objects, varies in size according to our position; it may be a large or a small portion of the trunk, or of the limbs: the part of the head of which an image can be formed in the retina is very small, such as the sides or tip of the nose, the eyebrows when depressed, and sometimes also the lips. This image of our own body occupies, in nearly all pictures on our retina, regularly some determinate space in the upper, middle, or lower part of the field of vision; it remains constant while the other images are continually changing.

The image of its own body being constant in its position, will in this way be soon distinguished by the child from those images which change their place when the body or eyes of the child are moved. From the movements, also, of this image of a part of its own body, the child will soon still more certainly conceive the idea of its possessing a body distinct from the absolutely external bodies; for these movements of the image in the retina will be observed to correspond to real movements of its body determined by the will. With the visual perceptions of its body will become connected perceptions of touch. The child, touching another part of its body with its hand, will see this act performed by the image in the retina; the image of its hand will touch the image of the other part of its body. In this way certain ideas become so inseparably connected with the sensations of vision, that not only does the image, which consists essentially merely in an affection of aliquot parts of our retina, seem to be external to, and removed to a distance from us, but the sensations come to be regarded as perfectly identical with the objects themselves, notwithstanding their difference of size.

Even the superficial expansion of the field of vision is soon converted by the imagination into a space extending in all directions; for, with every movement of our body, with every step forwards, the forms of the images undergo a change, the remote become near, and the near objects present other surfaces to our view. This change in the images depicted on our retina during the locomotion of our body, must convey to the mind the idea of our moving in space between the different images,—of our advancing through the midst of them; for, during this locomotion, the image of our own body in the field of vision becomes constantly associated with new images of external objects, and the locomotion is the cause of this displacement of the images.

From the foregoing considerations, we conclude that it is owing to the combined action of the mind and the nerves, and not to the action of the sense alone, which would merely perceive the changes produced in itself, that the sensation really seated in the nerve seems to us to be something exterior to the body.

X. *The mind not only perceives the sensations and interprets them according to ideas previously obtained, but it has a direct influence upon them, imparting to them intensity. This influence of the mind, in the case of the senses which have the power of distinguishing the property of extension in objects, may be confined to definite parts of the sentient organ; in the sense gifted with the power of distinguishing with delicacy intervals of time, it may be confined to particular acts of sensation. It also has the power of giving to one sense a predominant activity.*

The attention cannot be directed to many impressions at the same time: in proportion as coetaneous impressions on the senses become numerous, the sensations diminish in intensity, or the mind receives one only with distinctness; while the others are only obscurely, or not at all perceived. If the attention be withdrawn from the nerves of sense, and engaged in intellectual contemplation, deep speculations, or an intense passion, the sensations of the nerves make no impression upon the mind; they are not perceived,—that is to say, they are not communicated to the conscious "self," or with so little intensity, that the mind is at the moment, on account of being quite preoccupied by some other idea, unable to retain the impression, or only recollects it some time after, when the equilibrium of the sensorium is restored, and it is freed from the preponderating influence of the idea which had occupied it. The acuteness which individual senses acquire when others are quite inactive, is therefore readily intelligible; the attention is no longer divided between the several senses, but is wholly engaged in the analysis of the sensations of one.

The blind man acquires such an extraordinary acuteness of touch, as to distinguish with facility the minute elevations on the surface of money, for example; sometimes, indeed, he is able to discriminate between the corpus or grain of one colouring matter and that of another.

By an effort of the mind, however, the detail of a single sensation may be analysed. Since the mind is not capable of directing an equally accurate attention to every part of the cutaneous surface excited to sensation, an acute perception of the state of every part can be attained only by the mind being rapidly directed from the nervous fibres of one part to those of another. By this influence of the mind, an extraordinary degree of troublesome acuteness and permanence may be given to a slight itching sensation at any point of the skin of the face, while it ceases spontaneously when forgotten. The same influence of the mind is evinced in the sense of vision. If we endeavoured to direct our attention to the whole field of vision at the same time, we should see nothing distinctly; but our mental activity is directed first to this, then to that part, and analyses the detail of the sensation, the part to which the mind is directed being perceived with more distinctness than the rest of the same sensation. This does not arise from the middle of the retina, at which the sensibility is greatest, being turned towards the different parts of the object in succession; for, while the position of the axes of the eyes remains the same, we can by a mental effort render the perception of side objects more vivid than they were previously. Without changing the direction of the axis of vision, we can observe in succession the separate elements of a compound mathematical figure, which we are regarding, more accurately than the rest of the figure, which for the time we disregard. A polygonal figure, divided in its interior into different parts by lines, produces a different impression according as the attention is directed to this or that part of the whole: a single triangle in the figure may wholly occupy our attention; at the next moment the attention may be transferred to another figure intersecting the triangle, which, though it existed before, was not observed while the mind was directed to the triangle. The same process takes place in examining architectural ornaments, as roses and arabesques; and the charm which these figures possess, consists in great part in their exciting a vivid action of the attention on different parts of the objects so as to cause them even to present to us an appearance of life. We ordinarily see with both eyes simultaneously when their power of vision is equal; but the mental influence is able to render predominant in intensity the visual impression of one eye, as we shall hereafter prove by experiment; and it may be distinctly demonstrated that, in seeing with both eyes, although under ordinary circumstances we are unconscious of it, a striving for predominance of the sensation takes place between them, and that the sensation perceived is quite different according to the relative intensity of their actions. The experiment of looking upon a sheet of white paper through two differently coloured glasses at the same time, may serve as an illustration for the present. The impressions of blue and yellow, for example, are found in such an experiment not to mingle readily; at one moment the blue, at another the yellow is predominant. Sometimes blue nebulous spots are seen upon the yellow field; at other times, yellow spots of varying magnitude upon the blue field: sometimes one colour alone prevails, and has absorbed the other; sometimes the reverse is seen. The appearance of one colour in spots upon a ground of the other colour, shows indeed that the attention can be directed at the same time to one part of one retina, and to other parts of the other retina.

The influence of mental action upon the sense of hearing, which is not, like the senses of sight and touch, capable of the perception of corporeal extension in space, but has the most vivid perception of the succession of intervals of time in relation to impressions, is of another kind. The discriminating power of the organ of hearing, as to place, amounts at the most to the capability of determining whether the sound be heard with the one or the other ear, or by which it is heard most acutely; and then, when different words are addressed to the respective ears, the attention may be directed more to one impression than to the other. The influence of the attention, however, in distinguishing feeble sounds is highly remarkable: usually we do not perceive the more feeble tones of strings and other musical instruments; but, by attention, we cause their impression, as well as that of the slightest noise, upon the sensorium to become vivid. Still more remarkable is the faculty we possess of distinguishing by attention each of the many tones simultaneously emitted by an orchestra, and even of following the weaker tones of one instrument apart from the other sounds, of which the impressions are then less vividly perceived.

In concluding this introduction to the physiology of the senses, the question naturally presents itself: Is the number of the senses limited? may not some animals be endowed with other senses besides those which we possess? The error into which Spallanzani fell, in ascribing a peculiar sense to bats on account of their expertness of flight along the surface of walls when they could not see them, is well known. Many persons again have ascribed to animals a peculiar sense by reason of their foreknowledge of the changes of weather. Since the state of the atmospheric pressure, the quantity of watery vapour in the atmosphere, temperature, and electricity, have so marked an influence on the animal œconomy of our own bodies, that we are sensible of changes which they undergo, the possibility of such and even greater influences on animals may very well be conceived; but even great dependence on the state of the atmosphere with reference to sensation does not require a new sense.

On the contrary, the state of the atmosphere may be perceived by its influence on the whole nervous system, and particularly through the sensations of the nerves which are most numerous, and most exposed to the atmosphere, namely, the nerves of touch or common sensation. The supposed existence of a special sense for the perception of electricity in some animals is, *à priori*, not admissible; for electricity acts, as we have already shown, upon all the senses, exciting in each the sensations peculiar to it.

The essential attribute of a new sense is, not the perception of external objects or influences which ordinarily do not act upon the senses, but that external causes should excite in it a new and peculiar kind of sensation different from all the sensations of our five senses. Such peculiar kind of sensation will depend on the powers of the nervous system; and the possibility of the possession of such a faculty by some animals cannot, *à priori*, be denied: no facts, however, are known which establish the existence of such a new mode of sensation, and it is, in fact, quite impossible to have any experience of the nature of a sensation in any other beings than ourselves.

Some physiologists have regarded the internal sensations of the sense of touch by which we are made acquainted with the different states of our body, as something different from that sense, and have ranked the conscious perception of the different parts of our frame (Gemeingefühl, cœnæsthesis, or common feeling,) almost on a level with the other senses. This is an error; for the sensations here alluded to are of the same nature as those of the skin which are excited from without, only that in many organs they are more undefined and obscure. Moreover, it is indifferent whether a sense be excited to action from within, or from without; in no sense do we perceive any essential difference between the sensations thus produced. The designation, "sense of touch," expresses certainly a special relation of that sense to the external world; but the act of "touch" merely renders manifest the energies of this sense, which everywhere resides in the same nerves—the mixed cerebral and spinal nerves with double roots. Something analogous to the act of touch is observed in the other senses; it is an action of the sense voluntarily directed; and in the same way there is a voluntary hearing (listening), seeing (looking), tasting, and smelling.*

* The general treatises on the physiology of the senses are: Le Cat, Traité des Sens. Amst. 1744.—Elliot, Observations on Vision and Hearing. London, 1780. (Über die Sinne. Leipz. 1785.) — Steinbuch, Beiträge zur Physiologie der Sinne. Nürnberg, 1811.—Tourtual, Die Sinne des Menschen. Münster, 1827.

SECTION I.

Of Vision.

CHAPTER I.

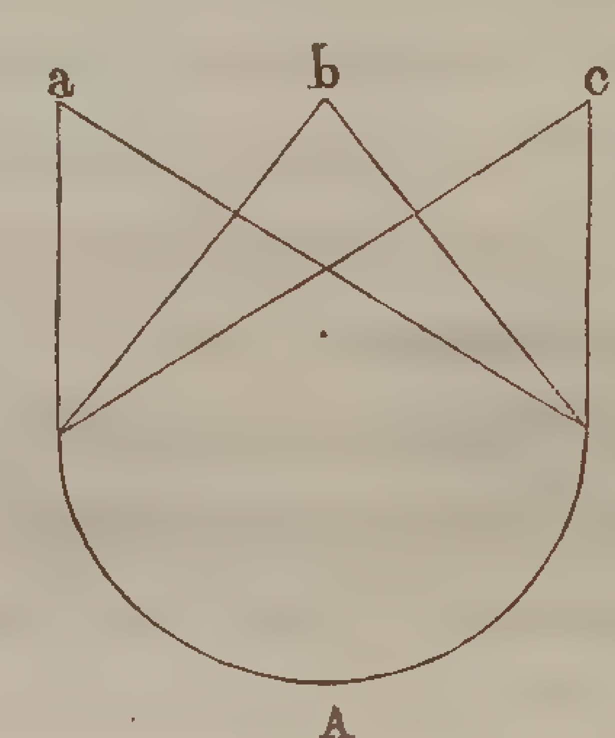
OF THE PHYSICAL CONDITIONS NECESSARY FOR THE FORMATION OF LUMINOUS IMAGES.

a. Of the possible forms of organs of vision.

From the facts stated in the introduction to the physiology of the senses we have learnt that light and colour are sensations of the optic nerve and retina, and that the appearance of darkness before the eyes is the sensation proper to the state of repose, or unexcited condition of the retina. The sensations of light and colour are produced, in the midst of this darkness, wherever aliquot parts of the retina are excited by any internal stimulus, such as the blood, or by an external stimulus, such as mechanical pressure, electricity, &c. The seat of the sensation varies with the part of the retina acted on by the stimulus. The luminous spectrum produced by pressing upon one side of the closed eye is always seen upon the opposite side; and those produced by exerting pressure upon the upper or lower part of the retina are also seen at the opposite points of the field of vision. If the pressure is made by means of a small body, such as, for example, the blunt point of any instrument, and the parts of the retina affected by it consequently of limited extent, the luminous image is also small. If, on the contrary, the pressure be made over a greater extent at the angle of the eye with the edge of some body, the image produced has a corresponding extent. These images are not defined, on account of the pressure upon the eye-ball through the eye-lids and coats of the eye being necessarily diffused to a certain distance around the space which the pressing body itself would act upon. If, however, it were possible to confine the pressure accurately to determinate portions of the retina, we should doubtless be able to produce perfectly defined images by mechanical means. The physical imponderable principle which has received the name of light, because the luminous affections of the retina are usually caused by it, produces, when the whole of that nervous expansion is uniformly affected by it, the sensation of a diffused light occupying the whole field of vision, in place of the darkness seen before the eyes when the retina is not excited. But if this well-adapted and salutary stimulus of the retina acts only on definite parts of the retina, luminous images are formed at those parts, and the shadows of these images are the intervening parts of the retina which are not stimulated to the sensation of light, and consequently retain the sensation of darkness, as when the eyes are closed. It is thus that we are enabled to see bodies, which either themselves radiate the principle called light,—luminous bodies, or, being impermeable by that principle, reflect it when they receive it from other bodies, and so direct it into the sentient eye. The sensation of light is then produced at a determinate part of the eye, and we think to see the body, which, however, merely reflects into the eye the principle capable of exciting the sensation of light, which it has itself received from elsewhere.

But that the light should produce in the retina luminous impressions or images of the objects from which it comes, it is necessary that the light emitted or reflected from determinate parts of the external objects should stimulate corresponding parts only of the retina; this requires the concurrence of certain physical conditions. Light radiates from a luminous body, in all directions, when the media offer no impediment to its transmission. A luminous point will therefore illuminate all parts of a surface opposed to it, and not merely one single point: in the exposed surface of the retina consequently the luminous point would excite the sensation of light in every part and not in one point only; and the same applies to all points from which light is radiated towards the retina. For example, if A, (fig. 60,) were the concave surface of the retina, red light emitted from the point *a*, colourless light from the point *b*, and yellow light from the point *c*, would each respectively illuminate every part of that surface, and the whole retina would consequently see red, white, and yellow light; that is to say, every point of it would be at the same time excited to sensation by three kinds of light, and the impression would necessarily not correspond to the differently coloured points *a*, *b*, and *c*, but would be a mixed impression of three different lights, of which neither would be distinguished separately. The same would be the result if the retina were convex anteriorly, as in insects and crustacea. A retina, therefore, without any optical apparatus placed in front of it to separate the light of different objects, would see nothing distinctly, but would merely perceive the general impression of daylight, and distinguish it from the night.

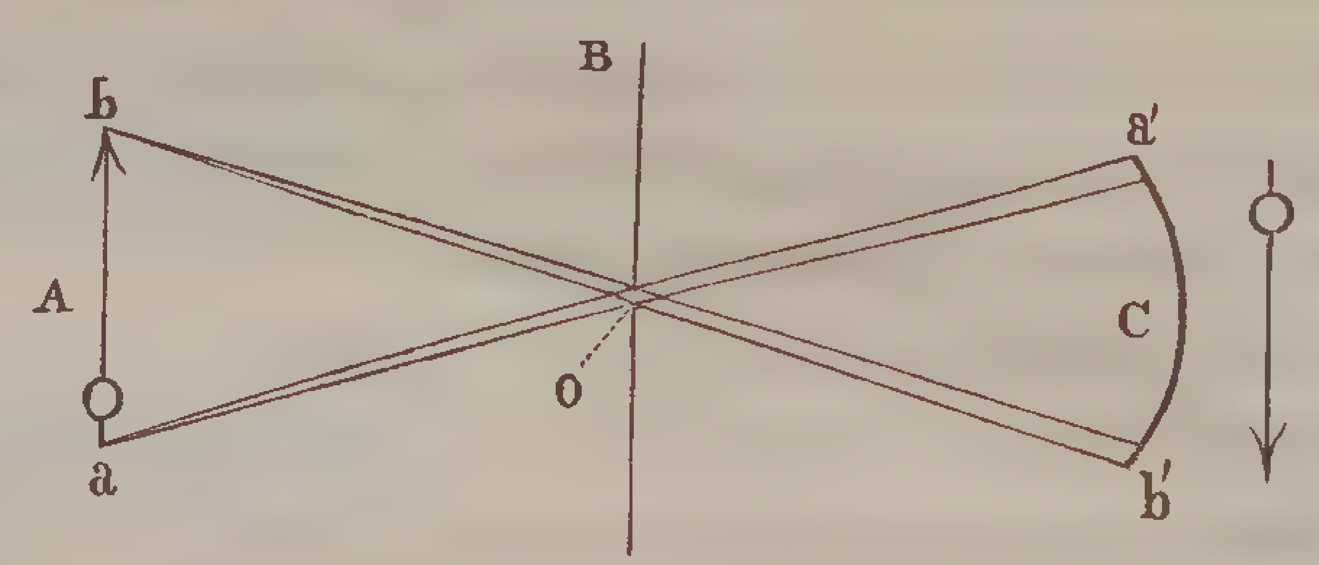
Fig. 60.



We see, therefore, that for the production of a luminous image in the eye, corresponding to the bodies emitting or reflecting the light, it is necessary that there should be apparatus to cause the light from the separate points *a*, *b*, and *c*, to act only upon separate points of the retina in the same order, and to prevent the light from different points of the external objects from acting on one point of the retina. There are three modes in which this can be effected, and nature has made use of two of these in the construction of eyes for distinct vision.*

1. Let A, (fig. 61,) be the luminous body, C the retina, B an opaque screen intercepting the light, except at the point *o*, where there is an opening. Through this opening the retina can alone receive light, and will consequently be in the greater part of its extent quite darkened. In such a case the luminous rays from *a*, passing through the opening *o*, will fall on the retina at *a′* only, those from *b* at *b′* only, and every point of the object between *a* and *b* will be represented at special points of the retina between *a* and *b′*. *a* and *b* in the body A, are mathematical points; *a′* and *b′* in the illuminated retina are small spots, which will be larger, and the image consequently less distinct, in proportion as the opening *o* is larger. The smaller the opening *o*, the more defined will be the image, but it will be proportionally fainter, for the smaller will be the cone of light which passes from each point of the body A through the opening.† Nature has made no use of this means of forming images; probably because the result obtained is too inconsiderable, and because intensity of light at each point cannot be attained without simultaneous loss of distinctness.

Fig. 61.



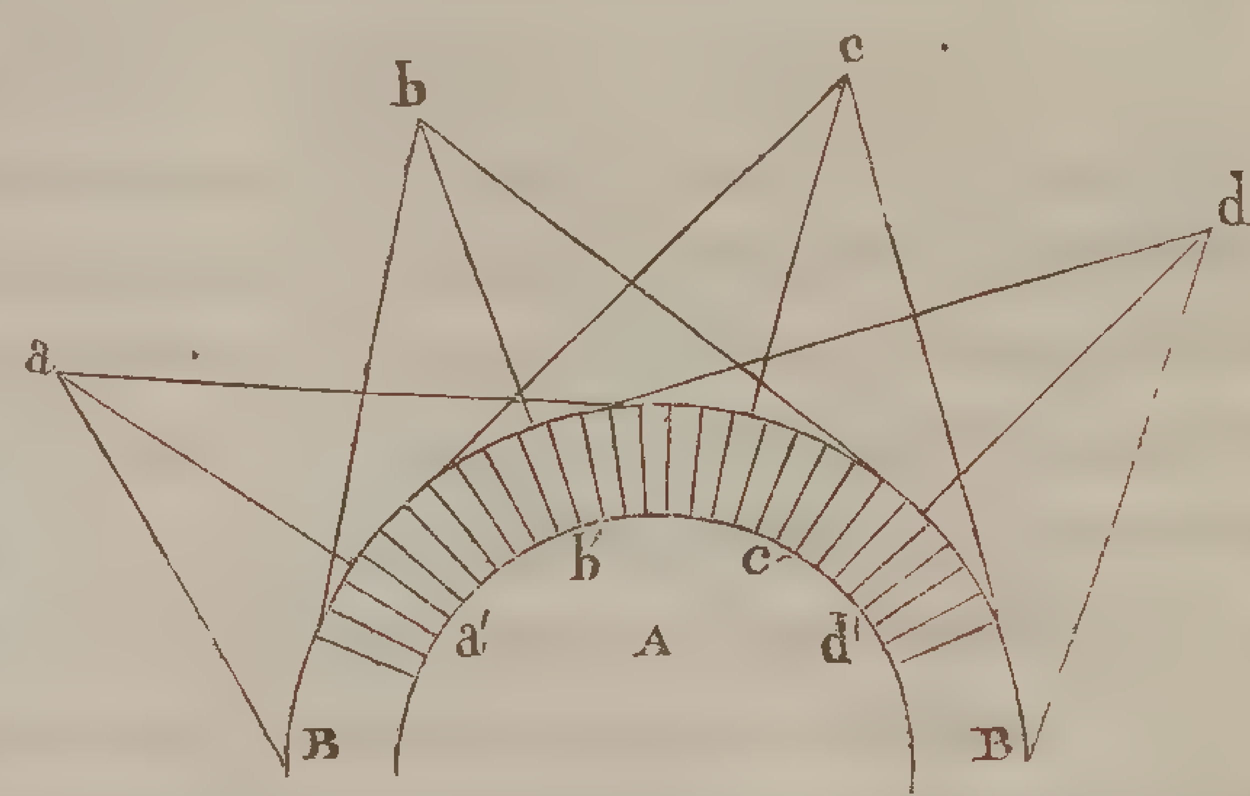
2. The second mode of separating the rays of light so as to form an image upon the retina, to which I first directed attention in 1826,‡ is the following:—In front of the retina, and perpendicularly to its surface, are arranged side by side in immense numbers transparent cones which allow the passage of that light only to the retina which comes in the direction of their axis; while all the light which enters them laterally, and therefore must fall obliquely upon their walls, is absorbed by the pigment which invests them. Let A, (fig. 62,) represent the retina, which has a convex spherical surface, in the direction of the radii of which the transparent cones B B, are arranged. Those rays

* See J. Müller, Vergleichende Physiologie des Gesichtssinnes. Leipz. 1826, p. 307.

† For further observations on this mode of forming images see Dr. Roget's Animal and Vegetable Physiology, London, 1834, vol. ii. p. 451; and Kunzek, Die Lehre vom Lichte, Lemberg, 1836, p. 28.

‡ In my treatise on the physiology of vision, just referred to.

Fig. 62.



only of the light issuing from the points *a*, *b*, *c*, and *d*, will be able to reach the retina, which have the direction of the radii of the convexity. Thus the point *a*, although it illuminates the whole surface of the eye, will throw its image only at one point, *a'*, of the retina; the point *b*, its image at *b'* only; and so on All the rest of the light from these points, falling obliquely upon the surface of the eye, is excluded.

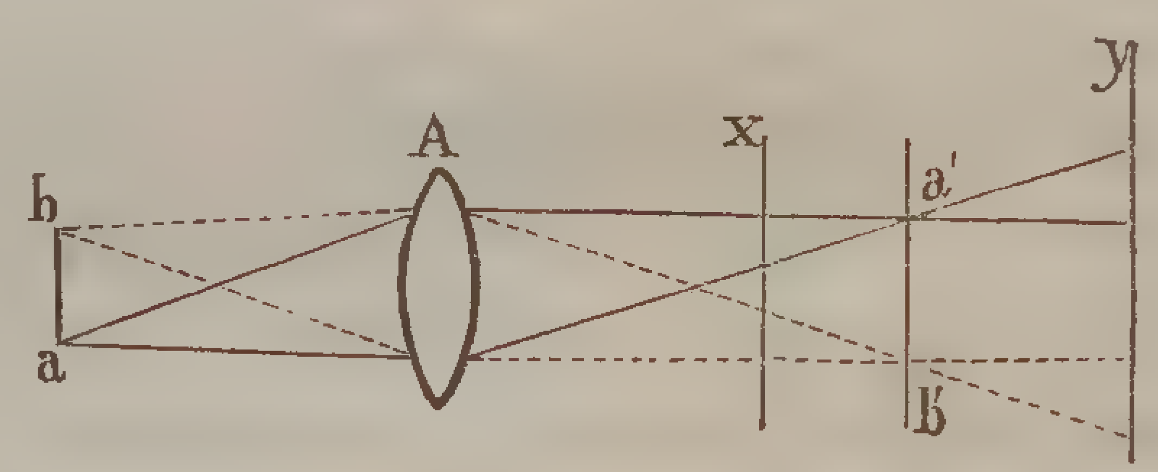
It is evident that the distinctness of the image must be greater in proportion to the number of the transparent cones arranged like radii upon the surface of the retina; and that, if there were a thousand of them, a thousand portions of the field of vision would be depicted in the image; and that, if their number were ten thousand, the distinctness of the image would be ten times greater. This arrangement of parts, which might be conceived as a possible form of visual organ, I have found really to exist in the compound eyes of all insects and crustacea. Such an organ of vision must, of course, be spherical, or a segment of a sphere. If its circumference approach the form of a plane surface, the exterior cones—those nearest to the margin of the eye—will necessarily be less divergent, and will correspond to a small portion only of the external world. In proportion, however, as the convexity of the eye, and the portion of a sphere which it forms, is larger, the extent of the field of vision will increase.

An image formed by several thousand separate points, of which each corresponds to a distinct field of vision in the external world, will resemble a piece of mosaic work; and a better idea cannot be conceived of the image of external objects which will be depicted on the retina of beings endowed with such organs of vision, than by comparing it with perfect work of that kind. A disadvantage which attaches to such an organ of vision is, that the quantity of light transmitted from one point of an object through the transparent cones must be extremely small. It appears, however, as we may observe in the evening when daylight is departing, that, for the mere discernment of objects even by the human eye, a very slight intensity of light is sufficient, — a light extremely feeble compared with that to which the eye is exposed during bright daylight; and even in our eye nature has been at more pains to moderate the quantity of light than to admit all that could enter. The smallest possible pupil is in a bright day adequate for vision.

This kind of optical apparatus may be called the mosaic dioptric instrument, in contradistinction to the concentrating collective organ.

3. In the forms of apparatus hitherto described, the light, issuing from the different points of the external body, was kept isolated and confined to different points of the receiving organ by separating and excluding the rays which would interfere with this object; but the same end may be attained with more perfect definition and greater intensity of light by collecting together again into one point the different diverging rays emitted by each point of the external body. Here, however, it is, of course, requisite that the organ destined to receive the image should be situated exactly at that distance at which the rays are again collected to a point,—that is to say, at the apex of the cone of light. In the other forms of optical instrument, this condition was not necessary; here it is absolute. If, for example, we suppose the transparent body A, (fig. 63,) to have the power of collecting the light issuing from the point *a*, and illuminating the whole surface of A to a point *a′* on its opposite side, and all the light issuing from *b* to the point *b′*, and in like manner of reassembling all the rays from different points between *a* and *b*, to corresponding points between *a′* and *b′*, the most perfect image of *a b* will necessarily be formed at *a′ b′*, and will be seen distinctly if the expansion of the optic nerve be situated at *a′ b′*; while, if the expansion of the nerve be either in front or behind *a′ b′*,—for instance, at *x*, or *y*,—the image will be very imperfect; for, in that case, the light from the point *a* will not be represented by a similar point, but will be dispersed over a considerable space, and so also will the light from each point of the object.

Fig. 63.



The bodies capable of collecting the rays of light in this manner are the transparent refracting media, and the most perfect form for the purpose of the organ of vision is that of the lens, as we shall now proceed to show more particularly.

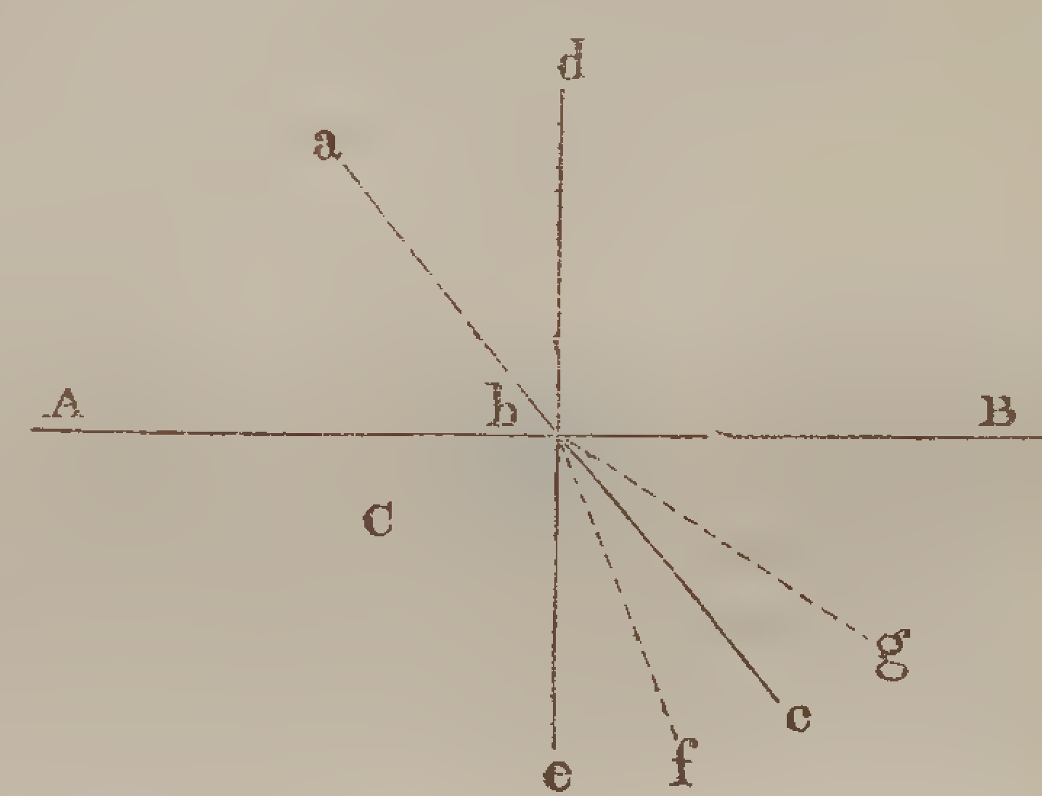
b. Of the physical conditions on which the formation of images by refracting media depends.

The importance of the theory of the refraction of light in explaining the function of vision in man and animals, whose organs of sight have refractive media as essential parts of the apparatus, requires that the principal laws of this theory should be kept in mind.*

* I have extracted the account of the general laws of refraction of light from the best treatises of optics; those of Porterfield, Priestley, Fischer, Biot, Kunzek, and Brandes. Porterfield's treatise, On the Eye, the Manner and Phenomena of vision, 2 vols. Edinb. 1759, contains much very important matter.

When rays of light pass from a vacuum into a transparent body, or from a rarer into a denser medium, if their direction be perpendicular to the surface of the medium which they enter, they continue their course in the same direction; but, if they impinge upon the surface of a denser medium in a direction removed from the perpendicular, they are bent out of their former direction towards that of a line perpendicular to the surface of the medium. Thus, if A B, (fig. 64,) be the surface of the denser medium, the ray of light *a b*, instead of being continued in the direction *b c*, will be bent towards the line of the perpendicular *d e*, so as to have the direction *b f*.

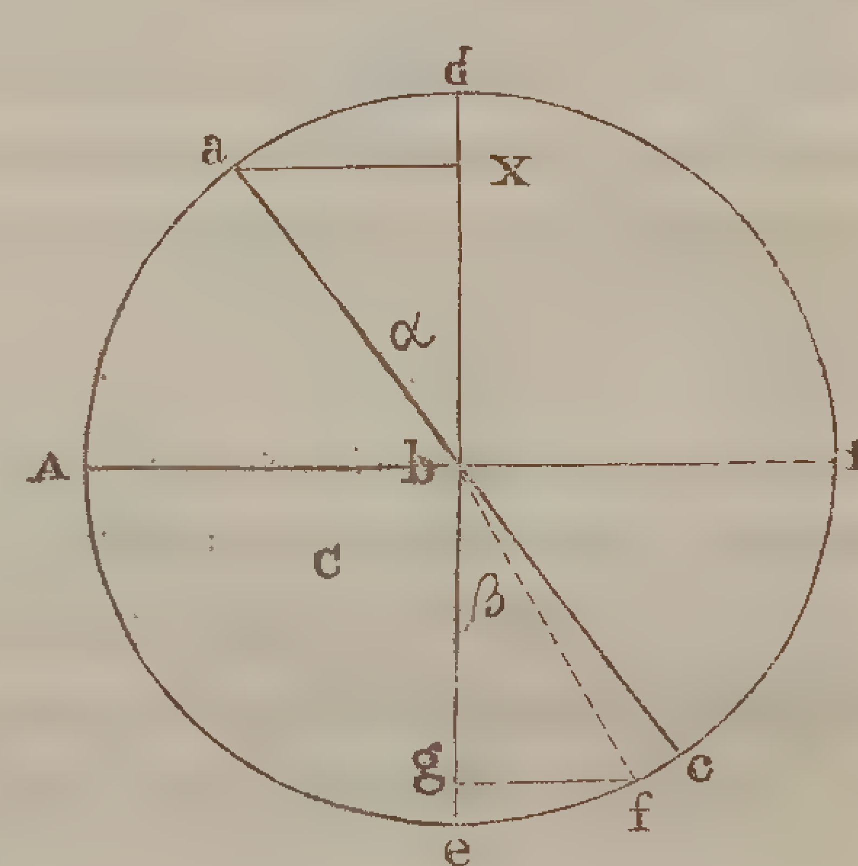
Fig. 64.



When, on the other hand, a ray of light passes obliquely from any transparent medium into a vacuum, or from a denser into a rarer body, it is bent from the perpendicular direction, and, instead of following the line *b c*, will take the direction *b g*.

The incident ray, the refracted ray, and the perpendicular line, lie in the same plane. The law regulating the degree of refraction is the following:—The angle between the incident ray *a b*, (fig. 65,) and the perpendicular *d b*, is called the *angle of incidence*; the angle between the refracted ray *b f*, and the perpendicular *b e*, is called the *angle of refraction*; the line *a x* is the *sine* of the angle of incidence, and the line *g f* the *sine* of the angle of refraction. Experience has taught that, if the two media remain the same, the relation between the sine of the angle of incidence α, and the sine of the angle of refraction β, will also remain the same, whatever be the inclination of the incident ray towards the surface of the refracting medium. The relation of two media in their refracting power will therefore be expressed by $\frac{\text{Sin. } \alpha.}{\text{Sin. } \beta.}$ The sines of the angles only,

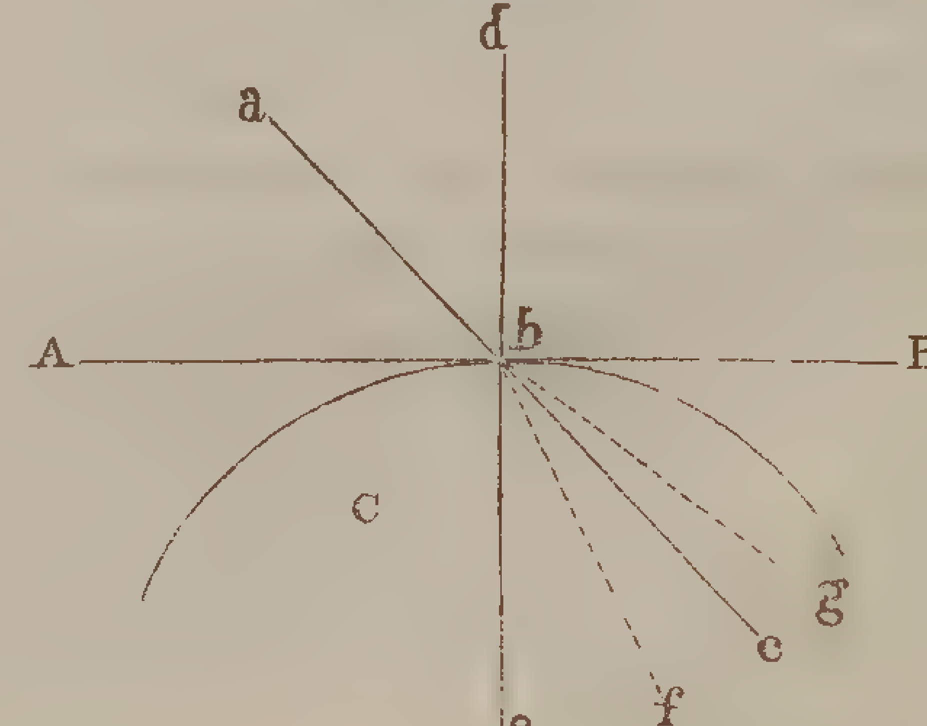
Fig. 65.



and not the angles themselves, have this uniform relation at every possible degree of inclination of the incident ray to the refrangent medium: as long, however, as the angles remain small, as in the case of the central rays passing through lenses, there will be no great error in assuming the relation of the angles also to be constant.

Since a curved surface may be regarded as composed of an infinite number of plane surfaces, the tangent A B, (fig. 66,) of the point of incidence *b*, of a ray of light *a b*, falling upon the curved surface of a refrangent substance, may be taken as the refracting surface, and the perpendicular, *d e*, of the tangent, will be the line towards which the ray will be bent so as to follow the direction *b f*, if the refracting medium be the denser, or from which it will be

Fig. 66.

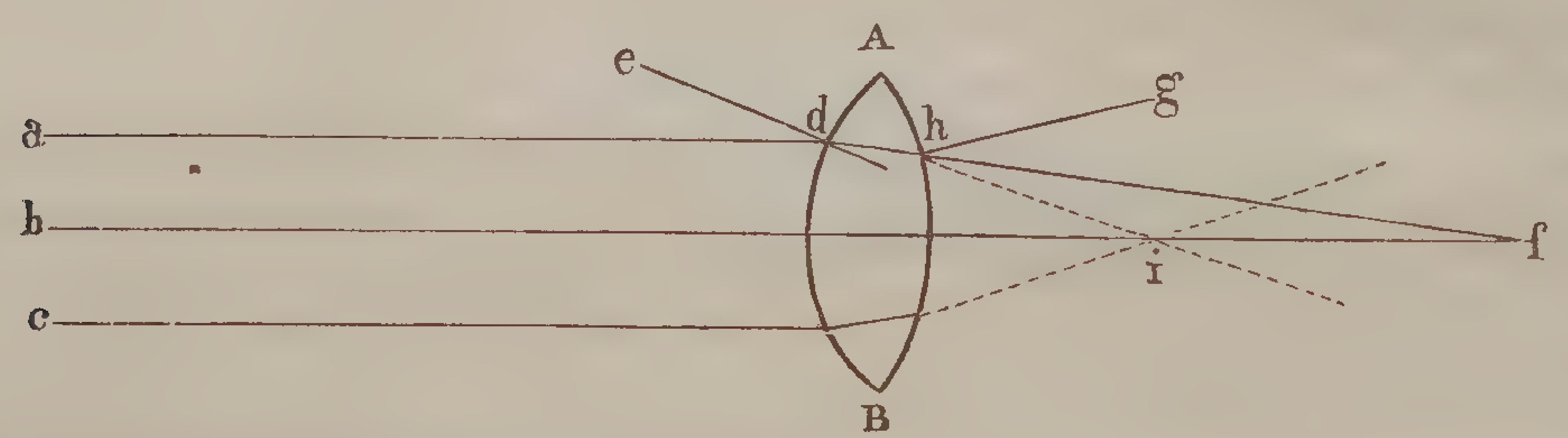


bent to the direction $b\ g$, if the medium which causes the refraction be rarer than that which the ray has previously traversed.

A knowledge of the laws of refraction of light by spherical lenses is important in relation to the study of the function of vision ; for such lenses are, under certain circumstances, capable of reuniting the rays of light issuing from a luminous point into one point, so as to form an image of that point.

If parallel rays of light, or rays of light issuing from a luminous point at a very great distance, impinge upon a plane refracting surface in an oblique direction, they are refracted, but their parallel relation to each other is not altered ; but, if such parallel rays fall upon a lens with a spherical surface, they are made to converge.

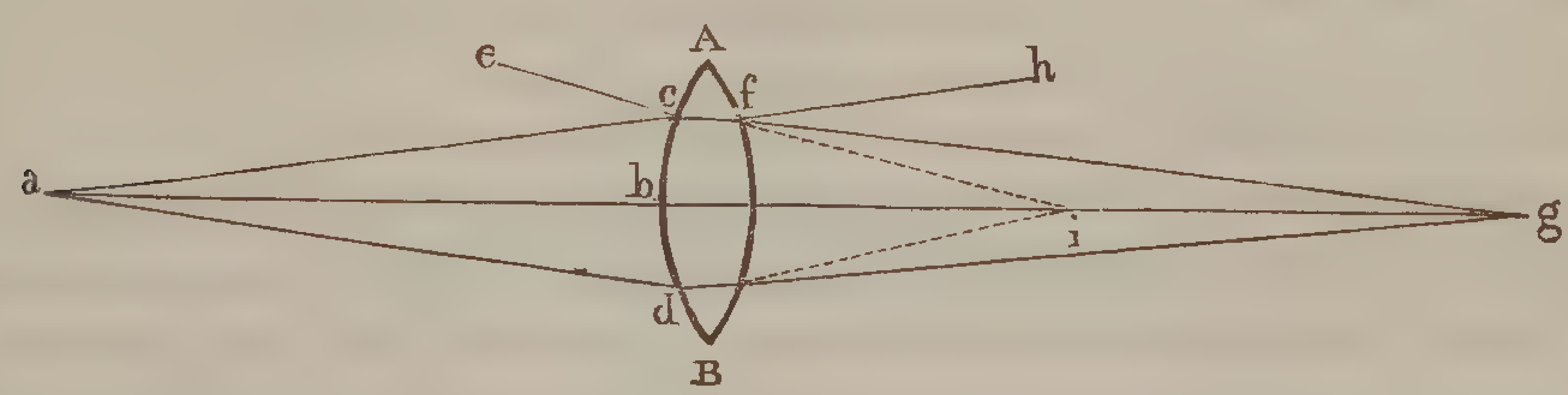
Fig. 67.



a, *b*, and *c*, (fig. 67,) are parallel rays of light ; the ray *b* coincides with the axis of the lens A B, and passes through it without suffering refraction ; but the other rays fall obliquely upon its surface, and issue from it obliquely with regard to its opposite surface, and are consequently refracted : the ray *a* is bent towards the perpendicular *e d*, of the incident surface, and passes through the lens in the direction *d f* ; but at its exit, where it re-enters the rarer medium, it is again refracted and bent away from the perpendicular, *h g*, of the point of surface at which it issues, taking the direction *h i*, so as to approach still more rapidly the ray *b f*. If the rays *a* and *c* be equally distant from the ray *b*, which is coincident with the axis of the lens, the ray *c* will be refracted in precisely the same manner as the ray *a* ; so that both will, after their exit from the lens, intersect the ray *b* at some one point, *i*, where consequently all the three rays will be collected together ; but beyond this point they will diverge. Now, inasmuch as what applies to the rays *a*, *c*, will also apply to all parallel rays which are equally distant from the ray *b*, and impinge together with this upon the lens, all these rays will intersect each other at a common point *i*, which is called the focus. The distance of the focus of parallel rays from the lens depends on the refracting power of the substance composing the lens, and on the degree of convexity of its surfaces ; this focus will of course be, *cæteris paribus*, nearer to the lens the greater the convexity of its two surfaces.

If the incident rays issue from a body situated in the focus of the lens, they will be so refracted by it as to have a parallel course after their exit from it. It follows from this and the preceding law, that, if the rays come from a point further distant from the lens than its principal focus or the focus of parallel rays, but yet not so far distant that the rays may be regarded as parallel, they can neither be concentrated to a point at the principal focus, nor be rendered parallel. On the contrary, such rays will necessarily intersect each other at a point between the principal focus and infinite distance ; and, the nearer the luminous point from which they issued is to the focus of the lens, the further distant will the point of their reunion or intersection be behind the lens, and the more will they approach the parallel direction ; while, the further the luminous point is distant from the principal focus, the less will be the distance of the point to which the rays are made to converge, until at length, the distance of the luminous point being such that the incident rays are essentially parallel, the point of their intersection becomes coincident with the principal focal point of the lens.

Fig. 68.



a, (fig. 68,) is the luminous point further distant from the lens A B than its principal focus ; $a\ b$ is a ray coincident with the axis of the lens, which it traverses therefore without undergoing refraction ; but the ray $a\ c$ is refracted twice, namely, at the anterior and at the posterior surface of the lens, being at the anterior surface bent towards the perpendicular, $e\ c$, of the tangent of the point of incidence, so as to receive the direction $c\ g$, and at the posterior surface bent away from the perpendicular, $f\ g$, to the direction $f\ i$. If the rays $a\ c$, and $a\ d$, impinge on the lens at equal distances from the point b, the ray $a\ d$ will be refracted in exactly the same manner, and to the same degree, as the ray $a\ c$, and both will intersect the central ray at the same point, i. All rays emitted from the point a, which are equally distant with $a\ c$, and $a\ d$, from the central ray $a\ b$, will likewise be assembled at the point i: $a\ c\ d$ may therefore be regarded as the periphery of a cone, which periphery is formed by luminous rays all converging to the point i. The distance of the point i from the lens is called the focal distance for diverging rays, which must not be confounded with the focal distance for parallel rays, or the principal focus. Diverging rays always come to a focus at a point further distant from the lens than the focus of parallel rays, and is more and more distant the nearer the luminous point from which the incident rays diverge is to the lens.

The distance of the focal point at which the luminous rays are collected from the lens, is dependent on three conditions: 1, on the refracting power of the lens in relation to the medium from which the rays enter the lens (n : 1) ; 2, on the degree of convexity of the two surfaces of the lens, which are expressed by the length of the radii of the spheres of which they form part ; 3, on the distance of the object from which the rays issue.

These three conditions being known, the focal distance of the image can be calculated for every distance of the object. The algebraic formula for this calculation is :

$$\frac{n-1}{f}+\frac{n-1}{g}=\frac{1}{a}+\frac{1}{\alpha}.$$

$\frac{n}{1}$ expresses the refracting power of the lens, or the relation of the angle of incidence to the angle of refraction, which, for glass receiving rays of light from air, is $\frac{3}{2}$. $n-1$, therefore, for air and glass would be $\frac{3}{2}-1$. f and g are the radii of the convexities of the lens ; a is the distance of the luminous point from the lens, and α is the desired focal distance of the image. If, for example, the medium be air, and the lens be of glass, and if the radii of the lens be 10 and 12 lines, and the distance of the luminous point from the lens 100 lines, the equation will be as follows :

$$\frac{\frac{3}{2}-1}{10}+\frac{\frac{3}{2}-1}{12}=\frac{1}{100}+\frac{1}{x},\ \text{or}\ \frac{3}{2}-1\left(\frac{1}{10}+\frac{1}{12}\right)=\frac{1}{100}+\frac{1}{x}\ .$$

The distance of the focus for parallel rays may also be found by the formula $\frac{n-1}{f}+\frac{n-1}{g}=\frac{1}{a}+\frac{1}{\alpha}$. The distance of the luminous point from which parallel rays proceed being considered as infinite, $\frac{1}{a}$ here equals 0; hence the formula may be stated thus, $\frac{n-1}{f}+\frac{n-1}{g}=\frac{1}{\alpha}$; or, if α be employed to designate more especially the focal distance for diverging rays, the formula for finding the focus of parallel rays may be, $\frac{n-1}{f}+\frac{n-1}{g}=\frac{1}{p}$.

By combining the formula for finding the focal point of diverging rays with that for the focal point of parallel rays, a yet simpler fundamental formula for the solution of these optical problems is obtained; for, since the first half of the equation is in both instances the same, it follows that $\frac{1}{p}=\frac{1}{a}+\frac{1}{\alpha}$. Here p is the focal distance for parallel rays, a the distance of the luminous point, and α the focal distance of the image from diverging rays; hence the focal distance of the lens for parallel rays, and the distance of the luminous point, or object, being known, the focal distance of the image may easily be found. The equation will be, $\alpha=\frac{a\,p}{a-p}$.

The focal distance of the image of any luminous point is, therefore, found by multiplying the distance of the object from the lens by the focal distance for parallel rays, and dividing the product by the difference between them.*

If the surface which receives the image be not placed at the focal distance, the rays from each luminous point will, of course, fall upon it, not in a point, but dispersed over a larger surface, which is the section of a cone of light. Whether the opaque surface be placed in front or behind the focal point, the effect will be the same: in the one case, the rays of the cone of light will be intercepted before they have been collected to a point; in the second case, they will not strike the surface until they are diverging again in the form of a cone after having intersected each other.

Hitherto the refrangent power of lenses has been considered only in relation to rays issuing from a single luminous point; but if the object have a certain extent of surface, and the points radiating the light from it lie in a plane perpendicular to the line of the axis of the lens, the images of those points will also lie in the reverse order in a

Fig. 69.

similar plane. If $a\,b$, (fig. 69,) be the object, the cone of light issuing from a being refracted by the lens will be concentrated to a point again at α, the cone of light from b will be brought to a focus at β, and those from the intermediate points of the object in corresponding order. The image of the object is inverted,—the part

* For further details of this calculation, I refer to Fischer's Mechanischer Naturlehre, ii. 213; and to Kunzek's Lehre vom Lichte, Lemberg, 1836, 115.

[Rules for finding the focus of parallel, converging, and diverging rays, for lenses of glass in the air, by simple numerical calculation, are given by Dr. Brewster in his Treatise on Optics, p. 39. See also Sir J. Herschell's Treatise on Light, in the Encyclop. Metropol. § ix.]

which was above is below, that which was to the right is on the left side; but the relative position of the individual parts remains exactly the same. The middle rays of the cones of light $a\ \alpha$, and $b\ \beta$, like the central ray of a luminous point lying in the line of the axis of the lens, are scarcely or not at all altered in direction. The other rays of the cone of light converge after refraction towards the middle ray; the image of the luminous point falls in the line of this ray, which consequently determines the position of the image of each luminous point, and the middle rays of the cones of light from the different points determine also the size of the image.

The points towards which the rays from the luminous points of the object, not coincident with the axis of the lens, are refracted to a focus, may be found by calculation; and it is ascertained that if such luminous points, though not in the line of the axis, yet be near it, so that the rays issuing from them and falling upon the lens do not form large angles with its axis, the different points of the image will fall in a plane parallel with the object.

Gregory* observed that the image of an object perpendicular to the axis of a lens of which the surfaces formed parts of spheres was not straight, but bent so as to appear concave towards the lens; and that, to form a straight image, the surfaces of the lens must have the form of the section of a cone (as an ellipse or hyperbole). Priestley admits this; but remarks that the error thence resulting is imperceptible, because the surfaces of the lens are very small parts of a sphere. Kaestner, however, adds that, if the aberration of the rays from the focus be disregarded,—that is, if the angles be regarded as proportional to their sines,—the most exact calculation will discover no curvature in the image of a plane figure.† That the plane of the image is parallel to the plane of the object, when the latter is perpendicular to the axis of the lens, is a matter of experience; and for an image of small extent, the mathematical proof of the axiom is not difficult, and is given with the mathematical calculations in extended works on physics.‡

Optical centre of lenses.—Since the two surfaces of a lens near the central point of these surfaces are parallel, or as good as parallel, rays which pass obliquely through the middle of the axis of the lens will not, after their transit, vary much from their previous direction, provided the points of incidence and exit lie within the parallel part of the two surfaces. Their refraction will be the same as that of rays passing obliquely through a glass plate with two parallel surfaces. The ray at its exit will be bent from the perpendicular to the same degree as it was bent towards it on entering the glass; it maintains, therefore, the same direction. Hence it is, that the middle ray of a cone of light passing with a moderate obliquity through the centre of the axis of a lens, is to be regarded as unchanged in its direction, and that its direction is to be regarded as determining that of the image. The point through which the rays must pass in order not to be refracted from their original direction, where the two surfaces of the lens are of unequal convexity, is not exactly the middle of the axis of the lens, but some point, either in front or behind that middle point, with which it is coincident only when the convexity of the two surfaces is equal. The knowledge of the optical centre of the lens is important for the better understanding of the theory of vision; I shall give here the mode of determining its situation, as stated by Fischer.§ Let n (fig. 70) be the centre of the sphere, of which the anterior surface of the lens is a portion, and m the centre of the posterior surface. a is a given point of the anterior surface, and $a\ n$ consequently the radius of this surface. Let the radius of the

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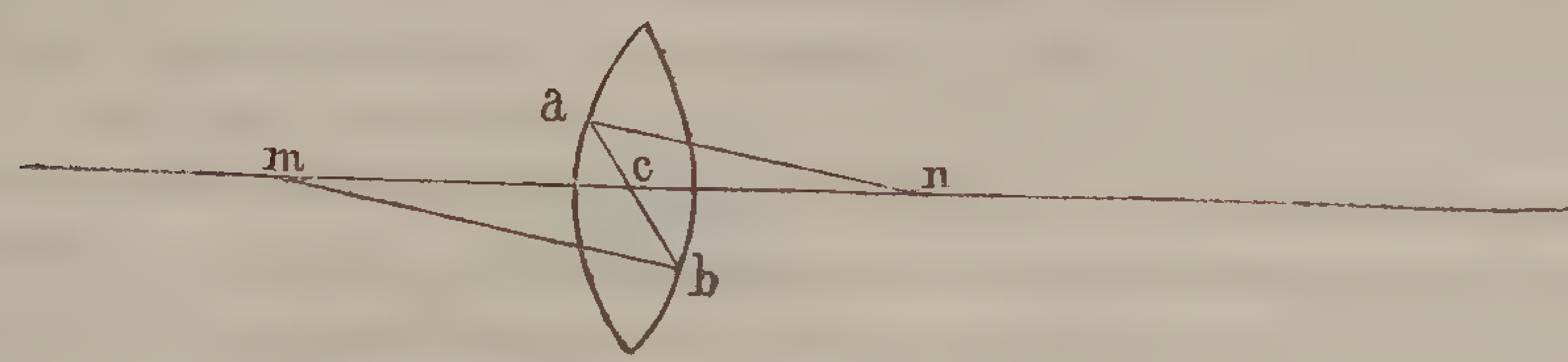
* Priestley's History of Light and Colours.

† Kaestner has given an example of such a calculation in the second volume of the Deutsche Schriften der Götting. Gesellschaft der Wissenschaften.

‡ See Kunzek, Lehre vom Lichte, 120.

§ Loc. cit. p. 217.

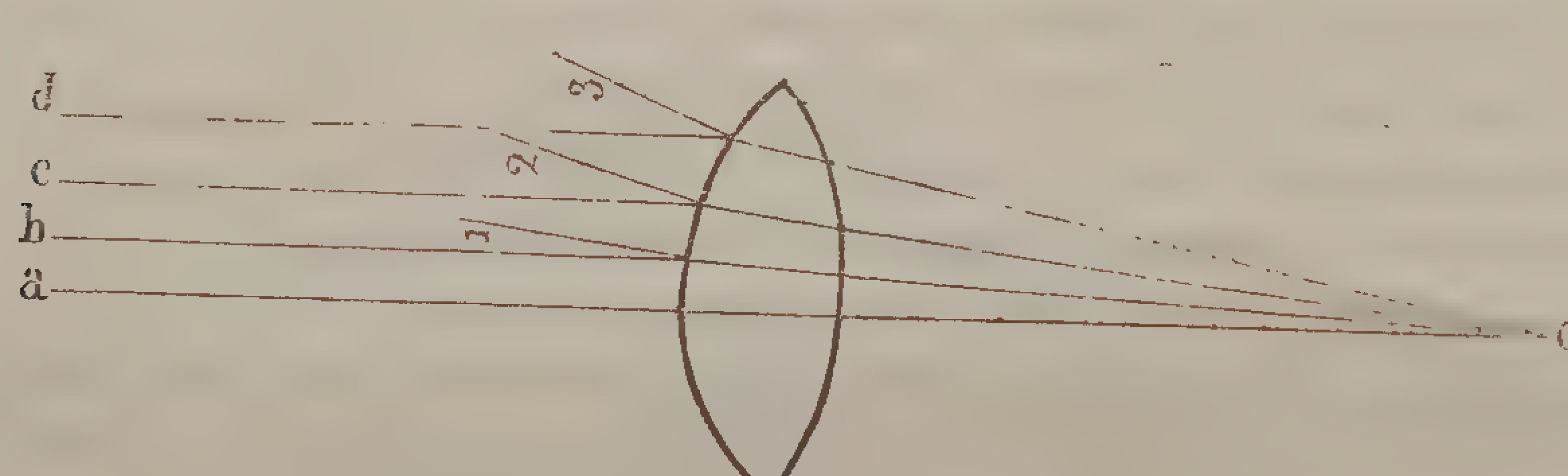
Fig. 70.



posterior surface, *m b*, be parallel with *a n*. The point *c* of the axis of the lens, at which the line *a b* intersects it, is the optical centre ; for, since *a n* and *m b* are parallel, the angles *n a b* and *m b a* will be equal. If *a b* be a ray of light, the angle which this ray makes with the perpendicular *a n* will be equal to the angle which it makes with the perpendicular *m b*. The angle of incidence of the ray entering the glass from the air bears the same relation to the angle of refraction, *n a b*, as the angle of refraction of the ray leaving the glass to the angle of incidence *m b a ;* consequently the angle of incidence of the ray entering the lens is equal to the angle of refraction of the ray leaving the lens, and hence the direction of the ray after its transit must be parallel to that of the incident ray, and the ray must be regarded as unrefracted. In a double convex lens, with unequally convex surfaces, the optical centre will lie nearer to the more convex surface.

Spherical aberration of lenses.—Hitherto we have considered principally the refraction of the rays which traverse the central portion of the lens ; we must now direct our attention to those which pass through its circumference, and to their relation to the focal point. Whatever be the form of a spherical plano-convex or bi-convex lens, it is a constant law that those parallel rays which enter it at an equal distance from its axis are concentrated to the same point; for their angles of incidence and of refraction are equal. In the same manner, in a cone of light, of which the axis is coincident with the axis of the lens, all those rays striking the lens in a circle, and at an equal distance from the axis of the lens, will be concentrated again to one point. But what course do the other rays of the cone take? Are they also brought to the same focus? or have they another focal point? To bring the parallel rays *a, b, c, d,* (fig. 71,) to the focus *o*, the refraction of these rays must increase in

Fig. 71.

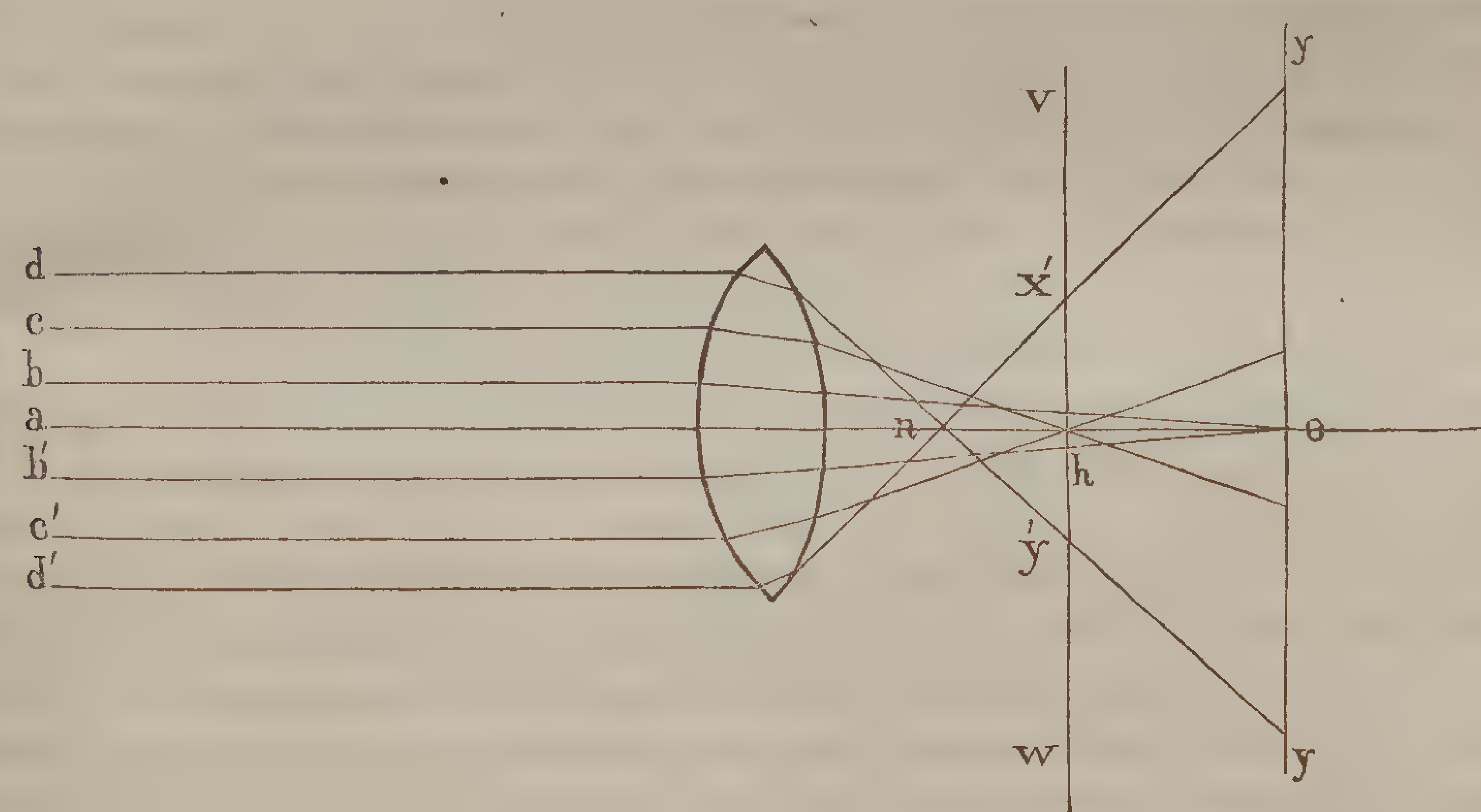


proportion as they are further distant from the line of the axis of the lens. This condition is afforded by media with convex surfaces, for in them the angles of incidence, 1, 2, 3, become greater in proportion as the rays, *b, c, d*, are further removed from the axis *a*. To condense parallel rays to a focus, it is therefore necessary that the surface of the refracting media be convex.

The question now comes, however, in what ratio must the angles of refraction of the parallel rays increase from the axis of the lens to its circumference, in order that they shall meet in a focus? or, in other words, what kind of curve must the surfaces of the lens have? Experience and calculation have shown that the object cannot be completely attained by means of lenses with spherical curves ; and that the forms of the surface necessary to concentrate the rays to a perfectly defined focus differ from that of the segment of a sphere, the only form which can be given to the surfaces of lenses by grinding. With such spherical surfaces the refraction of the rays increases too rapidly towards the circumference; and the rays most distant from the axis of the lens are consequently not brought to the same focus as the central rays. This is called "aberration from sphericity," or "spherical aberration." The focus for each circle of rays from the axis to the margin of the lens is different, becoming nearer to the lens the more remote the rays are from the centre.

I am not acquainted with any mathematical demonstration of this fact which would be readily intelligible, and shall therefore content myself with an empyrical statement of it.* *d, c, b, a, b′, c′, d′*, (fig. 72,) are parallel rays. The rays *b b′* traverse the

Fig. 72.



lens at the same short distance from its axis *a*; and, the refraction being there inconsiderable, they intersect the line of the axis at the point, *o*, furthest removed from the lens. The rays *c, c′*, which pass through the lens at a greater distance from its axis, are brought to a focus at *h*; the rays *d, d′*, which are nearest to the circumference, intersect each other at *n*. If an opaque surface to receive the image be placed at *o*, there will be seen, not merely the bright focus of the central rays, but also a halo produced by all the other rays, which come to a focus, not at *o*, but at *h, n*, and other points of the axis *a o*; and the diameter of this halo will be *y y*. If the opaque surface be placed at *h*, the focus of the rays *c, c′* will be seen with a halo *x′ y′*, and so on.

If the rays *d, c, b, a, b′, c′, d′*, in place of being parallel, were the base of a cone of light emitted from a point at a definite distance, they would still not be collected to a point by a lens with spherical surfaces; and on an opaque surface placed to receive them would be seen the focus of some of the rays surrounded by a halo formed by the others. The halo will, of course, be most considerable when the rays fall at the same time upon the centre and on the circumference of the lens, whether the image be received by a surface at *o* or by one at *h*; for then, with the focus of the one set of rays, there will be received the others not brought to a focus. If, on the contrary, all the rays which pass through the circumference of the lens can be excluded while the passage for the central rays is left free, the opaque surface placed at *o* will receive the

* For the mathematical discussion of the question, Gehler, Physikal. Wörterbuch, vi. 1. 396, [and Sir J. Herschell's treatise on Light,] may be consulted.

focus of the central rays as a definite image, without any halo produced by rays refracted by the border of the lens. This object can be attained by covering the peripheral portion of the lens with a ring-shaped screen, or *diaphragm*. The image will be defined also if the light be allowed to pass through the circumference of the lens only, and not through its centre, for then the halo formed by the central rays around the focus of the marginal rays will be avoided. But the latter mode of avoiding the effects of aberration is not employed in optical instruments, because the aberration is greatest in the case of the rays refracted by the circumference of the lens. All optical instruments, however, require diaphragms to enable the lenses to give definite images.

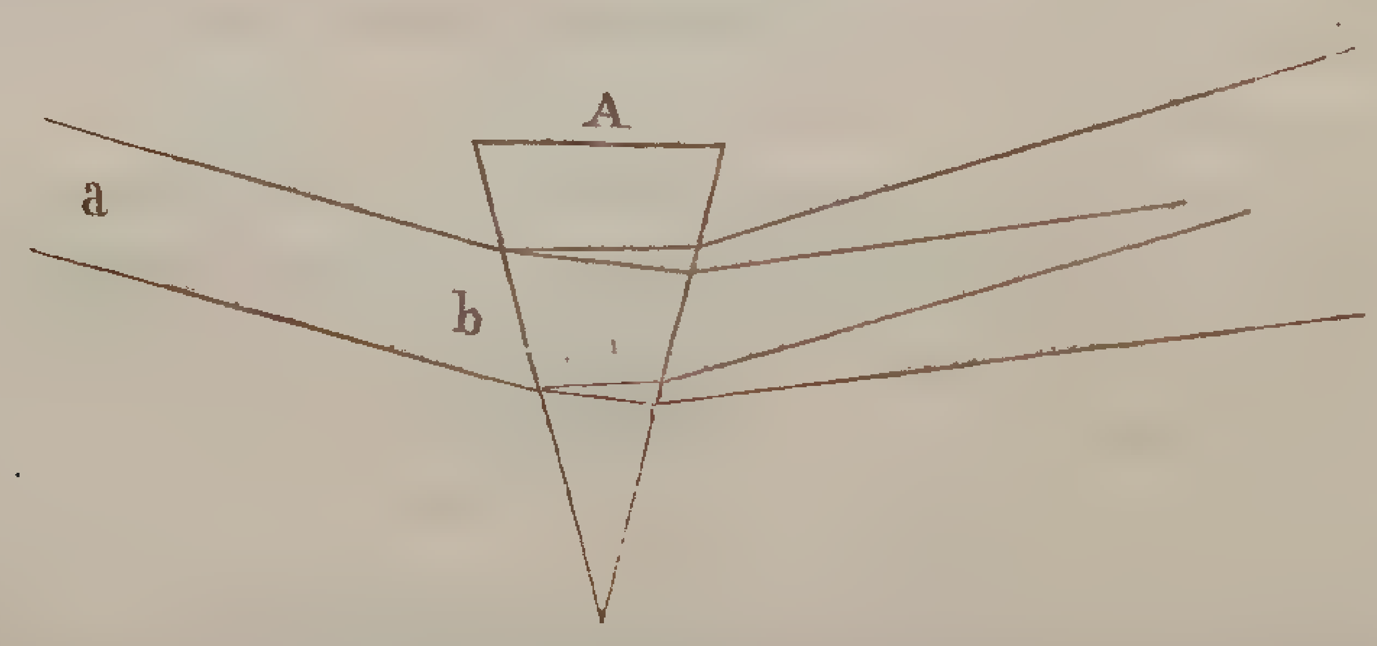
If the opening in the diaphragm be very small, new phenomena, resulting from the rays being bent by the edge of the diaphragm, arise, and interfere in a marked degree with the distinctness of the image.

The aberration from sphericity may be diminished to a very great extent by altering the relation of the curves of the two spherical surfaces. The slightest degree of aberration, according to Herschell, is produced when the radius of the posterior surface of the lens is from six to seven times as great as that of the anterior surface. If two thin lenses be combined, the relation between the radii of their surfaces may be made such that spherical aberration is wholly avoided. Increasing density of the lens towards its centre also must diminish aberration; for, by such a medium, the focal distance of the central rays is shortened, and approximated to that of the peripheral rays. Lenses which produce no spherical aberration are called "aplanatic."

*c. Of the physical conditions for the production of colours.**

1. *Dioptric colours.—Newton's theory of colours.*—By refraction, light is not merely bent out of its original direction, but, under certain circumstances, is rendered coloured. Coloured borders, indeed, are seen to surround the images produced by lenses. The phenomena of the production of colours is, however, most remarkable when prisms are used to refract the light. If a beam of the sun's light, *a*, *b*, (fig. 73,)

Fig. 73.

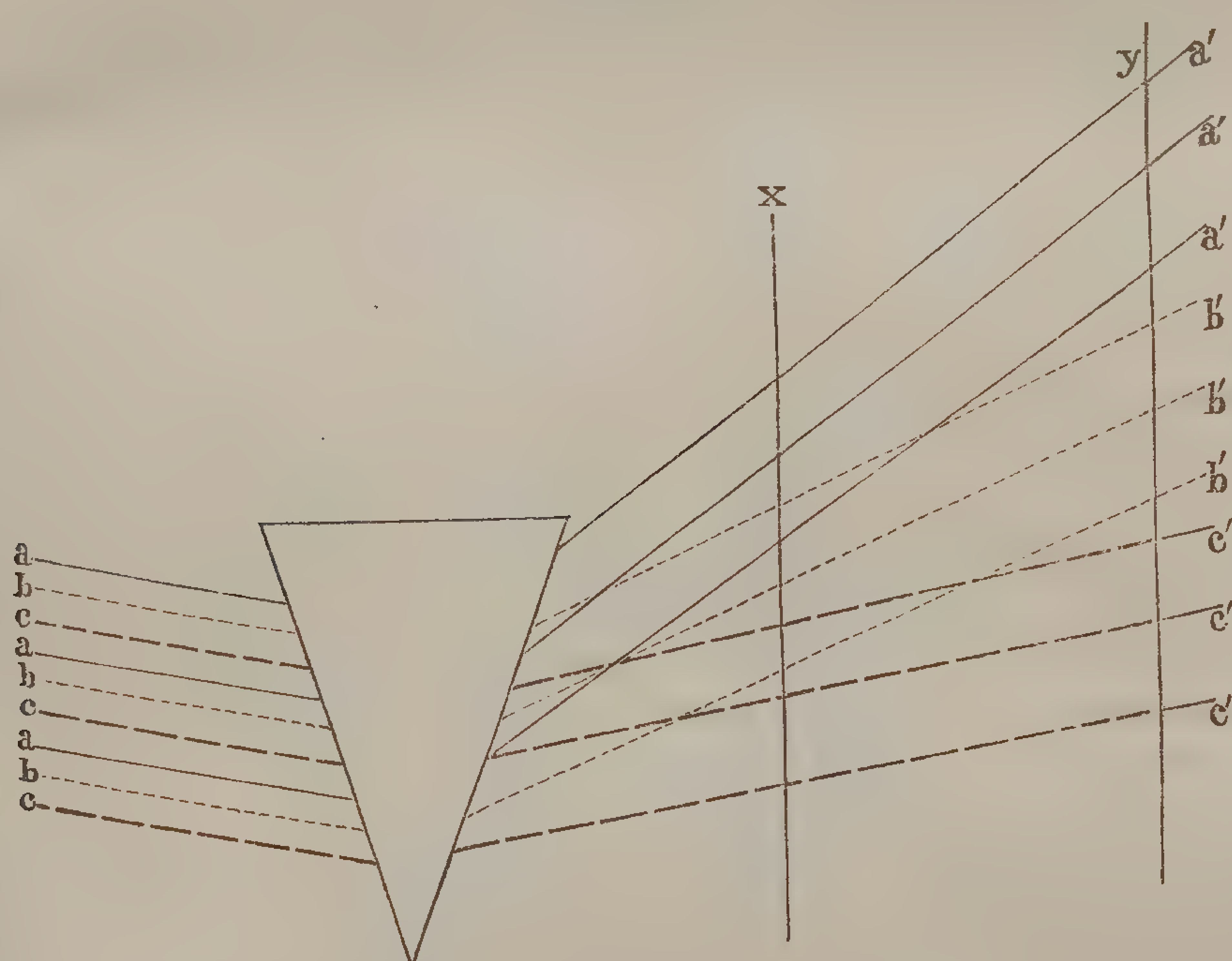


composed of parallel rays, fall obliquely upon the prism A, it will be refracted twice; namely, by its anterior and by its posterior surface; but, instead of the rays continuing parallel in their new course, the beam is spread out, and, when received upon an opaque surface, presents the colours of the rainbow. To observe these colours, it is not necessary to throw the light into a dark room through an opening in the window-shutter; the phenomena can be seen in open daylight, if the light of the sun after it has

* The works which may be consulted on this subject are,—Newton's Optics; Goethe's Farbenlehre; Brandes, in Gehler's Physik. Wörterb. art. Farben; Fischer's Mechanischer Naturlehre; and Pfaff über Newton- und Goethe-'sche Farbenlehre. The three treatises last named are referred to more especially, as containing critiques on Goethe's theory of colours.

passed through the prism be received upon some opaque surface; the colours, however, are much more vivid, and the borders of the image much more defined, in a dark room. The spectrum produced by the beam of light refracted by the prism, in place of being round and colourless, is elongated, with straight lateral borders and rounded extremities, and presents in succession the colours violet, blue, green, yellow, orange, and red. According to the laws of the simple refraction of light, the rays of light passing through the prism should receive a new direction, but ought to remain parallel. Inasmuch, however, as the spectrum is elongated, it is evident that the rays of light, while they have lost their parallelism, have undergone an unequal refraction. This fact suggested to Sir I. Newton his theory of colours. From the action of the prism on light, he concluded that in the sunbeam different elements or rays must be contained which have different degrees of refrangibility, and that those only which are homogeneous, or have the same refrangibility, follow the same direction after passing through the prism. If, for example, in the beam of parallel rays, *a*, *c* (fig. 74), the rays

Fig. 74.



a, *a*, *a* have equal refrangibility, the rays *b*, *b*, *b* also equal refrangibility, but a different degree of refrangibility from the rays *a*, *a*, *a*, and the rays *c*, *c*, *c*, again, agree in refrangibility among themselves, but differ in that respect from the rays *a*, *a*, *a* and *b*, *b*, *b*, it will follow that after refraction all the rays *a′*, *a′*, *a′* will be parallel, but that the rays *b′*, *b′*, *b′*, though parallel among themselves, will have a different direction from the rays *a′*, *a′*, *a′*, and also from the rays *c′*, *c′*, *c′*, which again will be parallel amongst themselves, but neither with the rays *a′* nor the rays *b′*. The homogeneous rays *a′*, *a′*, *a′* will appear with the same colour, namely, violet; the homogeneous rays *b′*, *b′*, *b′*, with the same colour, namely, blue; and the homogeneous rays *c*, with the same colour, green; and so other similar rays with the colours yellow, or orange, or red. Violet and red lie at the extremes of the spectrum; the violet rays having the greatest, the red rays the least refrangibility. The colours are not seen, however, unless the spectrum is received upon an opaque surface at the proper distance from the prism; for instance, at *y*, where the diverging rays of different kinds, *a′*, *b′*, *c′*, are no longer mingled with each other. If the surface which receives the spectrum is placed nearer to the prism, for instance at *x*, the dissimilar rays *a′*, *b′*, *c′*, are mingled in the middle of the image, which in such case appears white, while the upper and lower extremity only are coloured; and, the nearer to the prism the rays are intercepted, the less will those of different kinds be separated from each other; the larger will be the white middle portion of the spectrum, and the smaller the coloured borders.

These facts and considerations lead to the inference that a white body receives, and reflects upon the eye at the same time, all the different kinds of luminous rays; that colour, on the contrary, results from the impression upon the retina being produced by one kind of rays; in other words, that white light is composed of the different coloured rays which combined give the sensation of the white, but which, on account of their different refrangibility, may be separated from each other by refrangent media.

This inference is confirmed by the fact that the different coloured lights may be combined again so as to produce white light.

1. If the spectrum is received behind the prism by a condensing glass, the colours are combined at a certain point into a beam of uniform white light, although the coloured rays beyond this point again continue their separate course.

2. The same thing is effected by allowing the sun's light to pass through two prisms of equal refracting angle, placed in opposite directions. In this case the one prism, by refracting the rays in the opposite direction, neutralizes the action of the other, and the spectrum is consequently white.

3. Or the coloured lights may be collected to a point by means of a concave mirror, upon which they are received obliquely, so as to be reflected downwards upon a white surface, which then presents a colourless bright spot in place of a coloured prismatic spectrum.

The prismatic colours are produced, though not in such intensity, by the refraction of light by means of lenses instead of the prism: the images of objects formed by lenses have a border of prismatic colours. A lens may be regarded as a prism of which the refracting angle increases towards the margin, and in which the decomposition of the light is effected, not in one direction only from above downwards or from below upwards, as in the prism, but in all directions from the centre towards the periphery. The coloured margins are the more evident the further distant the point where the image is formed is from its proper focal distance.

The use of the word "rays" in the statement of Newton's theory of colours has induced in some persons the incorrect belief that, according to this theory, each ray of white light is composed of several rays of coloured light, — its elements as it were. But, to have an accurate conception of the results deducible from Sir I. Newton's discoveries, it is necessary to refer to the organ of vision, which has a share in the production of the phenomena of colours and light. The surface of the retina is, we know, composed, like mosaic-work, of the ends of an extraordinary number of nervous fibres, and each papilla of this mosaic-work represents the smallest elementary portion of the organ of vision which is capable of sensation. While the different-coloured lights fall upon the composite surface of the retina in such a way that each of the elementary portions receives one simple kind of light only, *a* receiving blue, *b* yellow, and *c* red light; so long will their impressions of colours be perceived as existing distinct from each other. But if the same minute portions of the retina are acted on at the same time by all the principal colours, so that the same papillæ of the retina receive at the same time the impressions proper for the sensations of yellow, red, and blue, none of these colours will be distinguished, but from the mixed impression the sensation of white will result. This is all that can be concluded from Newton's experiments. The simultaneous impression of all the colours on the same parts of the retina produces the sensation of white.

Sir I. Newton admitted, without sufficient reason, the existence of seven dioptric colours resulting from the decomposition of white light by refraction, and this arbitrary view was too long adopted; it ought to have been corrected before the time of T. Mayer and Goethe. There are three primitive colours only, yellow, blue, and red; the others may be explained by the mixture of these. Between the yellow and blue of the spectrum lies green, which results from their admixture; between blue and red lies violet; and between red and yellow, orange. If red and blue light fall upon the same elementary portion of the retina, neither of those colours will be perceived, but in place of them violet; and so of the other colours producing mixed impressions. Hence the combination of a mixed colour with a simple homogeneous colour is equivalent to the combination of all the three simple colours, because the mixed colour must always contain the two other simple colours; for instance, two-thirds orange and one-third blue is equivalent to one-third blue, one-third red, and one-third yellow, since the union of the two latter colours constitutes two-thirds orange.

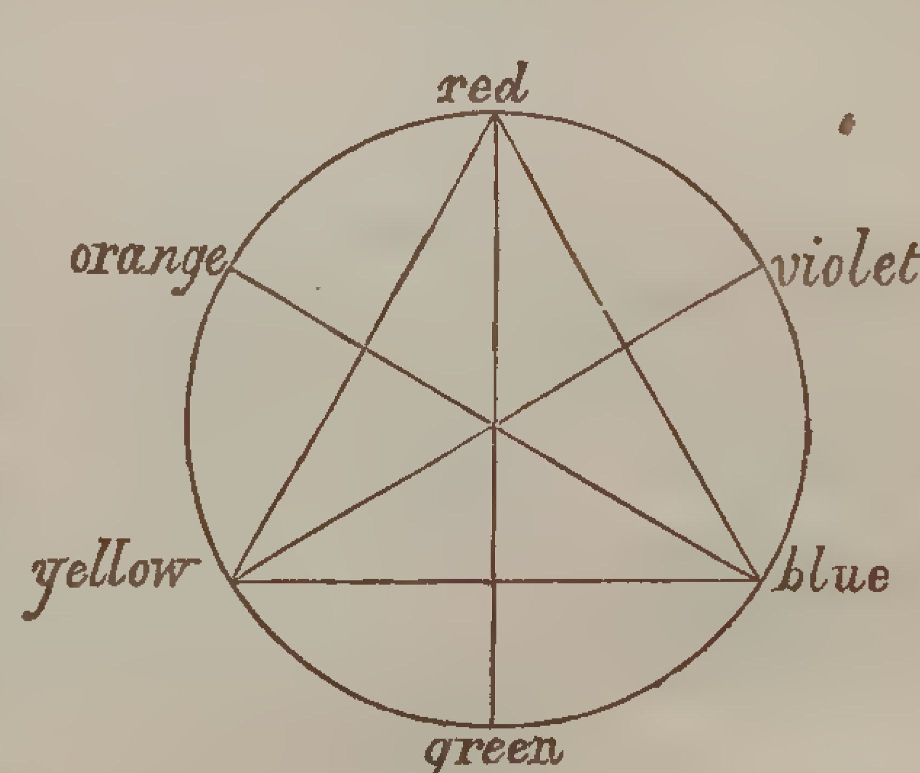
If the prismatic orange and the prismatic blue be by a special contrivance made to fall together upon the same surface, the impression will be white, as when produced by the union of all the three primary colours; in the same way white may be produced by the union of red with green (which contains blue and yellow), or of yellow with violet (which contains blue and red). A mixed prismatic colour, and a simple homogeneous colour, which produce white when combined, are said to be "complementary." Green and red are complementary of each other; so, likewise, are violet and yellow, and blue and orange. Absolute darkness, or the black colour, is the mere negative result of certain parts of the retina, or its entire surface, being in the state of repose or freedom from excitement. If the impression of colours unmixed with white be feeble, they necessarily appear more or less dark. If the impression of white light be sufficiently weak, the retina has the sensation of "grey;" as when a grey colour is produced by the admixture of white and black. The grey colour may, however, result from the mixture of different colouring matters; red, yellow, and blue pigments, when mixed produce a grey colour. Two pigments will yield a grey, if one be a simple homogeneous colour and the other a mixed colour, that is, a colour composed of two simple colours which with the other simple colour would afford the three primary colours of the spectrum.

Thus, red	and	green yield grey.
yellow	..	violet . . . —
orange	..	blue . . . . —

Two colours, which together yield a grey colour, are therefore also called "complementary."

In figure 75 the three simple colours are placed at the angles of an equilateral triangle, which are connected together by means of a circle; the mixed colours are placed intermediate between the corresponding simple or homogeneous colours; and the complementary colours, of which the pigments when mixed would constitute a grey, and of which the prismatic spectra would together produce a white light, will be found to be placed in each case opposite to each other, but connected by a line passing through the centre of the circle. This figure also is useful in showing the further shades of colour which are complementary of each other. If the circle be supposed to contain every transition of colour between the six marked down, those which, when united, yield a white or grey colour, will always be found directly opposite to each other; thus, for example, the intermediate

Fig. 75.



tint between orange and red is "complementary" to the middle tint between green and blue.

If we divide the surface of a circular disk into three equal portions, separated by three radii (sectors), and paint each with one of the three simple colours, these colours will disappear when the disk is made to revolve so rapidly that the images of the different coloured sectors change their place on the retina before the effect of the previous impression is lost, and the disk appears grey. The revolving disk will also appear grey if its surface present two complementary colours only in a definite proportion as to the space they occupy; for example, a mixed colour occupying two-thirds of the disk, and a simple colour occupying one-third. But if one of the colours is in too great proportion, it will be seen when the disk is made to revolve, and the grey will not be perfect. Two simple homogeneous colours, without their third complementary colour, never produce a grey when mixed, but merely intermediate or mixed tints; for instance, green results from the mixture of blue and yellow, violet from the mixture of blue and red, orange from the mixture of red and yellow.

These facts have been regarded as proofs of the incorrectness of Newton's theory, according to which all the primary colours, and therefore the complementary colours also, should when mixed produce white, and not grey. But, if Newton's theory be correct, the result can scarcely be other than it is; for the pigments are so dull, and absorb so much light, that grey is necessarily produced instead of white. A coloured body owes its colour, according to Newton's theory, to its absorbing one or more of the simple colours of the sun's light, and its reflecting the rest; which constitutes its colour. The impression produced by the different coloured images of a revolving disk cannot be white, for a white disk reflects all the light which strikes it, while the coloured one reflects merely a portion. Hence the united impressions of the different colours upon the same spot of the retina must produce a feeble sensation of white, or a grey which is lighter or darker according to the brightness or dulness of the pigments. But if we concentrate the brilliant colours of the prismatic spectrum to a focus, we obtain a pure white image; and the same is the case, as Von Grotthuss* has shown, when two complementary dioptric colours are made to combine.

Lastly, it must be remarked, that the intermediate tints produced by the union of two prismatic colours can be resolved by means of the prism into their original elementary colours, but that the intermediate colours of the true prismatic spectrum cannot be decomposed any further by the prism. This seems to prove that more than three primary colours exist in the sun's light, and that it probably contains an infinite number of rays differing in refrangibility. That the intermediate colours of the prismatic spectrum, and those produced artificially by the mixture of simple colours, should make the same impression on the retina, exciting the sensation of green, for example, while they are so different with respect to their susceptibility of decomposition by the prism, may be explained according to the undulatory theory, by supposing that undulations of the rapidity of the green rays of the prismatic spectrum produce the same impression upon the retina as undulations of yellow and blue rays of different rapidity striking the same part of the retina at the same time. The rapidity of the undulations of the green rays is, indeed, intermediate between that of the yellow and that of the blue rays; but the rapidity of the undulations of the violet rays is greater than that of the undulations either of the blue or of the red rays.

[Sir D. Brewster, by the use of media capable of absorbing certain of the coloured rays of light, has been enabled not only to explain why the orange and green rays of the solar spectrum cannot be decomposed by the prism,—a circumstance apparently

* Schweigger's Journ. iii. 158.

incompatible with the hypothesis of three primitive colours, but also to demonstrate more exactly than had hitherto been done the true constitution of the spectrum. The colours of transparent media depend on their absorbing some of the colours of white light, and transmitting others. Thus blue glass, the colour of which is not the pure blue of the prismatic spectrum, absorbs all those rays which with the rays producing its compound blue colour would form white light. If the solar spectrum be viewed through a plate of such blue glass of a certain thickness, the middle of the red space will disappear, and with it the whole of the orange, a great part of the green, a considerable part of the blue, a little of the indigo, and very little of the violet. The yellow space, which has not been much absorbed, will have increased in breadth, occupying part of the space formerly covered by the orange on one side, and part of the space formerly covered by the green on the other. Hence it follows that the blue glass has absorbed the red light, which, when mixed with the yellow light, constituted orange; and also the blue light, which, mixed with the yellow, constituted the part of the green space next to the yellow. The orange and green rays, therefore, though they cannot be decomposed by prismatic refraction, can be decomposed by absorption, and actually consist each of two different-coloured rays, possessing the same degree of refrangibility. Difference of colour is, therefore, not a test of difference of refrangibility. By analysing the spectrum in this way, by means of various coloured media, Sir D. Brewster has arrived at the conclusion, that red, yellow, and blue light exist at every point of the solar spectrum; and, consequently, that as a certain portion of red, yellow, and blue constitute white light, every point of the spectrum may be considered to consist of white light mixed with the predominating colour or colours.]

The theory of colours proposed by Newton is not essentially affected by the adoption either of the undulation or the emission theory of light; for impressions, which according to the latter theory, are produced by rays of coloured light of different nature, may also be due to differences in the undulations, and to the different rapidity of motion of the different coloured lights which suffer unequal refraction in passing through refracting media.

The objections brought by Goethe against Newton's theory of colours are, in the main, founded on erroneous views. Goethe* and Seebeck† regard colour as resulting from the mixture of white and black, and ascribe to the different colours a quality of "darkness" (σκιερὸν), by the different degrees of which they are distinguished, passing from white to black through the gradations of yellow, orange, red, violet, and blue, while green appears to be intermediate again between yellow and blue. This remark, though it has no influence in weakening the theory of colours proposed by Newton, is certainly correct, having been confirmed experimentally by the researches of Herschell, who ascertained the relative intensity of the different coloured rays by illuminating objects under the microscope by their means. The illuminating power was greatest in yellow and yellow-green, less in orange, still less in red, less again in blue, and least of all in violet (which, however, we should have expected to have been intermediate in illuminating power between red and blue). The brightness of the green rays was less also than that of the yellow-green. Another certain proof of the difference in brightness of the different coloured rays is afforded by the phenomena of ocular spectra. If, after gazing at the sun, the eyes are closed so as to exclude the light, the image of the sun appears at first as a luminous or white spectrum upon a dark ground; but it gradually passes through the series of colours to black,—that is to say, until it can be no longer distinguished from the dark field of vision; and the colours which it assumes are successively those intermediate between white and black in the order of their illuminating power or brightness, namely, yellow, orange, red, violet,

* Farbenlehre. † Schweigger's Journ. i. 4.

and blue. If, on the other hand, after looking for some time at the sun, we turn our eyes towards a white surface, the image of the sun is seen at first as a black spectrum upon the white surface, and gradually passes through the different colours from the darkest to the lightest, and at last becomes quite white, so that it can no longer be distinguished from the white surface. But, although the remark of Goethe relative to the different degrees of darkness of the colours is correct, yet it affords no proof of the correctness of his main principle, that colour is the result of the mixture of light and darkness. Darkness is, as we have already remarked, nothing positive; it is merely the expression of repose of the retina, or of parts of it.

A mixture of white and black, whether by the impressions of the two upon the same parts of the retina being made to succeed each other very rapidly, as by means of a revolving disk, or by both being allowed to act at the same time upon the same points of the retina, never gives rise to any colours, but produces "grey;" which shows merely that the impression which causes the sensation of white is moderated, so that the sensation of grey results

The fact of some semi-opaque media — as, white glass, or the air loaded with moisture, — causing light previously white to appear coloured when it has passed through them, was thought by Goethe to be a proof of the correctness of his theory of colours; but it is now known to result from certain media having the property of absorbing some of the component rays of white light while they allow the passage of others.

2. *Natural colours of bodies.* — *Pigments.* — The natural colour of bodies not themselves luminous, is due to the light which falls upon them, and is reflected by them towards our eyes; and in part also it depends on the affinity of the bodies for light, and for the different coloured rays, since they sometimes reflect all the coloured light; sometimes absorb it completely, becoming heated at the same time; sometimes partly reflect, and partly absorb it; while in other cases, again, they allow all the light to pass through them, or allow the transmission of some of the coloured rays, but absorb others. A white body is one which reflects all the different coloured rays simultaneously; a black body is one which appropriates all the different rays, and reflects none; while a coloured body is that which absorbs or transmits certain of the coloured rays of white light, and reflects the rest. A transparent colourless body transmits all the different coloured rays, as white or colourless light, reflecting only a very small part of each, so that no colour is produced. A transparent coloured body absorbs certain of the coloured rays, and transmits the remainder as coloured light. The dependence of the colour of opaque bodies upon the absorption or transmission of certain of the component coloured rays, and upon the reflection of others, may be proved by experiment.

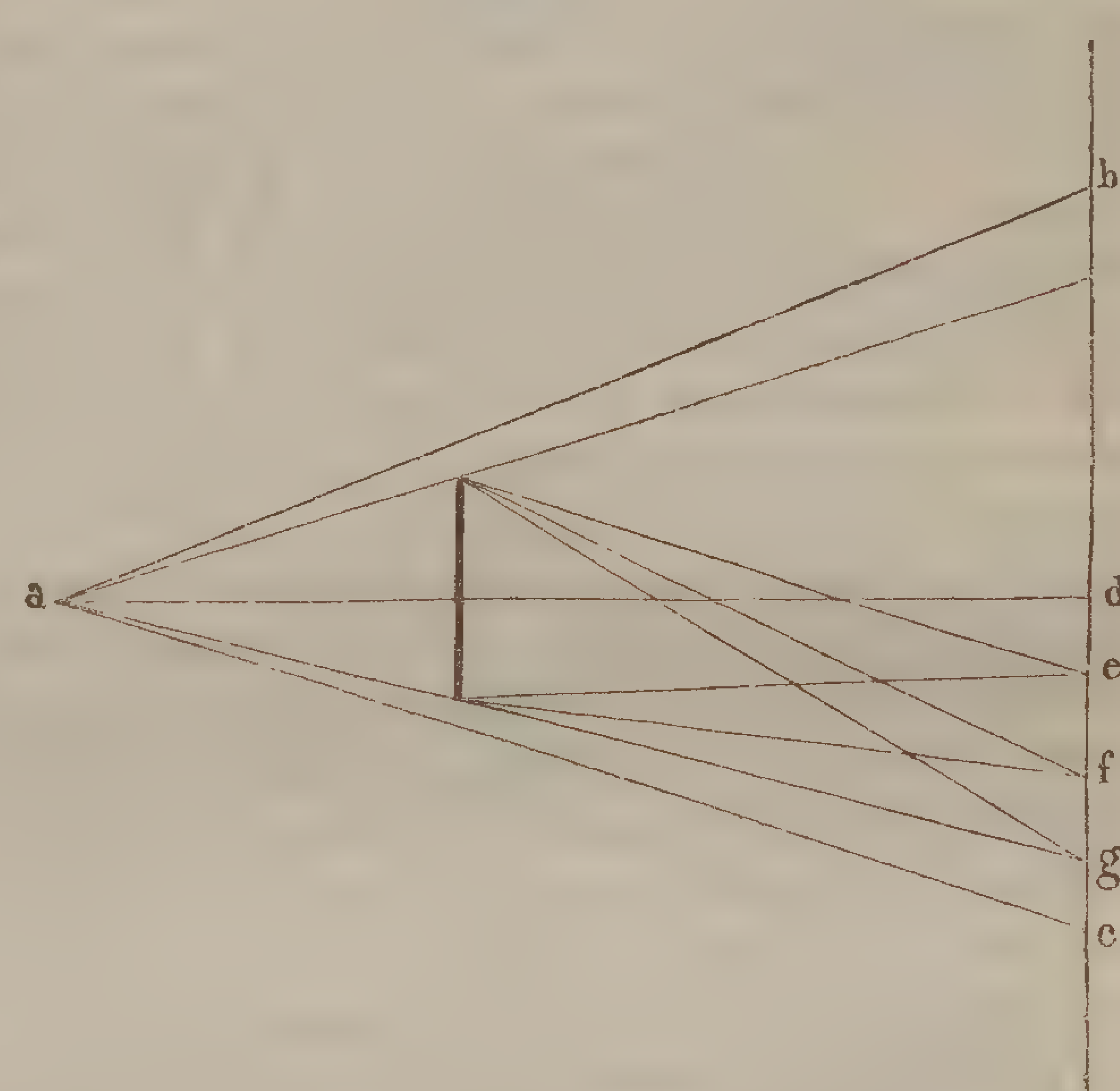
Coloured bodies which ordinarily reflect the coloured ray *a*, when illuminated only by a simple coloured light which contains none of the rays *a*, are, of course, no longer able to reflect these rays, and appear therefore perfectly colourless. A lamp-wick saturated with common salt, and burnt with alcohol, gives, as Brandes remarks, a homogeneous yellow light, in which all objects but those which are yellow appear devoid of colour. Most coloured lights are, however, not simple or homogeneous, and contain, besides the prevailing rays of one colour, white light.

Transparent coloured bodies sometimes appear of a different colour by reflected, from that which they have by transmitted light; in other instances, they appear of the same colour by reflected and by transmitted light. The same cloud may appear of a bluish colour by reflected, and of a yellow or orange tint by transmitted light. In the first case, we do not see the yellow and red rays which it allows to pass through it, but only the bluish rays which are reflected; in the second case, we see the transmitted rays, yellow and red, but not those which are reflected, — the blue. In this way Brandes explains the blue and orange tints of the atmosphere under different circumstances. When the atmosphere is clear, it appears in the evening blue towards the east, where it reflects towards us the blue rays, while it transmits the yellow and red, which are therefore invisible to us: in the west it appears at the same time of a yellowish red colour, because it transmits thence the yellow and red rays to our eyes, while it reflects back the blue rays. In the same manner, bluish white glass, when held towards the light, appears of a fiery red colour. Other transparent bodies have the same colour both by reflected and by transmitted light; they reflect one portion of the coloured light *a*, and transmit another portion of the same light *a*, while they absorb completely the other coloured rays *b*, *c*.*

3. *Of the colours produced by "interference" of the rays.* — The stability of Newton's doctrine of colours is not affected by the phenomena which require for their explanation the principle of "interference," or the reciprocal influence of the luminous rays upon each other, discovered by Dr. Young. Since many of the phenomena of colours hitherto difficult of explanation owe their production to this principle, an exposition of the most important points of the theory will be necessary to complete our account of the physical laws of colours.

The property of the luminous rays discovered by Dr. Young is this:—Two rays coming from one point, and after passing through paths of slightly different length meeting again at a very small angle in one point, under some conditions increase each other's intensity; under others, destroy each other. This reciprocal influence of the rays of light is called "interference."

Fig. 76.

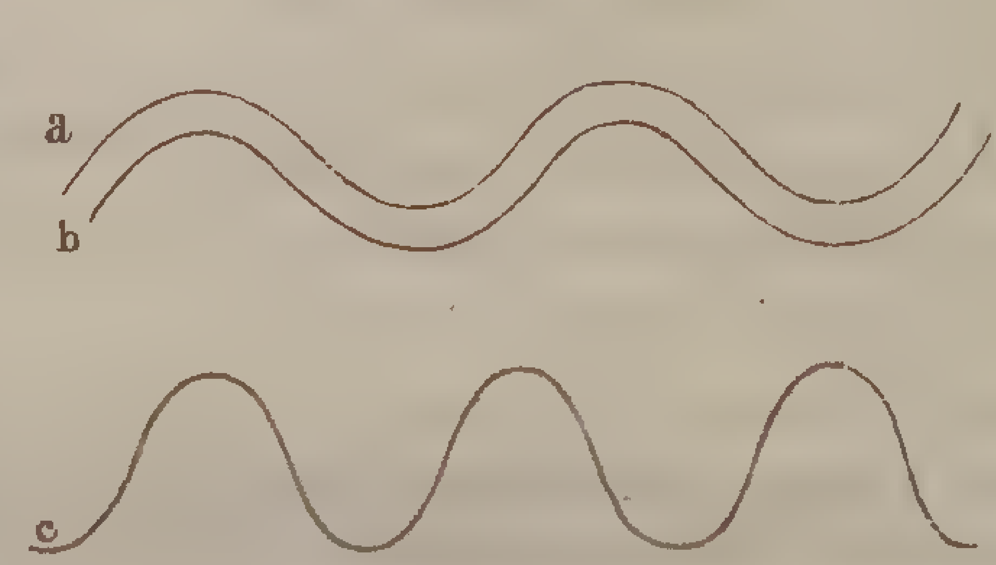


Admit into a dark room the cone of light *a b c* (fig. 76). At a short distance from the apex of the cone place a narrow strip of pasteboard, or wood. (This is made very broad in the figure, to render it more distinct.) Let *b c* be a surface receiving the shadow. If the light issuing from *a* be homogeneous, — for instance, the red light of the prismatic spectrum, — there will be seen upon the surface, *b c*, instead of a simple shadow, a series of alternate red and dark lines. If the surface *b c* be brought very near to the opaque body, the shadow will be defined and free from the lines of coloured light; and, the further it is removed from it, the more evident will those lines become. The middle band *d* will be red. If the passage of the light be interrupted at one border of the card, so that it can no longer reach the surface *b c* from that side, the coloured lines will cease to be visible; which proves that the phenomenon is due, not to the inflexion of the light at the margins of the card, but to the reciprocal action of the rays passing at the opposite borders on each other. It is, however, owing to the laws of inflexion, to which light is subject when it passes close to the edges of bodies, that the rays from the opposite sides meet on the surface *b c*.

* See Brandes, Gehler's Physik. Wörterbuch, art. Farben.

The rays passing the upper border of the card or pasteboard in the figure are inflected from their direction *a b* towards the points *g*, *f*, *e*, *d* ; the inflexion affecting those rays most which are nearest to the edge of the card, and diminishing as their distance from it is greater, until at a certain distance they maintain their original direction *ab*. By this "inflexion" or "diffraction," rays which issued from the point *a*, and were diverging from each other, are again brought together. The rays which thus meet will in the middle of the shadow be of equal length ; those meeting at all other points, as *e*, *f*, *g*, will be of unequal length. Now, since the image of the inflected rays emitted by the point *a* presents dark lines alternating with red lines, it follows that certain of the rays of red light inflected by the opposite borders of the opaque body have, by meeting at certain points of the surface *b c*, destroyed each other, causing these points to appear dark ; while other rays of the red light have not destroyed each other, and cause the parts of the surface which they fall upon to appear red. The same phenomena may be produced, as Fresnel has shown, by reflecting the rays issuing from a luminous point by means of two mirrors in such a manner as to produce interference ; reflexion doing here what was effected by inflexion in the experiment above described. The phenomenon of interference is easily explicable if the undulatory theory of light be adopted. The rays of red light which meet at the point *d*, are of equal length—have passed through an equal number of undulations, and at this point the red light is not lost ; but the rays which meet at the points *e*, *f*, *g*, are of unequal length, and each has passed through a different number of undulations. All such rays of unequal length either add to one another's intensity, or destroy each other. The difference in length of the rays meeting at *e* may be greater or less than the length of one of the undulations of red light, each of which undulations consists of a condensed and a rarefied portion. If one ray have passed through one entire wave more than the other ray which meets it at *e*, the waves of two rays will, according to the laws of all undulations, increase each other's intensity, and not destroy each other ; for the condensed portion of the wave of one ray will coincide with the condensed portion of the wave of the other ray, and the rarefied portion of the wave of one ray with the rarefied part of the wave of the other ray, or, in other words, the elevations and depressions of the one will coincide with the elevations and depressions of the other, as in fig. 77, *a*, *b*. The result of such a relation of the rays can only be an increase of intensity of the ray reflected from the surface *b c* (fig. 76) ; the elevations and depressions of the waves or undulations becoming exaggerated (fig. 77, *c*). The effect will be the same when the difference in the length of the rays amounts to three, four, five, or six, entire undulations ; for, in such cases, the elevations or depressions of the undulations of the two rays will always coincide.

Fig. 77.



If, on the contrary, one of the rays meeting at any point have passed through only half a wave more than the other ray, the rarefied portion or depression of the wave of one ray, *a*, will coincide with the condensed portion or elevation of the wave of the other ray *b*, as represented in fig. 78 ; and the elevation of one will neutralise the depression of the other, so that both will be destroyed, and the spot on which they fall will appear dark. If the difference in the length of the paths which the rays have traversed be less than an entire wave, but more than half a wave, the rays will interfere more or

Fig. 78.

less with each other, according to the amount of their difference in length. It may easily be perceived that these phenomena afford the means of calculating the size of the undulations of the different coloured rays. The relation of the dark and light lines in the image varies according to the kind of coloured light used in the experiment.

We have hitherto considered the case of the "interference" of rays of simple homogeneous light. If white light be used in the experiment, the peculiar phenomena of colours are produced, which it is our main object to explain. Instead of the alternate lines of black and a single colour, vivid stripes or fringes of the different homogeneous colours are seen. This is easily explained, on the same principle as the preceding experiment. The waves of each colour contained in white light have a different length; each of the simple homogeneous colours will consequently have its own separate coloured and black stripes, produced in the same way as when a simple colour is employed.

The theory of the production of colours by "interference" explains very readily the colours seen in thin plates of bodies with a fine laminated structure, and on very finely grooved surfaces. It is a fact well known, that light passing through a transparent body is reflected in part by its anterior and posterior surfaces. A ray falling perpendicularly upon a thin transparent lamina will be reflected in part by the anterior and in part by the posterior surface; the two parts of the ray meet again after reflection, and, if the difference in length of the paths which they have traversed is small enough, the appearance due to interference will be produced. The same is the case with rays falling obliquely upon such a body; for the ray reflected from the anterior surface will meet with part of some other ray reflected from the posterior surface of the lamina, and give rise to "interference." The colours seen on finely grooved surfaces are explained in the same manner. Of this nature, therefore, are the iridescent colours of laminæ of mica or glass, soap bubbles, mother-of-pearl, &c.*

In conclusion we give the table of the lengths and rate of the undulations in the rays of different coloured light, as calculated by Sir J. Herschell from the phenomena of interference.

Colours of the Spectrum.	*Length of an undulation in parts of an inch.*	*Number of undulations in an inch.*	*Number of undulations in a second.*
Extreme red . .	0·0000266	37640	458,000000,000000
Red	0·0000256	39180	477,000000,000000
Intermediate . .	0·0000246	40720	495,000000,000000
Orange . . .	0·0000240	41610	506,000000,000000
Intermediate . .	0·0000235	42510	517,000000,000000
Yellow	0·0000227	44000	535,000000,000000
Intermediate . .	0·0000219	45600	555,000000,000000
Green	0·0000211	47460	577,000000,000000
Intermediate . .	0·0000203	49320	600,000000,000000
Blue	0·0000196	51110	622,000000,000000
Intermediate . .	0·0000189	52910	644,000000,000000
Indigo	0·0000185	54070	658,000000,000000
Intermediate . .	0·0000181	55240	672,000000,000000
Violet	0·0000174	57490	699,000000,000000
Extreme violet .	0·0000167	59750	727,000000,000000

* On the theory of "interference," see Weber, Wellenlehre, Brandes, loc. cit.; and, on the undulation theory of light, Gehler's Physik. Wörterbuch, art. Licht; [and Sir J. Herschell's Treatise on Light.]

CHAPTER II.

OF THE EYE AS AN OPTICAL INSTRUMENT.

1. *Optical structure of eyes.*

The structure of eyes, regarded with reference to their function of the perception of light generally, and of distinguishing objects more particularly, presents three principal forms:—1. The simplest eyes or eye-dots of the Annelida and lower animals, which enjoy probably by means of their eyes merely the general perception of light, so as to distinguish, for example, day from night, or light places from dark. 2. The mosaic-like compound eyes of insects and Crustacea, furnished with transparent media calculated to insulate the rays of light coming from different objects, or from different parts of objects. 3. Eyes with transparent media for concentrating the rays to foci.

A. *The simplest eyes or eye-dots of the Annelida and other inferior animals.*—It can be distinctly demonstrated that the eyes of Insecta, Crustacea, and Mollusca have the apparatus necessary for separating the rays from different points of objects. The question is, whether the so-named eye-dots of the Annelida and other inferior animals have a similar provision, or whether these are wholly destitute of optical apparatus, possessing merely the faculty of distinguishing light from darkness, and day from night. The animals in which these eye-dots are met with will be enumerated at p. 1123. The Hirudo medicinalis has ten eyes, ranged in a semicircle at the anterior part of the head above the mouth. Weber describes them as being raised above the surface like warts, and as being prolonged as cylinders into the interior of the animal. The extremity of each is covered by a convex very transparent membrane, beneath which is a black lamina, and the lower portion of the cylinder is black. No pupil or transparent refracting media have been seen in these eyes, nor in the semilunar eyes of several Planariæ. I have examined the structure of the eye-dots in the Nereida. In the genus Nereis (Andouin and Edwards) there are four black eye-dots arranged in a quadrangle upon the surface of the head. They are not raised, but lie immediately beneath the epidermis of the head, are round posteriorly, towards the free surface flat, and consist of a cup-shaped black membrane, containing a round white opaque body which is prolonged into the optic nerve (see fig. 79). The four optic nerves enter the upper surface of the brain at separate points. The eyes of this animal are therefore destitute of optical apparatus. The light has access to the body contained within the choroid, for this presents a circular aperture on the side towards the light:

Fig. 79.*

[* Fig. 79.—A. Eye of Nereis, after Müller; B. the choroid partially removed, showing the bulb of the optic nerve within.]

but the round body appears to be merely the papillar extremity of the optic nerve; for it is opaque, has the same aspect as the nerve with which it is distinctly continuous, and has a fine granular structure. The animal in which I examined these eyes had certainly been preserved in spirit; but the transparent organs in the eyes of insects, spiders, and snails, preserved in spirit, keep their natural appearance.* Rathke† has likewise observed the pupil-like opening of the choroid in Nereis Dumerilli; but he has also described a second form of the eye in the family of the Nereida, namely in the genus Lycoris, in which this pupil is absent, and the choroid of a nearly black colour surrounds the whole eye. In this form still less than in the former can we suppose that the eye has the power of distinguishing forms, or is capable of anything more than a mere vague discrimination of light from darkness by means of the rays of light which are able to penetrate through the covering of pigment. Rudolph Wagner,‡ who confirmed by his observation of fresh specimens of Nereida my description of the papillar enlargement of the optic nerve, and the absence of transparent optical apparatus, believed that he could distinguish, in young examples of the Hirudo medicinalis just escaped from the ovum, transparent parts in addition; namely, a bell-shaped vitreous body, with red granules of pigment loose upon its surface, and, in front of this, a portion like a lens. It is certain, however, that of the Nereida some have a pupil, but no internal transparent media, and that others have not even a pupil; and we are therefore justified in ascribing to these animals merely the faculty of distinguishing light from darkness.

The existence in a genus of Nereida of true organs of vision totally covered with pigment without any pupil, and the similarity of these organs to the eyes of other Nereida which have a pupil, render it probable, that even in other inferior animals the black or dark-coloured eye-dots, though destitute of pupil, are with justice regarded as having a relation to the perception of light.

One example only of eyes unprovided with optic refracting apparatus is known among the Vertebrata. In the Myxine glutinosa I found a small eye, not merely beneath the skin, but really beneath the muscles; though in the allied genus, Bdellostoma, the eye lies at the surface. The eye of the Myxine glutinosa has no lens; but contains merely a bulb-like body filling the whole eye, which bears more resemblance to the bulb of an optic nerve than to a vitreous body. The perception of light is still possible here, although the eye is still covered by the muscles; for we are able to see the light through the thickness of our fingers and entire bones. These animals, therefore, will have merely the power of distinguishing light from darkness, day from night.

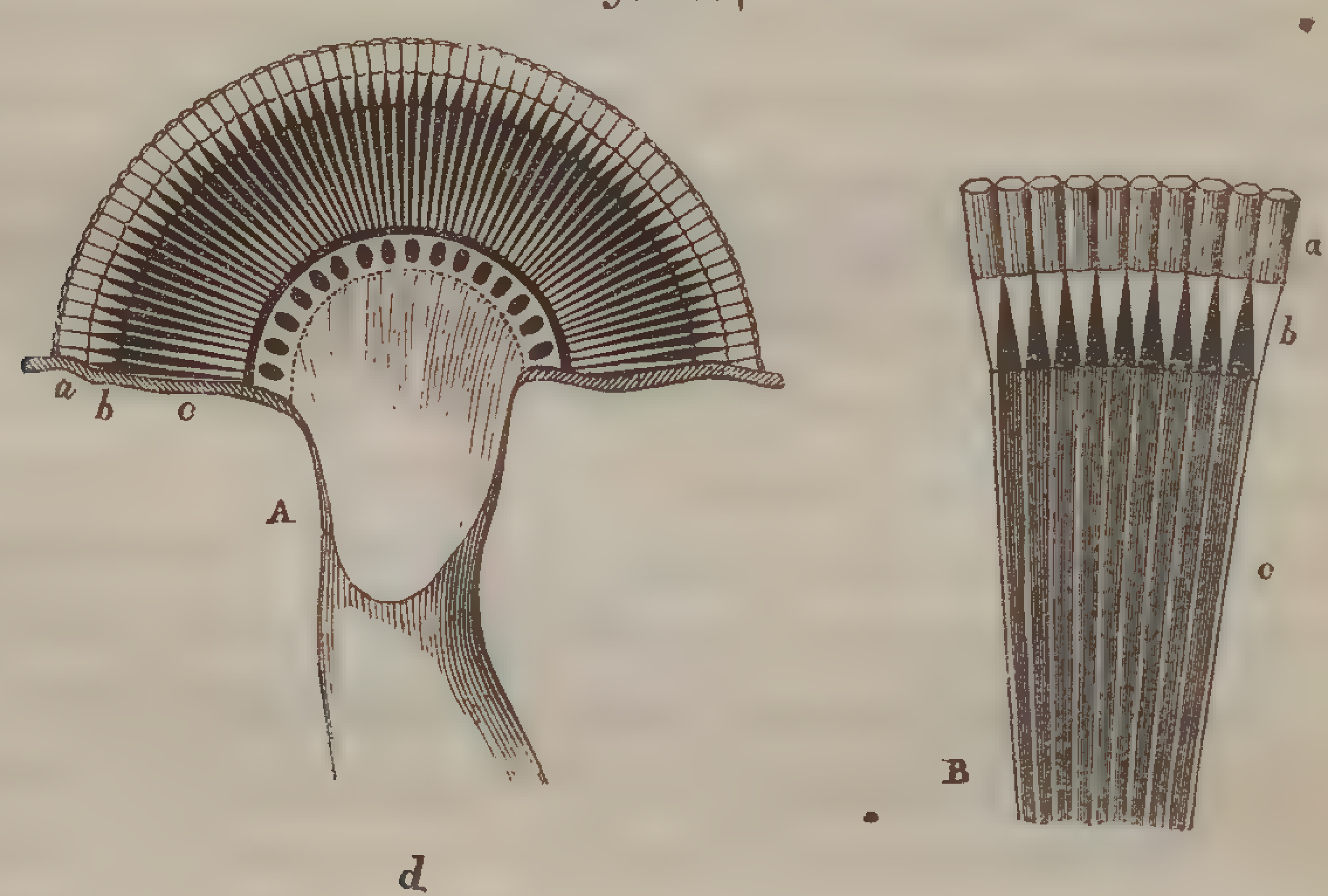
* J. Müller, Ann. des Sc. Nat. t. xxii. p. 19.

† De Bopyro et Nereide. Riga, 1837.

‡ Vergleichende Anatomie, i. p. 428.

B. *Compound eyes of Insecta and Crustacea with a mosaic-like structure.** The compound eyes of insects and Crustacea are more or less considerable segments of spheres sessile and fixed in the insects; but, in the Decapoda and some other Crustacea, moveable upon pedicles. The optic nerve also swells out in these eyes into a large ball or segment of a sphere, from the surface of which thousands of primitive nervous fibres rise, and are directed like radii towards the surface of the organ. They do not, however, reach the transparent covering or cornea of the eye; on the contrary, as I have demonstrated, in all orders of insects, and also in the Crustacea, the ends of the fibres of the optic nerve and the cornea are separated by transparent cone-like bodies likewise arranged in a radiate manner against the inner surface of the cornea, with which their bases are united, while their apices are received upon the ends

Fig. 80.†



of the fibres of the nerve (fig. 80). The length of these cones is very different in the different genera: in general, namely in most Coleoptera (beetles) and Lepidoptera (butterflies), they are five or six times as long as they are broad; in rare instances they are very short, — thus in the flies among dipterous insects their length scarcely at all exceeds their breadth. In insects, and the decapod Crustacea, the cornea is composed of numerous portions like mosaic work, each small portion or facet corresponding to one of the transparent cones connected with the fibres of the optic nerve. The facets of the cornea are hexagonal in insects; they have rarely this

* J. Müller, Physiologie des Gesichts-sinnes; Leipz. 1826. Ann. des Sc. Nat. t. xvii. pp. 225. 365.—Continued observations in Meckel's Archiv. 1829; 38. 177.

† [Fig. 80.—A. Section of the eye of Melolontha vulgaris, after Strauss Durckheim. *a*. facets of the cornea; *b*. parts supposed by Straus to be enlarged extremities of the nervous fibres, but by Müller shown to be transparent cones surrounded with pigment; *c*. the fibres of the optic nerve; *d*. the trunk of the optic nerve.—B. Portion of the eye of Melolontha, after Müller; *a*. prismatic segments or facets of cornea; *b*. transparent cone-like crystalline bodies; *c*. fibres of optic nerve.]

form in Crustacea, but in them are generally more nearly quadrangular, though the lines which divide them cannot here be right lines, in consequence of the surface of the eye being convex, but must be curves. In some instances, as in the Lepidoptera (butterflies), the facets are slightly convex, both externally and internally, that is, lens-shaped; generally, however, they are nearly plane, and indeed of considerable thickness, as in the Orthoptera and Coleoptera. The similarity of their anterior and posterior surfaces will not allow us to ascribe to the facets of the cornea any important influence in general upon the light: and in a great number of Crustacea, in the Entomostraca namely, according to my observations, they are wholly wanting, although the transparent cones remain; the surface of the cornea being in this case both externally and internally completely smooth. It is only where the cornea is thus smooth, and devoid of facets, that the bases of the cones, which are ordinarily united with the facets of the cornea, are rounded. Between the transparent cones, and even between the fibres of the optic nerve, there is pigment, of which the colour is sometimes dark, at others light; it may be nearly black, dark violet, dark blue, purple, brown, brownish yellow, light yellow, or green. Sometimes, indeed, several layers of different colours lie one over the other. The pigment rises between the cones as far as the cornea, and in some instances even covers the anterior surface or base of the cones to such an extent as to leave only a central pupil to each cone; this pupil is particularly evident when the cones are very short, as in dipterous insects. In other instances the bases of the cones are quite free from the pigment, which extends no farther than the lines of separation between the facets of the cornea. In the eyes of the lower Crustacea, where the cornea is destitute of facets, the cone-shaped transparent bodies are in the greater part of their length imbedded in the pigment, while their larger rounded extremities project out of it, and are turned to the inner surface of the perfectly smooth cornea. The number of the facets of the cornea and of the cones varies very much; it is generally very great, amounting to several thousand,—for instance, twelve or twenty thousand in one eye; in rare instances, as in some entomostracous Crustacea, they are few in number. R. Wagner has investigated the exact mode of connexion of the fibres of the optic nerve with the cones. In insects the fibre of the nerve is prolonged as a sheath over the sides of the cones; and, since the nervous fibres in the higher animals consist of a tube and contained matter, it is possible that this tube contributes chiefly to form the sheath of the cone.*

I have mentioned that according to my observations the eyes of many Crustacea have a cornea destitute of facets and transparent cones with

* On this point see Wiegman's Archiv. 1835. i. 372, and Müller's Archiv. 1836, 613.

rounded bases. This induced me several years ago* to divide the compound eyes into two principal classes. There is, however, a third modification of the structure of the compound eyes, which has been observed by Edwards, Burmeister, and myself, in several of the Crustacea. It is that where lenticular bodies exist between the cornea and the transparent cones. These lenses must concentrate the rays of light which fall upon them, and throw them towards the axis of the cones. M. Edwards† observed this structure in Callianassa, in many brachyurous decapods as Cancer maculatus, in Amphitoe, and in several of the Edriophthalmida. I saw with M. Edwards small lenses in the facets of the cornea of Hyperia. Branchiopus paludosus also has, according to Burmeister's observations, lenses with longitudinal axes of considerable length behind the facets of the cornea, and in front of the cones.‡ Some of these animals, as Amphitoe, and several Edriophthalmida, Hyperia, and Branchiopus, have two corneæ, of which the external is smooth, while the internal one is marked with facets, or has fenestræ behind which the lenses lie, as in Branchiopus. It appears then that the following may be set down as the modifications of compound eyes:—

1. Compound eyes with cornea divided into facets and transparent cones without lenses. Observed in insects and most decapodous Crustacea.

a. The cornea with simple facets.

b. The cornea with marked lens-like elevation of the internal surface of the facets. Ex. Meloe.

2. Compound eyes with cornea destitute of facets, and no lenses.

a. The transparent cone-shaped bodies rounded at their base. Observed in Daphnia, Apus, Gammarus, Cyanus, &c.

b. The bases of the cones united with the cornea. Ex. Limulus.

3. Compound eyes with lenses in front of the transparent cones.

a. The cornea divided into facets. Observed in Callianassa and several Brachyura, as Cancer maculatus.

b. Two corneæ; the external smooth, the internal divided into facets. Observed in Amphitoe, several Edriophthalmida, and in Hyperia.

c. Two corneæ; the external smooth, the internal with fenestræ. Ex. Branchiopus.

Allied to these compound eyes with lenses and cone-shaped vitreous bodies, is the fourth kind of compound eye pointed out by me as early as 1829.

4. Aggregates of simple eyes, of which each contains the essential parts of a simple eye, namely, lens and globular vitreous humour. This form is met with in several Isopoda, as Cymothoe; and in the Myriapoda,

* See Meckel's Archiv. 1829.

† Hist. Nat. d. Crustacées, t. i. p. 116. Paris 1834.

‡ Müller's Archiv. 1835, p. 529; and 1836, p. cii.

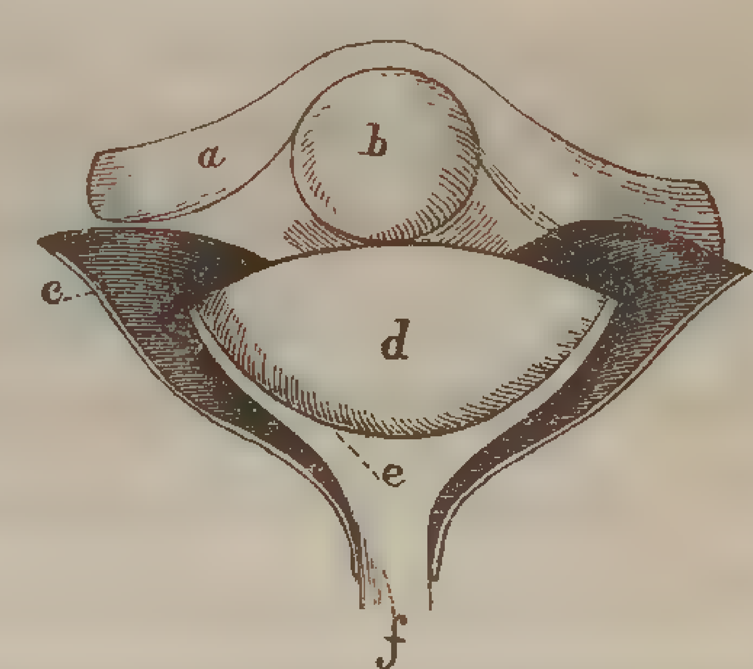
Julus. This is the transition form between mosaic-like compound eyes unprovided with concentrating apparatus, and the organ of vision with such apparatus.

C. *Simple eyes of Insecta, Arachnida, Crustacea, and Mollusca, provided with concentrative refracting media.**

a. Simple eyes with lens.

1. *Arachnida.*—The eyes of the Arachnida are constructed upon the principle of those of man and vertebrate animals generally. Behind the cornea is a spherical lens, and behind this a vitreous body. The black choroid forms a ring around the lens (fig. 81.) Usually the Arachnida have several of these eyes; the scorpion, for example, has two upon the upper surface of the head, and six of smaller size upon its margin: in the Scorpio teter (Mus. Entom. Berol.) from the Cape, and in the Scorpio occitanus, I found as many as ten eyes at the anterior margin of the head ‡

Fig. 81.†



2. *Crustacea.*—Eyes with concentrative refracting media or lenses are rare in Crustacea. Where they occur, they are given as accessory organs, the compound mosaic-like eyes being also present. They are here commonly called "simple eyes," to distinguish them from the compound. Thus the Limulus Polyphemus has, in addition to the compound eyes, two "simple eyes."

3. *Insects.*—In this class the simple eyes with lenses occur both alone and associated with compound eyes. The former is the case in several apterous insects, as the Scolopendra, which has four eyes on each side of the head, the Poduræ, and parasitic Aptera. The larvæ of carnivorous Coleoptera also have simple without compound eyes; thus the larvæ of Cicindela and Aristus have two, the larvæ of the water-beetle, Dytiscus, twelve (six on each side). The larvæ of Hymenoptera are, for the most part, destitute of eyes; but the larvæ of bees have two simple eyes. The larvæ of Lepidoptera are ordinarily provided with several simple eyes on each side of the head. Some insects in the perfect state, as the Orthoptera, the Hemiptera, Neuroptera, Hymenoptera, and the families Sphynx and Phalæna, or crepuscular and nocturnal Lepidoptera, have from two to three simple eyes together with compound eyes.

* J. Müller, Physiol. des Gesichts-sinnes, p. 315.—Ann. d. Sc. Nat. t. xvii. p. 232.—Ann. d. Sc. Nat. t. xxii.—Meckel's Archiv. 1829, pp. 38 and 208.

† [Fig. 81.—Eye of scorpion, after Müller. *a.* cornea; *b.* lens; *c.* choroid; *d.* lenticular vitreous body; *e.* cup-shaped retina; *f.* optic nerve.]

‡ On the structure of the eyes of Arachnida, and the union of the characters of compound with those of simple eyes; see Brants, in the Tydschrift voor natuurlyke geschiedenis. 4. 1 and 2 Stück. p. 135.

According to my observations, the simple eyes of these insects have the same structure as those of the Arachnida. They certainly contain a spherical lens close behind the cornea, and probably a substance analogous to a vitreous humour. Sometimes these eyes are elongated transversely; one of the eyes of the Scolopendra morsitans has this form, as have also two of the circle of eyes on each side of the head of the larvæ of Dytiscus marginalis; in this case the lens also is oblong.

The function of the simple eyes of insects is probably confined to the perception of very near objects. This may be inferred partly from their existing principally in larvæ and apterous insects, and partly from several observations which I have made relative to the position of these simple eyes. In the genus Empusa the head is so prolonged over the middle inferior eye, that, in the locomotion of the animal, the nearest objects only can come within its range. In the Locusta cornuta, also, the same eye lies beneath the prolongation of the head. The same is the case in the genus Truxalis. In Gryllus vittatus (Fabr.) the simple eye lies beneath, just above the helmet, or *galea:* and it has the same position in most species of Gryllus with a conical head; for example, in the Gryllus serrulatus, and G. crenatus. In the Gryllus lithoxylon (Klug) the middle simple eye lies entirely concealed in a furrow between the antennæ, so that its field of vision must be very small, and confined to very near objects. In Acheta monstrosa the simple eyes are scarcely perceptible, being seated on the radicle portion of the antennæ, and nearly included in the articulation of those organs with the head. In Orthoptera generally, also, the simple eyes are, in consequence of the depressed position of the head, directed downwards towards the surface upon which the insects are moving. In most Hymenoptera, on the other hand, the eyes are placed more posteriorly, as in Malaxis, Cimbex, Tenthredo, Leucopsis, Sirex, Ichneumon, Chrysis, Lasius, &c. From these facts, I consider myself justified in concluding that the simple eyes of insects are intended principally for myopic vision. The simple eyes bear a similar relation to the compound eyes, as the palpi to the antennæ. Both the antennæ and compound eyes are absent in the larvæ of insects.

4. *Mollusca.*—Organs of vision of similar structure to the simple eyes of Arachnida and insects are also possessed by many Mollusca, namely, by the whole order of Gasteropods. They contain a lens, and traces, more or less distinct, of a vitreous body.* These organs appear to the naked eye like black points, and are seated either at the extremity of the tentacles, upon a projection at the middle of their outer surface, or at their base. Those of the Helix are situated somewhat to the side of the extremity of the great tentacles. In their general structure they resemble the eyes of the higher animals, have a cup-shaped choroid

* J. Müller, Ann. d. Sc. Nat. xxii.

which forms a zone anteriorly, a lens and a vitreous humour, as was known to Swammerdam. The eye of the Murex Tritonis has, at least, one of the refracting media, a transparent body of considerable size and nearly round. With regard to the optic nerve of gasteropods, anatomists were formerly in error, mistaking for it the great nerve of the tentacle, which is the nerve of touch; the optic nerve is much more minute, and looks like a branch of that larger nerve, but may be traced backwards to the cerebral ganglion. The organ of vision in gasteropods appears to be adapted for the perception of the nearest objects only; for the Helix pomatia does not avoid an object placed near it until it is within two or three lines of the tentacle.

The eyes of cephalopod Mollusca contain all the essential parts of the organ of vision of the higher animals, even the iris and corpus ciliare.

b. Aggregates of simple eyes.—We may thus designate the organs of vision of some animals, which are produced by the aggregation of a great number of simple eyes into one mass, but in which each single eye either has the structure of the simple eyes of Arachnida and Mollusca, or is formed upon the model of the eyes of the higher animals. I met with such eyes in some insects and Crustacea, namely, in the genus Julus among insects [or Myriapoda]; and in some of the isopodous Crustacea, [German, Asseln], for instance, in Cymothoa. The surface of the organs of vision in these animals presents a number of convexities corresponding to the individual eyes. About as many as forty eyes may be united in one such aggregate organ. Behind each convex cornea is a roundish lens; and behind this a nearly spherical vitreous body, which is surrounded by retina and choroid. The aggregate forms the link between the simple eyes with refracting media for concentrating the rays of light and the compound mosaic-like eyes with lenses and conical transparent bodies.

D. *The eye of man and vertebrate animals.* — This is not the place to treat of the structure of the different parts of the eye, and to describe its general anatomy. It is our object here to refer merely to the principal structural relations important for the function of vision, and to the most essential differences presented by the eye in the different classes of vertebrata.

Appendages of the eyes. — *The eye-lids.*—The eye-lids may be entirely wanting, the skin passing in that case simply over the surface of the eye, as in many fishes and several Amphibia,—for example, in the Proteida and Pipa; or the skin forms eye-lids (palpebræ), which may be either single or double, or be united into a circular zone with a central opening, as in the chameleon. In addition to the ordinary eye-lids, there is seen in some animals the membrana nictitans, or third eye-lid, which exists in a rudimentary state even in Mammalia, is most fully developed in birds and reptiles, and exists again in a less perfect form in fishes, namely, in several genera of the shark family. In birds this membrana nictitans, which is a translucent membrane, can be drawn from the inner side over the anterior surface of the eye by means of a peculiar muscular apparatus subject to the nervus abducens. The sharks in which this membrane exists are the genera Carcharias and Galeus, and several others allied to them; in the genera Scyllium, Lamna, Selache, Alopecias, Notidanus, Spinax, Centrina, Scymnus, and many others it is wanting.

Of similar nature to the membrana nictitans is a spectacle-like transparent space in the inferior eye-lid of some lizards, as several of the Scincoid family, which can be drawn over the eye; and, while it corresponds to the cornea, does not prevent vision. The immoveable capsule in front of the eye in serpents is, on the contrary, quite a peculiar structure. The eye-lids are in other animals replaced by a transparent capsule lying in front of the eye, and continuous at its margin with the skin of which it is an attenuated prolongation. This capsule is composed of three laminæ: of an external one, which is a continuation of the epidermis, and is therefore cast off when the skin is shed; of a middle layer prolonged from the cutis; and of an internal layer, which corresponds to the conjunctiva palpebrarum, and, like it, is reflected at its circumference so as to be continuous with the conjunctiva covering the globe of the eye. Between this capsule and the anterior surface of the eye of serpents is a cavity into which the tears are poured, and whence they escape, as usual, through the lachrymal canal. The last-mentioned provision was first discovered in serpents by Cloquet: it exists even in those which have the eyes covered by a thick skin, as in Amphisbænæ, &c.; and I have also detected it in a mammiferous animal, Spalax typhlus, the eyes of which are covered by a thick hairy cutis, but have under this skin a cavity formed by conjunctiva. Lizards have generally eye-lids; but in one family, the Geckos, I have discovered the remarkable peculiarity that the eyes are covered by a transparent capsule, as in serpents.

The *lachrymal apparatus* is absent in cetaceous Mammalia, in Amphibia, and in fishes.

The tunics of the eye.—The *sclerotica* in many animals exhibits a tendency to be cartilaginous or bony. In birds, Chelonia, and lizards, the anterior part of the sclerotica immediately around the cornea contains a ring of osseous plates, of which the edges either lie one over the other in an imbricated manner, or are merely in apposition; and the sclerotic coat in fishes generally contains two large plates of cartilage.

The *choroid* is in animals divisible into two laminæ, — the external proper choroid, and the internal membrana Ruyschiana; in fishes the external lamina has generally a silvery lustre, while the internal is covered with pigment. Between the two at the point of entrance of the optic nerve is situated the glandula choroidalis, a body of a horse-shoe shape which receives a large quantity of blood.* The *ciliary ligament* is in man and Mammalia of fibrous structure, but in birds appears to be muscular. The inner surface of the choroid is in all animals covered by the *membrana pigmenti,* which is composed of flattened cells, often of hexagonal form, containing the granules of pigment. In albinoes these cells contain no pigment. In several animals it is normally deficient at certain parts of the eye, which then either are white, or have a metallic lustre, and are called the *Tapetum.* The tapetum at the posterior and external part of the eye in ruminant animals is covered with the cells of the pigment membrane, but the pigment itself is wanting. The metallic lustre and iridescent colour of the tapetum in these animals appears to be owing to the structure of the choroid producing "interference" of light, and not to the presence of any material colouring matter; they are therefore lost when the choroid is dried.† The perfectly white colour of the tapetum, which occupies an accurately defined triangular space at the bottom of the eye of carnivorous animals, is not destroyed by drying, and is due to a peculiar pigment. The smallest quantity of light entering the eye is reflected by the tapetum; and hence it is that the eyes of animals provided with this structure are luminous in a very faint light, though not in perfect darkness (see page 93).

The *corpus ciliare,* or *ciliary processes,* do not exist in fishes, with few exceptions; but a *falciform process* passes through a cleft in the retina, and attaches itself firmly to the margin of the lens, which is also held in its position by a small pear-shaped body (the campanula Halleri).

The *iris* is mobile in most animals, but in the osseous fishes is scarcely, if at all, so. In the horse, narwhale, lama, and rays, it presents at the upper border of the pupil a veil-like appendage. The *pupil* is sometimes round; sometimes elongated transversely, as in the Ruminantia; sometimes in the perpendicular direction, as in the cat family and the crocodile; sometimes triangular, as in the brown or fire toad, Rana bombina, &c.

The *pecten* or *marsupium* is characteristic of birds; it is a pyramidal

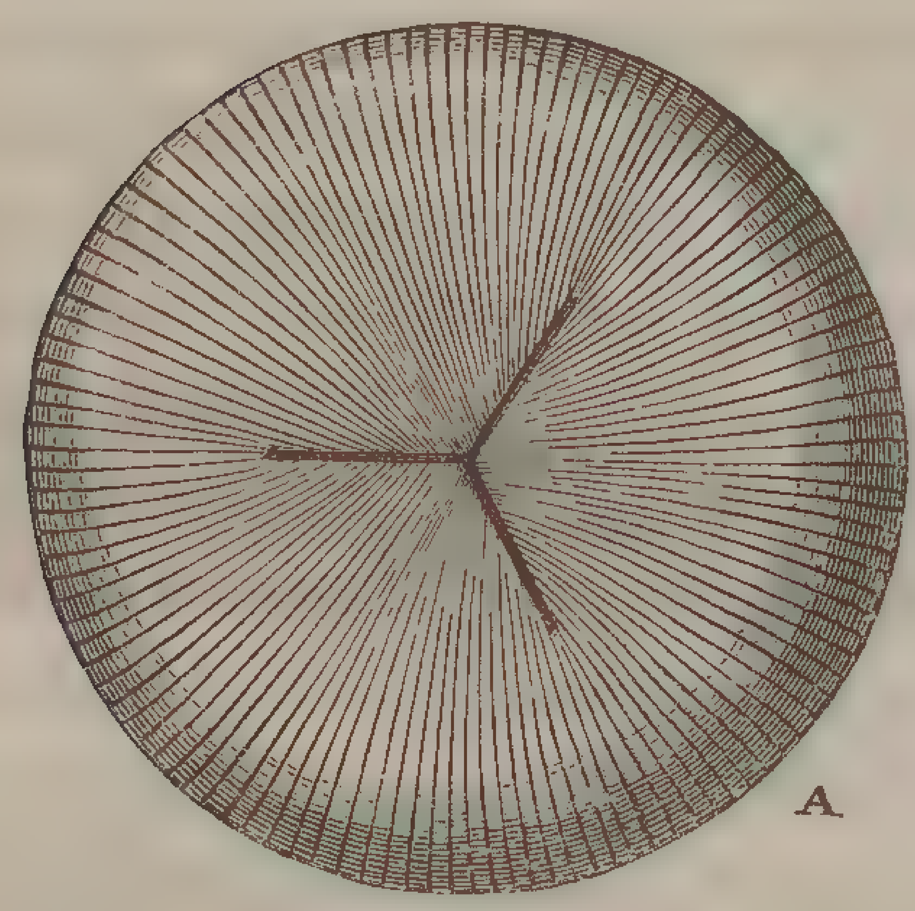
* [On the structure of this body, see Mr. Owen's remarks in the third volume of the Physiol. Series of the Catalogue of the Hunterian Museum; and Mr. Wharton Jones's paper in the twenty-first volume of the Med. Gazette, p. 650.]

† [It has been shown by Hessenstein, Valentin (Repertor. 1837, p. 246), and Mr. H. J. Carter, (Medical Gazette, Jan. 5, 1839,) that the action of the tapetum of ruminant animals in decomposing light depends on its being formed of parallel waving fibres like those of tendon. The influence of these fibres in producing the iridescent colours is explicable on the principle of "interference," see page 1107.]

plicated process provided with pigment, which has its origin in the choroid coat, passes through an opening in the retina, at the bottom of the eye, into the middle of the vitreous humour in the direction of the margin of the lens; its situation is the posterior and external part of the cavity of the eye. Lizards have a trace of the pecten, and the processus falciformis of fishes is perhaps an analogous structure.

Transparent media of the eye.—The fibrous structure of the lens has been already described at page 396. [Fig. 82, A, represents the disposition of the fibres in the lens of Mammalia; fig. 82, B, shows the

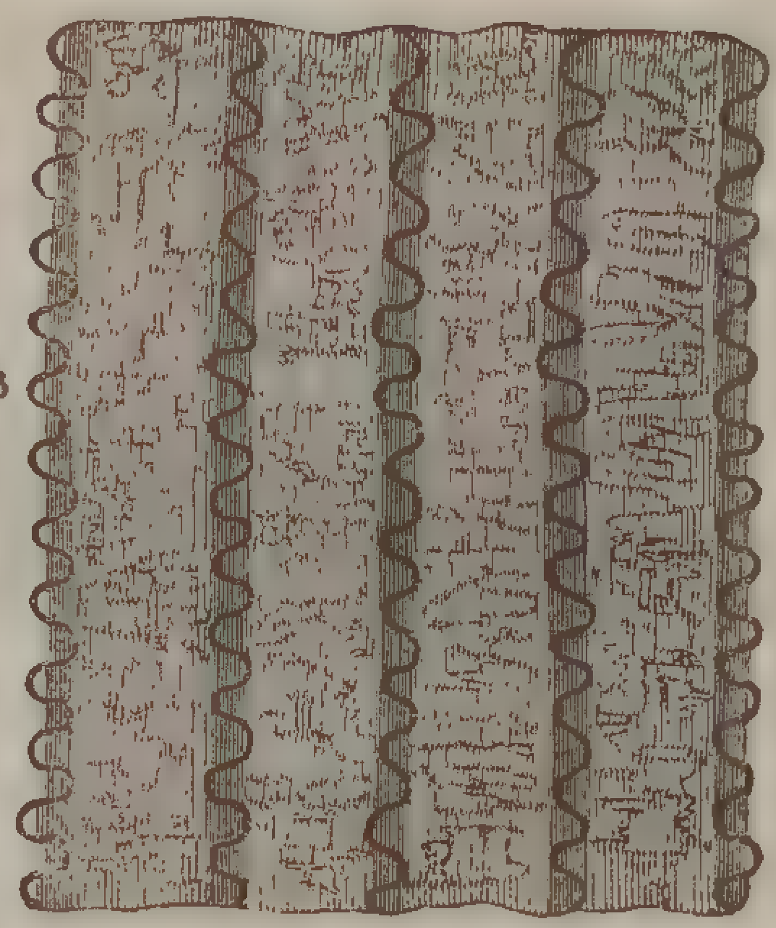
Fig 82,



A.

Fig. 82, B.

B



mode of union of the different fibres by their toothed margins.]* The arrangement of these toothed fibres is very different in the different classes and orders of animals.† The internal laminæ of the lens are always more firm than the external; in fishes the former have an extraordinary hardness, almost like that of horn. In aquatic animals the lens is always more convex than in those which live in the air; in fishes it is spherical, and in the cuttle-fish (Sepia) elongated in the direction of its axis. Convexity of the cornea would have been of no service in these animals, since the refracting power of the aqueous humour differs little from that of the water in which they live; though in animals living in the air the refraction produced by the cornea and aqueous humour is very great. Hence it was necessary that the refracting power should be provided in these aquatic animals by greater convexity of the lens. The anterior half of the lens in fishes projects through the pupil into the anterior chamber of the eye.

Optic nerve and Retina.—The most remarkable peculiarities of structure are presented by these parts. The optic nerve is always constituted of primitive nervous fibres, which are similar to those of the

* [Figs. 82, A and B, are copied from Sir D. Brewster's paper in the Philos. Transact. 1833.]

† Brewster, Philos. Transact. 1836.

brain, being very minute, much more so than those of other nerves. The nerve thus composed either presents a merely fibrous structure, as in man: or these fibres are arranged in particular situations, as at the chiasma, into laminæ; the laminæ of one nerve passing at this part between those of the other, as in birds, reptiles, and Amphibia: or, lastly, the whole optic nerve, in its course from the brain to the eye, is membranous; this structure, which Malpighi discovered in the sword-fish, appears to be characteristic of all fishes. When the sheath of the optic nerve in these animals is laid open, the optic nerve is seen, having the form of a membrane with free borders folded together like a curtain; and it would seem that the retina is formed simply by the unfolding of this membrane.* The retina in the eye of fishes has at least two corresponding free borders, being cleft and gaping from its anterior margin to the fundus of the eye.

The union of the two optic nerves soon after their origin, or the optic commissure or chiasma, next requires our attention. The varieties in structure with relation to this part may be stated as follows:—1. The structure which exists in osseous fishes. Here the two nerves are connected after their origin by a slender transverse commissure; and then form no chiasma, but simply decussate without their fibres mingling, the right nerve going to the left eye, and the left nerve to the right eye. 2. The structure proper to cartilaginous fishes. Here the nerves do not decussate as in osseous fishes, but are closely connected by a commissure, the internal structure of which is not known; this form approaches very nearly to the chiasma of the higher animals. 3. The chiasma of Amphibia, reptiles, and birds, which in external appearance is similar to that of Mammalia, but has an internal laminated structure; the laminæ of one optic nerve passing between those of the other nerve, like the crossed fingers of opposite hands. It is not yet known whether all the fibres of the two optic nerves decussate here, or whether a portion is continued to the eye of the same side as that of their root. 4. The chiasma of Mammalia and man. The laminated structure is here absent. There is a partial decussation of the fibres of the two nerves, while another portion is continued to the retina of the same side. This structure is more evident in mammiferous animals than in man. The superior and external portion of each root of the optic nerve is, in the horse, continued to the eye of the same side; the rest of the fibres decussate, and form part of the nerve of the opposite side.†

The microscopic structure of the *retina* has been recently elucidated by the discoveries of Treviranus,‡ with which the observations of Gottsche §

* J. Müller, Physiol. des Gesichts-sinnes, tab. 3, fig. 19. † Ibid. tab. 2. figs. 4, 5.

‡ Beiträge zur Aufklärung des Organischen Lebens. Bremen.

§ Pfaff's Mittheilungen aus dem Gebiete der Medicin, 1836. Heft 3, 4. The most internal fibres of the cerebral portion of each optic nerve are, according to Mr.

also are in accordance. The following description takes account of all the most important points in the structure of this part:—The retina consists of three principal layers; an external pulpy or pavement-like layer of granules, a middle fibrous layer, and an internal layer composed of erect cylinders, which is the continuation of the fibrous layer. The optic nerve, at its entrance into the eye, divides into the cylindrical nervous fibres which radiate out in the middle fibrous lamina of the retina. Each nervous fibre, or each fasciculus of several fibres, bends, as Treviranus discovered, at a certain point of its course, from the horizontal direction towards the opposite internal surface of the membrane,

Fig. 83*

where it ends as a papilla (fig. 83). The diameter of the nervous fibres was in the hedgehog 0·001 millim. [$\frac{1}{2116}$ of a line]; the diameter of the papillæ in the rabbit 0·0033 millim. [$\frac{1}{641}$ of a line]; in birds from 0·002 to 0·004 millim. [$\frac{1}{1058}$ to $\frac{1}{529}$ of a line]. In frogs the fibres measured 0·0044 millim. [$\frac{1}{481}$ of a line], and the papillæ 0·0066 [$\frac{1}{320}$ of a line] in diameter. The retina in all classes of Vertebrata,

Mayo, continuous in the commissure with corresponding fibres of the opposite nerve; these would be, as Mr. Solly remarks, strictly commissural fibres. The innermost fibres of the nerves beyond the commissure are also described by Mr. Mayo to be united in a similar manner by a sort of loop, and not to be continued backwards through the chiasma.

* [Fig. 83. Structure of the retina, after Treviranus.—A. Portion of retina of a sheep seen from the outer side, showing the cylindrical fibres, and at the right hand border some of the papillæ, in which the fibres terminate on the inner surface of the retina; B. papillæ seen on the inner surface of the same retina; C. a thin perpendicular section of the retina of the hooded crow (Corvus cornix), which had been hardened by maceration in spirit; *a.* internal lamina of choroid; *b.* layer of cellular tissue, in which the fibres of the retina radiate out; *c.* perpendicular portion of the fibres of the retina; *d.* second layer of cellular tissue, containing a network formed by branches of the arteria centralis retinæ, and giving a sheath of this vascular layer of retina to the nervous fibres; *e.* larger nervous fibres which have acquired this sheath; *f.* third cellular layer perforated by the papillæ (*g*).]

if examined in the fresh state, is seen to have on its internal surface a layer of cylinders arranged closely side by side, with one extremity directed towards the cavity of the eye. These cylinders, or rod-shaped bodies, separate very easily from the subjacent membrane, and are seen floating free in the field of the microscope. In fishes they have small enlargements or papillæ, of which Gottsche has given an exact description. These rod-shaped terminations of the nervous fibres upon the internal surface of the retina must be examined in the perfectly fresh state. They very quickly undergo change after death, particularly in the summer season; and in their place there is seen merely a layer of granules, which were frequently observed in the earlier investigations into the structure of the retina. Although the three layers of the retina certainly exist, and although the rod-shaped bodies composing its internal lamina are very distinct, having been seen by Volkmann, E. H. Weber, Gottsche, Ehrenberg, and myself, yet the essential nature and mode of connexion of these bodies with the fibres of the fibrous layer are still involved in obscurity. It is a question, namely, whether the rod-shaped bodies correspond exactly in number to the nervous fibres, and whether each fibre actually corresponds to one of those bodies; or whether the latter are superposed in series upon the fibres of the fibrous layer.

Conditions necessary for vision.—Owing to ignorance of the physical conditions necessary for vision, it has become a current opinion that there are animals endowed with the perception of light by their skin. It cannot be doubted that many animals which have no eyes are sensible of the influence of the principle of light; thus, Rapp* observed that the Veretillum cynomorium, one of the Polypifera, avoids the light, and prefers shaded situations.† But, with respect to the mode of action of light on such animals, we have no facts to prove that it produces in their skin, or the entire surface of their body, really the sensation of light, and not another kind of sensation. We ourselves are sensible of the action of light on our skin by the sensation of warmth which it produces, but do not thence derive any sensation of light; for, as far as we can judge from facts, the optic nerve alone is susceptible of that sensation. The action of light on the lower animals destitute of eyes

* Nova Acta Acad. Nat. Cur. xiv. p. 2.

† With respect to the Hydræ no decided result has been obtained, notwithstanding the experiments of Trembley, Baker, Hanow, Roesel, Schaeffer, Bonnet, and Goeze. Ingenhouss and Goldfuss relate that the green matter of Priestley collects especially in places exposed to a bright light. This green matter, which collects in such situations, may certainly consist of living infusory animalcules, since many of these creatures have a green colour, and many indeed have, according to Ehrenberg's observation, eye-dots. What is usually called the green matter of Priestley, however, often consists merely of the dead remains of green Infusoria, as the Euglena viridis and others.

may be similar to its action on the surface of our body. Even plants are strongly affected by its influence; the direction in which they grow and spread their branches is regulated by their tendency to bend towards the light.

The connexion of the sensation of light solely with special nerves endowed with a specific sensibility is proved by the actual existence of eyes in many of the animals lowest in the scale of organisation. Many of the Annelida, as several of the Nereida, several species of Eunice, Phyllodoce, Spio, and Nais, almost all the Hirudo family, and the Aphrodrite heptacera, have dark eye-dots on their head. An annelide nearly allied to Sabella, and observed by Ehrenberg, Henle, and myself, has two such dark points at each extremity of its body; and it creeps both forwards and backwards. The Hirudo medicinalis has, as E. H. Weber pointed out, ten dark eye-dots on its head, which in the embryo are distinctly visible, the body being yet transparent. The Planariæ have on their head eye-dots rendered visible by pigment. Similar eye-dots have been observed in several Cercariæ and Rotifera by Nitzsch, Dutrochet, Gruithuisen, and Ehrenberg. The last-mentioned naturalist has discovered the existence of such dots of pigment, or eyes, in many Infusoria, and also in the Asterias family, at the extremity of the divisions of their body, which they elevate in swimming; and he has rendered it probable that the bodies containing pigment, which exist at the margin of the disk in the Medusæ, have a similar function.* I have demonstrated the optic nerves in the dot-like eyes of the Annelida, and Ehrenberg has shown that the nerves in the arms of the Asterias are continued to the eye-dots at their extremity.

Gruithuisen† supposes that every dark spot of the skin has in some degree the nature of an organ of vision, since it absorbs more light than other parts. This is evidently an error; for the primary condition for vision is the specific sensibility of a nerve having other endowments than those of the nerves of mere common sensation or touch.

The very structure of the eyes in the Annelida proves, moreover, that, even for the mere distinguishing of day from night, a special nerve and an organ are necessary; for, as I have already shown at page 1110, the eyes of these animals are totally destitute of optical apparatus for the formation of images, and are consequently incapable of distinguishing any objects. Nature, therefore, where it aimed merely at the power of distinguishing light from darkness, has formed organs for that purpose; and it is probable that the eye-dots of the Planariæ, Asterias, Rotifera, and Infusoria have this function.

A second critical remark, which suggests itself in connexion with this

* Müller's Archiv. 1834.

† Isis, 1820, 251.

subject, relates to the opinion that, by virtue of the exaltation or transposition of sensibility, it is possible for persons to see with the skin.

It is a known fact that we cannot, by means of the fingers, recognize colours as such; although it may be possible to distinguish the corpus or grain of some colouring matters when laid thickly upon a surface, since they are uneven, and adhere to the skin which touches them. The necessity for an optical apparatus for the production of an image upon a percipient membrane sufficiently refutes the notion of persons being able to see with their epigastrium, or with the fingers, when in the so-named magnetic or mesmeric states. Even though the skin of the epigastrium or fingers were susceptible of the sensation of light, which they are not, the perception of objects would yet be impossible, unless there were optical apparatus for collecting the light radiated from certain points of the object upon certain corresponding points of the sensitive surface; and, without such apparatus, the epigastrium and fingers, though they possessed the sensibility for light, would merely be able to distinguish light from darkness. Since, however, these parts are not susceptible of the sensation of light, and since no sense can be transferred from one part to another, it is quite impossible for a person in the magnetic state to have even an obscure perception of light and darkness by means of any other parts than the eyes. Moreover, when the eyes are bound, it is still possible to distinguish the light, and even objects, by slightly raising the eye-lids, as every one well knows who has played at the game of "blind-man's buff;" and persons lying, like the subjects of the pretended magnetic sleep, in the horizontal posture with their eyes bound, can see every part of the room by looking under their bandage. But what well-informed physician can put faith in the fables told by the upholders of animal magnetism? It is quite in accordance with the laws of science that a person sleeping shall have ocular spectra,—we experience them sometimes when the eyes are closed, even before falling asleep,—for the nerves of vision may be excited to sensation by internal as well as by external causes; and so long as a "magnetic" patient manifests merely the ordinary phenomena of nervous action that are seen in other disorders of the nervous system, it is all credible enough. But when such a person pretends to see through a bandage placed before the eyes, or by means of the fingers or the epigastrium, or to see round a corner and into a neighbouring house, or to become prophetic, such arrant imposture no longer deserves forbearance, and an open and sound exposure of the deception is called for.

II. *Theory of vision deduced from the structure of the eye.*

Vision, or the formation of images, requires a very different theory, according as the eyes are constructed of transparent cones disposed in a radiate manner, and having their lateral surfaces so covered with pigment, that the light which passes in the direction of their axis can alone reach the retina, which is the case with the compound eyes of insects and Crustacea, — or like the simple eyes of insects, Arachnida, Mollusca, and Vertebrata, have concentrating refractive media, a cornea with or without aqueous humour, a lens, and a vitreous body.

A. *Of the mode in which vision is effected by the compound eyes of Insecta and Crustacea.**

The process of vision in insects and Crustacea with compound eyes is the more interesting, inasmuch as it is totally different from that which subsists where the eyes have a structure similar to the human eye, and affords an insight into the nature of vision generally. The structure of the compound eyes of insects has been described in the preceding pages.

As long as the transparent cones coated with pigment, which are intermediate between the cornea and retina, received no attention, or the fibres of the optic nerves were supposed to extend to the facets of the cornea, the vision of insects was quite inexplicable. If the fibres of the nerve extended as far as the cornea, each luminous point, *a*, *b*, *c*, or *d*, lying in front of the eye, would cast rays of light upon all the fibres of the nerve, *a*, *b*, *c*, and *d*, at the same time; in other words, the points *a*, *b*, *c*, and *d*, could not be distinguished from each other, but merely a certain general impression would be produced. The cones, however, prevent any light from reaching the nervous fibres corresponding to them, except that which enters them in the direction of their axis or of the radii of the eye; while all the rays of light which fall upon the sides of these cones are absorbed by the pigment covering them. In consequence of this, each cone represents an aliquot portion of the image, which is composed, like a mosaic-work, of as many parts as there are cones in the eye, and the distinctness of the image necessarily increases with the number of the cones.

Distinctness and indistinctness of the image.—The image formed in the eyes of insects and Crustacea, and that received upon the retina of eyes constructed with concentrating refractive lens-like apparatus, owe their distinctness respectively to very different causes. In the latter case, distinctness is due to the retina being situated at the proper focal distance from the lens. In the former, it depends merely on the size of the eye, and the number of cones or facets which contribute to compose the image. When the eye contains 12,000 such bodies for isolating the rays of light, 12,000 divisions of the field of vision will be separately

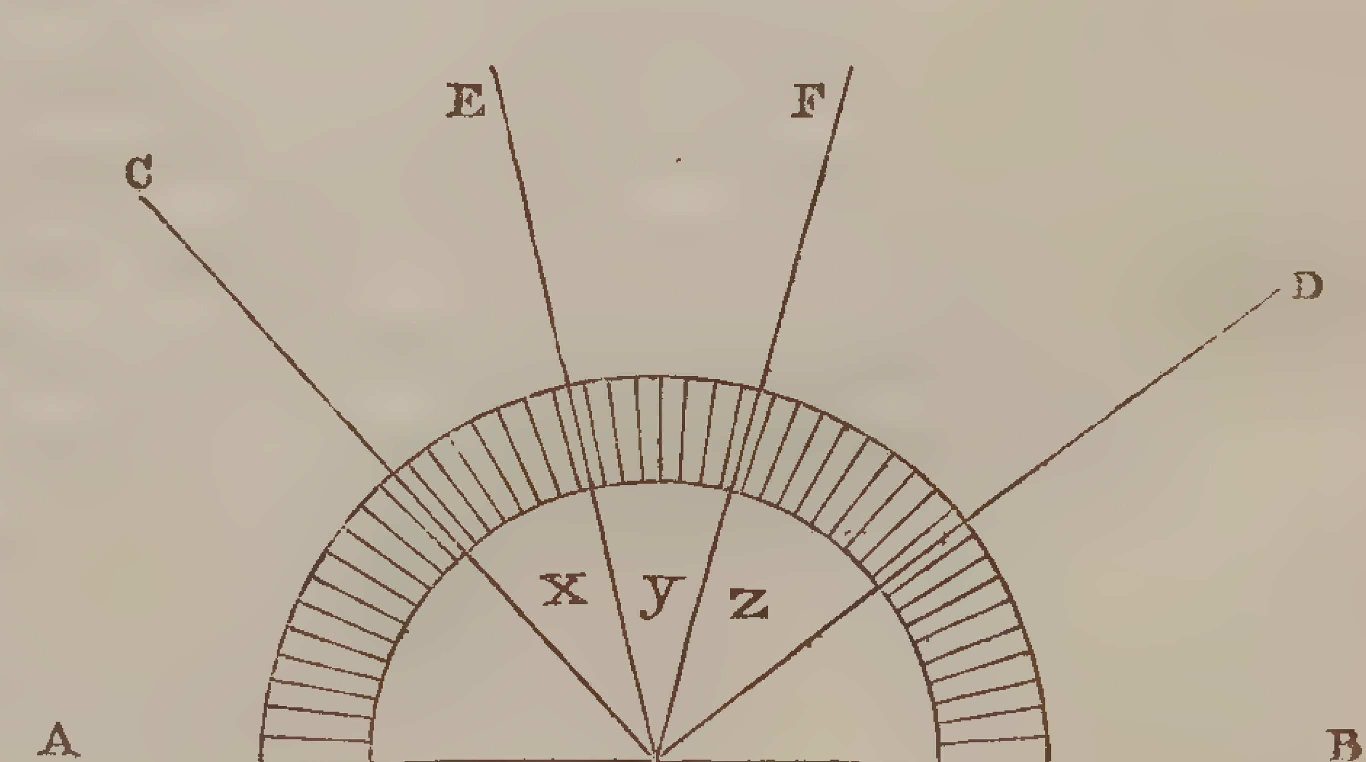
* J. Müller, Physiol. des Gesichts-sinnes, p. 315.—Ann. d. Sc. Nat. t. xvii. p. 232.

represented in the image. But, when the number of these bodies is small, each cone and each facet will admit the rays from a much larger portion of the visual field, and the image in each of these areæ will produce a confused impression, and not a distinct representation of the different luminous points; for all the luminous points from which the rays fall upon the same cone, and the same nervous fibre corresponding to this cone, will excite but one mixed sensation. The length of the cones also must have an influence on the distinctness of vision by these eyes; for, the longer the cones, the more perfectly will all the oblique rays be prevented from reaching the optic nerve, so that the impression of light will be more exclusively produced by the rays coming in the direction of the axis of the cone.

Vision of near and distant objects.—From the foregoing explanation of the process of vision in compound eyes, it follows that a great difference must exist between them and the eyes furnished with lenses in relation to the perception of near and distant objects. The action of the compound eyes remains the same whether the objects be near or distant: in neither case is any change of adaptation within the eye necessary; for a separate image will always be formed by those rays which traverse each cone in the direction of its axis, whether those rays come from a corresponding part of a near or of a distant body. The number of distinct points in the external world which are represented by one point only in the compound eye, will of course be greater as the distance of the object increases; but still there will be no halo produced, from the want of the rays being brought to a focus, and no change in the arrangement of parts in the interior of the eye will be necessary for the improvement of the image.

Size of the field of vision.—The extent of vision of an insect may be very exactly deduced from the form of the eyes; for, since no objects are seen but those which lie in the direction of the axes of the cones, or of the radii of the spherical surface of the eye, the axes of those cones which form the border of the eye, being extended onwards, will mark the limits of the field of vision. In other words, the greater the segment of a sphere which the eye of an insect represents, the more extensive will be its field of vision, and *vice versâ.*

Fig. 84.



An eye of hemispherical form (fig. 84) will receive the image of all bodies which lie in front of it, from the radius A to the radius B; an eye corresponding in convexity to the segment of a circle, C D, would receive the impression of the rays of light emitted by objects lying between the lengthened radii C and D; and the field of vision for an eye corresponding to the smaller segment of a sphere, E F, would only be such as would be included by the radii E and F. Since a body is less convex in proportion as the segment of a sphere which it represents is smaller, we may express this law by saying, that the less convex the eye is, the smaller will be its field of vision. The eye of a Libellula (or dragon-fly) has, for example, a field of extraordinary extent, for it forms more than half a sphere; it must receive the image of objects before and behind it, as well as at the side. The motions of this insect correspond with the developement of its eye, for they are very quick and sure; and their direction is changed at will, and often suddenly, towards either side. The slightly convex eyes of some Hydrocorizæ (water-bugs), which are scarcely raised above the surface of the head, and form a very small segment only of a sphere, must have a confined field of vision. In Naucoris and Notonecta these flat eyes lie at the front of the head, and we cannot therefore be surprised at the motions of these insects in the water being in accordance with the limited size of their field of vision. They move merely straight forwards, and do not vary their course from side to side.

It is evident that the absolute size of the eye cannot have the slightest influence on the extent of the field of vision. An eye may be very small, and yet have a large field, if it correspond in convexity to a large portion of a sphere; while, on the other hand, a large eye may have a very limited field of vision, if its surface be only slightly convex, so as to represent a small segment of a sphere.

Angle of vision.—It will be at once seen, from the remarks already made, on what depends the relative size of the images in comparison with the whole field of vision of an insect. The limits of the image of each object are determined by the rays of light which, issuing from the points of the object, fall upon the eye in the direction of the axes of the transparent cones. If we imagine these rays to be continued behind where they fall upon the eye until they meet, the angle included between them would be the angle of vision — angulus opticus. Or if we imagine the circle, of which the convexity of the eye in a section of it forms a part, to be completed, and the circle thus produced to be divided into degrees, minutes, and seconds, the distance of the points upon the surface of the eyes will be expressed in the measurements of angles. Now, since the relative size of the image, in comparison with the object, always depends on the position of the cones through which the rays of light from the individual points of the object pass, the size of the angle of vision for any object may be determined in degrees, minutes, and seconds, the distance from each other of the cones which admit the rays from the extreme points of the object being known. Objects at different distances from the eye, but transmitting their luminous rays to the optic nerve through the same cones, will, of course, form images of equal size, their angles of vision being the same. Thus, a body extending from the line C to the line E in the fig. 84, would always be seen under the same angle X; and its apparent size, in proportion to the field of vision, would be as X to 180°. The smallest angle of vision under which an insect will be able to distinguish one object from another, will be that which is included between the axes of two contiguous cones. Since many thousand cones are contained in one eye, we may form a general idea of the acuteness of vision of these animals.

From the consideration of the mode of action of these compound eyes in vision, it will be evident that no modification of structure is necessary to adapt them for the performance of their function in the air, or in water; for the conditions for vision remain the same in both cases, and, according to my observations, there are no structural differences between the eyes of aquatic insects and those of insects living in the air. In eyes in which the image is formed by the concentrating refractive action of lenses, a greater refractive power of the lens is necessary when the animal lives in the water than when vision is performed only in the air, on account of the difference between the density of the lens and water being less than that between the lens and air; but in the compound eyes of insects the refracting power of the transparent media has scarcely any share in the process of vision, and each cone transmits alike the rays from the object opposite to it, whether the surrounding medium be air or water.

The most perfect compound eye will be that which is fitted for seeing distinctly by its absolute magnitude, by the great number of its facets and cones, and by the length of these cones; and which has an extensive field of vision, owing to the convexity of its surface being such that it forms a great part of a sphere.

B. *Of the process of vision in eyes with concentrating dioptric media.**

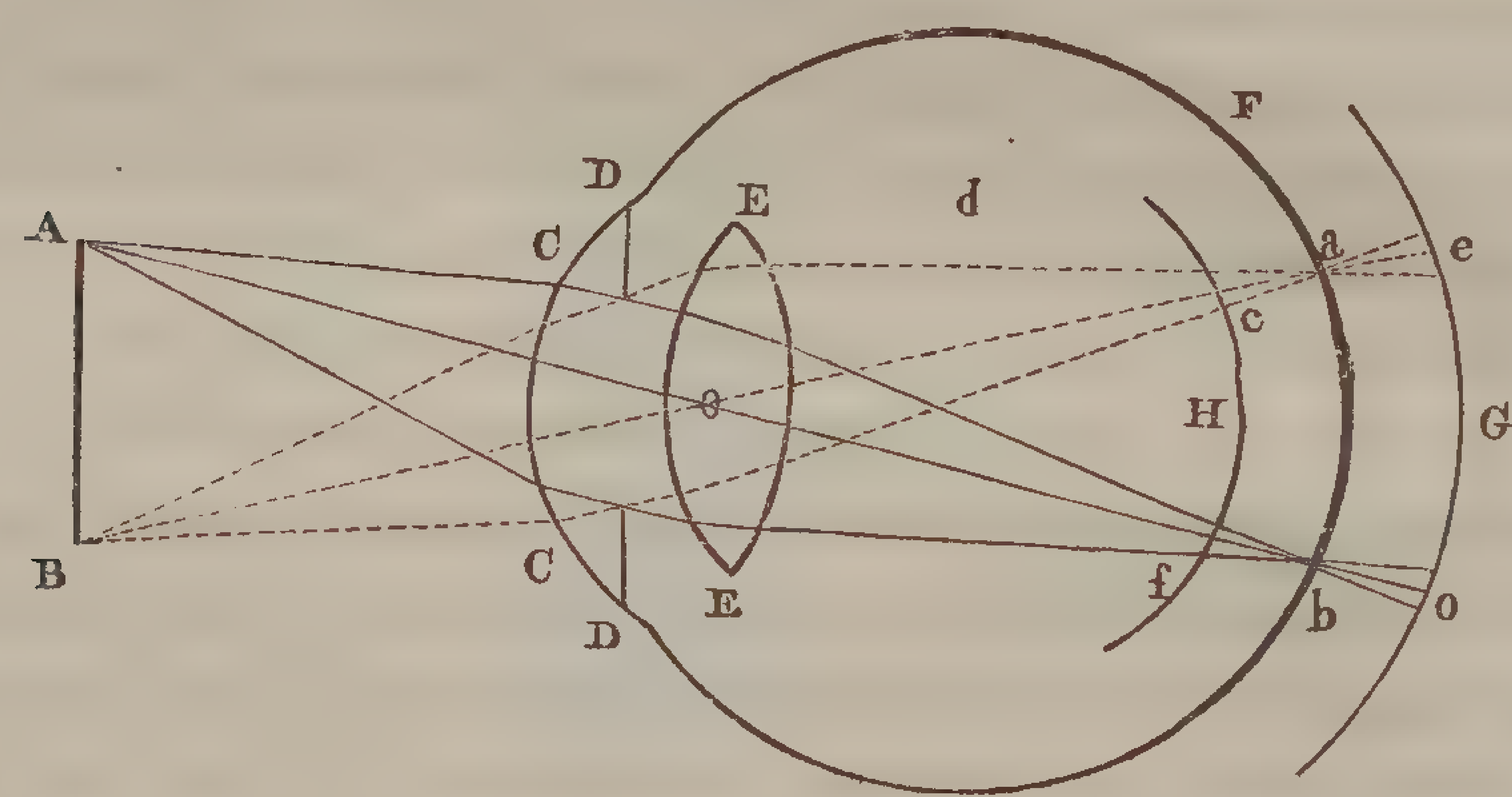
In the compound eye of insects and Crustacea vision is effected by the radiating cones transmitting to the optic nerve those rays only of the cone of light emitted by each point of the object, which have the direction of the axes of the cones, or of the radii of the eye, while the rest of the rays are absorbed. In eyes furnished with collective or concentra-

* After the treatises of Treviranus, Tourtual, Hueck, and Volkmann.

tive refracting media, the cone of light emitted by each point of the object is collected again to a point upon the sentient retina.

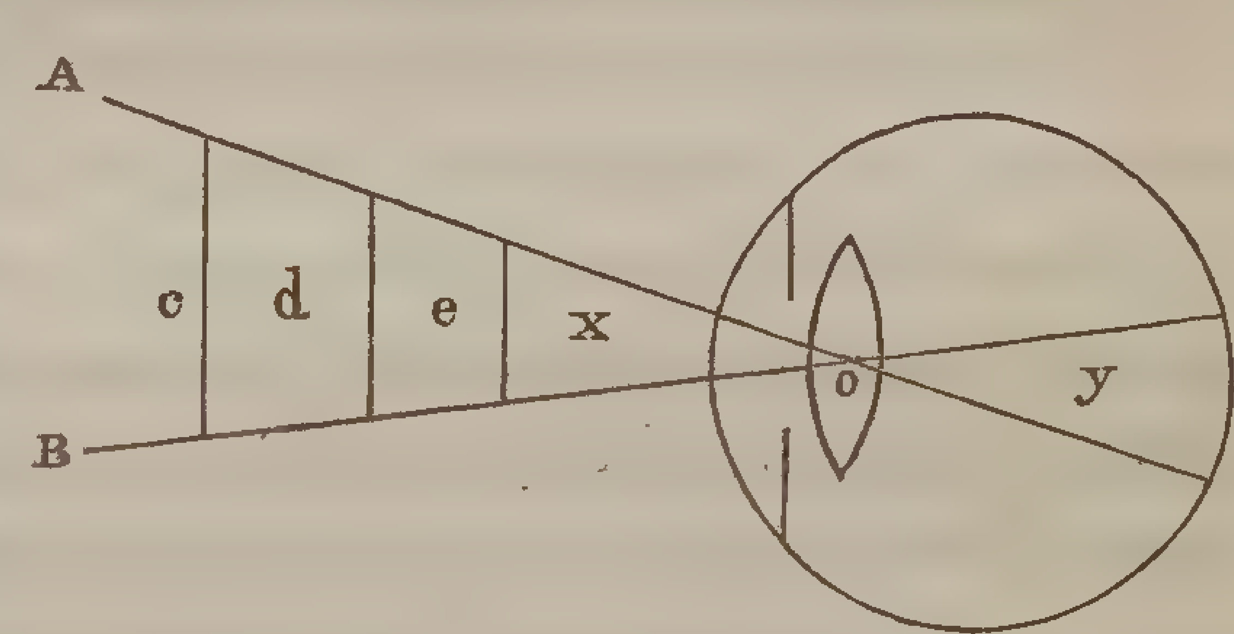
The refraction of the rays of light in the eyes of man and the higher Mammalia is, however, threefold. The rays of the cones of light

Fig. 85.



emitted by the points A B, and every other point of the object, (see fig. 85,) are first refracted by the cornea C C, and the aqueous humour contained between it and the lens, — that is to say, the rays are bent towards the axis of the cone of light; the media just mentioned having the power of refracting light by virtue of their density being greater than that of the air, and by reason also of their convexity. The rays of each cone of light are again refracted and bent still more towards its central ray or axis by the anterior surface of the lens E E; this body having a greater density than the aqueous humour, and its anterior surface being convex. The rays are again refracted in passing out of the lens into the less dense medium of the vitreous humour. It was shown in the preceding chapter, at page 1094, that a lens has the power of refracting the rays of a cone of light so as to bend them towards the axis of the cone, not only on their entrance from a rarer medium into the anterior convex surface of the lens, but also at their exit from its posterior convex surface, when they pass again into the rarer medium. In this manner the rays of the cones of light issuing from the points A and B are again collected to points at *a* and *b*; and, if the retina F be situated at *a* and *b*, perfect images of the points A and B will be perceived: but if the retina be not at *a* and *b*, but either before or behind that situation,—for instance, at H or G, circular luminous spots *c* and *f*, or *e* and *o*, instead of points, will be seen; for at H the rays have not yet met, and at G they have already intersected each other, and are again diverging. The retina must therefore be situated at the proper focal distance from the lens, otherwise a defined image will not be formed, or, in other words, the rays emitted by a given point of the object will not be collected into a point upon it. In the preceding chapter it was shown that the focal distance of the image is greater, the nearer the object to the lens, and *vice versâ*. The direction given to the rays by their refraction is regulated by that of the central ray, or axis of the cone, towards which the other rays are bent. The image of any point of an object is therefore always formed in a line identical with the axis of the cone of light, as in the line B *a*, or A *b*. The central ray of a cone of light will, it is true, itself suffer deviations from its straight path, if it do not pass through the axis of the lens, but impinge in an oblique direction upon it as well as upon the cornea. But these deviations may be disregarded for the present; and the spot where the image of any point will be formed upon the retina may be determined by prolonging the central ray of the cone of light, or that ray which traverses the centre of the pupil. Hence, for the preceding figure, the following (fig. 86) may be substituted. A *b* is the axis or central ray of the cone of light issuing from A; B *a*, the central ray of the cone of light issuing from B; the image of A is formed at *b*, the image of B at *a*, in the inverse position therefore; what in the object was above, is in the image below, and *vice versâ*,—the right-hand part of the object is in the image to the left, the left-hand to the right. These facts can be verified by an experiment on the eye of a quadruped. If an opening be carefully made in an eye at its superior surface, so that the retina can be seen through the vitreous humour, the image of any bright object, such as the windows of the room, will be perceived at the bottom of the eye. The experiment may be performed still more easily, as Magendie pointed out, by means of the eye of any albino animal, such as a white rabbit, in which the coats, from the absence of pigment, are transparent: such an eye being dissected clean, and held with the cornea towards a window, a very distinct image of the window completely inverted is seen depicted on the posterior translucent wall of the eye.

Fig. 86.



The angle *x*, included between the decussating central rays of two cones of light issuing from different points of an object, is called the optical angle—angulus opticus s. visorius. This angle becomes larger, the greater the distance between the points A and B (fig. 86); and since the angles *x* and *y* are equal, the distance between the points *a* and *b* in the image on the retina increases as the angle *x* becomes larger. Objects at different distances from the eye, but having the same optical angle, *x*,—for example, the objects *c*, D, and *e*,—must also throw images of equal size upon the retina; and, if they occupy the same angle of the field of vision, their image must occupy the same spot in the retina.

We have hitherto regarded those rays of the cones of light which traverse the middle of the pupil, and therefore pass through the crystalline lens near its centre, as determining the situation of the image on the retina. In this supposition, however, there is a slight inaccuracy,—that is to say, a line drawn from a given point of the object through the middle of the pupil would not fall exactly upon the corresponding point of the image on the retina; for even the central rays of a cone of light, when they fall obliquely upon the cornea and lens, suffer refraction from their original direction. Hence it follows that the actual direction of the central ray of a cone of light can be found only by experiment and calculation, and that the law laid down with regard to the optical angle requires some modification. The points of the image *a b* will not lie in the prolongation of the lines B *o* and A *o*.

It now remains to determine how far a straight line drawn from the object to the image would differ in direction from the central ray passing through the centre of the pupil.

I cannot enter into a full discussion of this problem, and will merely give the result of experiments instituted with a view to its elucidation. The valuable observations of Volkmann show that there is a point in the eye where the lines drawn from different objects to their images on the retina intersect each other; and that this point lies neither in the middle of the pupil, nor in the middle of the lens, but behind the lens.

Since the surface upon which the images are formed in the eye is concave, and from its centre towards its margins gradually approaches the lens, it necessarily follows that the images of objects situated at the sides cannot be so distinct as those of objects nearer to the middle of the field of vision, of which the images are formed at a distance behind the lens exactly corresponding to the situation of the retina. The indistinctness of the side images has, however, other causes besides this. The rays of a cone of light from an object situated at the side of the field of vision do not meet all in the same point, owing to their unequal refraction; but the main cause of the images of objects depicted on the retina becoming less distinct as they are more distant from its centre, seems to lie in a peculiarity of that membrane itself.

The refraction of the rays which pass through the circumference of the lens, and of those traversing its central portion, being unequal in consequence of "spherical aberration" (see page 1099), a contrivance for the prevention of indistinctness of vision from this cause was required in the eye, like that employed in optical instruments,—namely, a diaphragm to cover the circumference of the lens, and to prevent the rays from passing through any part of the lens but its centre; this diaphragm is the iris, and the central opening for the transmission of the rays, the pupil. The iris has, however, this advantage over the diaphragms of optical instruments, that it is mobile,—has the power of dilating and contracting. The dilatation of the pupil in the dark, or in a feeble light, has the good effect of admitting more luminous rays, even though the image is rendered less distinct. But even the image formed by the rays passing through the circumference of the lens when the pupil is much dilated may, under certain circumstances, be well defined; the image formed by the central rays being then indistinct or invisible, in consequence of the retina not receiving these rays where they are concentrated to a focus. The image must be most defined and distinct when the pupil is narrow, the object at the proper distance for vision, and the light abundant; so that, while a sufficient number of rays are admitted, the narrowness of the pupil prevents the production of indistinctness of the image by spherical aberration or unequal refraction.

With respect to the lens, we may remark that it must be more dense and more convex in proportion, as the difference between the density of the medium in which the animal lives, and that of the aqueous humour, is less. In fishes the lens is spherical, and the cornea generally flattened. In animals which live in the air, the cornea is more convex, and the lens much less so.

The interior of the eye, namely, the posterior surface of the iris and ciliary processes, and the inner surface of the choroid, immediately external to the retina itself, is coated with black pigment, which has the same effect as the black colour given to the inner surface of the walls of optical instruments. It absorbs any rays of light which may be reflected within the eye, and prevents their being thrown again upon the retina so as to interfere with the distinctness of the images there formed. This is the use of the pigment on the posterior surface of the iris and ciliary processes. But the coating of the outer surface of the retina by the pigment of the choroid is also important in the same respect; for the retina is very transparent, and if the surface behind it were not of a dark colour, but capable of reflecting the light, the luminous rays which had already acted on the retina would be reflected back again through it, and would fall upon other parts of the same membrane, the consequence of which would be not merely dazzling from the excessive action of light, but also indistinctness of the images. Animals in which the choroid is destitute of pigment, and human albinoes suffer in this way; they are dazzled by daylight, and see best in the twilight.

In many animals, which are most active, and hunt their prey when it is becoming dark, but are sluggish during the day, as in the cat family and other nocturnal animals, the portions of their choroid destitute of pigment, or rather covered with white pigment in place of black, are of service by increasing the action of the luminous rays upon the retina.

The distinctness of the image formed upon the middle portion of the retina is dependent on several very different conditions: namely, 1, on the rays emitted by each luminous point of the object being brought to a perfect focus upon the retina without any halo being produced; 2, on the sufficiency of the illumination; 3, on the small size of the elementary parts of the retina which are susceptible of distinct sensation.

The first condition, namely the necessity of the focus of the cones of light falling exactly upon the retina, is the cause of the different distances at which different persons see distinctly; some persons being short-sighted, others long-sighted; while in others, again, there are no such narrow limits to the sphere of distinct vision, their eye being able to adapt itself for the formation of the image upon the retina according to the distance of the object. Since, however, this power of adaptation of the eye for vision at different distances has its limits, there is in every individual a distance at which he sees most distinctly, and at which the focus of the image formed by the refracting media of his eye corresponds most accurately with the situation of his retina. This "distantia visionis distinctæ" may be stated at from five to ten feet [query, inches] in the majority of individuals. Objects which are too near the eye throw very indistinct images upon the retina; a slender body, such as a pin, held close to the eye, cannot be seen at all, or produces only an undefined impression on the retina. Few persons, on the other hand, are able to read print at a much greater distance than twenty inches. The refractive power of the transparent media of the eye is the source of great differences in this respect. Short-sighted or myopic persons see the nearest object distinctly, while they cannot discern distant objects; long-sighted persons can see a small body which is not very visible, only when it is held at a considerable distance from their eyes.

The second condition for distinctness of vision is an adequate quantity of light; excess as well as deficiency of light causes the images of objects to be indistinct.

The third condition is the minute size of the ultimate divisions of the retina capable of independent sensation. An illustration of this is afforded by bodies of which the surfaces are marked with very fine alternate black and white lines. Engravings viewed at such a distance that the images of the black and white lines fall together upon portions of the retina of a certain degree of minuteness, cannot be distinguished as separate lines, and produce merely the mixed impression of grey; the same remark applies to very fine lines of different colours regularly alternating with each other,—for instance, blue and yellow lines: in this case the impression of green will be produced. Hence it is that all mixtures of two different colouring matters are seen, not as two colours mixed, but as a single intermediate colour. There must therefore be ultimate portions of the retina in which all simultaneous impressions are perceived as one only, and are not distinguished as occupying distinct places in the field of vision, even when they really are distinct in the image formed by the refracting media. The idea immediately suggests itself, that these ultimate sentient portions of the retina may be the papillæ or rod-shaped bodies of its internal lamina; and it would appear probable that different luminous rays impinging simultaneously on the different points of the surface of such minute portion or papilla of the retina will not be perceived as distinct rays, but that each papilla will receive from all one mixed impression only, and will propagate such an impression to the optic nerve. On this supposition the image perceived in these eyes must be composite, like a piece of mosaic-work, in which each elementary portion is in itself homogeneous. In accordance with this view, it is found that the ultimate anatomical elements of the retina agree pretty nearly in size with the smallest portions of the retina ascertained by experiment to be capable of separate sensation. The smallest angle under which two points can be distinguished by many persons is 40″. From this, Smith calculated that the size of the smallest portion of the retina endowed with distinct sensation is $\frac{1}{8000}$ of an inch; and, according to the measurements of Treviranus, the diameter of the papillæ of the retina in the rabbit is 0·0033 millim; in birds from 0·002 to 0·004 millim. Now, 0·003 millim. equals 0·00011 of an English inch, and 0·00 4millim. = 0·00015 of an English inch. The mean between 0·003, and 0·004 millim. or, as an approximation, between $\frac{1}{6000}$ and $\frac{1}{10000}$ of an inch, being therefore assumed as the diameter of the papillæ of the retina, the size of these parts would agree very exactly with that of the smallest portions of the surface of that membrane capable of distinct sensation. The measurements of the globules of the human retina, taken by E. H. Weber some years since, also accord with this view: he found their diameter to be between $\frac{1}{8000}$ and $\frac{1}{8400}$ of a French inch.

According to other data, however, no such agreement is found to prevail; and Volkmann's observations render it probable that the discriminating power of the retina is much greater than it could be, were the nervous fibres its ultimate elements. Muncke assumes 30″ as the smallest angle at which an object can be distinguished; Treviranus could discern a black point 0·00833 of an inch in diameter, upon a white ground, at a distance of 48 inches; and Volkmann calculates that the diameter of the smallest image perceived by the retina is 0·000060″. Even this estimate of the discerning power of the retina he regards as too low; any eye of moderate power can, he says, see a hair 0·002 of an inch in diameter at the distance of 30 inches, when an image on the retina of 0·000023 of an inch only would result. A pupil of Von Baer could see a hair $\frac{1}{60}$th of a line in diameter at the distance of 28 inches, in which case Volkmann calculates that an image $\frac{1}{0,00000014}$ of an inch was perceived in the retina. Volkmann concludes, therefore, that, even disregarding the last extraordinary instance, the smallest images perceived in the retina are smaller than the most minute known anatomical elements of that structure.

III. *Adaptation of the eye to vision at different distances.*

It will have been perceived, from the facts already stated, that some changes in the internal condition of the eye are necessary for the purpose of distinct vision at different distances. The focus of the image of distant objects is somewhat nearer to the lens than that of the image of near objects. The amount of the difference in the focal distances for near and distant objects, as deduced from the refractive powers of the media of the eye, has been calculated by Olbers.* We shall extract some of the results of his calculations, in order to give an accurate idea of the degree of modification required in the eye. The distance of the image from the cornea when the objects were at the distances of 4, 8, and 27 inches, and at infinite distance, so that the rays were essentially parallel, was found to be respectively as follows:

Distance of the object.	*Distance of the image from the cornea.*
Infinite . . .	0·8997 of an inch.
27 inches . . .	0·9189 "
8 " . . .	0·9671 "
4 " . . .	1·0426 "

So that the difference between the focal distances of the images of an object at such distance that the rays are parallel, and of one at the distance of 4 inches, was only 0·143 of an inch. On this calculation the change in the distance of the retina from the lens required for vision at all distances, supposing the cornea and lens to maintain the same form, would not be more than about one line, which might be effected either by elongation of the eye, or by a change in the position of the lens. Dr. Young estimated the necessary change at $\frac{1}{6}$th of the length of the axis of the eye.

It will be conceived that the same object might be attained, without any alteration in the distance of the lens from the retina, by a change in the convexity either of the cornea or lens.

Olbers has also calculated the amount of change in the convexity of the cornea which would be required for distinct vision at different distances. The radius of the convexity of the cornea for vision

* See his excellent treatise, De Internis Oculi Mutationibus. Gött. 1780.

at certain distances, taken for the sake of examples, would be as follows:

Distance of the object.	*Radius of the cornea.*
Infinite	0·333 of an inch
27 inches	0·321 ,,
20 ,,	0·303 ,,
5 ,,	0·273 ,,

If the radius of the cornea were capable of modification between 0·333 and 0,300 of an inch, and the long axis of the eye capable of being lengthened the extent of half a line, distinct vision at all distances beyond four lines would be provided for. These results may serve as the basis of the following inquiry.

The absolute necessity of such internal changes in the eye to adapt it for distinct vision at different distances appears a matter of certainty. Nevertheless, some physiologists — as, De La Hire, and Haller, and more recently Magendie, Simonoff,* and Treviranus,† —have called in question the capability of the eye to undergo such internal changes: most cultivators of physics and physiology, however, regard the reality of these changes of adaptation as proved by certain facts. Magendie founds his scepticism on the observation that the image in the eye of a white rabbit does not diminish in distinctness when the distance of the object is altered; which is not, however, a constant fact. G. R. Treviranus, from a calculation of the action of lenses which increase in density towards their interior, arrived at the conclusion that with lenses of this structure the focal distance would remain the same whatever the distance of the object, and consequently that no adaptation of the eye for different distances is required.

Much as we may admire the elegant manner in which Treviranus has treated this subject with the aid of mathematics and the laws of optics, yet we must confess that the results of his calculation do not accord with the facts observed in the eye itself. Moreover, Kohlrausch ‡ controverts the accuracy of Treviranus's deductions. That the eye does undergo changes to adapt it for distinct vision at different distances is indeed proved incontestably by simple and accurate experiments. They are as follows:

1. The power which the eye possesses of accommodating itself to different distances is frequently much modified in a short space of time. Not only does the constant use of the eye in regarding near objects induce short-sightedness in children, but frequently the same condition

* Journ. de Physiol. iv. p. 260.

† Beiträge zur Anat. u. Physiol. der Sinneswerkzeuge, 1828; and his Beiträge zur Aufklärung der Erschein. u. Gesetze des Organisch. Lebens. 1—3 Heft.

‡ Über Treviranus' Hypothese. 1837.

is produced as a transient state of a few hours' duration by long-continued use of the microscope. Under such circumstances, the perception of objects at 20 feet distance in the street sometimes becomes indistinct, though, before, the eyes could accommodate themselves well both to near and distant objects. This has frequently happened to me. The state of myopia thus induced lasts sometimes several hours.

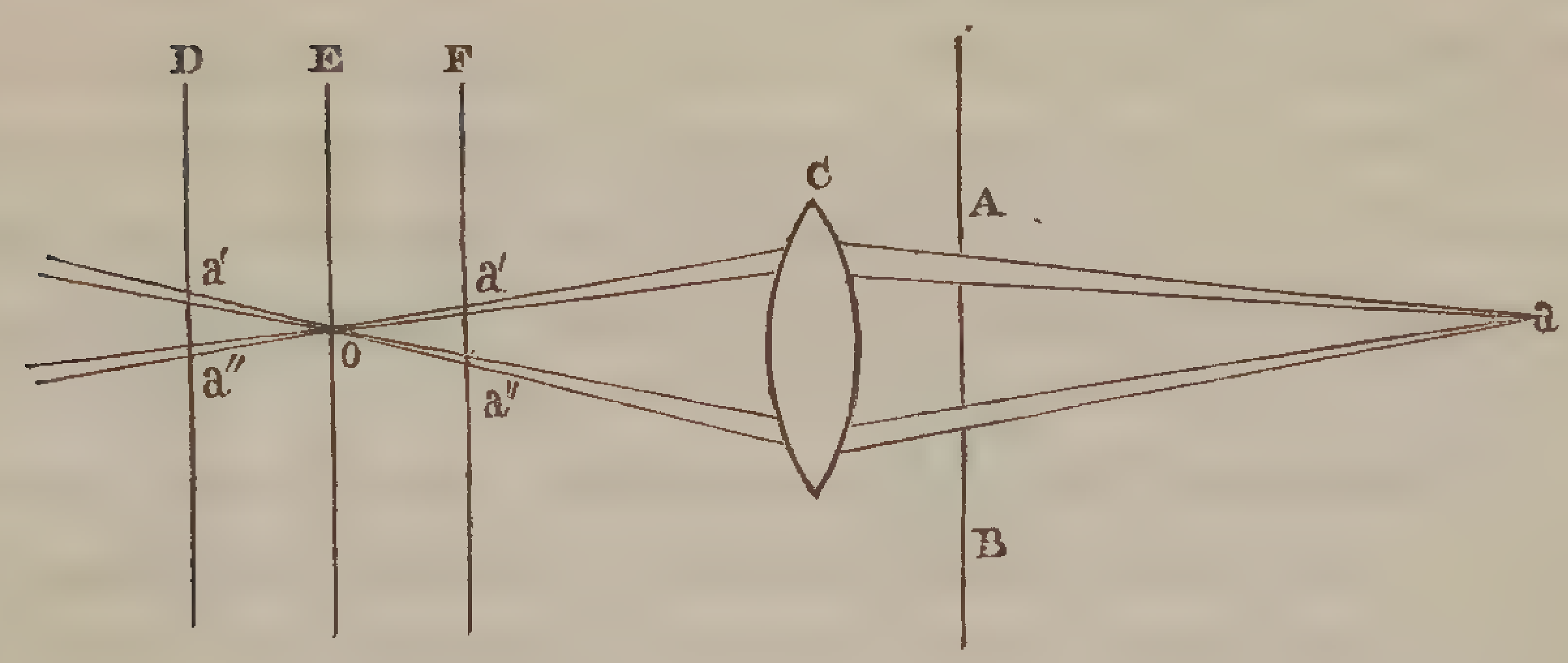
2. If we regard with one eye only (the other being closed) the ends of two needles placed one before the other at different distances in the line of the axis of the eye, one will be seen distinctly when the other appears indistinct, and *vice versâ.* Both the images lie in the axis of the eye, one over the other; and yet it depends on a voluntary effort, the exertion of which can be felt in the eye, whether the first or the second needle shall be seen distinctly. So that when with the pupil contracted, as it is for the vision of near objects, I fix my eye upon the nearest needle, the focal point of its distinct image being at the central point of the retina, the more distant one, though the central rays only of its cone of light can enter the eye, forms, nevertheless, an indistinct circle of light around the same central point of the retina; that is to say, the central rays of the more distant object do not meet in a focus at the central point of the retina, but anterior to it.* A variation of this experiment consists in looking at the head of a pin through a very small opening in a card. Here it is wholly dependent on the will whether the borders of the opening shall be seen distinctly, in which case the head of the pin becomes indistinct; or whether this should be seen distinctly, when the borders of the opening in the card cease to appear defined. Treviranus has not paid sufficient attention to these phenomena; and his explanation of them, by supposing the attention or nervous action being transferred from one part to another, is very unsatisfactory. The two images of the needles fall upon the same point of the retina, one lies over the other, and yet I see the nearer through the cloud-like image formed by the rays from the other more distinct needle, and *vice versâ.* There is here no transferring of the attention from one point of the retina to another. An entire leaf covered with letters appears indistinct to me, as soon as I produce the internal change in my eye necessary for distinct vision at a different distance, though no object be there.

3. Scheiner's experiment.†—If two pin-holes, A B, (fig. 87,) be made in a card, at a less distance from each other than the diameter of the pupil, and if these openings be held before one eye, so that a small object, *a*, can be seen through them, this object will appear single at one

* Jahrb. f. Wissenschaft. Kritik. 1829. Oct. 623.

† Scheiner, Oculus, sive Fundamentum Opticum.

Fig. 87.



particular distance from the eye, but when it is at any other distance it will appear double. Thus, if the object, *a*, be at such a distance that its single image, *o*, falls upon the retina E, it appears single; but, if its distance be greater, the focus of the image will be formed in front of the retina, and the rays, after intersecting each other, diverge and fall separately as a double image, a', a'', upon the retina, as at D; and, of the two images, the lower, a'', will disappear when the opposite or upper opening, A, in the card is closed, and *vice versâ*. In the same way, if the object, *a*, be too near the eye, the single image is formed behind the retina, which in this case also receives a double image a', a'', as at F; and, of these, the lower a'' will disappear, when the corresponding opening B, in the card is closed.

The conclusions to be deduced from this experiment have been pointed out by Porterfield, Young,* Purkinje, Plateau, and Volkmann, and the last-mentioned physiologist has varied the mode of performing it in several ways. The experiment of Scheiner proves clearly the necessity of adaptation of the eye for distinct vision at different distances, and at the same time the incorrectness of the hypothesis of Treviranus, since it shows that the image of an object under certain circumstances falls in front of the retina, and under others behind it. An experiment of Beudant and Crahay has the same import. If a pin at the distance of five or six centimeters [2 or $2\frac{1}{3}$ inches] from the eye be viewed through a pin-hole in a card, and the card be moved from side to side, the needle will appear to move also, but in the opposite direction to the card. This is explicable in accordance with the phenomena of indistinct vision, resulting from the image of the object falling either in front of or behind the retina. Thus, if the rays meet at a focus in front of the retina, they will diverge again after having crossed at the focal point, and will form an indistinct spectrum upon the retina, not a definite image; and if in this case the card in its motion intercept a part of the decussating rays, those from one side only will reach the retina. Hence the apparent shifting of the image. The diffraction of the rays

* Philos. Transact. 1801.

at the margin of the opening in the card, however, has also a share in the production of this phenomenon.

The adaptation of the eye to distinct vision at different distances may be attributed to changes in several different parts, namely, to movements of the iris, to change of place of the lens, to elongation of the axis of the eye, or to alteration in the convexity of the lens or cornea.*

1. The movements of the iris have been considered the means of adaptation by some physiologists, amongst whom are Mile and Pouillet; Professor Mile supposed it to be effected by the inflexion or diffraction of the light at the margin of the pupil, by which the focal distance for the respective rays would be rendered very different. M. Pouillet thought the image would be formed by the central or by the peripheral rays, according as the pupil was contracted or dilated.

2. Elongation and shortening of the axis of the lens were regarded by Dr. Young as the means of accommodation. J. Hunter and Dr. Young ascribed to the lens a contractile power inherent in itself.†

3. Change in the convexity of the cornea was the explanation adopted by Sir E. Home, Englefield, and Ramsden: this change was supposed by Sir E. Home to be effected by the action of the proper muscles of the eye; or, in birds, by the peculiar muscle, discovered by Sir P. Crampton,‡ at the inner surface of the margin of the cornea.

4. The movement of the lens by means of the ciliary processes, or the zonula ciliaris, was assumed as the cause by Kepler, Scheiner, Porterfield, Camper, and many others.

5. Lastly, the influence of the muscles upon the form of the eye has been regarded as the cause of the internal change of adjustment by many writers, as Rohault, Bayle, Olbers, Home, and Schroeder van der Kolk, some of whom ascribe the influence in question to the m. recti, others to the m. obliqui.

That a connexion exists between the movements of the iris and the action of the eye, by which it accommodates itself to vision at different distances, cannot be denied; for, when distant objects are viewed, the pupil becomes dilated, when near objects, contracted: and, notwithstanding the continued presence of a strong light, as of a lamp held before the eye, the size of the pupil may be very much modified at will by looking at objects at different distances; in doing which we cause the axes of the eye to converge while we regard the near object, and, on the contrary, give them a more parallel direction while a very

* A full account of all the hypotheses relative to this subject is given by Haller, Element. Physiol. t. v. L. xvi. Sect. 4. § 20; by Olbers, loc. cit.; and by Treviranus in his Biologie, Bd. vi. p. 512.

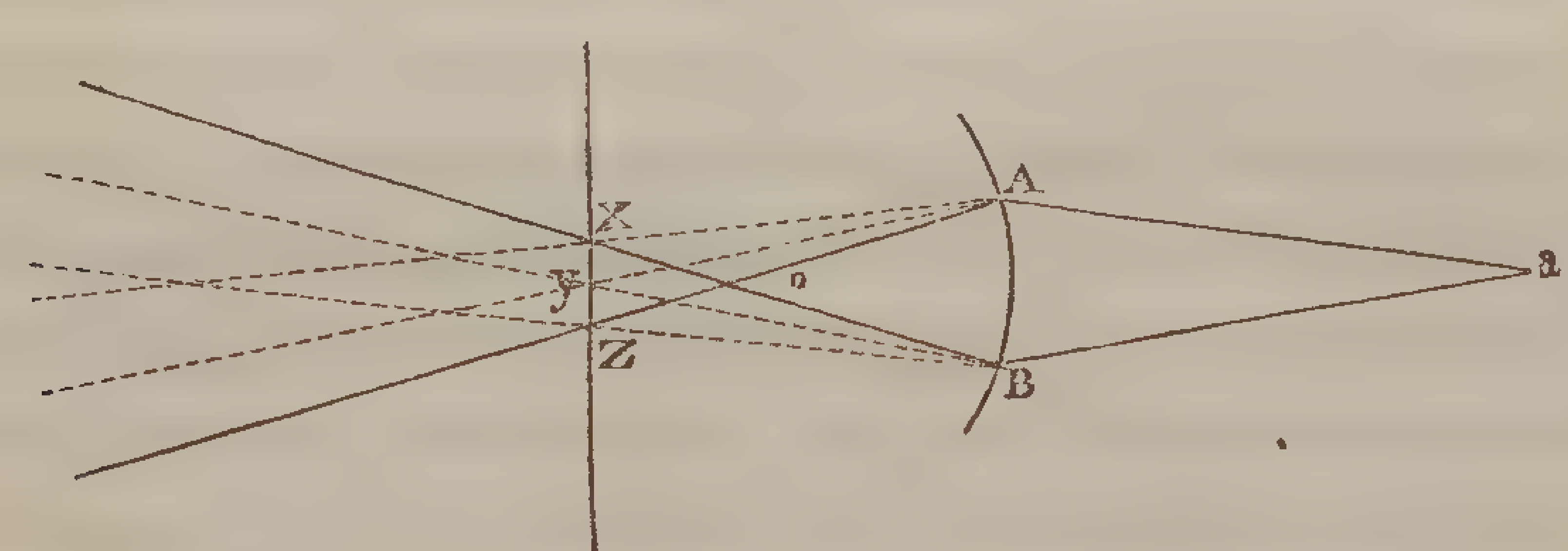
† Philos. Transact. 1794.

[‡ Thomson's Annals of Philosophy, vol. i. 1813, p. 170.]

distant object is the subject of our vision. These changes in the state of the iris are, however, merely associate movements, consequent on the nervus motorius oculi exerting an influence upon the ciliary or lenticular ganglion and the ciliary nerves, while it excites the action of the muscles of the eye-ball. Contraction of the iris always ensues as a result of associate or consentient nervous action, when even one eye only (the other being closed) is turned inwards, or inwards and upwards, and is in this way associated with the voluntary action of several muscles supplied by the third or motor oculi nerve. In these phenomena, therefore, we can recognise no immediate connexion between the motions of the iris, and the power of the eye to accommodate itself to different distances. But it remains to inquire how far distinct vision at different distances can be explained by these movements of the iris.

a. Mile* finds an explanation of the accommodating faculty of the eye in the motions of the iris, and the inflexion of the rays of light by its margin. The following is his view of the process. Let *a* (fig. 88)

Fig. 88.



be a given point in any object, the central rays of the cone of light emitted by which do not meet at a focus upon the retina, but in front of it; here, then, the point *a* cannot be seen through the medium of these central rays; but the peripheral rays of the cone, *a* A, and *a* B, which pass close to the margin of the iris, will suffer inflexion, and, instead of continuing their course in the direction A *o* and B *o*, will take the direction A *y* and B *y*, and meet upon the retina at *y*. The border of the iris, therefore, by producing this inflexion, lengthens the point in which the rays meet, or their focus, beyond the focal distance of the central rays; and since the inflexion of the rays becomes greater the nearer they are to the margin of the iris, the point at which they meet will be more and more distant behind the lens the nearer they are to the margin of the pupil. The focus of the central and peripheral rays will not therefore be confined to any definite point behind the lens, but will extend through a line of some length; and the eye will in consequence of this be able to see distinctly, through the medium of the rays inflected by the margins of the iris, an object which the other rays would no longer

* Magendie's Journal de Physiol. vi. p. 166.

depict distinctly on the retina. The defect of this theory is, as pointed out by Treviranus and Volkmann, that it supposes a small proportion only of the rays to be employed in the formation of the image,—those, namely, which pass close to the margin of the iris,—while the greater mass of the light is not taken into account; and moreover that the foci resulting from the meeting of the rays at other points, as at x and z, are not noticed.

b. Pouillet's theory is based, not upon the inflexion of the rays by the margin of the iris, but upon the different focal distance of the central and peripheral rays; the first of which, being refracted by the central denser portion of the crystalline lens, are, he supposed, brought to a focus sooner than the latter, which pass through its marginal portion. The pupil becoming dilated during the vision of distant objects, and contracted when the eye is fixed upon near objects, the marginal rays will in the latter case be intercepted, and the central rays only will be brought to a focus. On the other hand, the image of distant objects will be formed by the peripheral rays; for the rays from distant objects being concentrated to a focus nearer the lens than corresponding rays from near objects, the focal distance of the peripheral rays will here correspond to the situation of the retina, while the central rays will meet and intersect each other in front of the retina, and form indistinct luminous circles upon it, which, however, do not excite the attention of the sensorium, on account of the intensity of the image formed by the marginal rays concentrated to a focus. The experiment before mentioned, of fixing one eye (the other being closed,) alternately on the ends of two needles, placed one in front of the other at different distances from the eye, affords a complete refutation of this theory. While the needle nearst to the eye is seen distinctly the more distant one appears indistinct, and *vice versâ;* so that during the contracted state of the pupil for the vision of the near object, by which the peripheral rays of the cone of light are excluded, an imperfect image of the more distant object is still formed by the central rays proceeding from it, which have been concentrated to a focus in front of the retina. Whence this objection to the theory of Pouillet arises, that while the eye is fixed upon the more distant object and the pupil dilated, the central rays, notwithstanding the distinctness of the image formed by the peripheral rays, cannot be wholly without effect; and, if this be the case, the cause of distinct vision at different distances cannot be what Pouillet states.

c. This objection is of equal force against the view proposed by Treviranus, who admitted the change in the size of the pupil to be a cause, contributing with the varying density of the lens to effect the accommodation of the eye. According to his calculations, the crystalline lens will concentrate the rays from objects at any distance from the eye to a focus, if the size of the pupil be such as to modify, in accordance with a law which he states, the proportion between the central and peripheral rays.

To all hypotheses which regard the accommodation of the eye to distances as a direct effect of the motions of the iris, we may, lastly, object with Volkmann, that any change in the size of the pupil produced by variation of the light ought, in that case, to disturb the state of adaptation of the eye; which is not in accordance with facts. The distinct perception of an object through an artificial pupil in a card, and the power of seeing through such a pupil either of two needles placed one before the other in the line of the axis of vision, also prove clearly enough, that the power of adjustment is not directly due to the change of size of the pupil, and that the alteration in size which the pupil undergoes, according to the distance of the object, is an indirect effect of some other cause. Looking through a point-like aperture in a card held close to the cornea, I can see the letters of a book distant fifteen inches, either distinctly or indistinctly, by a voluntary effort of my eye, and quite independently of the size of the artificial pupil in the card, which remains constantly the same.

The hypothesis that the adjustment of the eye is effected by a change of the convexity of the cornea, appears to be sufficiently refuted by the calculations of Olbers; for the compression of the eye by the action of its muscles is not capable of producing changes in the length of the radius of the surface of the cornea to the extent of 0·273 or 0·333 of an inch. Home and Ramsden maintained, it is true, that they had observed such changes in the living eye during the vision of near and distant objects; but Dr. Young was unable to verify this observation, and it would be impossible to determine the reality of such a change accurately by experiment, on account of the mobility of the eye. The best means of ascertaining this fact would be to observe whether small images reflected by the cornea, such as the image of a light window, change their size and position while the eye is adapting itself to the perception of point-like objects situated at different distances in the same line.

The view which attributes the adjustment of the eye to the alteration of its form by the action of the external muscles, is also not free from objections. The phenomena of vision at different distances are certainly explicable on such a view; but that does not prove its correctness, for there are many different ways in which these phenomena might possibly be produced. The action of the straight muscles can, as Treviranus remarks, scarcely be conceived capable of producing elongation of the axis of the eye in the manner Olbers supposes. He imagines, namely, that by the action of these muscles the vitreous humour is compressed, and made to extend itself anteriorly and posteriorly. But the tendency of the straight muscles is merely to retract the eye, and, if resistance were afforded by the cushion of fat behind it, to flatten rather than elongate it; their action would therefore have the effect of adapting the eye to the vision of distant objects only, the image of which is formed nearer the lens than that of near objects: while it is in looking at very near objects, on the contrary, that we are conscious of an effort within the orbit. The compression and elongation of the eye might much more easily be effected by the oblique muscles; and Le Cameus, Rohault, and Schroeder van der Kolk have thus explained the accommodation of the eye. This view is in accordance with the circumstance that in the vision of near objects the axes of the eyes necessarily converge, to which movement the oblique muscles would contribute, as Luchtman has very ingeniously shown.* But this, as well as every other theory which attributes the adaptation of vision to distance to the action of the muscles of the eye, is open to objections. The state of adaptation of the eye can be entirely changed in a very short space of time by the local action of narcotics, the pupil becoming at the same time much dilated. This phenomenon cannot be explained by supposing the narcotic to be conveyed to the muscles of the eye and their nerves, since by imbibition the substance could reach only to a limited depth. Moreover, the motion of the eyes by means of the oblique muscles is not at all impeded by such local narcotization. The phenomenon in question is produced most readily by introducing a few drops of a weak solution of extract of belladonna into the eye. After a short time,—about a quarter of an hour,—the pupil becomes dilated, and at the same time the ordinary medium state of adaptation of the eye is found to be completely changed, though the power of adapting itself to different distances is not lost. Numerous observations relative to this phenomenon have been recorded. Most observers state that the eye is rendered long-sighted (presbyopic); while the experience of Purkinje, and a part of the observations of Volkmann, are opposed to this statement. The following is the result of my own observations:†—My vision is ordinarily perfect at all distances. It was remarkable that when the solution of the extract of belladonna was dropped into one eye, the other eye also was affected. When both eyes were open, that to which the narcotic was not applied had a refractive power adapted to the very nearest objects, which alone were seen distinctly, while the other eye did not perceive near objects distinctly. If it was desired to accommodate both eyes to distant objects, vision was more distinct, sometimes with the one eye, and sometimes with the other. If the eye immediately acted on by the belladonna was adapted for near objects, the other eye involuntarily

* Luchtman, De mutatione axis oculi secundum diversam distantiam objecti.—Trajecti ad Rh. 1832.

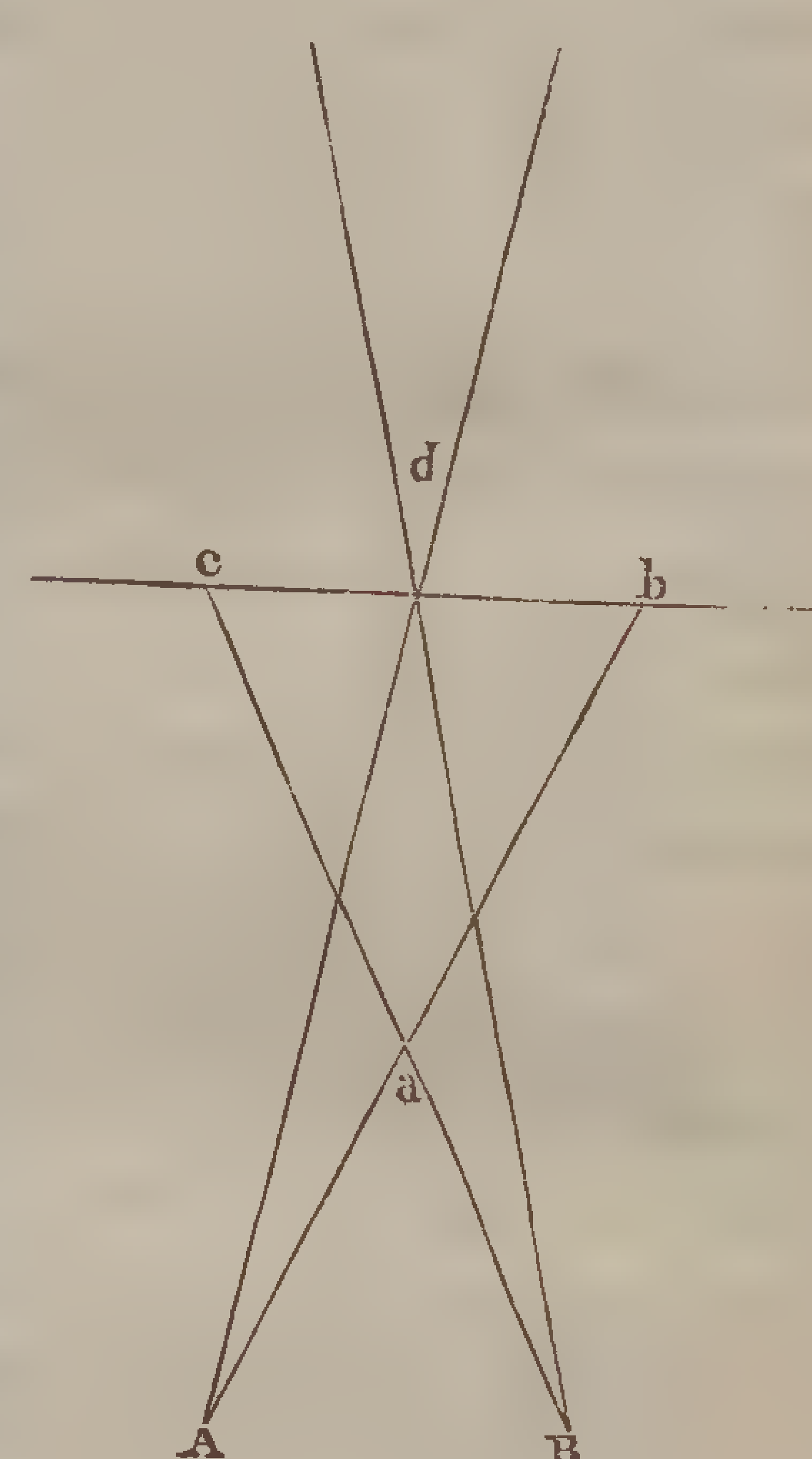
† Physiol. des Gesichts-sinnes, p. 200.

adjusted itself for the vision of the very nearest objects. The narcotized eye, therefore, though ordinarily presbyopic, had by no means lost the capability of adaptation. The iris also, although the pupil was very much dilated, had not quite lost its power of contracting. The eye could at will be made to discern, first near, and then distant objects distinctly; and, while the eye was fixed on distant objects, the iris was almost wholly retracted, but contracted somewhat, so as to narrow the pupil when the eye was voluntarily adapted to near objects. When objects were regarded with both eyes simultaneously, double images were generally seen, and the image appertaining to each eye was alternately more distinct, according as the simultaneous effort in both eyes brought the focus of the rays upon the retina of one or the other. When, by a voluntary effort, the narcotized presbyopic eye was accommodated to the vision of near objects, these appeared almost one-third smaller than natural, while the indistinct images depicted in the other eye (which under these circumstances saw only the very nearest objects distinctly) had their proper size.

If the hypotheses already considered be rejected, there will still remain those which place the means of accommodation to distances in the interior of the eye, — namely, in a change of position or form of the lens by the action of the ciliary processes, or zonula. Although these latter hypotheses cannot be directly refuted, they are equally incapable of proof; and such, in fact, is the state of the question generally; the phenomena may be explained in very different ways, but no one explanation can be proved to be more correct than another. Under these circumstances it will be more judicious to direct attention to some important facts, which are not taken cognizance of in any of the views above mentioned, and which, though they do not disclose to us the cause of the self-adjusting faculty of the eye, show its intimate connexion with other phenomena. The inquiries which I instituted in the year 1826 relative to double and single vision, led me to notice the connexion which subsists between the changes of adaptation to distances and the movements of the eye-balls themselves, by which their axes are altered in direction; a connexion as intimate as that between the changes of adaptation and the movements of the iris, or that between the movements of the iris and the movements of the axes of the eyes. Nearly all the writers who have treated of the accommodation of the eye to distances, have overlooked this important circumstance. Porterfield was, as Volkmann shows, the only one of the older physiologists acquainted with these phenomena.

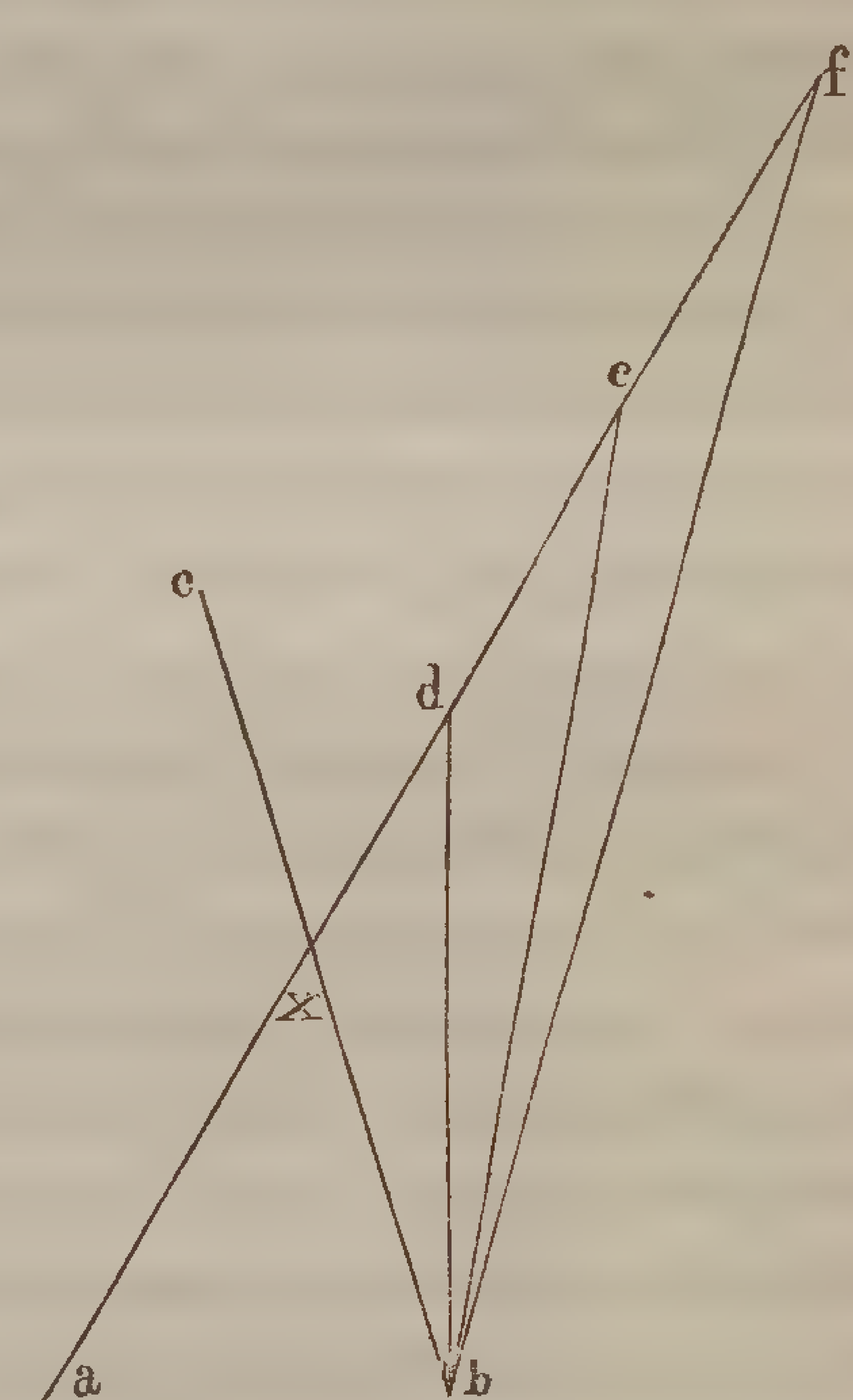
With the same constancy that the iris contracts when the axes of the eyes are made to converge, and dilates when they are moved outwards to the parallel direction, does the eye adjust itself for the vision of near objects when the axes of the eyes converge, and for vision even of the most distant objects when the eyes are turned outwards, so that their axes become parallel. It is well known that an object is seen distinctly when the eyes are fixed upon it, that is, when the axes of the eyes are made to converge towards it; but it is equally true that an object is always seen indistinctly—that the eye ceases to be adapted for the perception of it—when the object lies out of the line of the axis of vision, even though the lateral parts of the retina would otherwise perceive it distinctly. The false position of the axes of the eyes is attended with wrong adaptation, and the wrong adaptation with false position of the eyes; these changes of the eyes are to a certain extent necessarily attendant on each other. If, while we are regarding an object, the eyes be voluntarily adjusted for vision at a greater or less distance, the object appears double; that is to say, the axes of the eyes no longer converge towards it.

Fig. 89.



If, for example, *a* (fig. 89) be the object in which the axes of the eyes, A, B, meet, and we endeavour to see it indistinctly by inducing the internal adjustment for the perception of an imaginary object *d*, the eyes will immediately be directed towards *d*, so that *a* will be seen double, the image of it appearing to the eye A at *b*, to the eye B at *c*. The degree of indistinctness of these double images of *a* is dependent on the adjustment required for seeing distinctly the more distant object *d*. In proportion as the state of the eye, adapted for vision at *d*, is more similar to that adapted for seeing the object *a*, the double images will not only become more distinct, but will approach each other until, when the eye assumes the adjustment for *a*, they become one, the axes of the eyes then meeting at *a*. The double images in this experiment appertain to the opposite eyes,—*b* to the eye A, and *c* to the opposite eye B. Hence the image *b* disappears when the eye A is closed, and the image *c* on the closure of the eye B. The double images always appear to be situated on the opposite side to the eye by which they are seen when an adjustment of the eye for a distance more remote than the object is assumed. If, on the other hand, *d* be the object to which the eyes were directed, and an effort is made to accommodate the eye to vision at an imaginary point *a*, which is nearer than *d*, the object *d* again not merely becomes indistinct, but is seen double; for the eyes, while they are adjusted for vision at *a*, are involuntarily moved so that their axes converge towards that point; *d* then appears on the outside of the axis, A *b*, of the eye, A, and also on the outside of the axis, B *c*, of the other eye, B, and is consequently seen double and indistinct. In proportion to the indistinctness of the images does the distance between them increase. In this instance the double images lie upon the same side with the eye to which they belong: the image *d*, which belongs to the eye A, is seen on the same side of the object *a* as the eye A; and the image *d*, which belongs to the eye B, on the same side of the object *a* as the eye B; as is shown in the figure.

Fig. 90



Even when one eye is closed, the adaptation to distance, and the movement of the axes of the eye-balls, give rise to each other reciprocally, and it is here that the connexion of these phenomena with each other may be best shown. Let *a* (in fig. 90) represent the open eye, *b* the closed eye, and *x*, *d*, *e*, and *f*, objects situated at different distances in the axis of vision of the eye *a*. If, now the eye *a* be adjusted to see the point *x* distinctly, the axis of the covered eye *b* will be involuntarily directed towards *x*, and, if it be uncovered, the point *x* will be seen single at the convergence of the axes of the two eyes. If the eye *a* now pass from the refractive condition adapted for the object *x*, to other states adapted for more distant objects in the line *a f*, — for example, for the objects *e*, or *f*,—the covered eye will also be directed involuntarily towards *e* or *f*. On the other hand, by altering the inclination of the axes of vision, we are able to alter the state of adjustment of the eyes; and these changes are as completely simultaneous with each other, as the contraction and dilatation of the pupil with the convergence and parallelism of the axes of the eyes. If, for example, the axes of the eyes, *a* and *b*, are directed towards the imaginary point of space, *d*, and *x* consequently appears double, (one image being seen by the eye *a* in the direction *a f*, the other by the eye *b* in the direction *b c*,) the double images of *x* will also be indistinct, because the refractive power of the eye is accommodated to the distance *d*. If the axis of the eye *a* remain fixed in the direction *a f*, but that of the eye *b* be moved from the direction *b d* to those of *b e*, *b f*, &c , so that the inclination of the axes of vision is diminished, the refractive condition of the eyes will also be modified in adaptation to the distances *e f*, &c., while the double images of x will become more and more indistinct. The axis of one eye—namely, of that which is open,—may remain unmoved; but, if the axis of the closed eye be varied in direction, the internal adjustment to distance even of the open eye will be modified.*

In consequence of the power of modifying the refractive action of the eyes having a limit, while the optic axes are capable of any relative position with regard to each other, a want of accordance between the internal adjustment and the position of the eyes may happen when the objects are very distant; for instance, if one eye be fixed upon the moon while the other is covered by something held before it, the axis of the covered eye does not assume such a direction as to meet that of the other eye in the moon, though its refractive power is adapted for the distance from the eyes at which that object is situated; for, when the previously covered eye is left free, a second image of the moon is seen, but the two images soon become one from the error in the direction of the axes of the eyes being immediately corrected. This experiment, to which I first directed attention, afforded to one observer a different result. I mention it again, however, since in my case it always succeeded. The explanation of it offered by Treviranus is unsatisfactory.

From the foregoing facts it appears that change in the inclination of the axes of the eyes towards each other induces a change in the refractive power of the eye, by which this organ is accommodated to the distance of the object, even when one eye only, which is closed, alters its inclination towards the other, which is open. The same is the case with the motions of the iris: if one eye be fixed upon a given point, and the other eye closed, when the latter is moved, the size of the pupil even of the open eye undergoes a change proportionate to the degree of convergence of the two axes of vision, giving the appearance of a voluntary influence over the motions of the pupil (see page 684). The movement of the iris simultaneously with that of the axes of the eyes we have regarded as an associate or consensual movement, since it is observed to occur only when muscles supplied by the third or motor oculi nerve are in action, and that nerve is known to be the motor nerve of the iris, to which it sends filaments through the medium of the ciliary ganglion. In the same way the adjustment of the eye to vision at different distances may be an associate movement connected with the action of the muscles which draw the eye-ball inwards, and dependent either on an organic connexion in the nervous system, or on the influence of habit. The associate movement of the iris with the eye-balls can scarcely, however, be the result of habit.

* Compare Porterfield, A Treatise on the Eye; Edinb. 1759, v. i. p. 410: and Volkmann, loc. cit. p. 144. [See also Dr. Well's Essay on Single Vision, pp. 65 & 94.]

A slight influence upon the adaptation of the refractive power of the eye can be exerted by the will, without the direction of the axes of the eyes being necessarily changed; and this circumstance is itself a proof that the connexion between the two is not essential, and that the one is not the constant cause of the other. Plateau has stated, from observations made in his own person, that, by a voluntary effort, objects can be rendered indistinct through modification of the refractive power of the eyes, without any change in their position being induced. I had myself previously remarked that frequently, when a great effort was made, an object appeared to become indistinct without any double image being formed, though this appearance was only transient; but added that, in this case, though the double images were not seen in separate situations, they were both present, but in part placed one over the other. Experiments which I have since instituted lead me to agree entirely with Plateau in the observation that, intimately as the modification of the refractive power of the eye is connected with the alteration of the inclination of the axes of the eyes towards each other, yet with great practice the perception of an object upon which the eyes still remain fixed as before, may be rendered indistinct by the refractive power of the apparatus of vision being voluntarily modified so as to be adapted to another distance.

When the perception of an object is thus voluntarily rendered indistinct without the direction of the axes of vision being changed, the iris performs the usual motions, dilating when the eye is adapted for more distant vision, and *vice versâ*. This is an example of nearly perfect voluntary motion of the iris, inasmuch as here the motion is, at all events, not associated with any voluntary movement of the eye itself inwards and upwards.*

We perceive in this fact, as in all the phenomena previously described, the existence of an intimate connexion between the motions of the iris and the power of modifying the refractive action of the eye; but, nevertheless, we are not justified in ascribing to the motion of the iris even an indirect influence on the refractive power. It has been supposed that the motion of the iris may have an influence upon the ciliary body or processes, and through their medium upon the position of the lens, by virtue of the firm connexion of the ciliary body with the outer circumference of the posterior surface of the iris. This hypothesis, however, is easily refuted; for the movements of the iris may be excited by the stimulus of light independently of the will, and the same object appears to us equally distinct, whether it be illuminated with a bright light, when the pupil will be proportionally contracted, or the eye

* Müller's Archiv. 1837, p. cl.

screened from the action of light, when the pupil will be dilated.* It appears, therefore, most probable that the faculty of the eye which enables it to adjust itself to different distances depends on an organ which has certainly a tendency to act by consent with the iris, but yet is in a certain degree independent of it. Reasoning *per exclusionem*, it is certainly most probable that the ciliary body has this motor power, and this influence on the position of the lens, but we have no positive proof of its possessing contractility.

The self-adjusting faculty of the eye is, according to the observations both of Dr. Young and Volkmann, impaired by the extraction of the lens in the operation for cataract.

VI. *Of Myopia and Presbyopia, of the means of remedying these defects of vision, and of the use of glasses.*

Indistinctness of very near objects. — *Action of diaphragms.* — There is in every individual a point at which objects brought nearer and nearer to the eye can no longer be seen distinctly. Objects at the distance of from one to three inches, or less, from the eye, do not produce a distinct image on the retina, because the point at which the luminous rays emitted by them meet in a focus is in all persons situated behind that membrane. If the object held before the eye be small, it produces only a glimmering or cloud-like appearance, through which, though the object covers the middle of the pupil, more distant bodies are seen. The perception of distant objects through the indistinct image of one held near to the eye is intelligible when we recollect that, although those rays of the distant body which would pass through the centre of the pupil are intercepted, other rays will pass at the sides of the near object and enter the eye. Hence it is a necessary condition for seeing distant objects through the glimmer of a near one held close to the eye, that the latter be smaller than the pupil. It may indeed be very nearly as large as the pupil; for the peripheral rays of the cone of light from the more distant object will, in this case, by inflexion at the edges of the near body, still gain entrance into the eye and produce an image.

A distant object is also discerned by means of the rays passing through the circumference of the lens—the peripheral rays of the cone of light—when it is looked upon over the margin of another body held before it. It is a generally known fact that, if, while we are looking at a distant object, a second nearer object is interposed from the side, the more distant one appears to shift its place somewhat, and to become enlarged, as soon as the margin of the nearer object approaches it. This seems to be owing partly to the image being formed by rays which pass

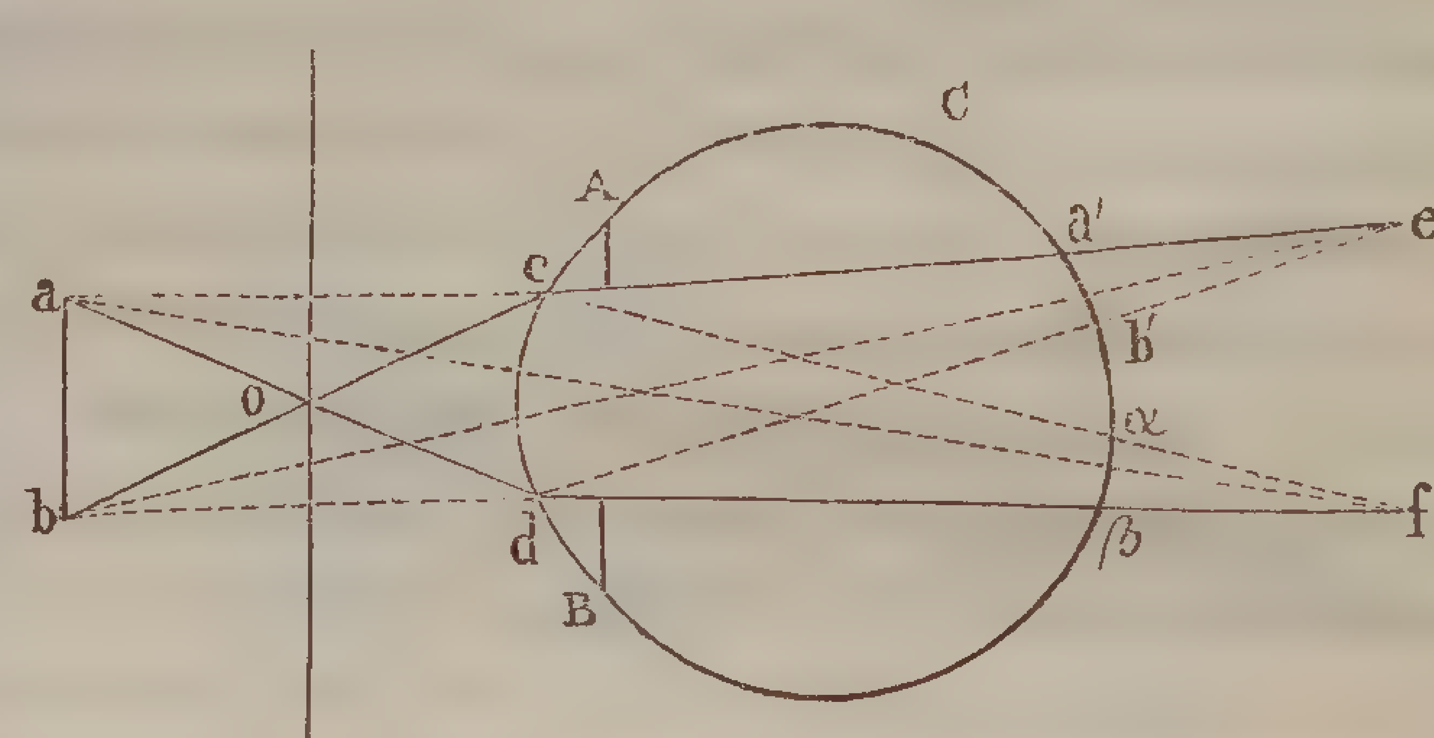
* Compare Volkmann, loc. cit, p. 156.

through the circumference of the lens, and partly also to the inflexion of the light by the edge of the interposed body.

The glimmering cloud-like spectrum which small objects held very close to the eye produce in place of a distinct image, is larger in proportion to the size of the pupil; for, inasmuch as the spectrum representing each point of the object is a section of the cone of light sent by it through the pupil, each point of the object will be represented in a larger space on the retina according as the pupil is wider. The appearance produced by a small body, such as a needle held very near the eye, is the result of the simultaneous impression on the same parts of the retina of the spectra of all points of the object. These considerations enable us to account for some interesting phenomena. If a pin be held at such a distance from the eye that it still produces an image, but one which is indistinct and hazy, this hazy image appears larger or smaller according as the eye is shaded or subjected to a strong light; in other words, according as the iris dilates or contracts. This is an excellent mode of observing the motion of the iris in one's own person by means of a phenomenon of vision.

Under certain conditions, however, objects held close to the eye may be seen distinctly, and then appear much enlarged, though no glasses to aid the eye be used. This happens, namely, when very near objects are viewed through a minute opening in a card. M. Henle, who has investigated this phenomenon, directed my attention to it and to its causes. It was known to Lecat, Monro, and Priestley. If we hold close to the eye the printed leaf of a book, we are unable to distinguish a single letter; but if, when it is at the same distance, we look at it through a pinhole in a card placed close to the eye, we immediately perceive very clearly both the letters and their white interspaces. It might be imagined that the cause of the distinct vision in this instance was that the central rays were isolated from the peripheral rays of the cones of light by the small size of the opening, and that, on account of the greater density of the nucleus of the lens of the eye, they are brought sooner to a focus, though in a lens of equal density throughout the central rays meet at a focus later than the peripheral rays; but, according to this view, the size of the object should not be increased. It may be said that the increase of size is merely apparent, and owing to the circumstance that, when the print is viewed closely without the interposition of the card, the nucleus only of the hazy image is taken cognizance of, and not its whole dimensions; but this objection is easily refuted by viewing the object simultaneously with both eyes, one with the perforated card, the other without it, and comparing the images. It is then seen that the white spaces between the letters, as well as the print itself, appear larger with the interposed card; three lines of one image being contained in the same space as two of the image seen with the other eye. Lecat* and Priestley† attribute the phenomenon to the inflexion of the rays at the margin of the opening in the card; the first of these writers referring for confirmation of his opinion to the change which the outline of a distant body suffers when the edge of a rod is interposed between it and the eye. The distant body appears, namely, to expand when the rod is moved into the line of the axis of vision. The distinctness of very near objects seen through an opening in a card may certainly be explained on the principle of inflexion, or more correctly diffraction, by which light is bent from its course in two directions. According to this view, the more exterior of the rays inflected at the margin of the opening in the card meet at a focus still farther behind the retina even than the rays of near bodies otherwise do; while the more internal of the inflected rays are brought to a focus sooner, and consequently meet no longer behind the retina, but upon it; and hence the distinctness and brightness of the image, notwithstanding the small quantity of the light engaged in producing it. The increaseof size of the image is, however, not easily intelligible from this theory.

Fig. 91.



Another explanation of the phenomenon is proposed by Henle. Let *a b* (fig. 91) be the body held close to the eye, A B the refractive media, C the retina. The cone of light emitted by the point *b* is concentrated to a focus at *e*; that from the point *a*, at *f*. The straight line, *b e*, will be the direction of the central ray of the cone of light emitted by the point *b*; the straight line, *a f*, that of the central ray of the cone of light from the point *a*: the focal points, *e* and *f*, lie behind the retina on account of the too great proximity of the object to the eye. The point *b*, therefore, is seen as a broad spectrum, *a′ b′*; the point *a* as a similar spectrum, α β. If now the card, with the small opening *o*, be interposed between the object and the eye, the rays of the two cones of light are partially intercepted, so that the bundles of rays, *b c* and *a d*, alone reach the eye through the opening *o*. The image of *b* is consequently seen distinctly at *a′*, that of *a* at β. Inflexion of the rays may contribute to render the image of the object distinct by causing the rays of each pencil of light which passes through the opening in the card to fall simultaneously upon a single point of the retina.

* Traité des Sens, p. 305.

† Geschichte der Optik. p. 391. History of Light and Colours; Lond. 1772.

The increased size of the image is owing to the rays α and β, which excite the sensation, being further distant from each other than the central rays of the cones of light would be.

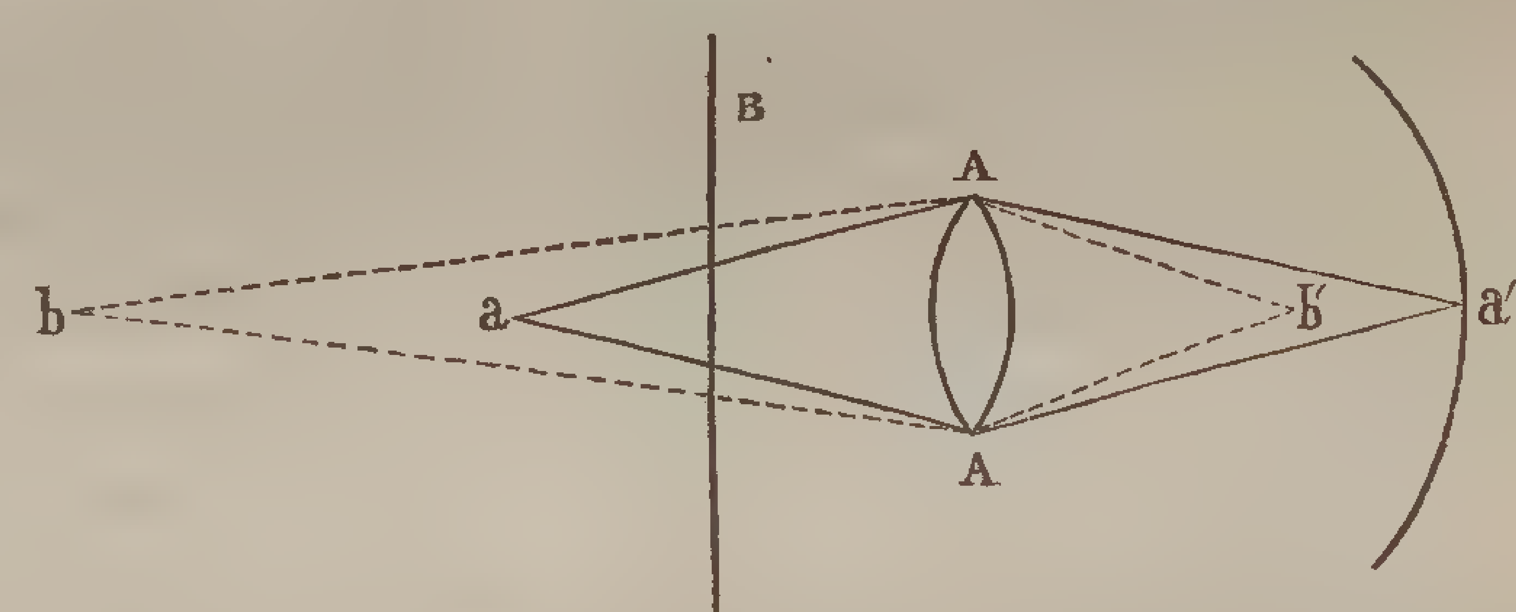
"Myopia," near-sight; and "Presbyopia," far-sight.— Spectacles and Optometers.— Many persons have not the power of accommodating their eye to vision at different distances, or have it in so slight a degree as to distinguish objects at a certain distance only; such persons are said to be either short-sighted or long-sighted. To individuals in this condition it is, of course, impossible to prove that the eye has the faculty of adjustment to distance; and this may have been the cause of the scepticism of Treviranus and others. Near-sightedness is most frequently observed in the middle period of life. Long-sightedness is more common in old age. The cause of these defects of vision is very often supposed to lie in the refracting media of the eye, as in the form of the cornea; and the cornea is, in fact, less convex in old age than in youth; but the convexity of the cornea is greatest in childhood, and, nevertheless, as Volkmann remarks, children are not frequently subjects of "near-sight." Myopia and presbyopia may with more reason be attributed, as regards their immediate cause, to want of the power of adjustment, or to great feebleness of this muscular act. With such a condition the eye would necessarily see objects distinctly at that distance only to which the form of its refractive media is best adapted. A strong proof of imperfection, or loss, of the power of adjustment being the cause of myopia, and presbyopia, is the circumstance that short-sightedness may be acquired merely by habitually using the eye for the perception of near objects only, and neglecting distant vision. Thus, children become short-sighted from accustoming themselves to read or write with the face too close to the paper. The constant use of the microscope may give rise to short-sightedness, and often does induce it as a transient condition lasting a few hours. The wearing of spectacles also is injurious in this respect, since they disuse the eye to self-adjustment for distinct vision at different distances

Sometimes the two eyes differ in their mean refractive power, though the pupils do not in these cases always present a corresponding difference in size. This unequal action of the eyes may also be acquired by employing one of them especially in the perception of near objects, as in the use of the microscope, &c. This inequality of the refractive power of the eyes is produced most rapidly, however, by narcotizing one eye by means of a few drops of solution of the extract of belladonna (see page 1144). In all these cases, the eyes, though differing in their mean refractive condition, may both retain the faculty of accommodation to different distances; the voluntary adjustment of one eye influences the other also, but yet the condition of the two remains unequal. Thus, if we express by two series of numbers the progressive change in the state of refractive power in the two eyes respectively, and the adjustment of the eye A be represented by 3, that of the eye B may be expressed by 1; and if the refractive power of the eye A becomes 5, that of the eye B will become 3. With a state of adjustment expressed by 1, the eye A sees distant objects distinctly, while the eye B discerns nothing. Within a certain limit both eyes, perhaps, may see distinctly when used simultaneously, since the indistinct image of the one eye may not disturb the perception of the other eye, and the two images are seen in the same position in the field of vision as one image; but the eye which was defective in the vision of distant objects has greater capability for close vision. The eye A has, perhaps, at 10 reached the limit of its sphere of adaptation; while the other eye, B, sees distinctly at 11 and 12. Inequality of the refractive power of the eyes is in many persons the original source of squinting, the eye of the most useful medium focus being employed by preference, while the other is not attended to, so that the image formed in it becomes no source of confusion. Even when eyes of equal refractive power are fixed upon the same object, one being furnished with an eye-glass, the other without any, the axes of the eyes do not meet in the object, which is apt to be seen double; this is also the case when spectacles of unequal power are used. The double images are still farther distant from each other, owing to the axes of the eyes not being both directed towards the object, when the refractive power of one of the eyes has been modified by the action of belladonna; in which case, while an object at a certain distance is seen distinctly by one eye, the image of the other is seen floating indistinct and hazy by its side. The cause of this want of coincidence of the images of the two eyes is intelligible from the considerations entered into, at page 1146, relative to the connexion between the refractive state of the eye and the position of the axes of the eye-balls. How it is that the image of an object depicted in the weaker eye does not disturb vision will be explained hereafter, when we come to state the facts which prove the existence of a kind of antagonism between the fields of vision of the two eyes, like that between the two scales of a balance, owing to the intensity of nervous action being greater sometimes in one, sometimes in the other eye.

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

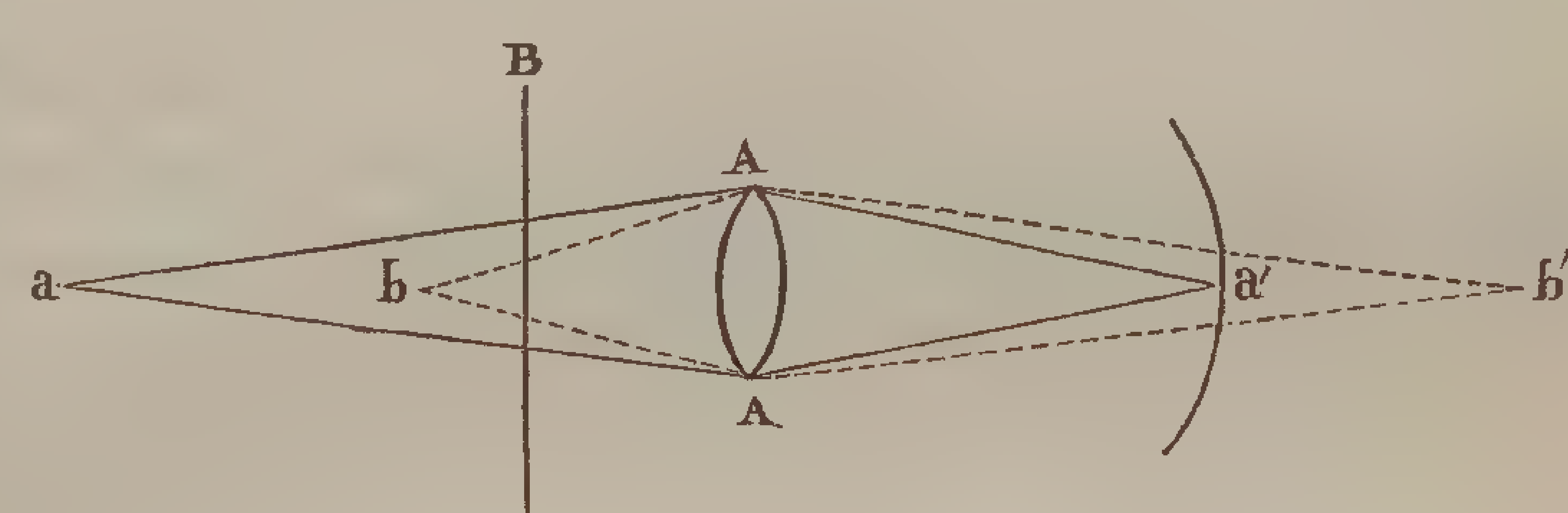
We may now, in a few words, explain the action of spectacles in aiding vision in persons labouring under myopia and presbyopia. The presbyopic, or long-sighted eye, is aided by a convex glass; the myopic, or short-sighted, by a concave glass. In the long-sighted eye, rays from distant objects are brought to a focus upon the retina; but the rays from objects less distant, or very close to the eye, not being made to converge so rapidly, meet behind the retina. A convex glass corrects this defect by causing the rays emitted by near objects to intersect each other at a point nearer the lens,—namely, in the retina itself. In the short-sighted eye the reverse condition subsists. The rays from near objects here meet in the retina, and produce a distinct image; but the rays of distant objects, which are more easily brought to a focus than those of near objects, meet before the retina, and form undefined spectra upon it. The concave glass corrects this by causing the rays to become more divergent, and therefore less readily concentrated by the eye to a focus, which is thus made to fall upon the retina. Figure 92 represents the direction of the rays in a short-sighted eye; A A being the refracting media of the eye. The rays emitted by a very near object, *a*, meet upon the retina at *a′*; those of a distant object, *b*, on the other hand, meet at a focus sooner, namely at *b′*. A concave glass at B causes the rays A *b′*, A *b*, to assume the direction A *a′*, A *a′*. A distant object, *b*, can therefore be seen distinctly at *a′* only by the use of the concave glass.

Fig. 92.



Again, let A A (fig. 93) represent the refractive media of a far-sighted eye; the luminous rays from a distant object, *a*, will, in this case, be concentrated to a focus at *a′*, that is, upon the retina. The image of the near object, *b*, will, on the contrary, be formed behind the retina at *b′*. A convex glass at B will here cause the rays of the near object to be brought to a focus more rapidly, so as to form the image upon the retina at *a′*, instead of behind it at *b′*.

Fig. 93.



The use of the optometer to determine the mean distance of vision for which the eye of any individual is adapted, is founded upon the experiment of Scheiner, detailed at page 1139. It consists in ascertaining the distance from the eye at which a small object viewed with one eye through two openings in a card, separated by a less distance than the diameter of the pupil, appears single; or the distance from the eye at which the double images of a thread, viewed without effort through two openings in a card, cross each other or unite to one image.—(Young's Optometer.) The distance thus ascertained is the mean length of vision of the eye. Before and behind this, an object viewed through the two openings in the card appears double; that is to say, its image falls either before or behind the retina. The application, however, of this method is always very imperfect, on account of the diffraction of the rays at the margins of the small openings in the card.

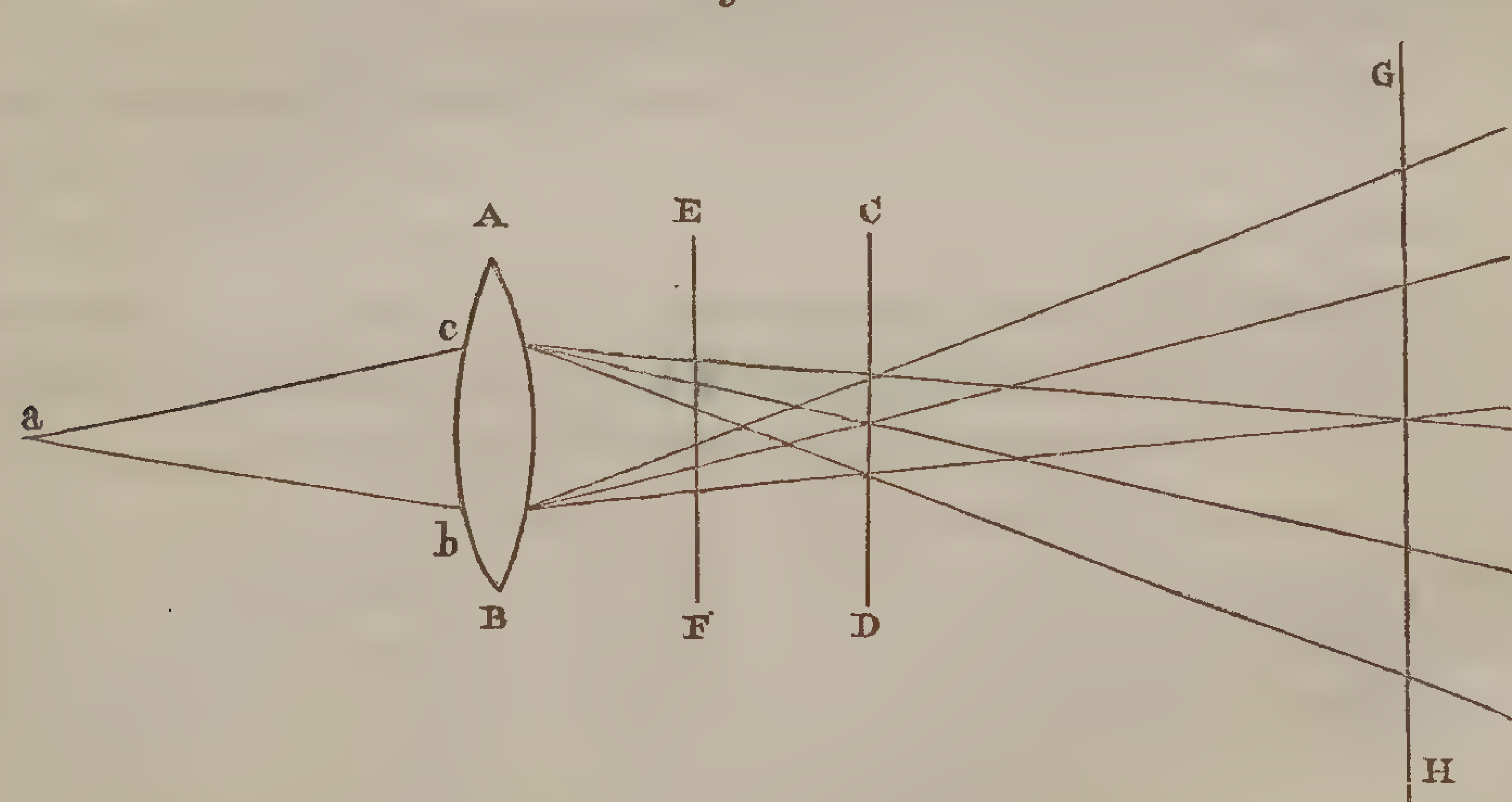
Influence of convex lenses upon the distance of distinct vision.—We have next to consider the action of glasses which increase the size of the image by altering the distance of distinct vision. The simplest kind of glass which has this effect is the common lens, or simple microscope. If a small object be brought very near the eye, it appears very large, but is wholly indistinct, because the point towards which the rays from it are made to converge lies behind the retina. The action of a lens interposed between the object and the eye is to shorten the focal distance of the image. If the lens be properly placed, so that the image falls upon the retina, all the details of its form are seen distinctly, while it appears of the same magnitude as when held close to the eye without the lens. In this case the increase of size is the result of the close approximation of the object; and the lens merely gives distinctness, which the image of so near an object would not otherwise have. In the telescope and compound microscope the image is formed, not in the eye itself, but in front of it. The rays meeting to form the image, not being received there by any opaque surface, diverge again from this point, in the same way as if the object from which they originally radiated were there situated. On this condition depend both the increase of size and the distinctness of the image in the eye; for an image near the eye is seen under a greater angle than the more distant object. And if the image occupies the situation of distinct vision at eight inches, it is not only increased in size, but has the distinctness of objects generally viewed with the naked eye at that distance. Telescopes serve to increase in size, and render distinct, the image of very distant objects; microscopes to enlarge, and render distinct, the image of near objects. The number of glasses employed in these instruments is very various. A second glass, placed behind the first, may either modify the image and its situation, or, if the image is already formed by the first glass before the rays traverse the second, this image stands in the relation of an object to the second glass. The image formed by the second glass may be still further modified by a third glass, or may become an object to it. The glass which receives the rays of light directly from the object itself is called the "object glass;" the glass next to the eye is the "eye-piece," or "ocular." In the microscope, the image formed by one or more lenses is viewed by means of the ocular, just as an object is viewed with a simple lens. The brightness of the image depends on the quantity of light which the object-glass receives from the object, or which, in the microscope, is thrown by artificial illumination upon the object. According as the quantity of light which goes to form the image in the telescope or microscope is greater or less than that which the naked eye receives from the object, will the image of the object be more or less vivid than when seen without the instrument. The image of objects viewed with the telescope is brighter than the object appears when viewed with the naked eye; because the object-glass of the telescope receives from the object, and applies to the formation of the image, more light than the pupil of the naked eye can admit.

V. *Of the chromatic and achromatic properties of the eye.**

a. Chromatic lenses.—Although the rays from a luminous object are by the refractive power of a lens concentrated so as to form a distinct image upon any surface, when spherical aberration is avoided, yet the image is not perfect unless the rays of light are homogeneous, that is, of one simple colour; for, even though spherical aberration be avoided, it is quite impossible, without further means, to bring the heterogeneous rays of white or mixed light to one focal point, since the different-coloured rays of white light have different degrees of refrangibility, and, therefore, with the same refracting medium have a different focal distance.

If *a* (fig. 94) be the luminous point, A B the lens, and *a b c* a cone of light containing rays of different colours, these rays will be refracted in different degrees; the violet rays, for example, which have the greatest refrangibility, will meet at a focus first, the yellow

Fig. 94.



* J. Müller, Physiol. des Gesichts-sinnes, pp. 195. 414.—Tourtual, Die Chromasie des Auges; Meckel's Archiv. 1830, p. 129.

later, and the red last. In place of a colourless, luminous point, therefore, there will be at the part where the light is most concentrated, at C D, a coloured spectrum, of which the centre will be white, on account of the coloured rays being there mingled; while the borders will be purple, owing to the presence of the red and violet rays without the yellow. The image will appear more coloured if the surface which receives it be placed before or behind the mean focal distance, as at E F, or G H. At E F, for example, the red rays, which are there most external and unmixed with other rays, form a fringe of red light; the most external of the yellow, mingled with red rays only, form a fringe of orange within the red, and around the colourless centre in which all the different-coloured rays are intermingled. At G H the violet rays will form the outer fringe; within this will be the blue, which are next to the violet in refrangibility; and the centre will be white.

The image formed by a convex lens is at the proper focus very slightly coloured: the outline of a white image received upon a dark ground has merely a margin of purple, which is scarcely perceptible; but, in proportion as the surface which receives the image is moved from the focal point, the more marked becomes the fringe of colours, in addition to the increasing indistinctness of the image formed by the white light itself.*

b. Achromatic lenses.—The dispersion of the coloured rays by a prism is counteracted by a second prism of the same refractive and the same dispersive power. Two prisms conjoined form a refracting medium with parallel surfaces, from which the rays of light transmitted through it will issue at the same angle as they entered, just as in passing through a plane plate of glass. Dollond, however, discovered that the dispersive power of media is not always proportionate to their refractive power; and that there are media which have a strong refractive action on light, but little dispersive influence. Flint-glass refracts light more strongly than crown-glass, but its excess of dispersive power is still greater. This led to the construction of achromatic prisms by the combination of prisms of unequal refractive and dispersive power. A prism of crown-glass, and one of flint-glass of the same refractive angle, united, bend the parallel rays which entered them out of their direction; and instead of transmitting them colourless, as two prisms of crown-glass of the same angle would do, disperse them so as to form a coloured spectrum, owing to the excess of dispersive power of the flint-glass. If, now, the refracting angle of the prism of flint-glass be so far diminished that both prisms disperse the light equally, the dispersive action of one neutralizes that of the other, and the rays are transmitted colourless; while the simple refraction remains, on account of the different angle of the two prisms.

* See Kunzek, Die Lehre vom Lichte, p. 157; and Tourtual, loc. cit.

An achromatic prism is formed by combining a crown-glass prism of a refracting angle of 30° with a prism of flint-glass having a refracting angle of 19° only. We may hence conceive the principle of the construction of achromatic double lenses which reciprocally correct each other's dispersive action. The most perfect achromatic doublet, however, does not prevent the production of colours when the image is not received at the proper focal distance; and, in the best telescope, objects appear surrounded with coloured fringes when the ocular is moved beyond the limits of distinct vision.*

c. *Achromatic property of the eye.*—The human eye is achromatic as long as the image is received at its focal distance upon the retina, or as long as the eye adapts itself to the different distances of objects. The cause of this achromatic property cannot with certainty be determined, although it is easy to show that the optical structure of the eye may very possibly give this property. The refractive media of the eye are of unequal refractive power, both as regards their convexities and their chemical constitution. The lens has two unequally convex surfaces, and the cornea and aqueous humour form a refracting medium of unequal chemical constitution. The cornea and aqueous humour taken together form a concavo-convex lens, the refractive power of which is different from that of the crystalline lens. The dispersive power of these two refracting media may perhaps be disproportionate to their refractive power, and this may be the source of the achromatic property of the eye. The achromatic and aplanatic double object-glasses of Sir J. Herschel have some distant resemblance in form and composition to the refracting media of the eye. They consist of a biconvex lens of crown-glass, the radii of whose convexities are of unequal length, and of which the more convex surface is turned outwards towards the object, and of a concavo-convex lens of flint-glass, the concave side of which is turned towards the lens of crown-glass, while its convex side is towards the eye.

d. *Chromatic property of the eye.*—It is an error to regard the human eye as perfectly achromatic. Whenever the image does not fall at its proper focal distance upon the retina, a more or less distinct appearance of colours is produced. The dioptric fringes of colours produced in our eye by its refractive media, and capable of being excited to a certain extent at will, appear to have been first observed by Scheiner.† To

* Kunzek, Lehre vom Lichte, pp. 172—177.

† Extended observations on the subject of these phenomena will be found in Comparetti's Observationes dioptricæ et anatomicæ comparatæ de color. apparent. visu et oculo; Patav. 1798, 4: in an article on the production of colours in the eye, in Schweigger's Journal, Bd. 16: in my work, Zur Physiol. des Gesichts-sinnes; Leipz. 1826, pp. 194—204: and in Tourtual's excellent paper in Meckel's Archiv. for 1830.

observe these phenomena in one's own person when the eye is in a healthy state, white objects upon a black ground, or black upon a white ground, must be held before the eyes while they are adjusted for nearer or more distant vision; the objects will then appear indistinct and surrounded with fringes of colours, and two images of each object will be seen, the cause of which will afterwards be explained. In proportion as the axes of the eyes deviate in their direction from that proper for distinct vision of the objects, the further distant do the double images appear from each other. The more indistinct the images, the more marked become the coloured fringes. At the commencement of the experiment they are not perceptible; but, by practice and attention, the narrowest line of colour around the image can be recognised. The image of an object can most easily be rendered indistinct at will by directing the axes of the eyes towards some body or ideal point nearer or more distant than it, and hence the coloured fringes are most readily perceived in this manner. With practice, however, it becomes possible to produce indistinct vision of an object with one eye only, while the other is closed, by causing it to adapt its refractive power to nearer or more distant vision. By this method coloured fringes may be seen with one eye, consequently without double images of the object being produced. The following are the results of my own observations:

1. If we look upon a white space on a black ground with one eye, adapting the refractive power of the eye to a more distant point than the object, the latter—that is, the white spot—will appear indistinct, and as if surrounded with a delicate and narrow fringe of colours passing from the white to the black ground through violet, blue, yellow, and red. Generally the blue and yellow have alone any degree of distinctness.

2. If we look upon the same object, and then adapt the refractive power of our eye to the perception of an imaginary object nearer to the eye, the coloured fringe of the image will present the same succession of colours—red, yellow, blue, and violet, but in the reverse order; the violet and blue are now nearer to the black, and the red and yellow next to the white.

When the vision of an object is rendered indistinct while both eyes are open, and two images are consequently seen, the colours in the surrounding fringes have the same arrangement as in the first case just described, if the axes of the eyes are made to converge to a point behind the object; while their order of succession is reversed as in the second case, if the axes of the eyes meet in front of the object.

The frames of the window also appear fringed with very vivid colours when we gaze at distant objects through it; or if, while looking at the window, we fix our eyes upon a nearer object, as the finger held before them.

The phenomena of coloured fringes dependent on dispersion of the coloured rays by the refractive media of the eye, are apt to become complicated with the accidental colours of the spectrum left by the long impression of an object upon the retina, this spectrum becoming manifest on a slight lateral movement of the eye. The "subjective" spectrum left by a white spot upon a dark ground is grey; that of a black spot on a white ground, white; that of a coloured spot, of the opposite complementary colour. While the eye is fixed on the object, the real image covers the spectrum; but, if the eye be slightly moved to the side, the margin of the physiological spectrum is perceived at the edge of the real image. The luminous borders or fringes arising thus are seen on that side of the image towards which the eye moves, and must be distinguished from the dioptric fringes of colour, which have their source not in an affection of the retina, but in the refractive media of the eye. Comparetti has described these two phenomena combined. It is quite an error to ascribe the dioptric coloured fringes of objects to an affection of the retina, as is done in some pathological works. When they occur as symptoms of disease, they are not a consequence of any change in the act of vision, but of an affection of the self-adjusting faculty of the eye by which it naturally adapts itself to vision at different distances. Many persons complain of seeing coloured fringes while their power of vision is otherwise perfect,—when there is no tendency to morbid changes in the retina, or to amblyopia or amaurosis. We have an instance of this phenomenon also in the red borders which surround the letters of print when, the adjusting power of the eyes is paralysed as a consequence of passion, of mental exertion, or inclination to sleep, &c. The coloured fringes are very evident also when the faculty of the eye to accommodate itself to distinct vision at different distances is suspended by the action of belladonna.*

The dioptric fringes of colours arising from refraction within the eye must not be confounded with the real coloured halos of luminous objects.

* See my work, Zur Physiol. des Gesichts-sinnes.

CHAPTER III.

OF THE ACTION OF THE RETINA, OPTIC NERVE, AND SENSORIUM IN VISION.

All the phenomena investigated in the preceding chapter are explicable by reference to the structure of the eye as an optical instrument,—that is, by the form and arrangement of the transparent media in front of the retina. There are a great number of other phenomena, however, of which the structure of these parts affords no explanation, but which are the results of vital properties of the retina, and of the co-operation of the sensorium in the act of vision. To these belong not merely the act of sensation itself, and the perception of the changes produced in the retina, as light and colours, but also the conversion of the mere images depicted in the retina into ideas of an extended field of vision,—of proximity and distance,—of the solidity (in the geometrical sense) and size of objects. To this class of phenomena belong also the effects of the reciprocal action of different parts of the sensitive apparatus on each other, and many phenomena in the retina either not excited by light at all, or not by its immediate action. These different phenomena will be treated of under the following heads: 1. Of the action of the retina generally, and of the co-operation of the sensorium in vision. 2. Of ocular spectra. 3. Of the reciprocal influence of different parts of the retina upon each other. 4. Of the simultaneous action of the two eyes. 5. Of the subjective phenomena of vision.

1. *Of the action of the retina generally considered, and of the co-operation of the sensorium in vision.*

Action of the retina and sensorium.—It has been shown already, in the Preliminary considerations on the Physiology of the Senses, that the retina is not a mere conductor of external impressions, but itself reacts against these impressions. Light and colour are actions of the retina, and of its nervous prolongations to the brain. The kind of colour and luminous image perceived depends on the kind of external impression. With this property of the retina, by virtue of which it becomes when irritated the seat of the sensations of colour and light we are so well acquainted, that we found upon it all inquiries concerning vision. The vibrations of a fluid existing in all space, the ether, when of a certain rapidity, produce in the retina the sensation of a certain colour; when of a different degree of rapidity, that of another colour; these colours or sensations being modes of reaction of the retina. The simultaneous impression of undulations of different rapidity upon the same points of the retina excites the sensation of white light. These same sensations of colours and light may, however, be produced, without the agency of the vibrations of an ether, by mere irritation of the retina by means of electricity or mechanical pressure.

If it be the change produced in the retina which we perceive in vision, we may with equal correctness say that in the act of vision the retina feels itself in a particular state, or that the sensorium perceives the retina in a particular condition. The condition of repose of the retina is the cause of the appearance of darkness before the eyes; the active state of the retina is the cause of the sensation of the illuminated field of vision. Under certain circumstances we see our own retina, and separate parts of it, when no images are produced in it by external objects. Besides the spectra produced by pressure and electricity, we have an instance of this in the following interesting phenomenon first observed by Purkinje:—If, in a room otherwise dark, a lighted candle be moved to and fro, or in a circle, at the distance of six inches before the eyes, we perceive, after a short time, a dark arborescent figure ramifying over the whole field of vision; this appearance is produced by the vasa centralia distributed over the retina, or by the parts of the retina covered by those vessels. There are, properly speaking, two arborescent figures, the trunks of which are not coincident, but on the contrary arise in the right and left divisions of the field, and immediately take opposite directions. One trunk belongs to each eye, but their branches intersect each other in the common field of vision. The explanation of this phenomenon is as follows:—By the movement of the candle to and fro, the light is made to act on the whole extent of the retina, and all parts of the membrane which are not immediately covered by the vasa centralia are feebly illuminated; those parts, on the contrary, which are covered by those vessels cannot be acted on by the light, and are perceived, therefore, as dark arborescent figures. In most persons this experiment succeeds readily; but in some individuals the phenomenon is produced with difficulty, or not at all. The figures of the vessels appear to lie before the eyes, and to be suspended in the field of vision. We have here a distinct demonstration of the axiom, that in vision we perceive merely certain states of the retina, and that the retina is itself the field of vision,—dark in the unexcited, illuminated in the excited condition.

One of the most difficult problems in physiology is that relative to the respective influence of the retina and sensorium in vision. This department of the physiology of the senses may be correctly styled the metaphysical, since we are at the present time totally destitute of any empyrical means of elucidating it. The question to be determined is the following:—Where is the state of the retina perceived; in the retina itself, or in the brain?

If the states of the minute portions of the retina are first perceived in the brain, they must be communicated along the optic nerve to the brain in the same order in which the affected parts of the retina stand in relation to each other; and to each ultimate sentient division of the retina there must be a correspondent nervous fibre in the optic nerve. Anatomical facts by no means accord with this view. A comparison of the thickness of the optic nerve with the extension of the retina is little favourable to the existence of such a relation between them. The number of nervous fibres in the optic nerve appears to be much less than the number of the papillæ on the surface of the retina. If, then, such a relation between the retina and optic nerve subsists, we can only suppose that the so-called primitive fibres of that nerve contain much more minute and numerous elementary parts. It must, however, be remembered that the sensibility of the retina is acute at its central part only; and if we assume that at this part the ends of the nervous fibres are aggregated closely together, while in the other parts of the membrane they are separated by intervals increasing in size from the centre outwards, we dispose of a part of the difficulty. The sensibility of the middle portion of the retina is in fact as acute, and that of the lateral parts as obtuse, as we might imagine them to be, if in the centre of the retina separate minute divisions of the image corresponded to the extremities of separate fibres, while at the sides one nervous fibre was subjected in some extent of its length to the impressions of many minute points of the image. It would be of especial importance in reference to this question, to know in what relation the papillæ of the retina, observed by Treviranus, stand to the subjacent fibrous layer; whether in fact each nervous fibre does, as he states, bend and become continuous with a single papilla, or whether it corresponds to a complete series of papillæ. But if the perception of locality takes place in the brain, how can the changes in separate successive portions of the length of a fibre be communicated to the sensorium? If we become conscious of sensations only by their being communicated to the brain by the ends of the separate nervous fibres, then the affections which aliquot parts of the length of one fibre have suffered will be perceived by the brain only at one point. If, on the other hand, the sensation of distinct locality be perceived in the aliquot parts of the length of a fibre itself, the mind must be in action in each portion of the length of such fibre; to which supposition, as applied to spinal nerves, the observations relative to the sensations in amputated limbs are opposed. This difficulty might be removed by supposing that the nerves of the higher senses have a more close participation in the action of the mind than other nerves; that the action of mind extends to the extremities of the nervous fibres in the retina; that, in fact, the nerves of the higher senses are merely prolongations of the sensorium. In the present state of our knowledge it is utterly impossible to solve this problem.

However the above question may be decided, it is at all events certain that, even after the retina and external portion of the optic nerve are lost, the internal or central portion of the organ of vision is capable of exciting not merely sensations of light, but also the same ideas of a field of vision in which images are perceived, as when the retina is present. The remarkable phenomena observed by Lincke are an instance of this. A patient, in whom an eye affected with fungoid disease had been extirpated, perceived on the day following the operation, while the sound eye was closed, different images,—such as lights, circles of fire, dancing figures, &c.—floating in front of the orbit from which the eye had been removed.* Similar phenomena have been several times observed in persons totally blind.† These facts would seem to prove that the affections of the fibres of the optic nerve are communicated to the brain before they give rise to the sensation of a field of vision; and, in that case, we must admit that each minute division of the retina is represented in the sensorium by a corresponding nervous fibre, though this cannot be demonstrated anatomically.

The mode of action of the peripheral and central parts of the apparatus of vision upon each other is, therefore, at present, involved in much obscurity; and we must rest satisfied with a knowledge of the fact, that the order of the images in the field of vision depends upon the relative position of the affected parts of the retina.

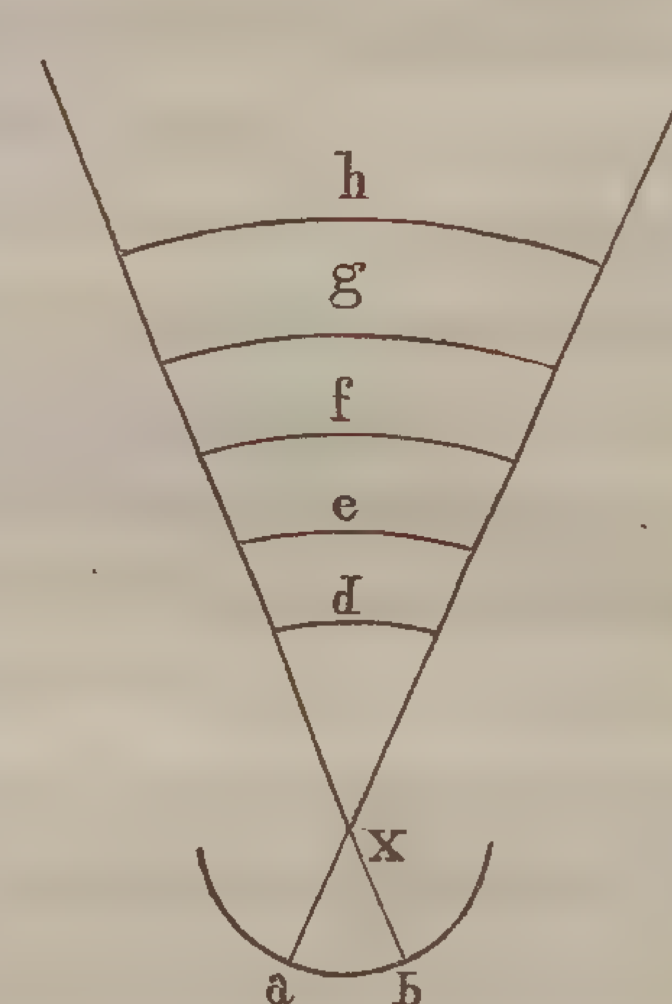
Ideal size of the field of vision.—The actual size of the field of vision depends on the extent of the retina, for only so many images can be seen at any one time as can occupy the retina at the same time; and thus considered the retina, of which the affections are perceived by the sensorium, is itself the field of vision. But to the mind of the individual the size of the field of vision has no determinate limits; sometimes it appears very small, at another time very large; for the mind projects the images on the retina towards the exterior, the cause of which will be explained hereafter. Hence the mental field of vision is very small when the sphere of the action of the mind is limited by impediments near the eye; on the contrary, it is very extensive when the projection of the images on the retina towards the exterior by the influence of the mind is not impeded. The mental field of vision is very small when we look into a hollow body of small capacity held before the eyes; it is large when we look out upon a landscape through a small opening; it is more extensive when we look at the landscape through a window; and most so when our view is unconfined by any near object. In all these cases the idea which we receive of the size of the field of vision is very different, and, nevertheless, its absolute size is in all the same, it being dependent on the extent of the retina; for,

* Lincke, De Fungo Medullari; Lips. 1834.

† See my tract, Über die Phantastischen Gesichtserscheinungen; Coblenz, 1826.

as was before said, we can not see at one time more than the extent of the retina is capable of containing. Nevertheless, although in looking upon a landscape through an opening, the whole image of the scene is not larger than the circumference of the opening through which it is viewed, and occupies the same space upon the retina; yet the idea conceived of it is extremely different. Hence it follows that the mind is constantly co-operating in the acts of vision, so that at last it becomes difficult to say what belongs to mere sensation, and what to the influence of the mind. In adult age it would only be by abstracting the action of the mind from the process of vision that we could obtain the mere sensation of vision, as it is perceived possibly in the new-born child; for the child which has as yet no idea of proximity and distance, would necessarily recognise no difference in the size of the field of vision, whether it looked into a tube closed at one end, or through an open one upon an extensive landscape. This consideration leads us also to the conclusion, that the simple perception of the images of objects must be an original faculty, quite independent of the ideas derived from them.

Fig. 95.



Every object seen under the same angle, *a x b* (fig. 95), has an image of the same size, *a b*, upon the retina; the objects *d*, *e*, *f*, *g*, *h*, which are of very different size, but are situated at different distances, are seen under the same angle, and therefore produce images of the same size upon the retina: and, nevertheless, these images appear to the mind of very unequal size when the ideas of distance and proximity come into play; for, from the image *a b*, the mind forms the conception of a visual space extending to *d*, *e*, *f*, *g*, or *h*, and of an object of the size which that represented by the image on the retina appears to have when viewed close to the eye, or under the most usual circumstances. A landscape depicted on the retina, as *a b*, and viewed under the angle *a x b*, is therefore conceived by the mind to have an extent of two miles perhaps, if we know that its extent is such, or if we infer it to be so from the number of known objects seen at the same time. And in the same way that the images of several different objects, viewed under the same angle, thus appear to the mind to have a different size in the field of vision, so the whole field of vision, which has always the same absolute size, is interpreted by the mind as of extremely various extent; and, for this reason also, the image viewed in the camera obscura is regarded as a real landscape,—

as the true field of vision,—although only a small image depicted upon paper. The same mental process gives rise to the idea of depth in the field of vision; this idea being fixed in our mind principally by the circumstance that, as we ourselves move forwards, different images in succession become depicted on our retina, so that we seem to pass between these images, which to the mind is the same thing as passing between the objects themselves

It is evident, therefore, that the field of vision conceived by our mind is extremely variable, while the field of the simple sensation of vision is entirely dependent on the extent of the retina, or of the central parts of the apparatus of vision in the brain. This latter field of vision is represented most nearly by sensations excited in the retina independently of any object which can call the mind to action,—for instance, by the sensation of darkness before the closed eyes, or by the sensation of light before the eyes when the lids are closed, but the light shines through them. In these cases the field of vision seems to be immediately before or in the eyes; but, as soon as the idea of an object already seen can associate itself with the sensation, the mental faculty of "projection" towards the exterior comes into play, and the size attributed to the object which excites the sensation depends on the former experience of the individual. Hence the difference in the statements of different persons respecting the size and apparent distance from the eye of the vessels of the retina perceived in Purkinje's experiment.

The action of the sense of vision in relation to external objects is, therefore, quite different from that of the sense of touch. The objects of the latter sense are immediately present to it; and our own body, with which they come into contact, is the measure of their size. The part of a table touched by the hand appears as large as the part of the hand receiving an impression from it, for a part of our body in which a sensation is excited is here the measure by which we judge of the magnitude of the object. The part of the hand brought into contact with the table forms a part of the whole sensitive surface, and the part of the table touched appears as large as the part of the hand which touches it is in proportion to our whole body; the power of distinguishing the different parts of our body depending on the possibility of distinguishing in the sensorium the nervous fibres coming from different parts. In the sense of vision, on the contrary, the images of objects are mere fractions of the objects themselves, realized upon the retina, the extent of which remains constantly the same. But the imagination which analyses the sensations of vision, invests the images of objects together with the whole field of vision in the retina, with very varying dimensions; the relative size of the images in proportion to the whole field of vision, or of the affected parts of the retina to the whole retina, alone remaining unaltered.

Volkmann remarks,* that the retina is in no case sensible of its own extension, and that even the sense of touch does not inform us of the definite extent and figure of the surface of our body. He founds this opinion on the facts observed by E. H. Weber, which have showed that the distance between two points is perceived very differently at different parts of the surface (see page 700). Volkmann, therefore, supposes that the skin, in measuring the size of objects, takes as unity the extent of the small division of its own surface capable of distinguishing distance. If we call this measure of unity x, an inch will to the point of the fingers be 12 x, to the middle of the arm 1 x; for every spot of the skin touched by an object will ascribe to that object a size which equals so many times x as it contains parts capable of distinguishing two points touching it from each other. According to this view, when I touch the middle of my arm with the point of the finger, the part of my finger which comes into contact with my arm should feel twelve times as large as the corresponding part of the arm. Volkmann applies this view to the retina also; and supposes that it also, in estimating the size of objects, takes as unity the most minute space capable of being distinguished by vision. The phenomena observed by Professor Weber are explicable, however, in another way, namely, as the result of the mingling or radiation of sensations (see page 697).

Relation of the sense of vision to the external world.—We have next to inquire how the action of the sense of vision in relation to the external world is first established. Several physiologists—as, Tourtual, Volkmann, and Bartels—suppose the interpretation of the sensations of the retina as objects forming part of the exterior world to be a faculty of the sense of vision itself. But what, in the first place, constitutes the external world? Since in the first acts of vision the image of the individual's own body cannot be distinguished from those of other bodies, the referring of the sensations of vision to something external can be nothing else than the discrimination between the sensations of vision and the subject of them,—between the sensations and the sentient "self." It is by the operations of the judgment that the objects of vision are recognised as exterior to the body of the individual; this has been already explained and illustrated in the Preliminary Considerations on the Physiology of the Senses. It is said that the new-born infant perceives from the first that the objects of vision are external to its body and to its eye; but the infant recognises neither its own eye nor its body in the form of sensations of vision, and only learns by experience which of the

* Beiträge zur Physiol. d. Gesichts-sinnes, Leipz. 1836.

images which it sees is its own body. We can, therefore, only say that the new-born infant distinguishes the sensations from the sentient "self," and in this sense only does it perceive the sensations as something external. In brutes the co-operation of instinct renders this re-action of the sensorium, under the impression of external objects, much less indefinite, for the young animal soon applies itself to the nipple of the mother; so that its sensorium must be the seat of an innate impulse to attain to the image which it sees, and which is an object or something external to the sentient self, by appropriate movements. Though the new-born infant be at first unable to distinguish between the image of its own body and those of external objects, it will soon remark that certain images in the field of vision are constantly re-appearing, and that these images move when its body is voluntarily moved. These are images of parts of its own body. All the other images in the field of vision either change quite independently of the body of the infant, or the changes which they undergo do not correspond with its voluntary movements. These are images of objects appertaining to the external world, which, now recognised as existing in a space external to the body of the individual, are henceforth continually presenting themselves in this space, which, according to the conception of the mind, is subject to the operations of vision. Of the eye as the organ of vision the new-born infant knows nothing.

We have, in fact, little opportunity of perceiving in the act of vision that the eye is its seat. It is only when the eye is the seat of sensation without any definite external objects being perceived, that it is really recognized to be the seat of these actions; for instance, when darkness is seen before the closed eyes, or when light shines through the closed eye-lids, so as to excite in the eyes the sensation of light. It is thus by the process which we have described that the newly born human being learns to distinguish between the visible external world and himself, or gains the idea of an exterior visible world.

Images of the individual's own body in the field of vision.—Certain parts of our body nearly constantly occupy a part of the field of vision, and therefore have a share in the ideas which the sensations of vision excite in the mind. When we look with one eye only, one side of the field of vision is occupied by the image of one side of the nose. If we depress the eye-brows, the upper part of the field of vision becomes occupied by them. If the cheek be raised, a part of it is seen at the lower part; and if the outer portion of the orbicularis palpebrarum muscle be contracted, a shadow thrown by the investments of the eye is seen at the outer part of the field of vision. Images of parts of our body may therefore appear in the entire periphery of the field of vision, and then the images of external objects will lie in the space surrounded by them. If we close one eye, and fix the other upon the point of the nose, the image of the nose will project from one side into the middle of the field of vision. If we direct both eyes simultaneously towards the nose, the image of the point of that organ will lie in the middle of the lower part of the field of vision; while the images of the sides of the nose will be in part deficient, since, at the part where one eye perceives an indistinct image of the side of the nose, the other will see external objects. If the eye be directed more downwards, not merely the nose, cheeks, and lips, but also the trunk and extremities, will appear at the lower part of the visual field. In every position of the eye, however, some one part of our body is always visible, occupying a determinate place in the periphery of the field of vision either above or below, or at the sides; and the image of some part of our body constitutes a part in most of the sensations of vision, and of the ideas attached to them.

Although the images of our body perceived by the sense of vision are merely images depicted on the retina, and by it communicated to the sensorium, they are confidently interpreted, like the images of external bodies, as real objects. The image of our hand, which we see, is not, in point of fact, our hand, but only its representation in the retina. When we grasp any object, the movement is represented in the retina: we see that we grasp the object, for the image of our hand is seen to grasp the image of the object. We are also made acquainted with the performance of the act by means of another sense, namely, by sense of touch in the hand, and the sense of movement in it. It appears an extraordinary circumstance that, although the perception of any part of our body by the sense of common feeling or touch, and by the sense of vision, takes place in such different localities, the two sensations never interfere with each other; they are brought into harmony and unison through the influence of the mind. That this is the case we can render evident to ourselves by an example in which the difference of locality is still more striking, and where nevertheless the two sensations are by the power of the mind not less closely brought into unison.

If while we look at our image in a mirror we move our hands, we are informed of those movements, as well by the sense of feeling as by the image in the mirror; and, although the seat of impressions on the senses of touch and sight is so different, we derive from them through our mental agency but one harmonious idea.

Inverted images and erect vision.—In accordance with the laws of optics, the images are depicted on the retina in an inverted position as regards the objects themselves; what in the object is above, is in the image represented below, and *vice versâ;* the right side of the object is to the left, and the left side to the right; while the relative position of its different parts remains precisely the same. The question now arises, whether we really see the images inverted, as they are in the retina; or erect, as in the object itself. Since the image, and the affected parts of the retina, mean the same thing, the question physiologically expressed is this: Are the minute divisions of the retina affected in vision perceived by the sensorium in their natural relation to the object?

The view which I take of the question, and which I proposed in my work on the physiology of vision, is, that even if we do see objects reversed, the only proof we can possibly have of it is that afforded by the study of the laws of optics; and that, if every thing is seen reversed, the relative position of the objects of course remains unchanged. It is the same thing as the daily inversion of objects consequent on the revolution of the entire earth, which we know only by observing the position of the stars; and yet it is certain that, within twenty-four hours, that which was below in relation to the stars, comes to be above. Hence it is, also, that no discordance arises between the sensations of inverted vision and those of touch, which perceives every thing in its erect position; for the images of all objects, even of our own limbs, in the retina, are equally inverted, and therefore maintain the same relative position. Even the image of our hand, while used in touch, is seen inverted. The position in which we see objects, we call therefore the erect position. A mere lateral inversion of our body in a mirror, where the right hand occupies the left of the image, is indeed scarcely remarked; and there is but little discordance between the sensations acquired by touch in regulating our movements by the image in the mirror, and those of sight, as, for example, in tying a knot in the cravat. There is some want of harmony here, on account of the inversion being only lateral, and not complete in all directions.

Volkmann agrees with this view of the question. He also argues that no explanation of erect vision is required, as long as all things equally, and not some objects only, appear to the eye inverted. Nothing can be inverted where nothing is erect; for each idea exists only in antithesis to the other.

The hypothesis, that erect vision is the result of our perceiving, not the image on the retina, but the direction of the rays of light which produce it, involves an impossibility, since each point of the image is not formed by rays having one determinate direction, but by an entire cone of rays; and, moreover, vision can consist only in the perception of the state of the retina itself, and not of any thing lying in front of it in the external world. The hypothesis, also, that the retina has an *outward* action, and that objects are seen in the direction of decussating lines, that is to say, in the direction of the perpendicular of each point of the concavity of the retina, (Bartels,) is a perfectly arbitrary assumption; since there is no apparent reason why one direction should have the preference rather than another, and each ultimate sensitive division of the retina, if it had the power of action beyond itself, would act in as many directions as radii might be drawn from it towards the exterior world.

The inversion of objects being a thing of which we can never become conscious in ourselves, it is not probable that nature has made in the brain, or elsewhere, any provision for the correction of the error, which would never have been known but for the institution of optical inquiries. The decussating course of the optic nerves cannot be adduced as an explanation of erect vision, since the decussation is only partial.*

If it were possible to produce an image of an object upon the retina without the aid of light, for instance by immediate contact, the image would in that case not be inverted; and, if it were possible to see the same object simultaneously by means of luminous rays from without, and by immediate impression upon the retina, the images produced in these two ways would appear to lie on opposite sides. This can in fact be shown experimentally. If, we press upon the retina with the finger through the sclerotica, a spectrum produced by the immediate impression of the finger will be perceived; while at the same time the finger may be seen through the medium of the external light. The two images will appear at opposite sides. If, while the eyes are closed in the dark, we press upon what appears to us to be the upper part of one eye with the finger, which is, therefore, seen above, the spectrum produced by the pressure becomes visible below; if the pressure be made upon the lower part of the retina, the spectrum appears above; if the right side of the retina be the seat of the pressure, the spectrum appears on the left side, and *vice versâ*.

Visual direction.—Before wholly quitting this subject, we must take into consideration what has been called by some writers "the direction of vision," or "visual direction." Objects, of which the images fall upon the same parts of the retina, lie in the same visual direction. With respect to the causes which determine the direction of vision, two views may be adopted, though one of these only appears to me to be correct.

1. The direction in which an object is seen depends merely on the part of the retina which receives the image, and on the distance of this part from, and its relation to, the central point of the retina; or, in other words, on the position which the affected part of the retina bears in relation to the entire mosaic-like expanse of the membrane. If, by the action of the mind, the images or affections of the retina are projected into the exterior world, the relation of the images to each other remains

* See the observations of Berthold, (Über das Aufrecht-erscheinen der Gesichts-objecte: Gött. 1830,) and of Bartels, (Beiträge zur Physiologie des Gesichts-sinnes: Berlin, 1834,) on this subject.

the same; and the idea which the sensorium receives from the act of vision may be imagined by supposing the whole visual field of the retina to be projected forwards, its different parts maintaining the same relative position, the part which was above remaining above, that which was below still below. Thus if *d b a c e* (fig. 96) were the retina, and

Fig. 96.

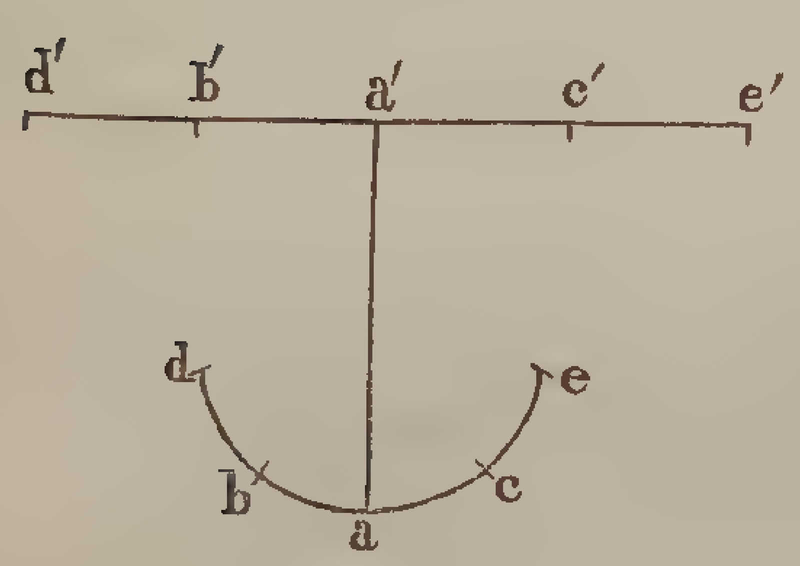
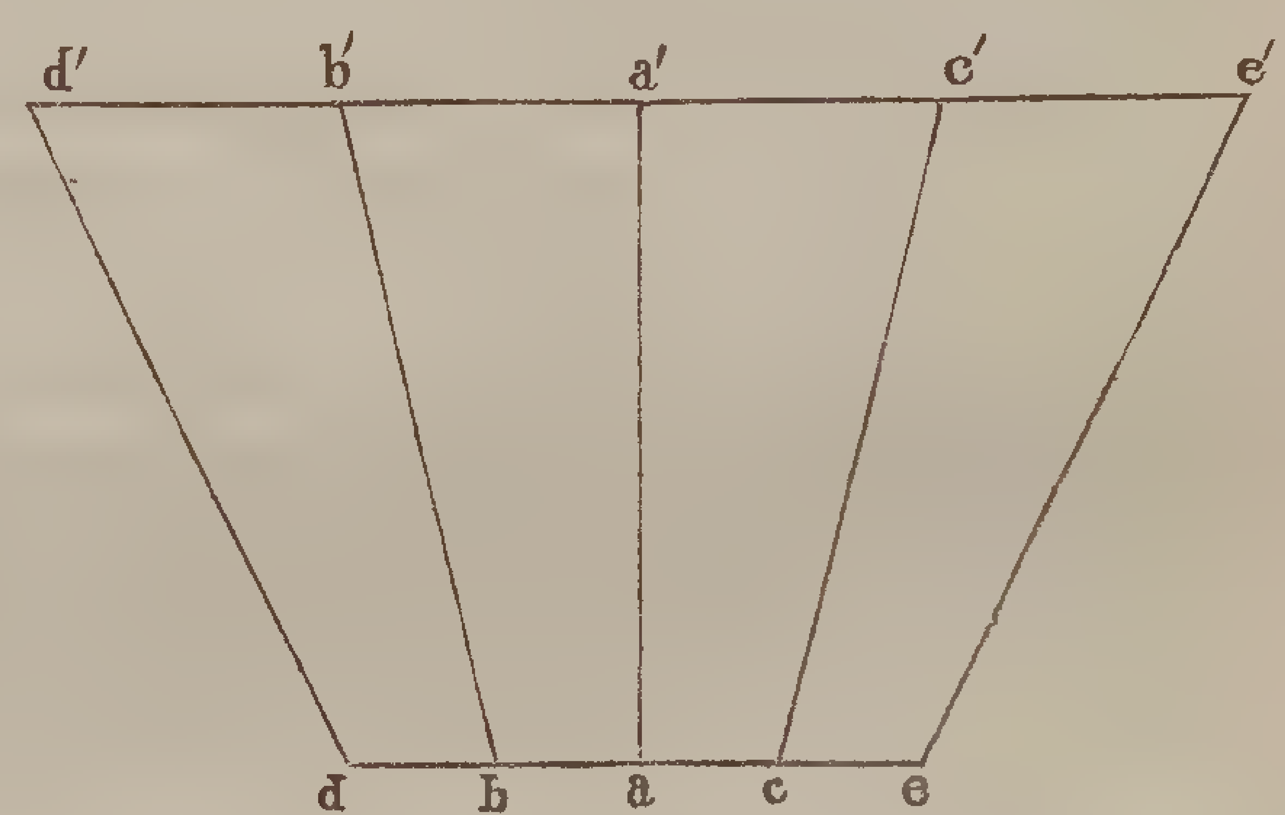


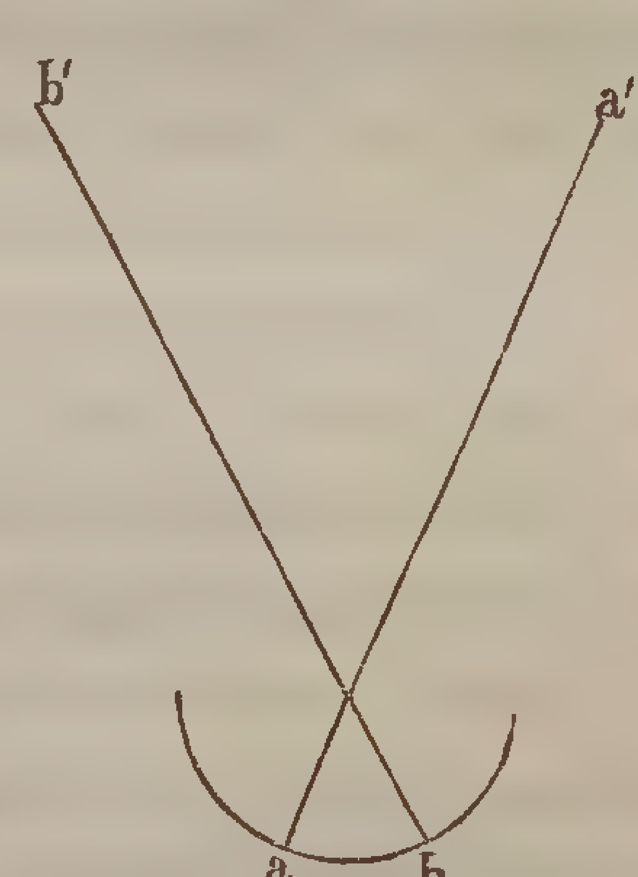
Fig. 97.



the images depicted on it were projected forwards, *a′* would be the situation towards which *a* would be projected by the agency of the mind, *b′* that towards which *b* would be projected, and so on; the points *b′*, *c′*, *d′*, and *e′*, of the image conceived by the sensorium lying respectively on the same sides as the corresponding points *b*, *c*, *d*, and *e*, of the image in the retina: or, if the retina be regarded as a plane surface, the projection of the image would be as in fig. 97. Here the extent ascribed to *d′ e′* would depend on the mind itself; and merely the relative positions of the different points *a′*, *b′*, *c′*, *d′*, and *e′*, would remain the same.

2. Opposed to this view is the hypothesis that the images are projected forwards in decussating lines, as in fig. 98; the point *a* of the image on the retina being, for example, projected forwards towards the opposite side, and seen in the direction *a′ a*. Of this hypothesis there are various modifications, dependent on the situation in which the lines of visual direction are supposed to decussate.

Fig. 98.



a. Thus some physiologists suppose that the direction of the light itself is perceived, and that we see consequently in the direction in which the light comes to us; this view, which was shown by Porterfield, and more recently by Volkmann, to be untenable, is, curious to say, adopted in many treatises on physics.

In ordinary vision, every point of the image upon the retina is produced by the apex of a cone or pencil of light, of which the base is the circumference of the pupil. Which, then, of the rays composing this cone determines the direction of vision? If it be said, the ray occupying the axis of the cone, we may answer that the peripheral rays also are adequate for vision, as in looking through an opening in a card in such a manner that the peripheral rays only enter the eye. If the point *a* (fig. 99) of any object be at such a distance from the eye that the rays issuing from it meet in a focus in front of the retina at *o*, and if

Fig. 99.

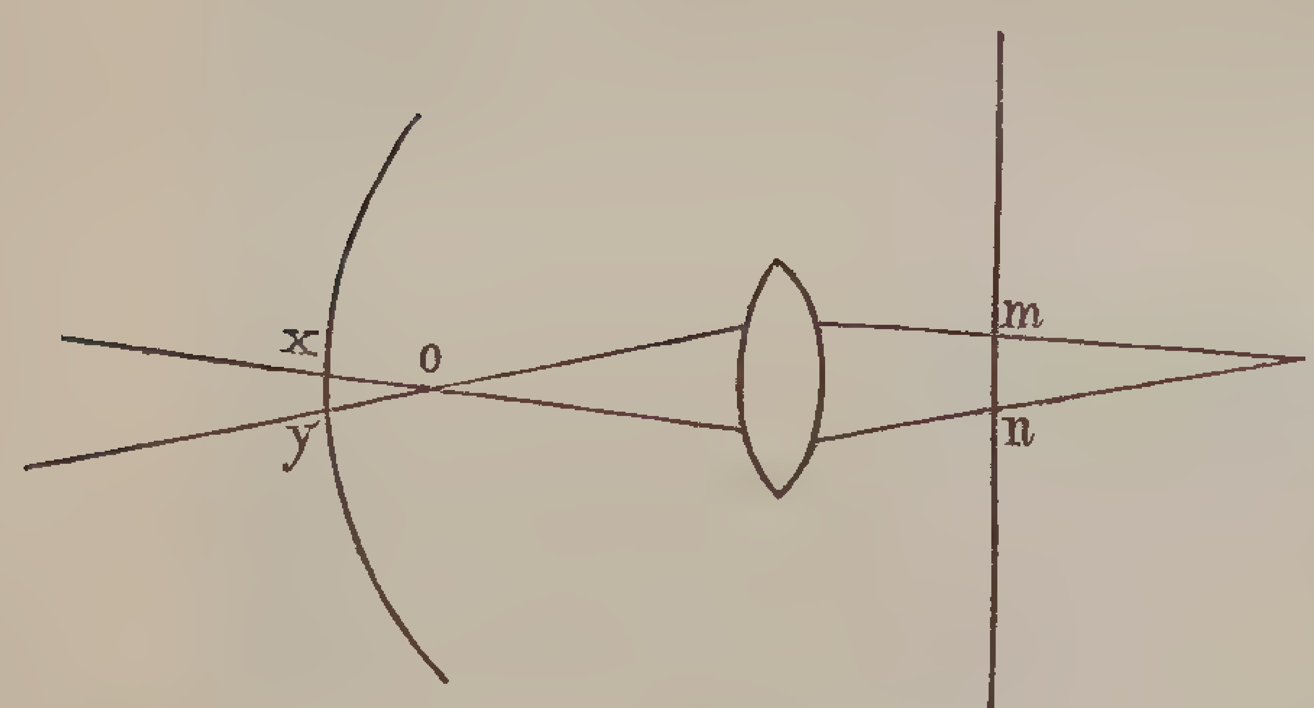
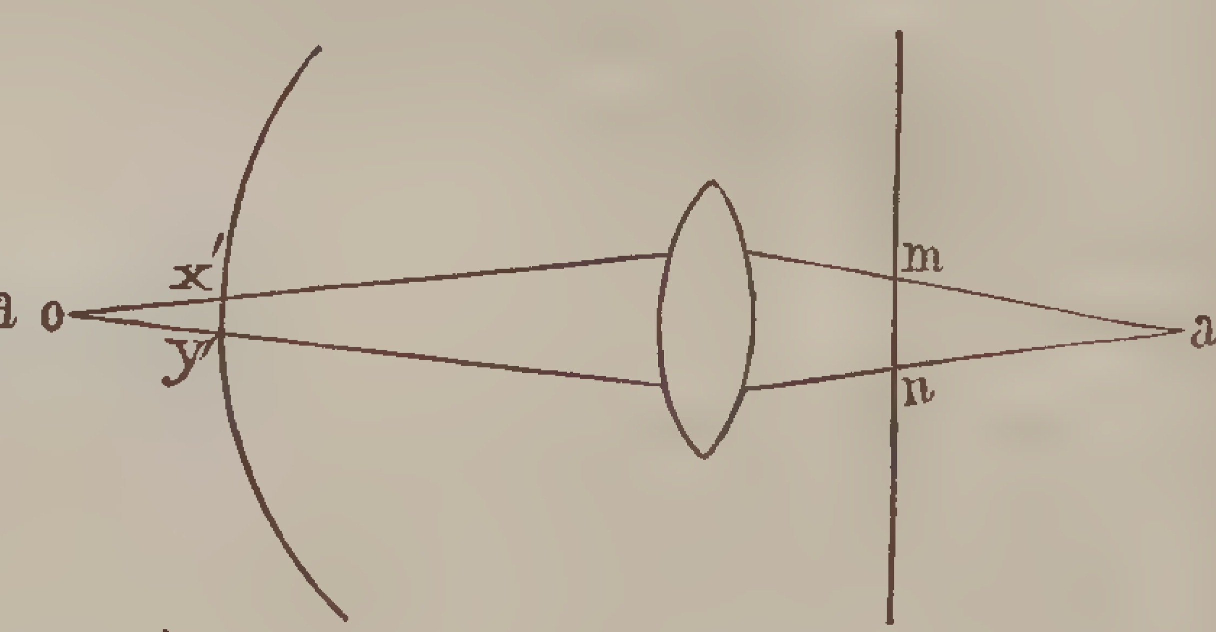


Fig. 100.



m, *n*, be two perforations in a card, two images of the point *a* will be formed at *x*, *y*, by the peripheral bundles of rays passing through the perforations in the card.

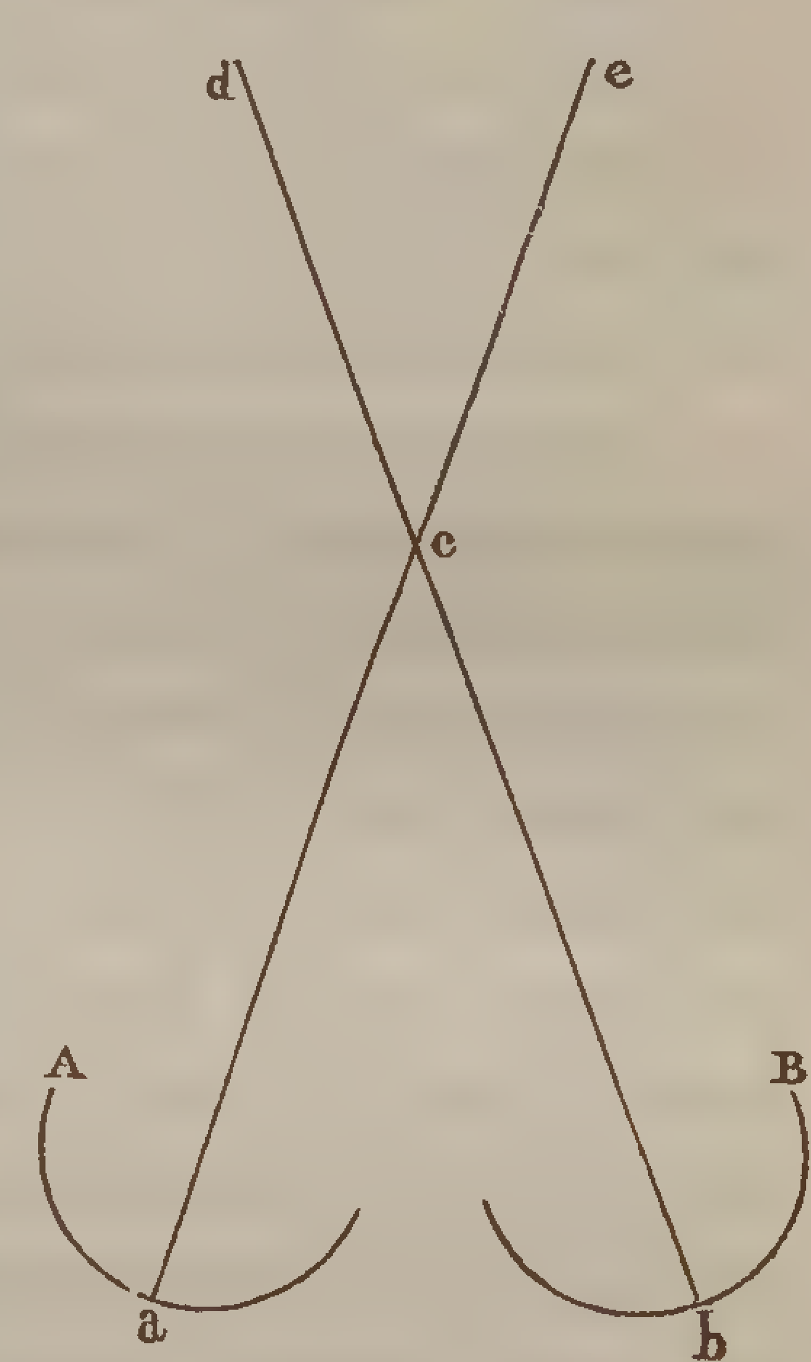
If, on the contrary, the point *a* be too near the eye, (as in fig. 100,) so that the focus of its cone of light falls behind the retina, and *m*, *n* be again openings in a card, two images will still be produced at *x*,′ *y*,′ by the bundles of peripheral rays transmitted by the openings in the card. The distance of the point *a* from the eye may be so regulated, that the images *x*′, *y*′ may be at the same distance apart in the second figure as the images *x*, *y* in the first, and the images will then appear in the same position, although the direction of the rays *x*, *o* in the first figure, and that of the rays *o*, *x* in the second, is so very different.

b. The second modification of the hypothesis above mentioned is that proposed by Porterfield and Bartels, namely, that each point of the retina sees the object in the direction of a line perpendicular to itself, or to its tangent. This is an entirely arbitrary assumption.

c. Volkmann proposes a third modification of the same view. According to him, the direction of vision is regulated by the position of the sentient point of the retina in relation to the decussating point of the visual rays; which point is, according to his inquiries, situated in a line drawn between the image on the retina and the object (see page 1132). That the direction of vision is thus regulated, he supposes to be owing to an innate and inexplicable law. It is certain that the most perfect accordance, in a physical point of view, subsists between the objects and their images on the retina, and that lines drawn from the one to the other do all pass through such a point of decussation. Nevertheless, I cannot ascribe to the optic nerves a power of exterior action in a determinate and exclusive direction. Volkmann presupposes the existence of an inexplicable innate relation between the separate sensitive points of the retina and a point of decussation situated behind the lens. But the former view of the subject does not require the assumption of any such inexplicable condition. The direction in which each image is seen is there supposed to be determined merely by the situation which it occupies upon the retina, and by the relation which this spot bears to the rest of the membrane; and the images to be projected forwards by the action of the mind in the same order as that in which they exist on the retina, but not in decussating lines. The projection of the images towards the exterior cannot be regulated by the mere curve of the retina, but must, in my opinion, be dependent on the arrangement of the elementary parts of that membrane with regard to each other.

All explanations of the direction of vision which are founded on the hypothesis of the projection of the images in decussating lines have one defect in common. The phenomena of vision with two eyes simultaneously are wholly at variance with them. If visual direction be dependent on an exterior action of the retina in any determinate direction, either in the direction of the point on which the eye revolves, or in a direction perpendicular to the retina, single vision with two eyes becomes inconceivable; for, by the eye A (fig. 101), the image of the object *c* falling upon the central point of the retina *a* will be seen in the direction *a c e*; while, by the eye B, the image of the same object, *c*, falling upon the central point of the retina *b*, will be seen in the direction *b c d*. Hence, according to this hypothesis, the image of the same object, *c*, will be seen at two different parts of the field of vision. This objection is not answered by saying that the central points of the two retinæ always see the object singly, or have but one perception from their two impressions; for, if they see the same object in the same spot of the field of vision, they cannot project the images of it in the directions *a c e* and *b c d*. But if the direction in which an object is seen depends simply on the relation which the affected portion of the retina bears to the whole membrane, the image of *c* falling upon the identical points of the two retinæ will be seen single, and will occupy the middle of the common field of vision of the two eyes.

Fig. 101.



Estimation of form, size, distance, and motion.—The estimation of the form of bodies by sight is the result partly of the mere sensation, and partly of the association of ideas. Since the form of the images perceived by the retina depends wholly on the outline of the part of the retina affected, the sensation alone is adequate to the distinction of mere superficial forms from each other, as of a square from a circle.

Molyneux proposed to Locke the question, whether a person born blind, who was able by the sense of touch to distinguish a cube from a sphere, would on suddenly obtaining his sight be able to distinguish them by the latter sense. It is difficult to conceive wherefore these two philosophers answered the problem in the negative; for the senses of touch and sight are both based on the same fundamental faculty by which we are rendered conscious of the extension of our own organs in space. Hence a new-born animal, when it sees the nipple of its mother, immediately perceives the definite form of that object; and this alone proves that the comprehension of simple forms is not a faculty acquired by education.

The estimation of the different dimensions of bodies from their images on the retina is, on the contrary, a result of experience; since all the ideas obtained by vision refer originally to superficial extent only, and the idea of a solid body, or a body of three dimensions, can only be attained by the action of reason constructing it from the different superficial images seen in different positions of the eye with regard to the object. To the youth restored to sight by Cheselden all objects appeared at first as if painted on one surface, as, in fact, they are; but from the changes which the images on our retina undergo during progression, in which we pass, as it were, between the images, the idea of the depth of the field of vision is originated in our mind; the field of vision is, indeed, merely a conception of the mind, and not a perception of sense.

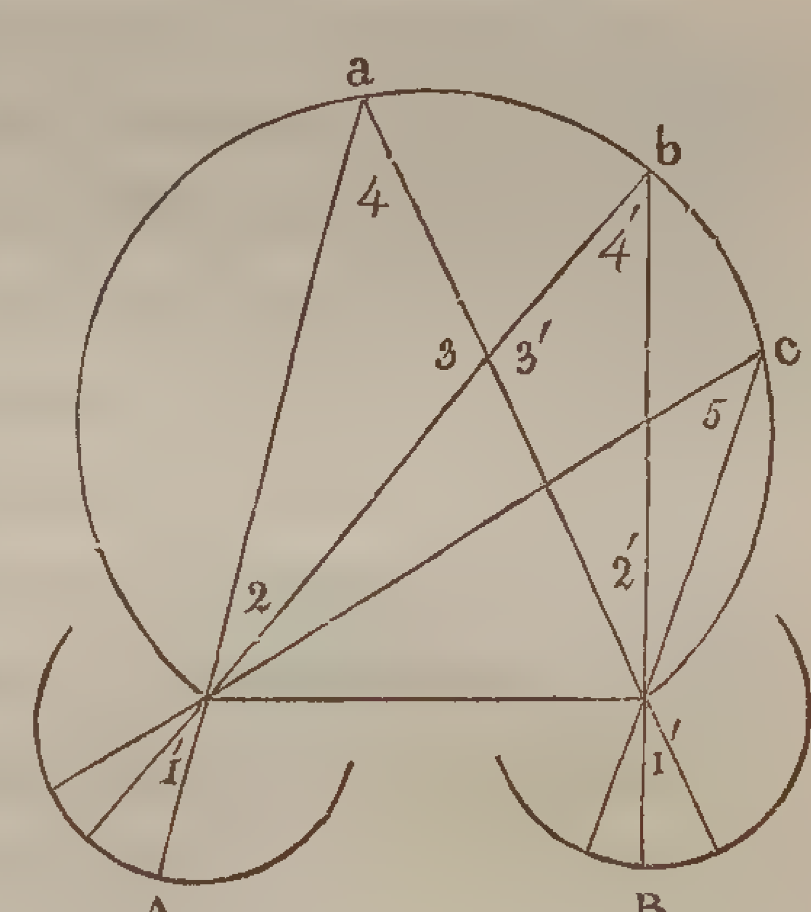
[From the interesting facts observed by Mr. Wheatstone relative to binocular vision, it appears that our belief in the solidity of a body of three dimensions, such as a cube, arises in a great measure from two different perspective projections of it being presented simultaneously to the sensorium by the two eyes (see page 1205). The influence of this circumstance is greater in proportion as the object is nearer to the eyes, and ceases when it is so distant that the optic axes in regarding it are parallel, the pictures then received by the two retinæ being exactly similar. A person who has lost one eye is destitute of this aid in distinguishing the form of near objects, but he supplies the defect by the motion of his head, by which means he causes his single eye to receive different pictures of an object, such as would be received by the two in binocular vision.]

The apparent size of objects depends primarily on the size of the affected parts of the retina, or on the size of the angle under which the objects are viewed by the eye (see page 1131). The idea of the true size of objects from their apparent size is the result of practice, and of the combination of previous ideas of distance, proximity, &c. [Mr. Wheatstone has ascertained that the degree of inclination of the optic axes with which an object is viewed has a great influence on our idea of its magnitude.]*

The estimation of proximity and distance is not obtained directly from the sensation, but by an action of the reasoning powers. An object is regarded as distant when the visual angle under which its image falls upon the retina is smaller than it is when the object is known to be near the eye. An object appears more distant than others when it is in part concealed by the others, or appears relatively smaller than it should do if it were situated at the same distance as the other objects. This idea of distance is acquired, and in man, at least, is not innate. To the child everything appears equally distant, and it grasps at the moon as at the nearest object.

Most physiologists maintain that the position of the axes of the eyes required for distinct vision of an object also contributes in a great degree to enable us to estimate its distance; the axes of the eyes converging more and more, the nearer the object is to them. The influence of this circumstance is, however, estimated too highly. When the objects lie in a straight direction in front of the eyes, it may certainly have considerable effect; but, when they lie laterally, the position of the axes of the eyes cannot longer be of any assistance in judging of their distance; for distinct vision of objects situated at the sides of the field of vision requires an inclination of the axes of the eyes very different from that necessary for the perception of objects in the middle of the field of vision even when they lie in the same plane. Thus the degree of convergence of the axes of the eyes for the perception of the points *a*, *b*, and *c* (fig. 102) is the same; and, nevertheless, *a* is very distant from the eyes, the lateral object *c* very near to them. The angles 4, 4′, and 5 are equal, if the line *a b c* be a circle; for it is the property of a circle that triangles erected towards its periphery, and having a common chord for their base, have equal angles at that periphery. Hence, from the circumstance of objects requiring the same inclination of the axes of the eyes for their distinct perception, we do not learn that they lie at the same distance from the eye, but that they lie in a circle, as the points *a*, *b*, *c*.

Fig. 102.



[The circumstance of objects being viewed from two different points of sight simultaneously by the two eyes, which has been shown by Mr. Wheatstone to afford great aid to the mind in estimating forms, was distinctly pointed out by Le Cat in the following paragraph, as assisting us in judging of the distance of objects, although he attributed more import-

* Mayo's Physiology, 4th Ed. p. 284.

ance to our consiousness of the degree of inclination of the optic axes:—"I do not doubt that the more or less extended succession of different bodies between the objects and ourselves aids this judgment; but the concurrence of the optic axes of the two eyes is itself necessary to enable us to distinguish well this series of interposed bodies: thus, this concurrence of the axes, and the length of the angle they form, are the fundamental principles for estimating the distance of objects: hence it is, that when we look with one eye only, we are unable to distinguish distances, and cannot place the end of the finger directly upon an object indicated to us, though it be very near, for the finger hides the object, and appears to correspond to it as exactly when it is at the distance of a foot as if it were only a line removed from it. But, if our other eye be open, it will see the finger and the object from the side, and will therefore discover a considerable interval between them if they are a foot distant from each other, but only a very small interval if they are very near; and thus we are enabled to place our finger with certainty upon the desired object." *]

We judge of the motion of an object, partly from the motion of its image over the surface of the retina, and partly from the motion of our eyes following it.

If the image upon the retina moves while our eyes and our body are at rest, we conclude that the object is changing its relative position with regard to ourselves. In such a case the movement of the object may be apparent only, as when we are fixed upon a body which is in motion, such as a ship. If, on the other hand, the image does not move with regard to the retina, but remains fixed upon the same spot of that membrane, while our eyes follow the moving body, we judge of the motion of the object by the sensations of the muscles in action to move the eye, or by the currents of nervous energy sent by the sensorium to those muscles. If the image moves over the surface of the retina while the muscles of the eye are acting at the same time in a manner corresponding to this motion, as in reading, we infer that the object is stationary, and we know that we are merely altering the relation of our eyes to the object. Sometimes the object appears to move when both object and eye are fixed. This is the case in the vertigo produced by moving our body round on its axis; surrounding objects then, when our body and eyes cease to move, appear to perform a circular motion in the opposite direction to that in which our head had moved. Some remarkable observations, by Purkinje, seem to show that these apparent motions are owing to an impulse to motion in the determinate direction imparted to the brain; for the direction of the apparent rotation of objects maintained a constant relation to the head, although the position of the head were changed after its own movement was remitted (see page 847). With

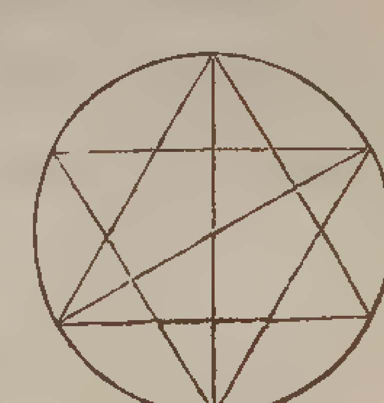
* Le Cat, Traité des Sensations, &c.; Paris, 1767, t. ii. p. 475.

these phenomena of apparent motion we must not confound others dependent on spectra left by strong impressions on the retina, of which we shall speak in treating of those spectra. The sensations of rotatory movement of objects, produced by turning the body on its axis, are quite independent of the previous impressions on the retina; for they can be produced by moving round with the eyes closed.

Influence of the "attention" on vision.—Before leaving the subject of the reciprocal actions of the retina and sensorium, we must notice the influence of the mental action upon the act of sensation itself.

The mind can, by the faculty of "attention," concentrate its activity more or less exclusively upon the senses of sight, hearing, and touch alternately. When exclusively occupied with the action of one sense, it is scarcely conscious of the sensations of the others. The mind, when deeply immersed in contemplations of another nature, is indifferent to the actions of the sense of sight, as of every other sense. We often when deep in thought have our eyes open and fixed, but seeing nothing; which is owing to the action of the fibres of the optic nerves being unable to excite the sensorium to perception while it is acting in another direction: for vision, therefore, "attention" of the mind is necessary. But by this faculty of "attention" we also analyse what the field of vision presents. The mind does not perceive all the objects presented by the field of vision at the same time with equal acuteness, but directs itself first to one and then to another. The sensation becomes more intense according as the particular object is at the time the principal subject of mental contemplation. Any compound mathematical figure produces a different impression, according as the attention is directed exclusively to one or the other part of it. Thus, in figure 103, we may in succession have a vivid perception of the whole, or of distinct parts only; of the six triangles near the outer circle, of the hexagon in the middle, or of the three large triangles. The more numerous and varied the parts of which a figure is composed, the more scope does it afford for the play of the attention. Hence it is that architectural ornaments have an enlivening effect on the sense of vision, since they afford constantly fresh subject for the action of the mind.*

Fig. 103.



2. *Of the "ocular spectra" consequent on impressions on the retina.*

The duration of the sensations of the retina is much longer than that

* On the influence of attention in the sense of vision, see Purkinje, Beobachtungen und Versuche zur Physiologie der Sinne; Prag. 1823, 1: and Tourtual, loc. cit. On the subject of the influence of the mind on the sensations of vision generally, see Heermann, Über die Bildung der Gesichtsvorstellungen aus den Gesichts-empfindungen; Hannover, 1835.

of the impressions which produce them: according to Plateau,* the sensation persists 0·32 to 0·35 of a second after the impression has ceased; and the duration of the "after-sensation," or "spectrum," is greater in a direct ratio with the duration of the impression which caused it. Hence the image of a bright object, as of the panes of a window through which the light is shining, may be perceived in the retina for a considerable period, if we have previously kept our eye fixed on the object for some time. The duration of these images in the closed eyes may also be very much prolonged, by passing the hand up and down before them, so as to permit the light to fall upon them only at intervals. The after-duration of sensations consequent on impressions on the retina explains the appearance of a circle of light produced by moving a luminous body in a circle before the eyes, as well as that of the confusion of the images of the spokes of a rapidly revolving wheel, or of the prismatic colours painted upon a spinning-top.

[It has been noticed by several observers, that the ocular spectra frequently disappear, return, and again disappear. This fact, which any person can readily verify, may assist in explaining the following phenomena.]

If we gaze for a considerable time upon a body which presents a continued motion of different parts of its surface in succession, the spectra left on the retina have also an appearance of motion in the same direction, owing to their disappearing from the eye in the same order. This is, in my opinion, the proper mode of explaining certain illusory appearances of motion in objects. If, after looking for a long time at the undulations of a stream of water, we suddenly turn our eyes to the ground at its margin, the ground itself appears to move, in the opposite direction to the waves of the water. I have frequently remarked this phenomenon, when, after gazing from my window upon the neighbouring river, I have directed my eyes to the pavement of the street. I observed it also when, being on board a steam-packet, and having looked for some length of time upon the waves which passed, I suddenly turned my eyes towards the deck of the vessel. If we suppose that in these cases spectra were left in the retina by the impressions of the waves, and that they disappeared in the order in which they arose, their successive disappearance while looking upon the fixed surface of the ground or deck would necessarily cause an apparent motion of this surface in the opposite direction.

The ocular spectra may be divided into three classes. They are either colourless spectra left by colourless images, or coloured spectra after colourless images, or coloured spectra after coloured images.

* Fechner's Repert. 2, 210.

*Colourless spectra left by colourless images of real objects.**—The spectra left by the images of white or luminous objects are ordinarily white or luminous; those left by dark objects are dark. Thus, the spectrum of a luminous body rapidly moved before the eyes is also luminous. If the eye, after being subjected to a vivid impression, be closed and turned away from the light, or, what is better, quite covered, white or luminous spectra of the objects which were white and luminous are seen, and dark or black spectra of those which were dark or black. Thus, if while sitting in our room we look for some time at the light window with its dark framework, and then suddenly close the eyes, turn them from the window and cover them with the hand, so that no light, not even that which would pass through the eye-lids, can reach the eye, bright spectra of the panes of the window, and a dark spectrum of the framework, are seen.

The relation of the light and dark parts in the image may, however, under certain circumstances, be reversed in the spectrum; what was bright may be dark, and what was dark may appear light. This occurs whenever the eye which is the seat of the spectrum of a luminous object is not closed, but fixed upon another bright or white surface, as a white wall or a sheet of white paper. Hence the spectrum of the sun, which, while light is excluded from the eye, is luminous, appears black or grey when the eye is directed upon a white surface. In the same way the spectra of the window-panes appear dark, those of the dark framework light, if we look with closed eyes towards the light of the window, so that the light passing through the eye-lids gently stimulates the retina. These phenomena are easily explained. The part of the retina which has received the luminous image remains for a certain period afterwards in an excited state, while that which has received a dark image is in an unexcited, and therefore much more excitable condition. If the eye in this condition be directed towards a white surface, the luminous rays from this surface produce upon the excited parts of the retina a much more feeble impression than upon the other parts which are as yet unexcited, and therefore more susceptible of their action. Hence the parts of the retina upon which the dark portions of the previous image had fallen receive a much more intense impression from the white surface than those upon which the luminous portions of the image were directed; and hence the inversion of the light and dark parts of the image in the spectrum thus seen.

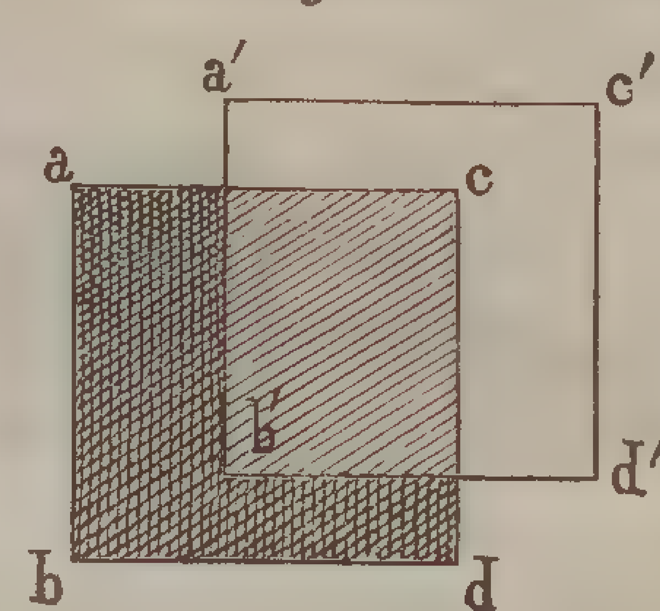
Similar phenomena are presented by the whole field of vision when a sudden change is made from light to darkness, and *vice versâ*. On coming from darkness into a bright light, every object appears exces-

* J. Müller, Physiologie des Gesichts-sinnes, p. 401.

sively bright, on account of the great susceptibility of the retina after its previous rest; and, on passing from light into moderate darkness, we at first see nothing, until the retina, exhausted by previous excitement, shall have recovered sufficient excitability to be acted on by the slight degree of light to which it is now submitted. A light object always appears brighter when viewed after a dark object, or even when viewed side by side with it. Similar phenomena are observed with relation to the other senses. Cold is felt most intensely when it follows the impression of heat, or warmth; and, after exposure to a great heat, a slightly different temperature, which under ordinary circumstances would feel warm, will produce the sensation of cold. The distinctions between light and darkness, heat and cold, are therefore merely relative.

Ocular spectra seem to change their place with relation to our body with every movement of the eyes, and, for an evident reason, are still seen, in whatever direction we may turn the retina. If we look for a long time at a black square upon a white ground, and then divert our eyes slightly, so as not entirely to leave the square, but rather to look more directly at its border, a portion of the spectrum which it has produced, *a′ c′ d′* (fig. 104), will appear free upon the white ground, as a bright margin to one part of the dark image *a, b, c, d;* while, to a certain extent, the true image and the spectrum will lie upon the same part of the retina, covering each other; another portion of the true image of the object (*a b d*) being left free. In such a case the free portion of the ocular spectrum (*a′ c′ d′*) appears very bright; the free portion of the true image (*a b d*) very dark; while the parts of the image and the spectrum which are coincident appear of a dark grey colour, as if the two conditions of black and light were there balancing each other. The explanation of the phenomenon is this:—The sensation of white in the part of the retina, *a′ c′ d′*, which was before the seat of the image of the black object, is more intense, because that part of the retina was previously unexcited; hence the bright margin *a′ c′ d′*. The part of the image where the true image and spectrum are coincident, remains unchanged. While the portion of the true image which is left free (*a b d*) appears blacker than before, because it now falls upon a part of the retina which had previously received rays from the white ground, and has consequently lost part of its excitability.

Fig. 104.



*Coloured spectra from the impression of colourless objects.**—If the impression of a luminous object on the retina be very intense, as when

* Goethe, Farbenlehre.

produced by the light of the sun's image, the spectrum consequent on it is not merely light when seen upon a dark ground, or dark when the eyes are directed upon a white surface, but assumes different colours in succession, which are expressions of the states which the retina passes through in its transition from the condition of dazzling to its natural state. The dark spectrum of the sun, when the eye is fixed upon a white surface, assumes different colours, from the dark to the light, in the following order:—black, blue, green, yellow, white. The appearance of these colours commences at the borders of the spectrum. When the spectrum has become white, it is no longer distinguishable from the white surface on which it is viewed; that is, the white surface produces now the same sensation in this part of the retina as in all the other parts which had not been submitted to the dazzling action of the sun. If the eye, after viewing the sun, be exposed to perfect darkness, that is, if light be entirely excluded from it, the colours of the spectrum will succeed each other in the inverse order, namely, from white through the lightest, and then the darker colours, to black; thus, in the order of white, yellow, orange, red, violet, blue, and black. When the spectrum has become black, it can no longer be distinguished from the surrounding darkness; the part of the retina which was its seat having regained the same unexcited condition as the other parts which were not acted on by the image of the sun.*

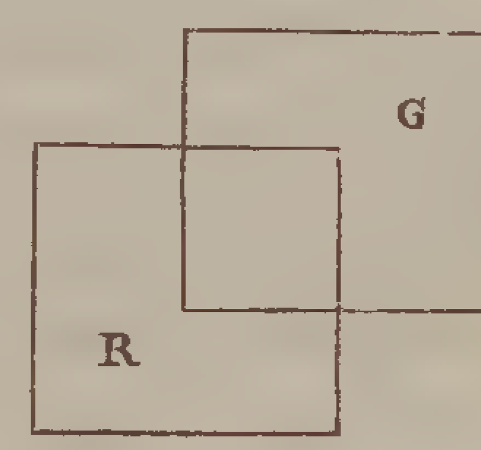
These phenomena, which cannot be explained by any external conditions acting on the eye, are another proof that colours have their immediate cause in the conditions of the retina itself.

Coloured spectra consequent on the impressions of coloured objects.—The ocular spectra which remain after the impression of coloured objects upon the retina are always coloured; and their colour is, not that of the object, or of the image produced directly by the object, but the opposite, or complementary colour. The spectrum of a red object is, therefore, green; that of a green object, red; that of violet, yellow; that of yellow, violet. The spectrum of a blue object is orange; that of an orange-coloured object, blue. The colours which thus reciprocally excite each other in the retina are those placed at opposite points of the circle in fig. 75, page 1103. If we fix our eye for any length of time upon a bright red spot on a white ground, and then suddenly turn it from the red spot and let it rest upon the white surface, we see an ocular spectrum of the red spot, of the same size and form, but of a green colour. If, on the contrary, we turn our eye only slightly to the side, so as to fix it upon the border of the red spot, the spectrum is seen partly covering the object, as in fig. 105. A portion of the true image of the object R appears free, and a portion also of the spectrum distinct from the true

* [Compare Sir D. Brewster's account of his experiments on this subject in his Treatise on Optics, p. 307.]

image; but this portion of the spectrum G is green. At the part where the true image of the object still falls upon the same part of the retina that is the seat of the affection producing the phenomenon of the spectrum, the colour of the object is seen, but it is faint and grey, because the retina is there rendered less susceptible of red, by the condition which causes it to have the sensation of green as an ocular spectrum, than at that part (R) of the true image of the object which now lies upon a part of the retina previously directed to the white surface. The mode of explaining these phenomena is twofold; the one theory is based on physical, the other on physiological principles.

Fig. 105.



1. The explanation on physical principles is this:—White light contains all the colours as its elements. The retina, when long fixed on a red object, is rendered insensible to the red light, but is still susceptible of the impression of the other coloured rays; if it be now directed towards a white surface, being no longer sensible to the red rays contained in the white light, it perceives only the remaining component rays of white light,—those which produce the colours complementary of red, namely, green.

2. The physiological explanation of the phenomenon is as follows:—The perception of any one of the three simple colours consists merely in the retina being in one of those conditions to which it has a tendency when in a state of excitement; if this condition be artificially excited in an intense degree, the retina acquires an extreme tendency to that of the complementary colour, which consequently is perceived as the ocular spectrum.

Either of these explanations is generally adequate to account for the phenomena; and the first, indeed, appears more definite and more probable, but there are facts at variance with it. For if the white light of the surface upon which the eye is directed be the source of the coloured spectrum, the complementary colour ought not to be seen when the eye is turned upon a black surface. But I have shown that the spectrum of any coloured object has the proper complementary colour even when the eye is directed upon a black surface, or into a perfectly dark cavity.*

All persons are not equally susceptible of the phenomena of the coloured spectra. Some individuals perceive them with difficulty, others without any trouble. When once seen, the observation is repeated with extreme ease. Most persons are little acquainted with the ocular spectra, owing to their attention not having been directed to them. When, however, they, and the laws of their production, are known, their

* Müller's Archiv. 1834, p. 144.

constant presence frequently becomes tormenting. Thus, the luminous borders which objects appear to have in twilight are owing to the ocular spectrum appearing at the one or other margin of the image in the retina; and the luminous appearance sometimes observed around objects, as flowers, in the faint light of evening, which by many persons has been regarded as something mysterious, is of the same nature. A devotee before an image may, in accordance with the laws of these phenomena, see a spectrum of the image whichever way he turns his eye.

3. *Of the reciprocal action of different parts of the retina on each other.*

Although each elementary part of the retina represents a distinct portion of the field of vision, yet the different elementary parts, or sensitive points, of that membrane have a certain influence on each other; the particular condition of one influencing that of another, so that the image perceived by one part is modified by the image depicted in the other part. A great number of phenomena, which have hitherto been regarded as different in their nature,—such as the vanishing of objects, the modification of their colour by that of the surface which surrounds them, the appearance of opposite colours under certain circumstances, the coloured shadows and the influence of light upon the sensation of the property of darkness in a neighbouring object, and *vice versâ*,—may be comprehended under one common head, as the result of this relation between the different parts of the retina. Such phenomena may, however, be arranged in two classes; the one including those where the condition existing in the greater extent of the retina is imparted to the remainder of that membrane; the other consisting of those cases in which the condition of the larger portion of the retina excites in the less extensive portion the opposite condition.

A. *Participation of different parts of the retina in each other's condition. "Irradiation of sensations."*—When two opposite impressions occur in contiguous parts of an image on the retina, the one impression is, under certain circumstances, modified by the other. If the impressions occupy each one-half of the image, this does not take place, for in that case their actions are equally balanced. But if one of the impressions occupies only a small part of the retina, and the other the greater part of its surface, the latter may, if long continued, extend its influence over the whole retina, so that the opposite less extensive impression is no longer perceived, and its place becomes occupied by the same sensation as the rest of the field of vision. The lateral parts of the retina, which do not lie in the axis of vision, are more prone to exhibit this phenomenon than the central part; but no portion of the membrane is entirely insusceptible of it. The point of entrance of the optic nerve is the spot where it is most readily produced.

Vanishing of images at parts of the retina not corresponding to the entrance *of the optic nerve.*—If we fix the eye for some time, until it is fatigued, upon a strip of coloured paper lying upon a white surface, the image of the coloured object will in a short time disappear, and the white surface will be seen in its place. This experiment succeeds most easily when the image of the coloured paper falls on the lateral parts of the retina; but the central part of that membrane is also capable of presenting the phenomenon. Purkinje [and Dr. Brewster*] have described these phenomena. They prove that the different parts of the retina, after being subjected to long-continued impressions, mutually participate in each other's condition, and that they are, in a limited degree, capable of exciting their own sensations in surrounding parts. Coloured images upon a white ground are best adapted for showing these phenomena; a small black spot upon a white ground disappears with difficulty, and very slowly, on account of the sensation excited by an impression being more vivid when it forms a contrast with surrounding impressions. The disappearance of images from this cause is only of a few seconds' duration; they then reappear.†

Vanishing of images which fall on the point of entrance of the optic nerve.—The disappearance of images at this part of the retina has been long known, having been discovered by Mariotte. If we direct one eye, the other being closed, upon a point at such distance to the side of any object that the image of the latter must fall upon the retina at the point of entrance of the optic nerve, this image is lost either instantaneously or very soon. If, for example, we close the left eye, and direct the axis of the right eye steadily towards the circular spot here represented, while the page is held at the distance of about five inches from the eye, the

cross will vanish, and the colour of the paper will be seen in its place. The distance of the object from the eye must be about five times as great as its distance from the point on which the eye is fixed. We can satisfy ourselves that this phenomenon arises from the image falling on the point of entrance of the optic nerve, by fixing the same eye upon the cross instead of upon the round dot; the latter object then does not disappear, or only after long persistence of the impression.

* [Journal of Science, vol. iii. p. 289.]

† [May not these phenomena be explained on the supposition that feeble impressions on the retina are inadequate to excite the sensorium to a sustained action? The appearance of the colour of the surrounding surface in the part of the field of vision corresponding to the point of the retina in which, for the moment, no sensation is perceived, may be due to an action of the mind of which we are unconscious. At all events, the analogous phenomenon of the alternate vanishing and reappearance of ocular spectra (see page 1180) can scarcely be attributed to the extension of the state of one part of the retina to another. On the contrary, it would seem more probable that the condition of the retina on which the ocular spectrum depends is persistent, and that the cause of the occasional disappearance of the image has its seat in the sensorium.]

The phenomenon here described has led to the erroneous conclusion that the part of the retina at which the optic nerve enters is insensible to light, while in fact it is sensible, but the impression which it perceives is that which affects directly the rest of the retina, or the more contiguous parts of that membrane. It differs from the rest of the retina only in possessing, in a higher degree, the property of participating in the condition of surrounding parts.*

The facts which we have been considering prove that the elementary parts of the retina are, in a certain measure, capable of a reciprocal action on each other; but the mode of this reciprocal action, or mutual reaction, may be very different from that hitherto described, as we shall now proceed to show.

B. *Excitement of opposite conditions in contiguous parts of the retina.*— In the phenomena hitherto described, the prevailing condition, or sensation of the retina, extends to parts of that membrane which are differently affected. In the phenomena now to be considered, the affection of one part of the retina influences that of another part not in such a manner as to obliterate it, but so as to cause it to become the contrast or opposite of itself. The former phenomena ensue gradually, and only after the images have been long fixed on the retina; the latter are instantaneous in their production, and are permanent.

Impressions of light and darkness rendered more intense by contrast.— A grey spot upon a white ground appears darker than the same tint of grey would do, if it alone occupied the whole field of vision. Every shadow is rendered deeper when the light which gives rise to it becomes more intense, owing to the greater contrast. The following instance may serve as an example of many such phenomena:—Let the light of a single candle fall upon a sheet of white paper, and the paper will appear white. Now, place a second candle at some distance from the paper, and between them some body, which shall throw a shadow upon the paper; this shadow will appear grey, although the part of the paper on which it falls will still receive the same quantity of light from the first candle as before made it appear white. The cause of the difference is the contrast with the other part of the paper, which now receives light from two candles. For the same reason, a shadow upon a white surface appears much less dark when viewed through a tube, so that

* [Not only will a black spot disappear from a white surface, but a white spot upon a black surface will also become invisible, when it falls upon the base of the optic nerve. In the latter instance, according to the author's theory, the condition of repose of the retina generally extends to the part excited by the rays from the white object, and renders their impression null. This is directly contrary to what occurs in the case of the "radiation" of sensations in the nerves of common sensibility; there, an excited state of one or more nervous fibres extends to others previously in an unexcited condition.]

the surrounding white surface does not produce an impression on the retina at the same time.*

Physiological colours produced by contrast.—A very small dull-grey strip of paper, lying upon an extensive surface of any bright colour, does not appear grey, but has a faint tint of the colour which is the contrast of that of the surrounding surface. Thus, for example:—A strip of grey paper upon a green field often appears to have a tint of red, and when lying upon a red surface, a greenish tint; an orange-coloured tint upon a bright blue surface, and a bluish tint upon an orange-coloured surface; a yellowish colour upon a bright violet, and a violet tint upon a bright yellow surface. For the production of this phenomenon it is necessary that the colour of the extended surface should be very bright, containing abundant rays of white light. Every coloured paper is not adapted for it. It is shown most distinctly by holding a coloured glass covered with thin paper before a lamp, and covering any spot on the glass and paper with a strip of a grey colour. The strip of paper is then readily seen to have the colour which is the contrast to that of the glass. The colours which are thus developed physiologically by contrast, are the complementary colours shown at the opposite points of the circle in fig. 75, at page 1103. The new colour is always that which, combined with the colour of the surrounding surface, would yield the sum of the three simple prismatic colours, red, yellow, and blue. The colour excited by the impression of yellow is, for example, violet, which contains blue and red.

The colour excited thus, as a contrast to the exciting colour, being wholly independent of any rays of the corresponding colour acting from without upon the retina, must arise as an opposite or antagonistic condition of that membrane; and the opposite conditions of which the retina thus becomes the subject would seem to balance each other by their reciprocal reaction. We have also in these phenomena a fresh proof that colours, physiologically considered, are merely certain states of the retina, which are capable of exciting each other reciprocally in different parts of that membrane. A necessary condition for the production of the contrasted colours is, that the part of the retina in which the new colour is to be excited shall be in a state of relative repose; hence the small object itself must be grey. A second condition is, that the colour of the surrounding surface shall be very bright, that is, it shall contain much white light.

Several other phenomena observed by Smith, Sir D. Brewster, and myself, seem to be also of this nature.†

* Tourtual has described many other phenomena of this nature in his tract, Über die Erscheinung des Schattens. Berlin, 1830.

† See an account of these phenomena in Müller's Archiv. 1834, pp. 144, 145; [and Sir D. Brewster in the Philos. Mag. Ser. iii. vol. ii.]

Coloured shadows. — The coloured shadows sometimes observed are phenomena belonging to the same category. But all coloured shadows are not of this nature; some are owing solely to the shadow being illuminated by a coloured light.

a. Coloured shadows dependent on a physical cause.—If a coloured light fall upon a shadow produced by colourless light, or by light of a different colour, the shadow of course appears coloured. In the faint light of evening, the shadows of bodies appear by candle-light blue or yellow, according as the bluish light of the sky or the yellow light of the candle falls upon them. The two kinds of light may produce two shadows of different colours from one body. Of two shadows thus produced by a small rod upon a sheet of white paper, the one which cannot receive any of the bluish light of the sky, but receives light from the candle, will appear yellow; while the other shadow, which receives no light from the candle, but is illuminated by the bluish light of the sky, appears blue. All other parts of the paper present no predominant colour, since they receive rays from both kinds of light. The purely physical nature of these coloured shadows was pointed out by Pohlmann.*

b. Coloured shadows dependent on a physiological cause. — If light transmitted through coloured glass, or reflected from a coloured body fall upon a white surface, and a shadow be produced upon this surface, which now appears coloured, by means of a narrow body raised upon it, this shadow, when illuminated by the white light of day, will appear of the colour which is complementary of that of the surrounding surface. The experiment succeeds also if the shadow be illuminated by the light of a candle. The illumination of the shadow by white light is a necessary condition for the production of the phenomenon. For, as Grotthuss has shown, if coloured light be thrown into a cavity otherwise perfectly dark, a shadow there produced does not appear coloured. Some of the earlier hypotheses offered in explanation of this phenomenon may be wholly passed over. It can only be referred either to a physical action of the coloured and white lights reciprocally on each other, or to the physiological principle of contrast.

Von Münchow has proposed an explanation of the former kind. His view is founded on the assumption, that coloured light has the property of rendering inert those rays of white light, traversing the space occupied by it, which are analogous to its own rays, and of transmitting only the rays of the colour complementary of itself.† According to this hypothesis of Von Münchow, white light traversing a space occupied by blue light would lose the blue rays which it contains, and would be transmitted with merely the remaining complementary orange. To prove that two

* Poggendorf's Ann. 37. 319.

† See Pohlmann, loc. cit. p. 323.

bodies of light, meeting from different directions, may exert an influence on each other, Von Münchow adduces the experiment of Frauenhofer, which showed that one ray of light can divert another from its course. Pohlmann, however, controverts the hypothesis of Von Münchow by the following experiment:—Coloured light was thrown by means of a plate of coloured glass upon a white surface within the cavity of a box, a shadow being produced on the white surface by a strip of some substance placed upon the glass. Instead, however, of illuminating the shadow by allowing the light of day to fall freely upon the white surface, he directed it by means of a tube, the lower end of which passed into the shadow, upon the shaded part only of the surface. But even here coloured light might certainly be reflected from the walls of the box so as to occupy the space of the shadow, and exert the influence which Von Münchow imagines it does, upon the white light.

The coloured shadows are usually ascribed to the physiological influence of contrast; the complementary colour presented by the shadow being regarded as the effect of internal causes acting on that part of the retina, and not of the impression of coloured rays from without. This explanation is the one adopted by Rumford, Goethe, Grotthuss, Brandes, Tourtual, Pohlmann, and most authors who have studied the subject.

An argument in favour of this view is the fact observed by Count Rumford, that the colour of the shadow does not appear different from that of an ordinary colourless shadow, when it is viewed through a tube in such a manner that the coloured ground is not seen at the same time.

Great probability is also conferred on this explanation of the phenomena by their analogy with the facts previously spoken of, those in which a small grey strip upon a surface of a bright colour appears of the opposite complementary colour. In the case of the coloured shadows, the experiment is complicated with many deceptive circumstances; but in that of the experiment just alluded to the phenomenon is reduced to its simplest conditions.

C. *Pleasing effect of the physiological contrasts of colours; physiological basis of the harmony of colours.**—The phenomena described in the foregoing pages prove clearly that the action of one colour upon the retina disturbs the equilibrium of its condition, exciting in it one predominant state; and that a tendency exists in it to the developement of the opposite state complementary of the one thus excited. We cannot, there-

* Goethe, Farbenlehre. [See, also, a memoir on colours, and a new chromatic scale, by M. Nobili, translated in Taylor's Scientific Memoirs, vol. i. from the Bibliothèque Univ. des Sciences, Genev. 1830; vol. ii. p. 337; vol. iii. p. 35.]

fore, be surprised at finding that the combinations of colours producing a pleasing and salutary impression both upon the eye and upon the mind, are those which contain the colours thus opposed to, or complementary of, each other. All complementary colours have an agreeable effect; and all bright colours which are not complementary a disagreeable one, if they predominate. In this sense the complementary colours may also be styled harmonic, and those which are not complementary of each other disharmonic. A combination of complementary colours is an harmonic combination; all other combinations of colours are disharmonic, in proportion as they belong to one simple prismatic colour, and are at the same time very bright. A predominant flaming red is as unpleasant as a predominant glaring yellow, or a uniform predominant blue. Hence we are accustomed to mingle white or grey with these colours, when it is requisite to employ them alone over any extent of surface, so as to soften them and render them more supportable. But the purest red is pleasing when associated with its complementary colour green; blue when combined with orange or gold; yellow when combined with violet. In figure 75, page 1103, the complementary or harmonic colours are placed at opposite points of the circle, and we see at once what mixture of colours will harmonize with another mixture previously determined. Women of good taste, when they have a single predominant colour in their dress, select a dull one; or, if they wear the pure colours, combine those which harmonize from being complementary of each other; for instance, they wear a red shawl over a green dress; combine lilac with yellow, or blue with orange. How beautiful and pleasing to the eye is the combination of a golden orange colour with blue; for instance, of an orange fringe with blue drapery! while the dress of a female, in which pure yellow were combined with red, or yellow with blue, or blue with red, would by every person be regarded as hideous and out of taste. Such striking combinations of disharmonic colours are chosen only for national signs and for the dress of soldiers.

Combinations of two of the simple colours, the third which would render them complementary being deficient, are the most offensive to the eye; for instance, combinations of yellow and red, blue and red, or yellow and blue. In these combinations there is complete disharmony; while, in the association of two colours of which one forms the transition to the other, there is neither harmony nor disharmony,—such colours are indifferent to each other,—as, yellow to green, red to orange, or violet to blue. The disharmony between two colours may, however, be removed by the interposition of a third colour, which is the harmonic of one of them, and is indifferent with relation to the other. We have examples of this in such combinations as red, green, and yellow; yellow, violet, and red; blue, orange, and red; or red, green, and blue, &c. The disharmony between red and yellow is removed by the presence between them of green, which is the harmonic of red, and is indifferent with regard to yellow.

Painters either intentionally, or without being aware of it, make constant application of these physiological principles; and the pleasing effect of the colours in a picture depends on the skilful combination of harmonic colours, and the prevention or solution of the disharmonies. The application of this principle is often carried so far as the imitation of the coloured shadows. By employing principally the dull grey colours the danger of disharmonies is avoided, but the whole charm arising from the harmonic combinations of colours is at the same time renounced.*

4. *Of the simultaneous action of the two eyes.*

The simultaneous action of the two eyes in vision gives rise to the phenomena of single vision by the two organs under certain conditions, of double vision under other conditions, and of the contention for predominance between the fields of vision perceived by the two retinæ.

Of single vision with the two eyes.†—The phenomenon of single vision, resulting from the simultaneous action of two organs of vision, has by some physiologists, as M. Gall, been thought to be most easily explained by supposing that we do not really employ both eyes simultaneously in vision, but always see with one only at a time. This especial employment of one eye in vision certainly occurs in persons whose eyes are of very unequal focal distance, but in the majority of individuals both eyes are simultaneously in action in the perception of the same object; of this it is easy to convince oneself by the observation of the double images seen under certain conditions. If two fingers be held up before the eyes, one in front of the other, and vision be directed to the more distant, so that it is seen singly, the nearer will appear double; while, if the nearer one be regarded more particularly, so as to appear single, the more distant will be seen double; and one of the double images in each case will be found to belong to one eye, the other to the other eye.

Single vision results only when certain parts of the two retinæ are affected simultaneously; if different parts of the retinæ receive the image of the object, it is seen double. We have, therefore, first to learn by experiment which are the parts of the retina in the two eyes which correspond to each other in the property of referring the images which affect them simultaneously, to the same spot in the field of vision. The knowledge of these parts, which for the sake of brevity may be

* This subject has been fully treated of by Runge in his work, Über die Farben, from which the materials for the above sketch have been chiefly derived.

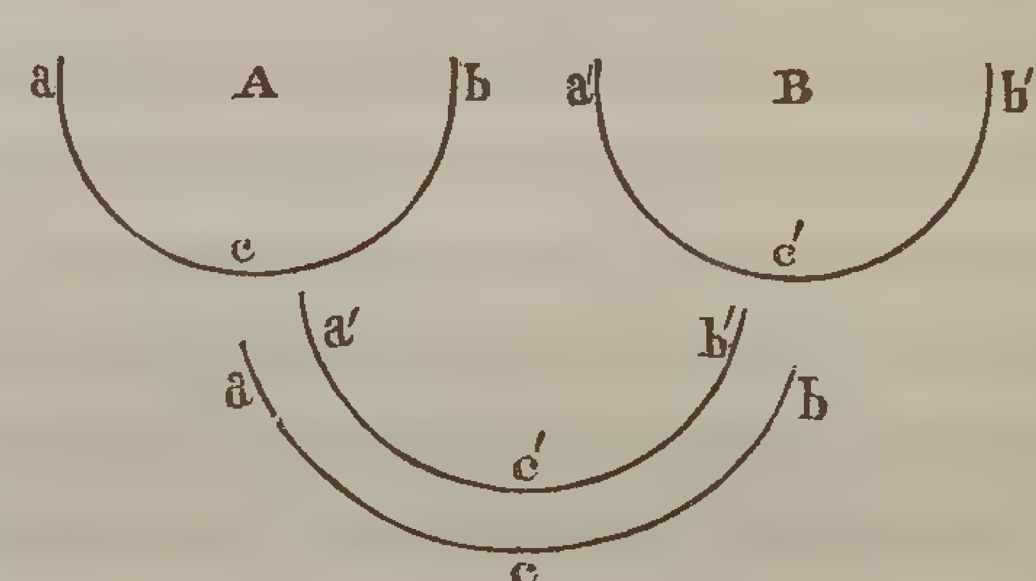
† J. Müller, Physiologie des Gesichts-sinnes; Leipz. 1826; p. 71.

termed the identical parts of the retina, is obtained in the following manner :—

If while in a dark room, our eyes being closed, we press with the finger upon any part of the ball of the eye, so as to affect the retina, a luminous circle is seen in the field of vision, and, for reasons stated at page 1172, at the opposite side of the field of vision to that on which the pressure is made. If we exert pressure with the finger at the upper part of one eye, and at the lower part of the other eye, two luminous circles are seen, one above the other; the upper circle resulting from the pressure made at the lower part of the one eye, the lower from the pressure made at the upper part of the other eye. These points in the retinæ of the two eyes are therefore certainly not identical; for affections of them are referred to perfectly different parts of the field of vision.

If pressure be made upon the outer part of both eyes, two figures are again seen, of which the one belonging to each eye is on the opposite side in the field of vision. If pressure be made on the inner side of each eye, two luminous circles are produced, but they lie at the extreme limits of the field of vision; the one on the right side belongs to the right eye, that on the left side to the left eye. It is certain, therefore, that neither the upper part of one retina and the lower part of the other are identical, nor the outer lateral parts of the two retinæ, nor their inner lateral portions. But the outer lateral portion of one eye is identical with the inner portion of the other eye; or *a* of the eye A (fig. 106) with *a'*, of the eye B. The upper part of one retina is identical with the upper part of the other; and the lower parts of the two eyes are identical with each other. If, for example, pressure be made with the fingers upon both eyes simultaneously at their lower part, while they are closed and no light is shining upon them, one luminous ring is seen at the middle of the upper part of the field of vision; if the pressure be applied to the upper part of both eyes, a single luminous circle is seen in the middle of the field of vision below. So also if we press upon the outer side *a* of the eye A, and upon the inner side *a'* of the eye B, or, what is the same thing, upon the left side of both eyes, a single spectrum is produced, and is apparent at the extreme right of the field of vision. Or if the point *b* of one eye, and the point *b'* of the other, receive the pressure, that is, the right side of both eyes, a single spectrum is again seen, namely, to the extreme left. In short, we may regard the spheres of the two retinæ as lying one over the other, as in the

Fig. 106.



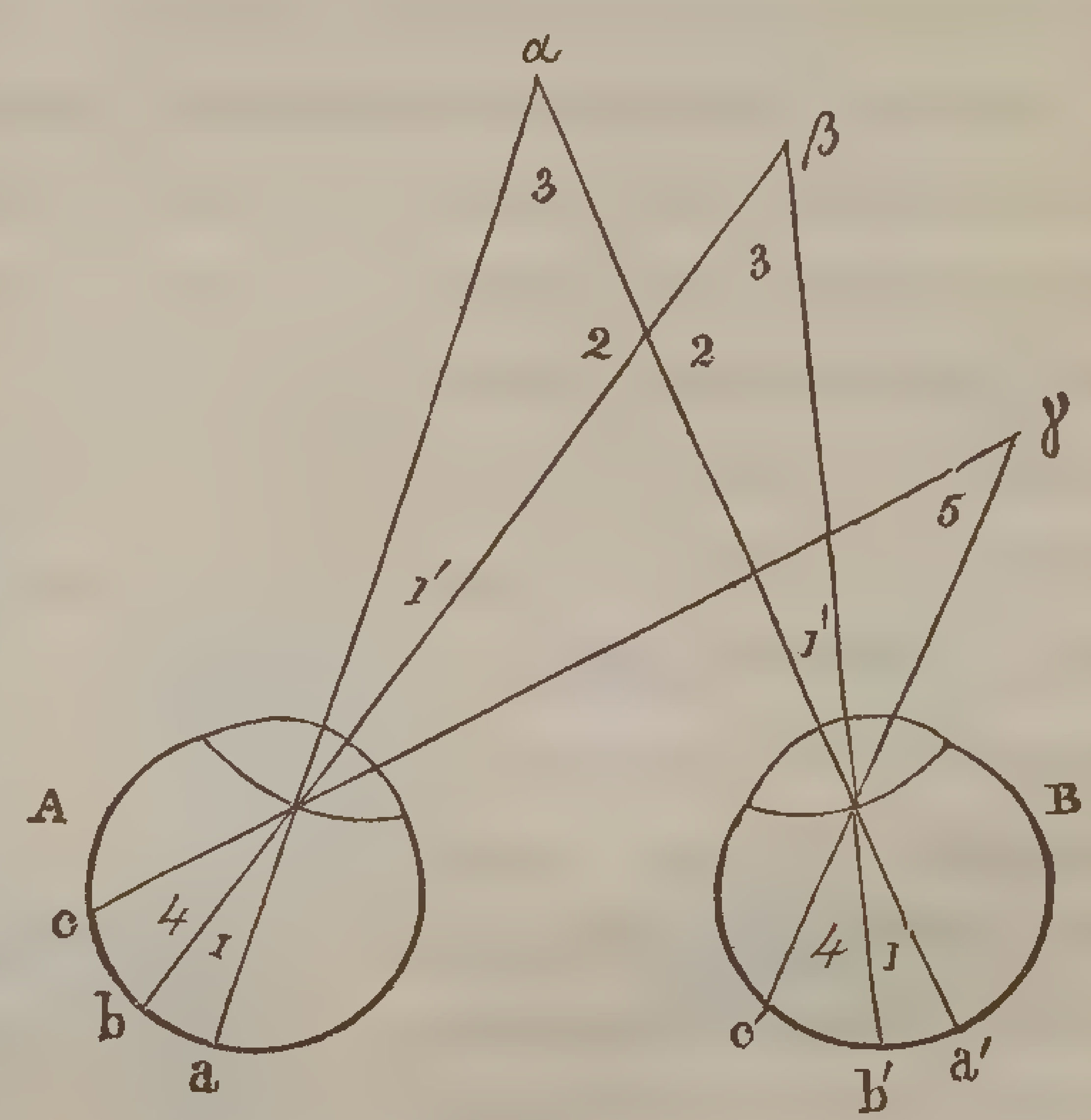
lower figure; so that the left portion of one eye lies over the identical left portion of the other eye, the right portion of one eye over the right portion of the other eye with which it is identical; and so with the upper and lower portions of the two eyes, a lies over a', b over b', and c over c'.

The points of the one retina intermediate between a and c, are again identical with the correspondent points of the other retina between a' and c'; those between b and c of the one retina, with those between b' and c' of the other. For if pressure commencing at identical points of the two eyes—for instance, on the left side of each,—be carried simultaneously upwards towards the upper part of each eye, the spectrum will remain single, and the pressure may in this way be made to travel in the complete circle in each eye, and still but one spectrum be seen. But, as soon as the finger in either eye is made to press upon a spot not identical with the point compressed in the other, double spectra immediately appear.

This experiment leads at once to the conviction that parts of the retinæ which correspond exactly in situation, are also completely identical in sensation. Parts of the retina which lie in the same segments of the sphere, in the same meridian and the same parallel of latitude, the middle point of the retina being regarded as the pole,—or which lie at equal distances in the same direction from the centre of the retina,—are completely identical. All other parts of the retinæ are non-identical; and, when they are excited to action, the effect is the same as if the impressions were made on different parts of the same retina; and the double images belonging to the eyes A and B, are seen at exactly the same distance from each other as exists between the image of the eye A, and the part of the retina of the eye A which corresponds to or is identical with the seat of the second image in the eye B; or, to return to the figure already used in illustration (fig. 106), if a of one eye be affected, and b' of the other, the distance of the two spectra a and b' will, inasmuch as a is identical with a', and b with b', lie at exactly the same distance from each other as spectra produced by impressions on the points a, b of the one eye, or a', b' of the other.

The application of these results to the phenomena of vision produced by external objects is self-evident. If the position of the eyes with regard to a luminous object be such that similar images of the same object fall on identical parts of the two retinæ, the object cannot be seen otherwise than single; but in any other case two images must be seen. That position of the eyes with regard to an object by which identical parts of the retinæ receive an image of the object, is attained when the axes of the eyes meet in some one point of the object, as always happens when vision is directed particularly to the object.

Fig. 107.



If the axes of the eyes, A and B (fig. 107), be so directed that they meet at α, an object at α will be seen singly at the same spot in the middle of the field of vision, for the point a of the one retina, and a' of the other, are identical. But other objects, also, which lie to the side of α,—for example, β and γ,—may also appear single. If the object β be so situated that its image falls in both eyes at the same distance from the central point of the retina, — namely, at b in the one eye, and at b' in the other,—the image of β affecting identical parts of the retina will be seen single. In the same way, the object γ will be seen single if the distance of the point of the retina c from the point a in the eye A, be the same as that of the point c' from the point a' in the eye B.

A straight line, or plane, passing through the point of convergence of the axes of the eyes, or the point towards which the eyes are directed, was called by the older philosophers the "horopter;" and it was imagined that even the lateral objects situated in this horopter were seen single. On closer inquiry, however, it is found, that the horopter can neither be a straight line nor a plane, but must have a circular or spherical form.* The problem to be determined is this:—If the points a, b, c of the one eye be identical with the points a', b', c' of the other eye, and, consequently, the angles 1 and 4 of the one eye equal to the angles 1 and 4 of the other eye, can the points α, β, γ lie in a straight line, or in what form of line must they lie?

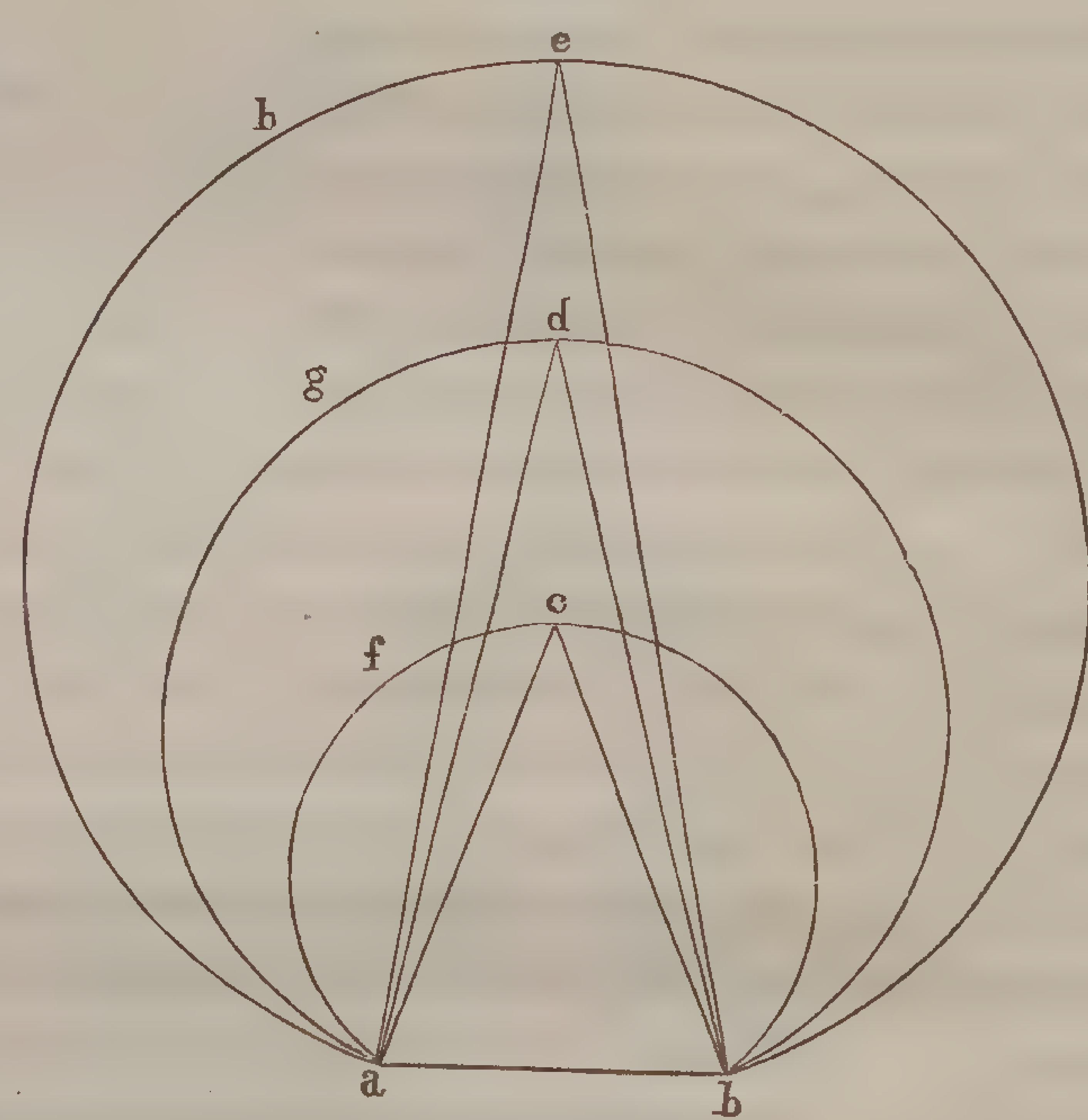
a, b being equal to a' b', and the angle 1 in the eye A equal to the angle 1 in the eye B, the angles 1′ and 1′ will be equal. And since the angles 2 and 2 are equal, the angles 3 and 3 must also be equal. In the same way it may be shown that the angle at γ,—namely, the angle 5, is equal to the angle 3. For $b\ c = b'\,c'$, $\angle\ 4 = \angle\ 4$. It being shown that the angles 3, 3, and 5 are equal, it follows that α, β, γ cannot lie in a straight line, for it is the property of a circle exclusively

* I demonstrated this in my work, Über die Physiologie des Gesichts-sinnes. Many physiologists have ascribed to me the discovery of the true form of the horopter, and I also imagined for a long time that I had first taken the above view of the matter; but in Gehler's Physik. Wörterb. iv. 2, Leipz. 1828, p. 1472, I see that Vieth had already shown, (Gilbert's Annalen, 58, 233,) that the horopter must be a circle.

that triangles erected upon the same chord, and reaching to the periphery, have at the periphery equal angles.

The horopter is therefore always a circle, of which the chord is formed by the distance between the eyes, or, more correctly, between the points of decussation of the rays of light in the eyes, and of which the size is determined by three points,—namely, by the two eyes, and the point towards which their axes converge. If *a*, *b*, fig. 108, be the distance of the eyes from each other, the circle *f* is the horopter for the object *c*, the circle *g* that for the object *d*, and the circle *h* that for the object *e*.

Fig. 108.



The cause of the impressions on identical points of the two retinæ giving rise to but one sensation, and the perception of a single image, must lie in the organization of the deeper or cerebral portion of the visual apparatus; it must at all events depend on some structural provision; for it is the property of the corresponding nerves of the two sides of the body in no other case to refer their sensations as one to one spot. It is exceedingly improbable that the identical action of the corresponding parts of the two retinæ is the result of a certain habituation, or of the influence of the mind. The co-operation of the two retinæ in one field of vision, whatever is its cause, must rather be the source of all the ideas to which single or double vision may give rise.

It has been urged as an objection to the constant identity in sensation of the corresponding points of the retinæ of the right and left eyes, that double vision sometimes occurs in syncope, intoxication, and nervous affections, where, nevertheless, the harmony of the movement of the eyes, it is asserted, is not lost. (Treviranus.) If double vision necessarily occurs where the axes of the two eyes do not meet in the object, or where this does not lie in the horopter, there are no conditions of which it should be a more natural and inevitable consequence than syncope, intoxication, and nervous febrile affections. The statement of Treviranus, Steinbuch, and of others before them, that the identity of the fields of vision of the two retinæ is acquired, and that though, at the commencement of squinting, objects are seen double, yet afterwards a new relation of identity, different from the former one, and according with the degree of distortion of the eyes, is established between the two retinæ, is also erroneous. Strabismus is a relative term. The position of our eyes required for the convergence of their axes towards a very near object is squinting, as compared with their position in looking at a distant object. In cases where the eyes have an unnatural direction inwards, objects situated in the horopter of this position of the eyes ought to be seen single, and it is not easy to conceive for what distance the new identity of the retinæ should be adapted, since the eye which is not affected with the strabismus can accommodate itself to all distances. Moreover, observations made upon persons affected with strabismus do not show that the original relation of the identical parts of the two retinæ is disturbed; but that the squinting eye in general does not co-operate in vision.* A presbyopic, or myopic state of the eye, is very often combined with strabismus. The squinting eye, in that case, being adjusted to a very different distance, its field of vision does not at all, or very slightly only, interfere with the impressions of the field of vision of the other eye. Thus even in looking with one eye into the microscope, while the other is directed upon the table at the side, the field of vision of the latter eye, though occupying the same place as that of the other, disturbs but little its perceptions; because the accommodation of the one eye for the perception of the image in the microscope induces a similar adjustment of the other, in consequence of which the table which occupies its field of vision is only indistinctly seen. In a person affected with strabismus, whom I examined recently, I found that under the ordinary conditions for the production of double vision (see page 1201), when one eye is directed so as to have a distinct perception of either of two objects held at different distances from the eyes, no second image of the other object is seen. He distinguishes objects with one eye only, therefore, though both are open.

The accordance of the identical points of the two retinæ is, therefore, an innate property, and never undergoes any change. The eyes may be compared to two branches with a single root, of which every minute portion bifurcates so as to send a twig to each eye.

Many attempts have been made to explain this remarkable relation between the eyes.

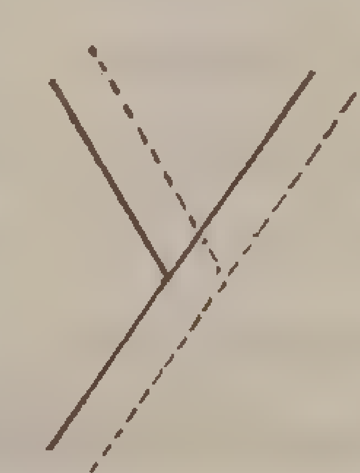
1. The circumstance of the inner portion of the fibres of the two optic nerves decussating at the commissure, and passing to the eye of the opposite side, while the outer portion of the fibres continue their course to the eye of the same side, so that the left side of both retinæ is formed from

* With reference to the causes of strabismus, see my work, Physiol. d. Gesichtssinnes; Priestley, History of Light and Colours; and I. N. Fischer, Theorie des Schielens veranlasst durch einen Aufsatz des Gr. Buffon. Ingolstadt, 1781.

one root of the nerves, and the right side of both retinæ from the other root, naturally led to an attempt to explain the phenomenon of single vision by this distribution of the fibres of the nerves. Such was the theory of Sir I. Newton* and Dr. Wollaston.† Dr. Wollaston applied this theory to the explanation of the cases which sometimes occur, in which the entire of one side of the retina, as far as the central point in both eyes, becomes insensible; supposing that in such cases the cerebral portion of one optic nerve is paralyzed.‡

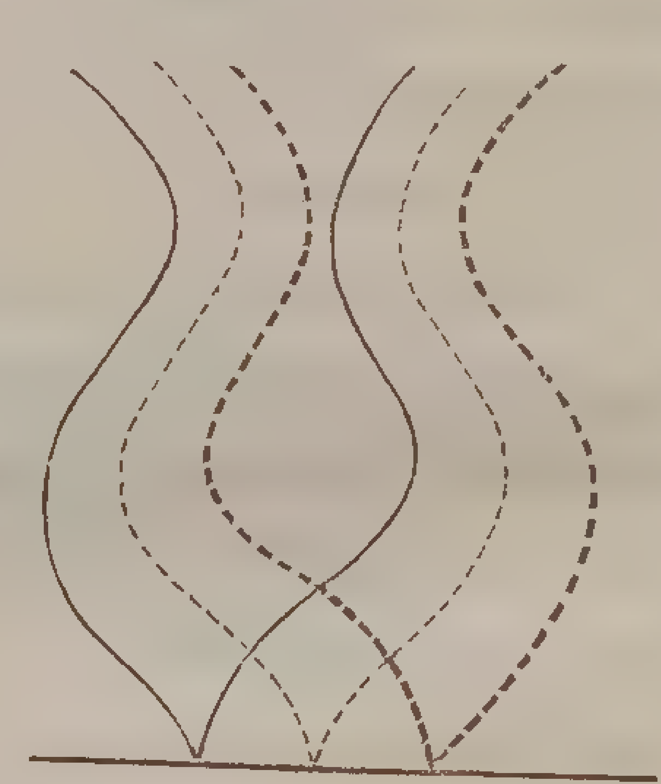
2. I have elsewhere shown that this theory is inadequate to explain the phenomenon, unless it be supposed that each fibre in each cerebral portion of the optic nerves divides in the chiasma into two branches for the identical points of the two retina, as is shown in the figure (fig. 109). A theory based on the structural relations of the fibres of the nerves might alone be sufficient to explain the phenomena; but such a theory is susceptible of several modifications. The idea of each fibre of the nerves dividing in the chiasma may possibly have occurred to Newton. Treviranus and Volkmann were, however, unable to detect any division of fibres in the chiasma, and I also was unsuccessful in my search for such dividing fibres. Moreover, if this theory were correct, the cerebral portions of the optic nerves ought to have only half the thickness of the ocular portions of the nerves. We must, therefore, remain satisfied with the simple fact, long known, that the cerebral portion of each optic nerve divides at the chiasma into two parts, of which the inner decussates with that of the opposite nerve, while the outer part continues its course to the eye of the same side.§

Fig. 109.



3. A third theory is that of Rohault,|| who, assuming it as a fact that each optic nerve contains exactly the same number of fibres as the other, supposes that the correspondent fibres of the two nerves are united in the sensorium (as in fig. 110). In this theory no account is taken of the partial decussation of the fibres of the nerves in the chiasma.

Fig. 110.



4. A modification, or amendment, of the two preceding theories would be the following, in which regard is paid also to the structure of

* Optics, Quer. 112. † Philos. Trans. 1824. Ann. de Chim. Phys. 1824. Sept.

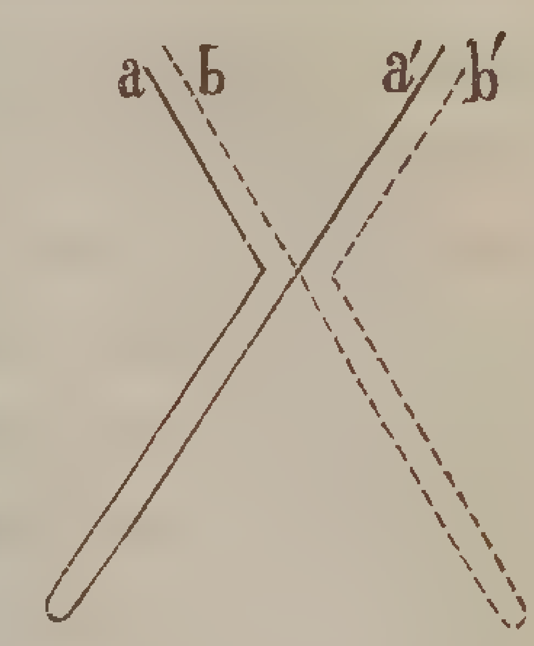
‡ For an account of cases of visus dimidiatus, see Vater, Oculi vitia duo rarissima, visus duplicatus et dimidiatus. Viteb. 1723. 4. recus. in Hall Diss. Med. Pract. t. i. and Ann. de Chim. Phys. 1824. Sept.

§ See the representations of this structure in my work on the sense of vision, already referred to. The partial decussation is most distinct in the horse.

|| Physic. p. i. cap. 31.

the chiasma:—The fibres *a* and *a′*, coming from identical points of the two retinæ, are in the chiasma brought into one optic nerve, and in the brain either are united by a loop, or spring from the same point of the sensorium, or the same ganglionic corpuscule in the cerebral substance. The same disposition prevails in the case of the identical fibres *b* and *b′*. According to this theory, the left half of each retina would be represented in the left hemisphere of the brain, and the right half of each retina in the right hemisphere.

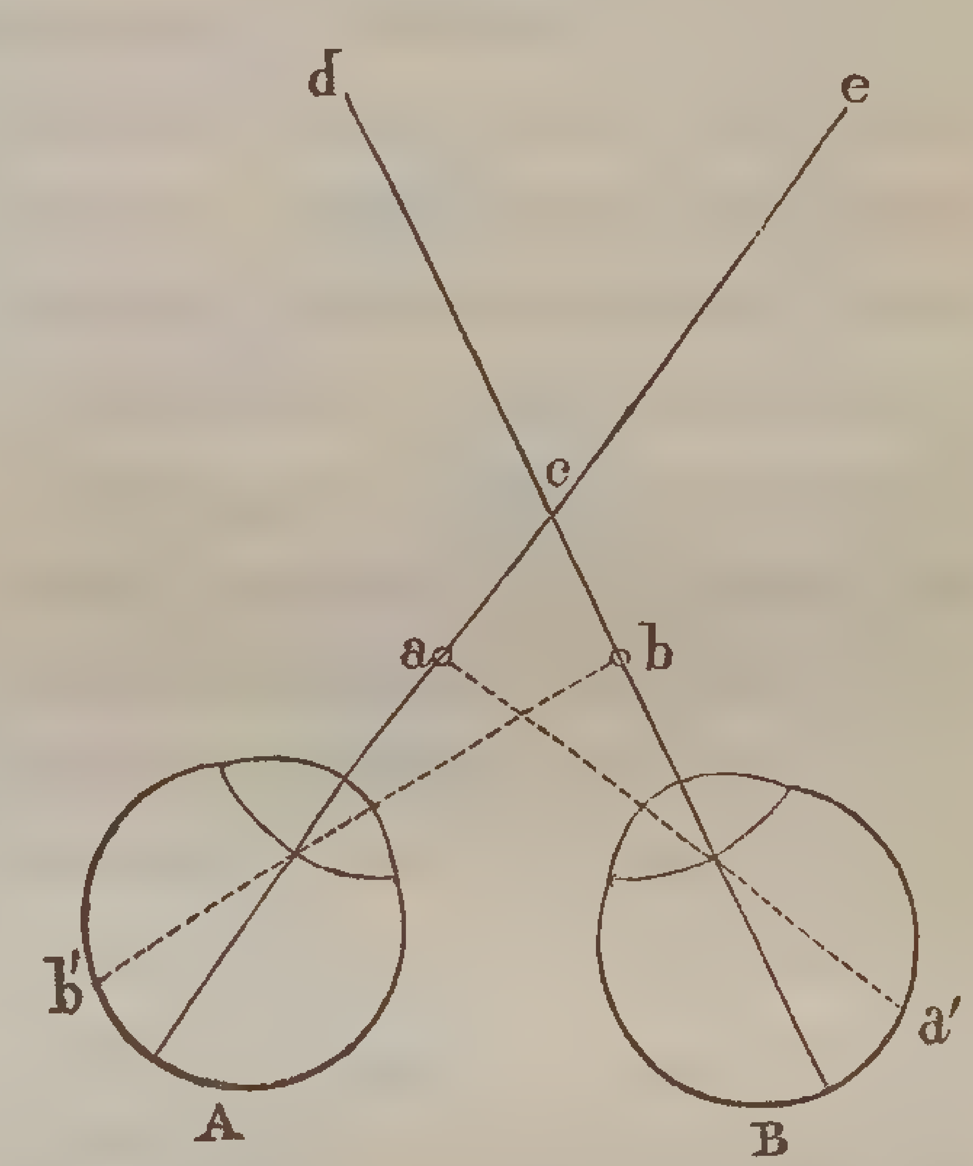
Fig. 111.



5. A fifth theory yet might be adopted; it might, namely, be supposed that a commissural union exists in the middle line in the brain between the identical fibres of the two retinæ.

Porterfield* maintains, that the true cause of our not seeing two images of objects viewed with both eyes, is to be found in the faculty we enjoy of seeing the objects in their real situation. But this view is not founded on correct principles, and may be easily refuted. For if the object *c*, which lies in the direction of the axes of the eyes A and B (fig. 112), be seen singly by these eyes merely because they see it in its proper place, the objects *a* and *b* ought to be seen separately by the two eyes for the same reason; but these objects, *a* and *b*, while the position of the axes of the eyes remains as represented in the figure, are not seen separately, but as one in the same spot of the field of vision as *c*, owing to their image falling in both eyes on the same central point of the retina. A double image of *a* is seen, it is true, by the eye B, namely by the point of the retina *a′* and a double image of *b* by the point of the retina *b′* of the eye A; but the images of the points *a* and *b*, which fall upon the centre of the retinæ of either eye, are not seen as if in the really separate situations of the objects but as one object, in one spot of the field of vision. We cannot, indeed, correctly say that we see the object *c* single, because we see it where it actually is. The seeing an object in its real place can merely be the seeing it in the direction in which it lies with regard to the eye. The object *c*, however, is seen by the eye A in the direction *c*, *e*; by the eye B in the direction *c*, *d*: it

Fig. 112.



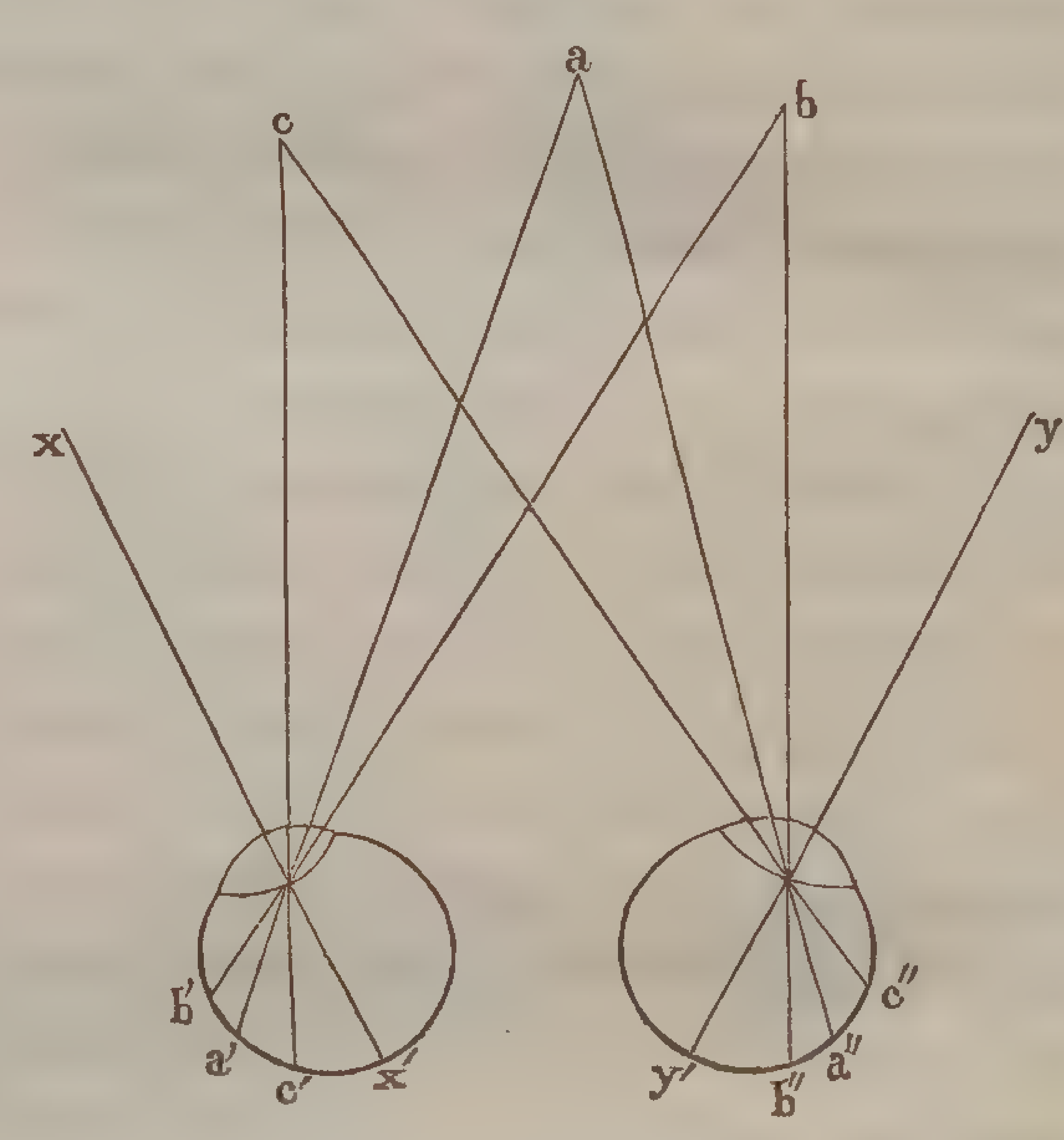
* Op. cit. ii. p. 293.

should, therefore, be seen double according to this theory, while, for reasons already explained, it really appears single.

The cause of the single sensation excited by impressions on identical points of the two retinæ must, therefore, be some organic or structural provision. There are many theories involving the supposition of such a structure, which would account for the phenomena; but not one of these theories can be proved to be the correct one, and, with regard to several of them, it can be shown that they are certainly erroneous. The sort of theory which the facts require is, however, sufficiently evident from the examples given above. [The remarkable phenomena of binocular vision observed by Mr. Wheatstone, (see page 1205,) prove, however, that the impressions on the two retinæ are communicated separately to the sensorium, and are combined to one perception by an action of the mind alone,—not by any organic union of fibres.]

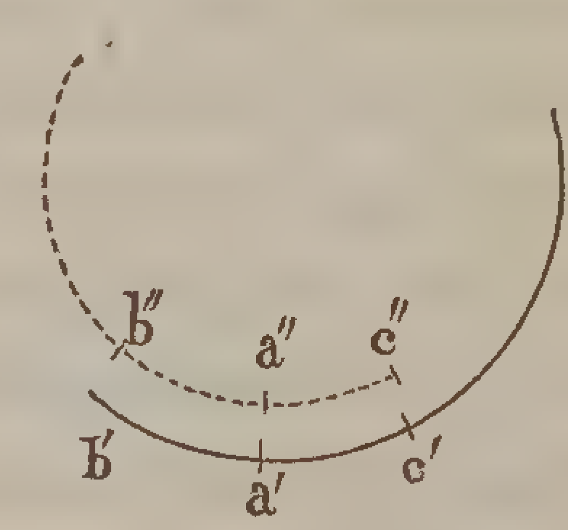
In quadrupeds the relation between the identical and non-identical parts of the retinæ cannot be the same as in man; for the axes of their eyes generally diverge, and can never be made to meet in one point of an object. When an animal regards an object situated directly in front of it, the image of the object must fall in both eyes in the outer portion of the retina. Thus the image of the object *a* (fig. 113) will fall at *a′* in one eye, and at *a″* in the other; and these points, *a′* and *a″*, must be identical; in fact, a dog alters the directions of his eyes according to the distance of the object situated in the direction of his body, just as we do. But the visual axes are not in the dog identical with the axes of the eye-balls; the visual axes in the dog are not the lines *y y′* and *x x′*, but the lines *a a′*, and *a a″*. For distinct and single vision of objects, *b* or *c*, lying in front of the animal, and visible to both eyes, it is necessary again that the points *b′* and *b″*, or *c′* and *c″*, in the two retinæ, on which the images of these objects fall, should be identical. All points of the retina in each eye which receive rays of light from lateral objects only, can have no correspondent identical points in the retina of the other eye; for otherwise two objects, one situated to the right and the other to the left, would appear to lie in the same spot of the field of vision. It is probable, therefore, that there are in the eyes of animals parts of the retina

Fig. 113.



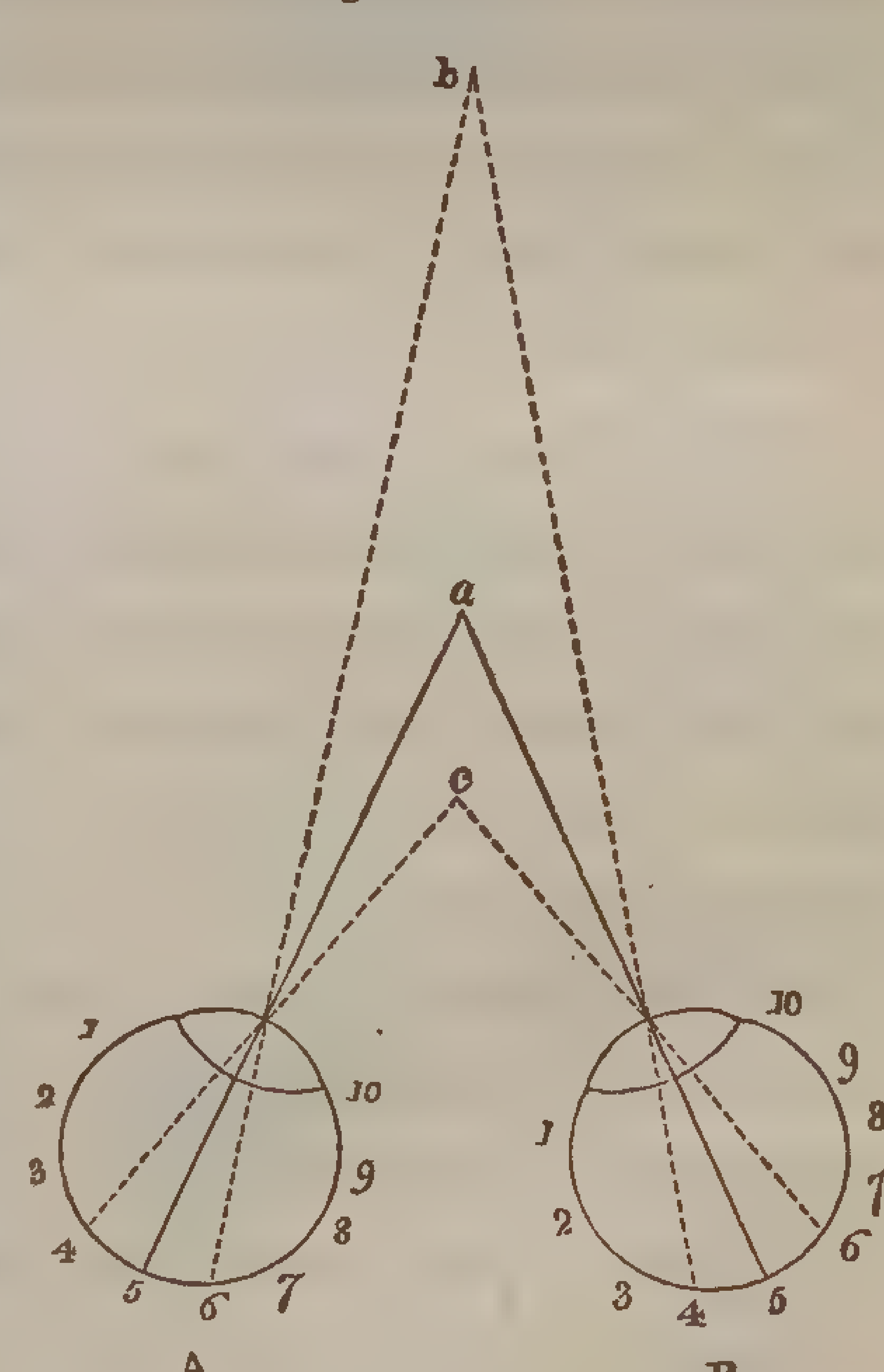
which are identical, and parts which are not identical,—which have no corresponding parts in the other eye. And the relation of the two retinæ to each other in the field of vision may be represented as in fig. 114.

Fig. 114.



*Of double vision.**—Whenever an object lies out of the "horopter" (see page 1195), its image falls on non-identical points of the retinæ, and it is seen double. The double images always lie at a determinate distance from each other; thus, if the image fall in one eye upon the point 6, in the other upon the point 4, the point 6 of the one retina being identical with the point 6 of the other retina, the distance of the two images from each other will be equal to the distance of 4 from 6,—that is to say, the space between the two images, as compared with the extent of the whole field of vision, will be the same as the distance between 4 and 6 in comparison with the diameter of the whole surface of one retina. The simplest experiment for the observation of double images is the following:—Two fingers are held in a straight line before the eyes; one close in front of them, the other at a distance from them. If we look at the first, directing the axes of the eyes towards it, the second is seen double; if we direct our eyes towards the more distant, the nearer finger appears double. The greater the distance between the fingers, the farther do the images of the one seen double appear removed from each other; the nearer the fingers are brought to each other, the more closely do the double images approximate, until at length, when both fingers come within the same horopter, they coalesce.

Fig. 115.

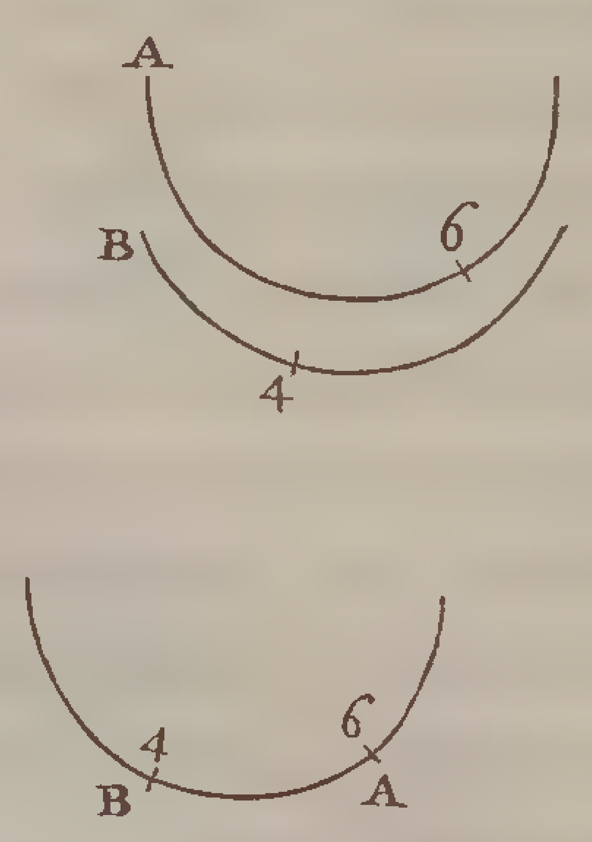


To illustrate this, let a (fig. 115) be a point towards which the axes of the eyes are directed, and b an object more distant from the eyes. An image of a will fall upon identical points of the two retinæ,—namely, upon the central points 5, 5; a will consequently be seen single. The image of b will fall in the left eye at 6, and in the right eye at 4. The points 4 and 6 of the two eyes being non-identical, since the identical point of one eye corresponding to the point 4 of the other is 4, b will be seen double, and the distance between the two images of b in proportion to the extent of the whole field of vision will be the same as that between 4 and 6, in comparison with the

* J. Müller, Physiol. des Gesichts-sinnes, p. 167.

distance between 1 and 10 in each retina. This relation of the double images with regard to each other will be still more evident if the surfaces of the two retinæ be imagined laid one over the other, as in fig. 116, where A is the retina of the left eye, B that of the right eye of the preceding figure; 4 the situation of the image of *b* in the right eye, and 6 that of its image in the left eye. Since the sentient surfaces represented in this figure are essentially identical, the lower figure may be substituted for it; with reference to which it is to be remarked that the image at 6 belongs to the left eye; that at 4 to the right eye.

Fig. 116.



If *c*, in fig. 115, be an object nearer the eyes than the point *a*, towards which their axes are directed, it also is seen double. For an image of *c* will fall in the left eye at 4, in the right eye at 6, points of the retinæ which are not identical; and the distance separating the two images from each other will be the distance 4—5 in the left eye, added to the distance 5—6 in the right eye; or, both eyes being regarded as one, their distance will be that between 4 and 6,—that is to say, the distance between the two images of *c* will bear the same relation to the whole field of vision, as the distance between 4 and 6 to the whole extent of the retina 1—10.

With regard to the position of the double images in relation to the eye to which they respectively belong, it is to be remarked that, when the axes of the eyes decussate at a point nearer than the object, the left-hand image seen in the field of vision belongs to the left eye, and the right-hand image to the right eye. If, on the contrary, the axes of the eyes meet or decussate at a point more distant than the object, the image seen by the right eye lies at the opposite, or left side, of the field of vision; that seen by the left eye, at the right side; as is easily ascertained by closing either eye.

This relative position of the images is important in a theoretical point of view. The position of the images in relation to the eyes, which we have just described, appears, at first sight, to be most easily explicable by the theory that we see objects in the direction in which they really lie, and not according to the position of the parts of the retina affected by their images. Thus, when the axes of the eyes decussate at *a* (fig. 115), the more distant object, *b*, is seen double; and the image seen by the left eye should, according to the diagram, appear to the left of the axis of that eye, *a* 5, the image seen by the right eye to the right of the axis *a* 5 of that eye; and so it is found to be by experiment. The phenomena of double vision might, therefore, be adduced as proof of the inverted position of images on the retina being corrected either by the projection of the images in lines of visible direction, or by a particular course of the fibres of the optic nerves in the brain. The phenomena are, however, explicable by the opposite theory; according to which, the images, or parts of the retina affected by them, are seen in their real position in the retina itself, and are not projected towards the exterior, and seen in the place of the objects.

In the experiment already described, the left of the double images of the object is seen on the left of the middle axis of vision; the object, therefore, according to optical principles, lies to the right. In the perceptions of the retinæ, no distinction of right and left eye exists; they are identical; but, inasmuch as rays of light are reflected by our own body upon the retina, an image of it is formed there, and, according to optical principles, its different parts are situated on the opposite side to that on which they are seen in the image; the apparent right side of the body therefore is really the left, and the apparent left properly the right. Hence the fact observed in the above experiment, that, when an object is seen double in consequence of the axes of the eyes converging towards a point nearer than it, the left image disappears on the left eye being closed, may also be expressed thus:—If we close the eye of the apparent left, but true right side, the left image of the object disappears; and this is confirmed, indeed, by the construction of the foregoing figures, for the image of *b* lies in the retina of the true right eye B to the left side,—namely, at 4.

The experiments which we have described in illustration of double vision may be varied in many ways; but all the variations are dependent on the same fundamental condition,—namely, that the image of the object falls on non-identical parts of the two retinæ.

Thus, if the axes of the eyes are directed, as in figure 117, towards *a*, all other points lying in the line *a, b, c* appear double, because their

Fig. 117.

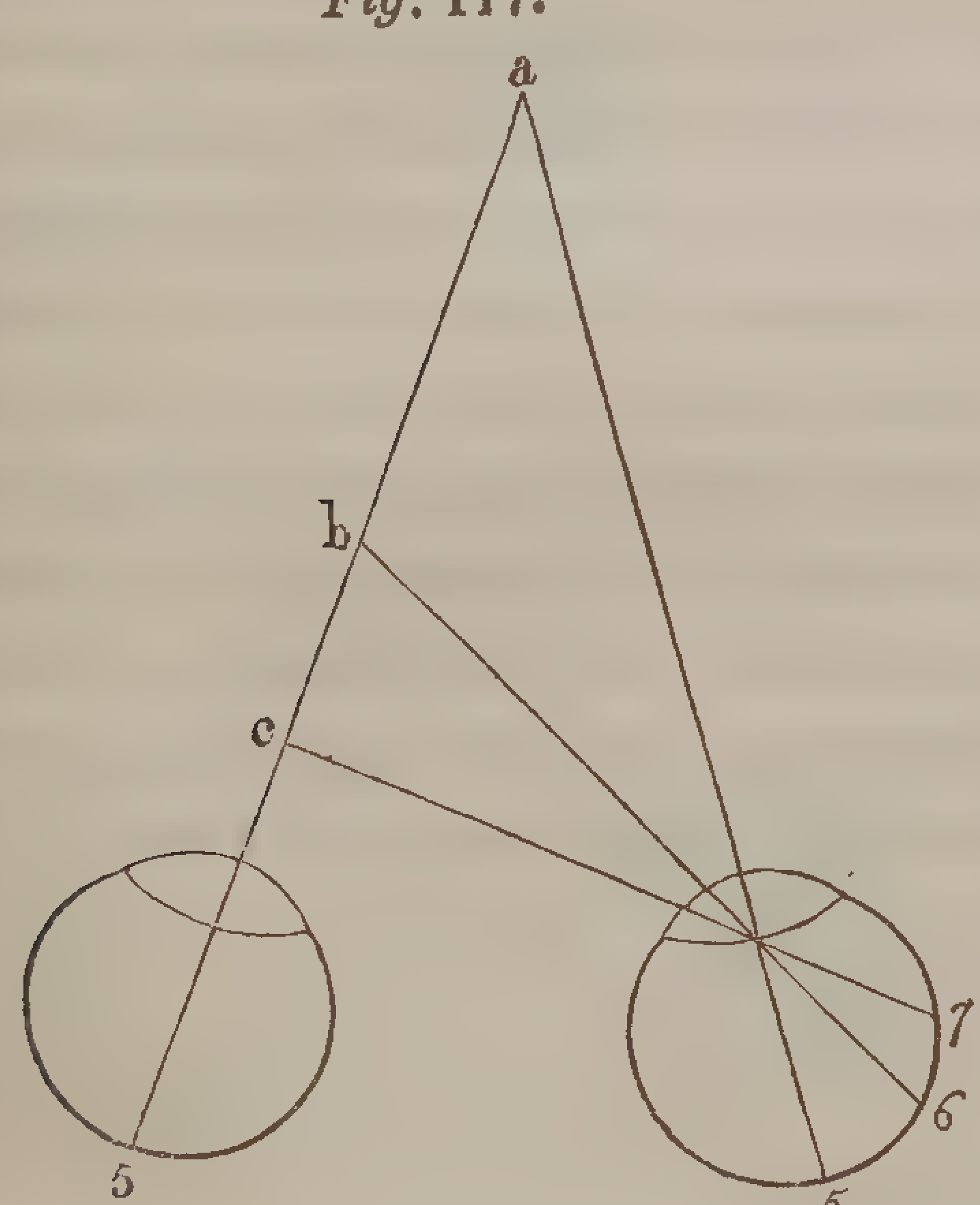
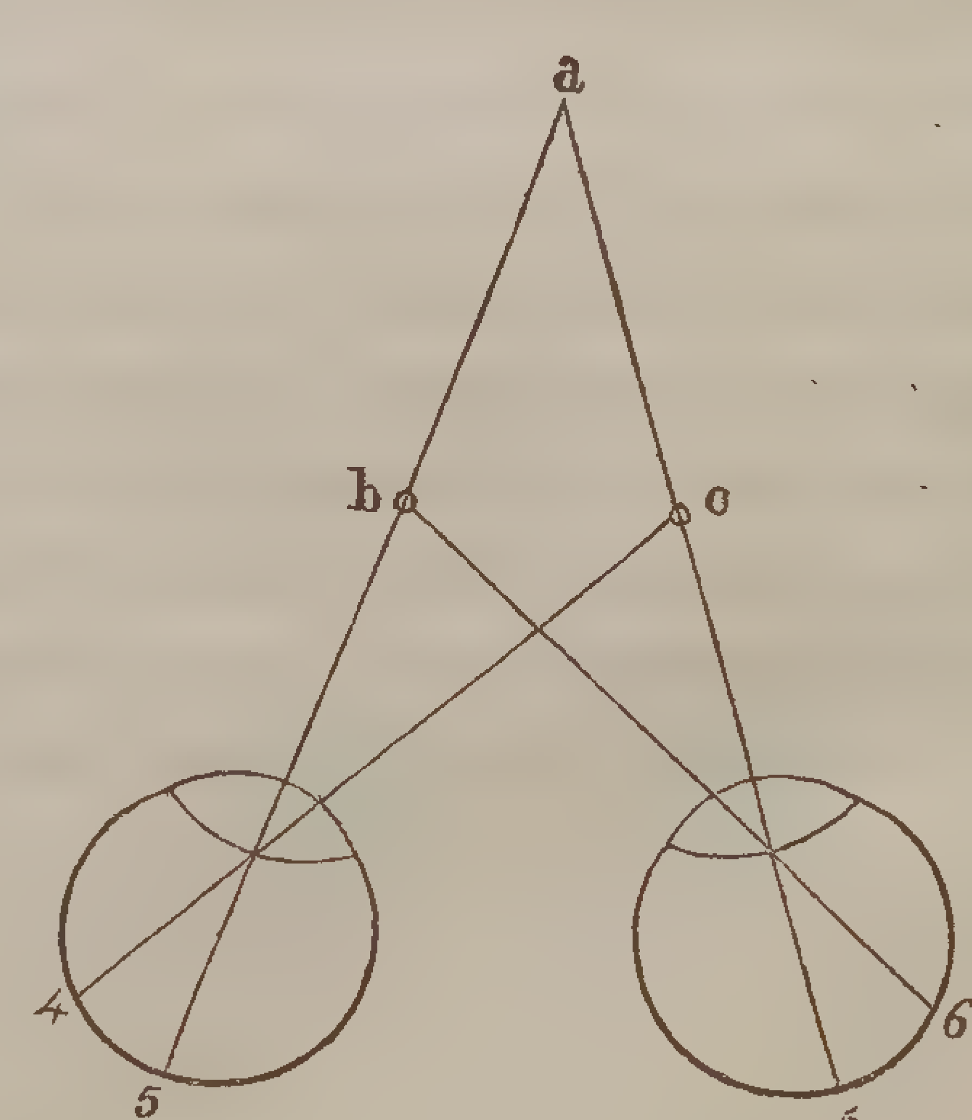


Fig. 118.



images fall in the one eye upon the central point of the retina 5, but in the other eye at different points, 6, 7, 8, 9, &c.

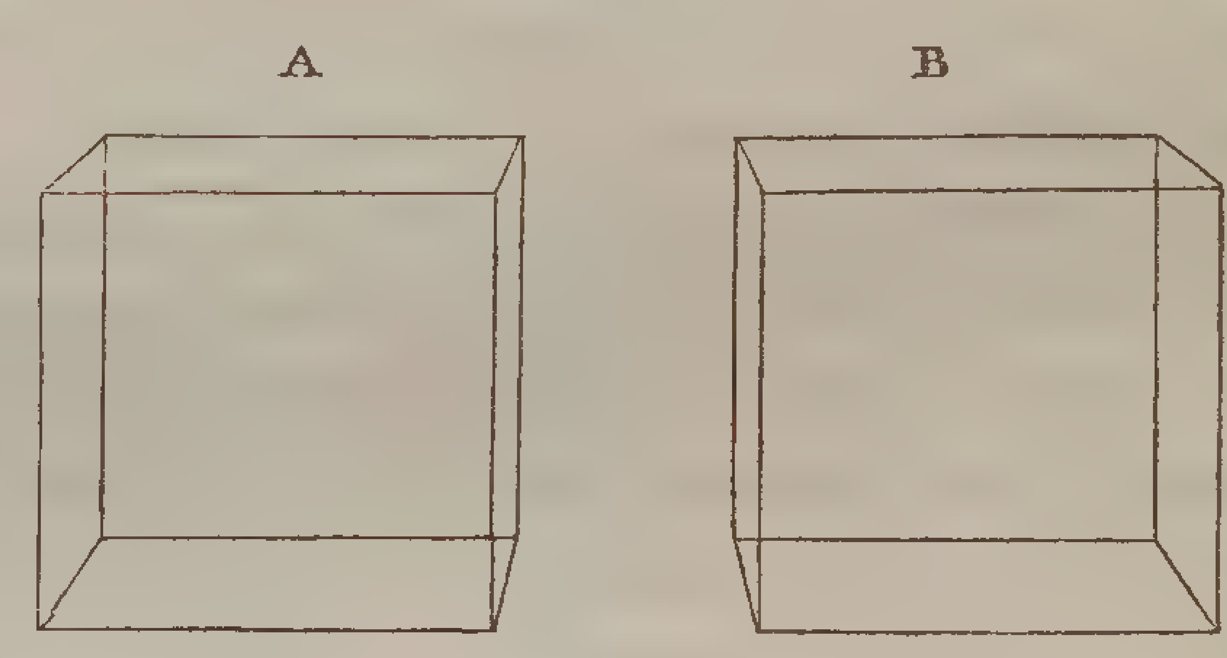
Or again, if, while the eyes are directed, as before, towards *a*, (fig. 118,) two needles are held at the points *b* and *c* in the lines of the axes of the eyes, then in place of two images of *b*, and two images of *c*, or four images, three only will be seen; for the image of the needle *b* will fall in the left eye at 5, that of the needle *c* in the right eye at 5; and, since the points 5 and 5 of the two eyes are identical, these two images will be seen in one point of the field of vision as one. An image of *c* will also fall upon the point 4 of the left retina, and one of the needle *b* at the point 6 of the right retina, which are non-identical points; three needles, consequently, are seen in the order, and at the distance from each other, corresponding with the points 4, 5, and 6 of either retina.

The indistinctness of double images of objects is a necessary consequence of facts with which we have already become acquainted, for they generally fall upon the lateral parts of the retinæ; and, even when one lies in the axis of the eye by which it is seen, the proper adjustment of the refractive power of the eye is wanting, since, as we have shown, the adaptation of the refractive power for distinct vision varies in direct accordance with the horopter in which the axes of the eyes decussate.

The phenomena of double vision are so necessary a result of the organization of the eyes, and are so intimately connected with the conditions on which single vision depends, that they must present themselves constantly during the ordinary employment of the eyes. Such, indeed, is the case: but commonly we do not pay attention to them; partly because the images of objects seen double are indistinct, and partly because our eyes are usually directed towards an object in such a way that it is seen single. In all cases, however, where two objects situated at different distances, and not lying in the same horopter, are seen simultaneously, one or other of them must necessarily appear double. Thus, when we look through a window upon a church steeple, either the window-frame or the steeple must appear double, according as the axes of the eyes are directed to the one or the other. Whenever the power of directing the axes of the eyes so as to meet in the object is lost from any cause, double vision must result; hence its occurrence in persons intoxicated, in nervous fevers, in the paroxysms of nervous or hysterical affections, in the state immediately preceding sleep, and in strabismus. This double vision is in no way dependent on any change in the central parts of the nervous system, or in the retina; but is the simple result of the inability to direct both eyes to the object. In the state preceding sleep, and at the moment of falling asleep, our eyes are always rotated strongly inwards; hence at those times all objects—even near objects—appear double. The too great convergence of the eyes can be recognised in the position of the double images; the left-hand image is found to belong to the left eye. In the state of intoxication, also, the eyes are directed inwards.

[Some important circumstances relative to binocular vision have been pointed out by Professor Wheatstone.* It can scarcely have escaped observation, that, when an object is placed so near the eyes that to view it the optic axes must converge, a different perspective projection of it is seen by each eye, these perspectives being more dissimilar as the convergence of the optic axes becomes greater. Thus, if any figure of three dimensions, an outline cube for example, be held at a moderate distance before the eyes, and viewed with each eye successively, while the head is kept perfectly steady, A (fig. 119) will be the picture presented to the right eye, and B that seen by the left eye. The importance of this circumstance in vision, however, has hitherto been disregarded by all writers on optics. Mr. Wheatstone has shown that on it depends in a great measure our conviction of the solidity of an object, or of its projection in relief. If different perspective drawings of a solid body, one representing the image seen by the right eye, the other that seen by the left, (for example the drawings of a cube A, B, fig. 119,) be presented to corresponding parts of the two retinæ, the mind will perceive not merely a single representation of the object, but a body projecting in relief, the exact counterpart of that from which the drawings were made. The two pictures may be made to fall on corresponding parts of the retinæ, by placing them one in the direction of each optic axis, at equal distances before or behind their intersection, (for example, at *d*, *e*, fig. 112; or *b*, *c*, fig. 118.) But a better method is, to employ the stereoscope, an instrument invented for the purpose by Mr. Wheatstone, the essential parts of which are two plane mirrors inclined with their backs towards each other, at an angle of 90°. The two pictures, A and B, are placed in the same horizontal line, and parallel to each other, at the sides of these mirrors, and at equal distances from them. The observer then, placing his eyes as near as possible to the two mirrors, their angle coinciding with the middle line of his forehead and face, sees the solid body, represented by the perspective drawings, standing forward in relief, provided the two drawings are so situated that their images reflected by the mirrors coincide with the lines of the convergent optic axes. As the drawings are reversed by reflection in the mirrors, the perspective of the object as seen by the right eye must be presented to the left-hand mirror, and *vice versâ*.

Fig. 119.



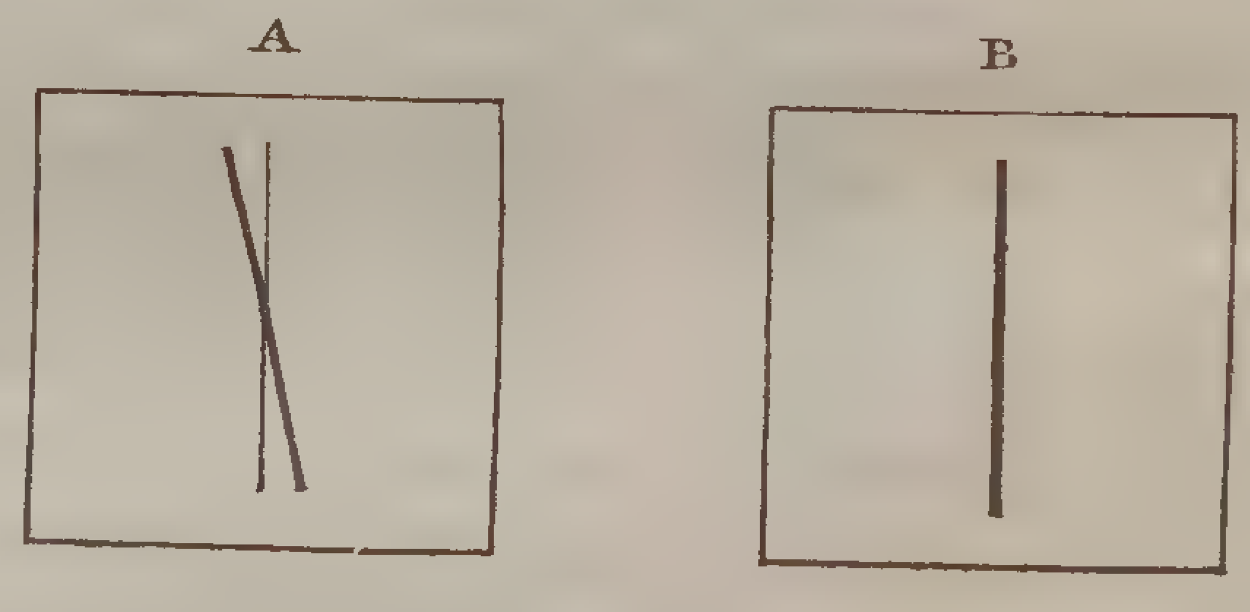
* Philos. Transactions, 1838, pt. ii. p. 371.

Mr. Wheatstone shows also by means of the stereoscope that similar images, differing to a certain extent in magnitude, when presented to the corresponding parts of the two retinæ, give rise to the perception of a single object, intermediate in size between the two monocular pictures. Were it not for this, objects would appear single only when the optic axes converge directly forwards, that is to say, when the object is equally distant from the two eyes; for it is only then that the images on the retinæ can be of equal size; the size of the image being dependent on the angle under which the object is seen, and this being less as the object is more distant. Thus, if a piece of money be held to the right side of the field of vision, and the optic axes made to converge to a somewhat nearer point, it will appear double, and the image seen by the left eye will be evidently smaller than that seen by the right.

If pictures of dissimilar objects are presented to the eyes simultaneously, phenomena are observed analogous to those perceived when different colours fall upon corresponding parts of the two retinæ; the two images do not coalesce, nor do they appear permanently superposed on each other, but at one time one image, at another time the other, will be seen, and, at the moment of change, fragments of the two intermingled will be visible. It does not appear to be in the power of the will, Mr. Wheatstone observes, to determine the appearance of either; but, if one picture be more illuminated than the other, that which is less so will appear during a shorter time.

The fact that two different perspective projections of an object, when they harmonize in suggesting to the mind the same idea, coalesce into one image, is sufficient proof of the incorrectness of the hypothesis that objects can be seen single only when their images fall on identical points of the two retinæ.* The following experiment, adduced by Mr. Wheatstone, shows that, under some conditions, similar pictures falling on corresponding points of the retinæ may appear double, and in different places; and, consequently, that there is no necessary physiological connection between the corresponding points of the two retinæ:—If to one eye we present in the stereoscope a vertical line B, (fig. 119,) tothe other eye a line inclined some degrees from the perpen-

Fig. 120.



[* But though it is not necessary that *exactly identical points* of the retinæ should be affected by *similar points of the two images*, yet the object will not in general be seen single, unless its images fall on *corresponding parts* of the retinæ, as is proved by the experiment of displacing the axis of one eye by pressing on it with the finger, when objects are seen double.]

dicular, we shall see a line, the extremities of which appear at different distances before the eyes. If now we draw a faint vertical line, intersecting the inclined line at its centre, as at A, and present the two drawings to the eyes as before, the two strong lines will still coincide, and the resultant perspective line will occupy the same place; while the faint line, though it occupies the same part of the retina as the vertical line B, appears in a different place, namely, at the intersection of the planes of visual direction of the two eyes. Here it is evidently an action of the mind, employing the impressions on the retinæ merely as suggestions for its judgment, which determines the image perceived, and the idea conceived. The influence of the mind on the perceptions of vision is evident even when one eye only is used. Thus, if we look with a single eye at the drawing of a solid geometrical figure, (as the cube A or B, fig. 119,) it may be imagined to be the representation of either of two dissimilar solid figures, the figure intended to be represented, or its converse figure, (which, in the case of the cube, is the frustum of a pyramid with its base remote from the eye.) If the former is a very usual, and the latter a very unusual figure, the imagination will fix on the original without wandering to the converse figure: but if both are of ordinary occurrence, which is generally the case with regard to simple forms, the original figure will be perceived distinctly at one time, and at another time the converse; and, while one continues, it is not in the power of the will to change it immediately. The apparent conversion of a cameo, or bas-relief, such as that of a piece of money, into an intaglio, and of an intaglio into a cameo, when viewed with a single eye, especially through a microscope, is a well-known instance of this indetermination of judgment, and is an illustration of the aid we derive in estimating the forms of solid objects from a different projection of them being presented to the two eyes.*]

* [The assertion of Gassendus, Haller, Gall, and others, that we see with only one eye at a time, though both remain open, is refuted, as Mr. Wheatstone observes, by the fact that in many cases (those where the optic axes converge to view a solid object) the simultaneous affection of the two retinæ excites a different idea in the mind to that consequent on either of the single impressions; the latter giving rise to the idea of a representation on a plane surface, the former to that of an object in relief: these things could not occur did we see with only one eye at a time. The above assertion, however, though itself incorrect, is founded on correct observations. In many persons one eye is, as Le Cat expresses it, "stronger or more vigilant than the other, and takes upon itself the larger share of the common task." With such persons M. Gall's experiment succeeds perfectly. A narrow body, such as a pencil or pen, held so as partially to obscure a candle, while both eyes are open, will still appear to have the same position when the weaker eye is shut, but will seem to lie much to one side when the eye, most used in vision, is closed, and the weaker opened. In those persons, on the contrary, whose eyes are equally employed in vision, the position which the body in this experiment holds, when both eyes are open, is intermediate between those which it appears to have when viewed with the respective eyes singly.

With the double vision with two eyes, we must not confound the phenomenon of double or manifold vision with one eye. Most persons, looking at the moon even with one eye, see several images of it, which lie in part one over the other; each, however, having its distinct outline. Like many other persons, I perceive this phenomenon only in looking at such very distant objects. In other individuals, however, it attends the vision likewise of nearer objects.* The cause of this kind of double or manifold vision lies in the physical structure of the eye; it is probably connected with the arrangement of the fibres of the laminæ of the crystalline lens into different compartments.

Alternate predominance of the sensations of the two retinæ.—One of the most interesting facts relating to the phenomenon of vision is, that the impression of different colours on corresponding "identical" spots of the two retinæ does not give rise to one mixed sensation, but that one of the colours predominates in part or in the whole extent of the field of vision, and that the impression made on the other retina is perceived only in spots where the first is wanting. A convenient mode of observing this phenomenon is to look upon a piece of white paper through two differently coloured glasses held close to the eyes; for instance, through a blue and a yellow glass.† The paper, under these circumstances, is not seen of a green colour, but appears in part blue and in part yellow. Sometimes the blue colour predominates, sometimes the yellow; sometimes a blue cloud or spot is seen upon a yellow ground, sometimes the reverse. At one time the blue obliterates the yellow; at another, the yellow the blue. This physiological difficulty was observed by me in another experiment, namely, in distorting the axes of the eyes so as to cause the double images of two objects of different colours to fall upon identical parts of the retina, and therefore to appear to lie one over the other; the two colours, I perceived, did not easily

The part which eyes unequal in power respectively play in vision may be determined more accurately by means of Mr. Wheatstone's stereoscope. In the case of the translator, it is the right eye which determines the position of objects in the field of vision; and the vision of this eye is more perfect, as tested by minute objects held at various distances. When two dissimilar outline perspectives of a solid body, as the cube (fig. 119) are presented to the eyes by means of the stereoscope, the body represented by them is seen standing forwards in relief; but, on closing each eye alternately, it is found that the position of the body, and of its bounding lines, corresponds exactly with the perspective projection presented to the right eye, and differs consequently very much from that viewed by the left eye. Here then the attention of the mind seems to be directed principally to the impression on the retina of the right eye, but yet takes cognizance of the impression on the left retina sufficiently to give rise to the idea and mental perception of a solid body, which would not be acquired without it.]

* See Steifensand in Graefe und Walther's Journ. 1835.—Müller's Arch. 1836, p. CXLVIII.

† For a further account of these experiments see my work Über den Gesichts-sinn, p. 79. Compare Müller's Archiv. 1836, p. CXLIV; and Volkmann and Heermann, loc. cit.

mingle to form an intermediate tint, as Huschke states, though I admitted the possibility of this occurring. The observations of Heermann and Volkmann agree with mine.

Völckers* has found that if the experiment with glasses of different colours, described above, be long continued, the mingling of the colours, to which there was at first no tendency, becomes more evident; but still, from time to time, one obtaining the predominance appears for a moment alone, or in isolated spots. The mingling of the colours in these experiments has no further physiological interest; but the antagonism of the retinæ, and the yielding of one colour to another in a part or in the whole extent of the field of vision, is of the greatest interest, illustrating as it does most distinctly, in a phenomenon which can easily be observed, the nature of the simultaneous action of the two eyes. For, that their action is the same in regard to other impressions besides colours, may be concluded from the above experiments, and is proved also by other facts.

The appearance at one time of one colour in spots upon the ground of the other; the complete disappearance at another time of one colour, simultaneously with its replacement by the other colour; and, lastly, the union of the two colours to form an intermediate tint, though this is observed only occasionally, prove — 1, that at certain moments the two eyes are both in action together; hence the appearance of spots or nebulæ of one colour upon the ground of the other; 2, that at other moments the impression on one retina is entirely, or nearly entirely, obliterated, and that of the other left predominant; and, 3, that at other periods again the impressions on the two eyes combine to produce one sensation. These states, alternating constantly with each other, present the actions of the eyes to us as phenomena of disturbed equilibrium, like the oscillation of a balance. The state of repose or balance of the impressions is attained with difficulty, though it is possible. The equilibrium is disturbed, however, in part by internal influences unknown to us, and in part probably by the mind being directed more especially to the one or the other eye. The phenomena showing this antagonism of the retinæ are, we may mention, quite distinct and vivid in persons whose eyes are perfectly equal in power, as in myself. The appearance of one colour in spots, or as nebulæ, while all around the other colour prevails, shows moreover the possibility of the different parts of the retina acting unequally; and the phenomenon is, indeed, of the greatest importance, as affording information with respect to the internal conditions of the retina.

The disturbance of the equilibrium between the sensations of the retinæ when both are acting simultaneously is frequently observed

* Müller's Archiv. 1838, p. 60.

under other circumstances. Sometimes, when the axes of the eyes are so directed as to produce double vision, one of the double images of an object suddenly disappears. If the two eyes are adapted for distinct vision at different distances, the image of each alternately prevails and completely supplants that of the other eye. The image of that eye is seen of which the adjustment corresponds to the distance of the object, and to which, consequently, the "attention" of the mind is directed. Sometimes the indistinct image of the other eye floats near the image of the eye which sees distinctly; but often it is not at all perceived, the "attention" not being directed to it. Thus it is also in strabismus, the faulty eye and the sound eye are generally adapted for vision at very different distances; the image received by the former is, therefore, indistinct when that of the other eye is clearly defined, and hence the mind is not directed to it. The total disappearance of the indistinct image under these circumstances is rendered intelligible by the phenomena which we have become acquainted with in the experiments with coloured glasses. Strabismus, indeed, often arises from the indistinctness of the image in one eye; for the eye thus useless in vision ceases to be properly directed towards the object which it is desired to view distinctly, and at last is wholly unemployed.

That the action of the sensorium can be confined to the sensations of one retina, may be observed also in viewing objects through magnifying glasses; for frequently the eye which is looking into the microscope alone sees or distinguishes its object, while the other eye either distinguishes no objects at all, or at least does not see any in that part of the field of vision occupied by the microscopic images perceived by the first eye. Sometimes, on the other hand, the eye not engaged in the microscopic observation resumes its activity, and the image it perceives then seems to floats over the image in the microscope and disturbs the observation.

5. *Of the "subjective" phenomena of vision.**

If we exclude from consideration those phenomena affording evidence of action of the retina, which are in some way dependent on the influence of the external light, such as the "ocular spectra," and the phenomena of double vision and the radiation of sensation in the retina, there still remain many others which are dependent on causes of a very different nature. The most remarkable of these phenomena, for a knowledge of which we are principally indebted to Purkinje, are the following:—

Appearances produced by pressure on the retina.—The luminous appearances produced by pressing with the fingers upon the eye (named by

* Purkinje, Beobachtungen und Versuche zur Physiologie der Sinne: i. Prag. 1823; ii. Berlin, 1285.

Purkinje "Druckfiguren") vary in form; they are sometimes annular, sometimes star-like, and sometimes regularly divided into squares; whence Purkinjė compared them to the figures produced by sonorous vibrations. When a plate of glass covered with water is struck with the bow of a violin, the plate not only divides into vibrating segments, and parts which remain at rest, but the water upon the vibrating parts of the glass presents a most regular distribution into rhombic figures or stationary waves. The figure in the eye calls to mind the appearance of decussating waves.

The vascular figure, described at page 1163, *is sometimes seen with a luminous character.*—It was sometimes seen thus by Purkinje as the effect of pressure, particularly in the morning; and I have frequently seen this luminous ramified figure in the dark field of vision, when, after ascending a flight of stairs, I have found myself suddenly in a dark place, and also when I have suddenly immersed my head in bathing. The luminous appearance is evidently the effect of the pressure of vessels filled with blood upon the retina.

Luminous appearance produced by the arterial pulse.—When the head is congested with blood, it is easy to perceive that each beat of the pulse is attended by a change in the degree of light perceived by the eyes, by a pulsating illumination of the field of vision. This phenomenon is very easy to observe. Some few times I have seen a similar change in the field of vision, or a rhythmic appearance of a small bright spot, in the middle of the dark field of vision, isochronous with the respiration and the corresponding movement of the brain; but this phenomenon cannot be excited at will, and has presented itself to me only a few times.

Visible movement of the blood.—There are many circumstances under which a general expression of the circulation is perceptible. It is seen, however, more particularly in looking at surfaces which are brightly illuminated, but not to a dazzling degree, as the sky; or after fixing the eyes for some time upon a surface of snow or white paper. The appearance consists in an indistinct confused movement, as of points crossing each other in all directions, or like the motion of vapours. The appearance is so undefined, that the direction of the movement cannot be determined. It evidently is due to the motion of the blood. Of the same nature is the much more definite appearance of dark bodies with tails, flying and moving about in all directions, which is seen sometimes by persons suffering under plethora, or congestion of blood in the head, on rising suddenly from the stooping posture. The sensation of ants creeping over the surface is an analogous affection of the nerves of common sensation or touch.

Luminous circles seen in the dark field of vision on a sudden lateral movement of the eyes.—This appearance is a constant result of suddenly turning the eyes to either side when in the dark. Two circles of light are always seen; they must therefore be produced by an affection of the retinæ at two different "non-identical" points,—perhaps, at the situation of the entrance of the optic nerve into each eye.

Appearances produced in the eye by electricity.—These phenomena have been investigated by Ritter, Purkinje, and Hjort. If the eye be made to form part of a galvanic circle,—one pole, for example, being applied to the conjunctiva of each eye-lid,—an appearance like a flash of lightning will be perceived when the circle is either closed or interrupted. The same thing takes place also when, although the eye does not lie in the direct line of the electric current from pole to pole, the electricity is nevertheless in part directed towards the eye; as when one pole of the battery is, for instance, applied to the lower eye-lid, and the other to the mucous membrane of the mouth. Even a simple pair of plates of zinc and copper are sufficient to produce the appearance above mentioned in a dark room. A small battery excites more remarkable phenomena: according to Purkinje's experiments, a yellowish light is seen at the zinc pole, a violet light at the copper pole. Under certain conditions, which Purkinje details, peculiar appearances are produced at determinate points of the field of vision, corresponding to the situation of the optic nerve, and to the central point of the retina.

Spontaneous appearances of light in the darkened eyes.—If we direct our attention to what takes place in the eyes when closed, not merely do we see sometimes a certain degree of illumination of the field of vision, but also occasionally an appearance of light developed in greater intensity; sometimes, indeed, this luminous appearance spreads from the centre to the circumference, in the form of circular waves, disappearing at the periphery. At other times the appearance has more the form of luminous clouds, nebulæ, or spots; and, on rare occasions, it has been repeated in me with a regular rhythm. Closely connected with these more indefinite appearances in the eye are the more distinct forms seen at the time of falling asleep, or in the period that precedes this, which are due to the action of the mind isolating different definite forms in succession from the cloud-like appearances in the eye, "the chaos of dreams," according to Gruithuisen.

Opposed to these phenomena is the transitory loss of sight, accompanied by the appearances of a mist, coloured smoke, or similar phenomena, before the eyes, which sometimes occurs in persons with a weak nervous system, and which is a state of temporary exhaustion of the retina. A person in perfect health may indeed induce this phenomenon, by looking for a very long time at a white or coloured surface.

Flickering before the eyes after taking narcotic substances.—Digitalis is most prone to produce this symptom. Purkinje has instituted observations upon it in his own person. If the action of the narcotic is strong, definite forms appear.

Apparent movement of objects consequent on repeated rotation of the body.—This phenomenon has been already described at pages 847 and 848. It must be distinguished with respect to its cause from the apparent movements seen after looking at objects really moving; which arise from the successive disappearance of the spectra left by the moving bodies (see page 1178). The apparent motion produced by the former cause occurs even though the eyes were closed during the rotation of the body.

Defect of the sense of colours.—Owing to an original disposition of the retina, many individuals have in an imperfect degree only the power of distinguishing colours. From numerous observations made on such persons, the younger Seebeck* has obtained the following results:—Besides those persons who find difficulty in determining the colours of objects generally, without however mistaking one colour for another, there are many individuals who are in a more or less complete degree incapable of distinguishing perfectly dissimilar colours from each other. But these persons differ, again, not only in the degree of their defect, but also in its character. Hence Seebeck has divided them, smaller differences being disregarded, into two classes. To the first class belong those who, though differing considerably in the degree of their imperfection of vision, agree pretty nearly in the circumstance of confounding the following colours:—

1. Light orange and pure yellow.
2. Intense orange, light yellowish green, or brownish green, and yellow-brown.
3. Pure light green, grey-brown, and flesh-colour.
4. Rose-red, green (rather blue than yellow), and grey.
5. Crimson, dark green, and hair-brown.
6. Bluish green and imperfect violet.
7. Lilac and bluish grey.
8. Sky-blue, grey-blue, and grey-lilac.

The individuals of this class have a very imperfect power of distinguishing the impression of colours generally; but the defect is greatest with regard to red, and the complementary colour green; these colours being to them scarcely or not at all distinguishable from grey: the colour of which the perception is next in degree defective is blue, which is imperfectly distinguished from grey. The perception of yellow is the most perfect, though objects of this colour also are distinguished from a colourless surface much less easily than by the eye in its normal state.

* Poggendorf's Annal. 42.

Individuals belonging to the second class likewise recognise yellow best; red is distinguished better, blue less perfectly, from the absence of colour, than in persons of the first class: but the distinction of red from blue is above all more imperfect here. The colours which they confound are as follows:—

1. Light orange, greenish yellow, brownish yellow, and pure yellow.
2. Bright orange, yellow-brown, and grass-green.
3. Brick-red, rust-brown, and dark olive-green.
4. Cinnabar-red and dark brown.
5. Dark carmine and blackish blue-green.
6. Flesh-red, grey-brown, and bluish green.
7. Dull bluish green and (somewhat brownish) grey.
8. Imperfect (somewhat yellowish) rose-red and pure grey.
9. Rose-red, lilac, sky-blue, and grey (inclining to lilac).
10. Crimson and violet.
11. Dark violet and dark blue.

It is the perception of the least refrangible rays only that is here very imperfect, which is not the case in persons of the first class.

We must distinguish from the subjective phenomena of vision the images of objects existing in the interior of the eye, and throwing a shadow upon the retina. Such are the thread-like convoluted figures in which rows of globules appear to be contained. These figures are not fixed; not only do the separate parts of the figures alter their relative position, but the whole figures change their place in the field of vision. By an energetic movement of the eyes we can cause them to shift their place somewhat to the side or upwards, but they soon return to their original situation, and, after having previously risen, they gradually sink again. Many persons have such figures in considerable number before their eyes, but those in the middle of the field of vision only are seen distinctly. In microscopic observations they often lie in front of the object, and interfere with the perception of it; in such a case I am in the habit of displacing them, by pressing on the eye at the side. In many individuals these appearances are not seen, while to others they are very troublesome. They are by some writers called muscæ volitantes, and confounded with certain symptoms which accompany the developement of amaurosis; but they are quite innocent in their nature, and exist in persons whose powers of vision are most acute. I have been subject to them from childhood. Whether they be owing to particles floating in the aqueous humour, or contained in the vitreous body, is not known.

SECTION II.

Of Hearing.

CHAPTER I.

OF THE PHYSICAL CONDITIONS ESSENTIAL TO HEARING.

A MECHANICAL impulse upon the organ of hearing excites in the auditory nerve the sensation of noise, or sound; and, if the impulse be rapidly repeated at regular intervals, a musical tone is heard, the acuteness of which is proportionate to the number of the impulses imparted to the nerve within a given time. Musical tones are most frequently produced by the vibrations of elastic bodies. The sounds produced by the separate impulses of the teeth of a saw, or of the wheel in Savart's experiments, or by the impulses of the water in the siren of Cagniard La Tour (see page 973), give rise, by their quick succession, to a continuous tone. From a vibrating elastic body which makes one thousand vibrations in a second, if we reckon the movement towards both sides, the organ of hearing receives five hundred impulses in a second, propagated to it by the air or other soniferous medium. The effect of these vibrations is the same as that of five hundred direct impulses of a body which does not produce sound by vibrations.

Whether the tones be excited by vibrations or mere impulses, the propagation both of the impulses and vibrations to the organ of hearing is effected in accordance with the general laws of undulatory or vibratory motion. The original production of the sounds which are due to vibrations is also regulated by the same laws, a knowledge of which is consequently necessary in studying the physiology of hearing.

I. *Of undulations in general.**

When the state of equilibrium of the different parts of any body has been disturbed by an external cause, the complete recovery of the previous state of repose is preceded by a movement in which the different parts of the body alternately approach the position of rest, and are removed from it. If a pendulum is driven towards one side, it continues to move in that direction until the moving force $= 0$; it is then drawn down by the force of gravity, falling with increasing rapidity, which prevents it from immediately resuming the state of rest, and causes it to ascend on the opposite side; and these movements are repeated until the equilibrium is restored. Movements, in which the parts of a body alternately approach and depart from the state of equilibrium, are called vibrations, oscillations, or undulations. *Undulations* are either undulations of

* E. H. and W. Weber, Wellenlehre; Leipz. 1825.—Eisenlohr, Lehrbuch der Physik; Mannheim, 1836. 121.

inflexion, or flexion-waves, consisting in the surface of the body being thrown into alternate elevations and depressions without any change in its density; or they consist in successive condensations and rarefactions, without the form of the surface being changed. The rarefactions in this case correspond to the depressions of the undulations of inflexion. Vibrations or oscillations are either progressive, when they traverse the different parts of a body in succession; or they are stationary, in which case, like those of a pendulum, they do not change their place.

A. *Undulations of inflexion, or elevation and depression, in incompressible fluids.*—The undulations of inelastic fluids are disturbances of the equilibrium of their surface to a certain depth. Gravity is the prime cause of this kind of undulatory movement. Such undulations in water are much too slow to give rise to sound. It is, however, important to become acquainted with their laws, since the laws of undulations generally can be most easily observed in them.

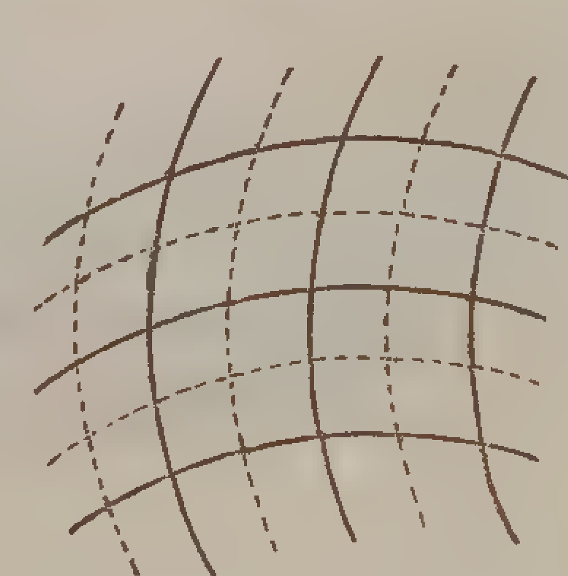
Progressive undulations.—If the equilibrium of a fluid is disturbed at any one point, circular undulations with circular elevations and depressions are formed around this point; each undulation extending outwards from it, and being followed by another. The stronger the impulse, the higher are the elevations of the waves, and the more rapid is their motion; though this is also influenced by the depth of the fluid. If undulations are excited in a fluid contained in a deep channel with parallel sides by an impulse acting on the whole breadth of the fluid, their motion is progressive in a straight line, and they do not form circles moving from a centre. The motion of waves is not produced by the progressive motion of the particles of water; on the contrary, the water itself is stationary, the waves only move over its surface. The particles of water in the situation of a wave merely suffer a movement of rotation: being in a hollow as the wave approaches them, they successively form the most elevated part of it; the wave still moving onwards, they come gradually to form the depression behind the wave, whence they again rise as the next approaches.

If two waves of equal height meet from opposite points, they intersect each other without the progress of either being disturbed. The elevation of the one, and that of the other, coincide, and form an elevation of double the height of either alone, and the depression of the one also coincides with that of the other. The particles of the fluid here receive impulses to rotation from two forces acting in opposite directions; and, in consequence of these impulses to rotation neutralizing each other, the particles of water are moved in the vertical direction only. After decussating with each other, the waves move on, each in its own direction.

If, when undulations meet from opposite directions, the elevation of one coincides with the depression of the other, they neutralize each other, and the surface of the fluid remains level; but, beyond their place of meeting, the waves again appear moving onwards in their original direction.

When parallel waves coming from different, but not directly opposite directions, intersect each other, both the effects above mentioned are produced at different points. Thus, if we suppose the continuous lines in fig. 120 to represent the elevations of the undulations, and the dotted lines the depressions, elevations of double height will be produced where the continuous lines cross, and depressions of double depth where the dotted lines cross each other; while, at the points where the continuous lines intersect the dotted lines, the elevation of the one wave will neutralize the depression of the other, and the surface will remain undisturbed. This is the "interference" of waves.

Fig. 121.



Waves are reflected by the surfaces of solid bodies;

and in the case of a wave, as of a ray of light, the angle of reflection is equal to the angle of incidence. If a wave be imagined to consist of a series of forces moving forwards side by side, each part of the wave will be reflected by the solid surface at the same angle as that under which it impinged on the surface, and thence will result a system of reflected portions of waves which will together form a reflected wave. The direction of the reflected wave may be either the same or different from that of the original wave. The reflected and incident waves have the same direction, when straight waves are produced in a channel, as above described, and when these waves impinge in a perpendicular direction on the reflecting surface, and also when circular concentric waves issuing from one point strike upon a surface which itself forms a concentric circle around that point ; in the latter case the reflected waves move back again towards the central point whence they arose.

A circular wave or undulation is reflected from a plane surface in the direction which a wave would have, that issued from a point at the same distance behind the surface as the central point of the original wave lies in front.

Waves originating at one focus of an ellipse, and falling upon a surface occupying the periphery of this ellipse, are reflected in such a manner that the central point of the reflected waves is the other focus of the ellipse ; for each point of a wave originating at one focus of an ellipse will, according to the law of equal angles of incidence and reflection, be reflected towards the other focus of this figure. For the same reasons, circular waves issuing from the focus of a parabola, and impinging upon a surface occupying the periphery of the parabola, are, by virtue of the properties of that figure, reflected in straight lines, and in a direction parallel with the axis of the parabola.

On the other hand, straight waves moving in a direction parallel with the axis of a parabola must be reflected by the parabolic surface, as concentric waves having the focus of the parabola as their common centre.

Circular waves, therefore, originating at the focus of a parabolic surface, and reflected by this surface as straight waves in a direction parallel with the axis of the parabola, will be reflected by a second parabolic surface placed directly opposite to the former as concentric waves meeting in the focus of the second parabola.

If waves are produced in water by an impulse communicated to its surface in the whole length of a line, every point of this line may be regarded as the centre of a circular wave. These waves issuing from all the points of the line of impulse at the same moment will remain all of equal size as they extend outwards from their respective centres, and, intersecting each other, will give rise to the production of a larger straight wave (*a* and *b*, fig. 122), before and behind the line of impulse, and parallel with this.

A body moving through the water gives rise to a constant succession of circular waves (fig. 123). Those last produced are small ; while the others at a greater dis-

Fig. 122.

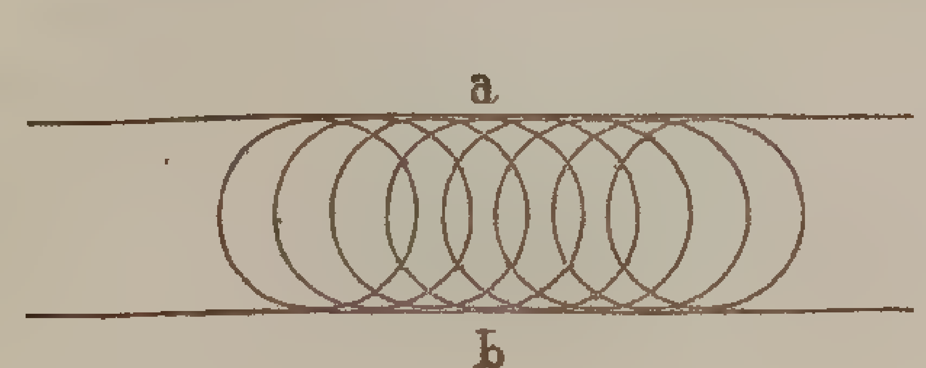
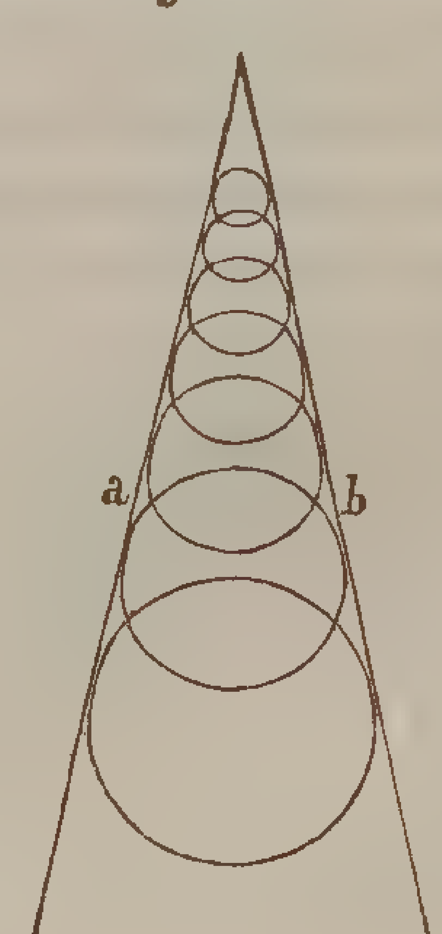


Fig. 123.



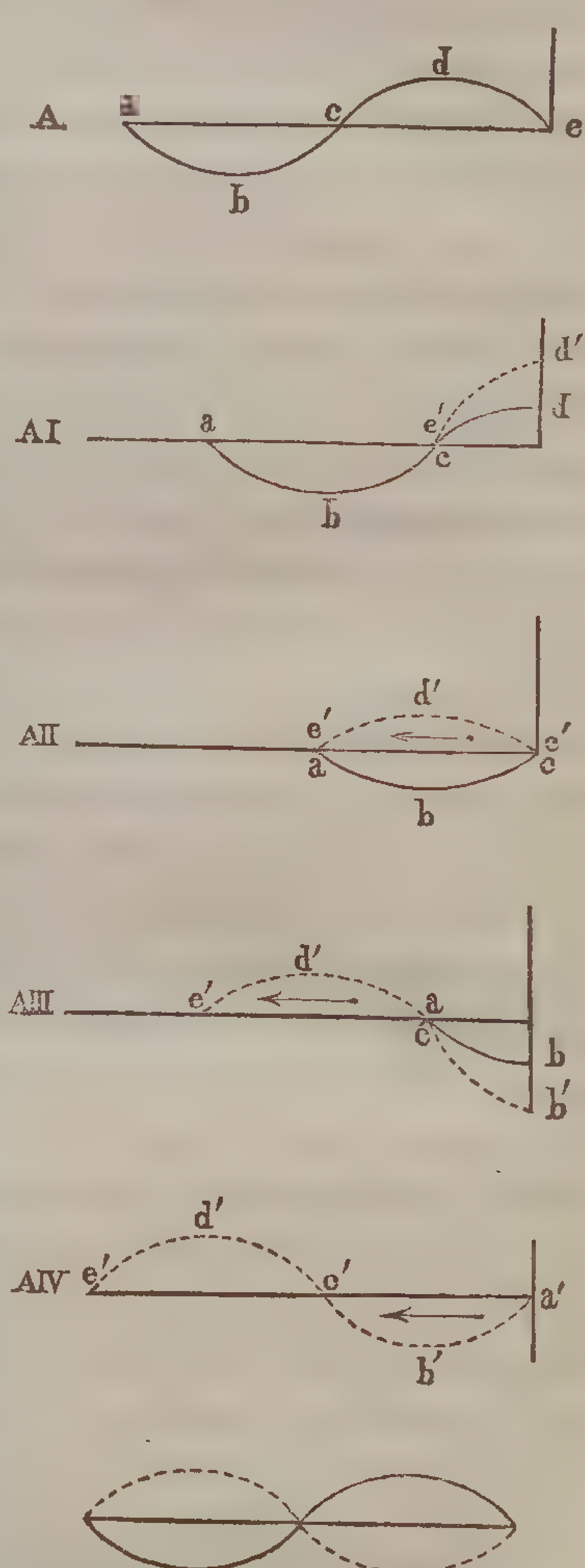
tance behind the moving body are larger and larger in proportion to the length of time that has elapsed since their production; and, in consequence of this, the larger waves which they produce by intersecting each other at the sides (*a* and *b*) diverge from the body which gives the original impulse.

Waves passing through an opening in any solid body do not retain the form which they had in the opening: on the contrary, their extremities which have passed the margins of the opening receive a circular inflexion around these margins, in consequence of which the waves, after their exit, not merely extend forwards, but also in the lateral direction. This is the "inflexion" of waves.

Stationary waves or vibrations.—If A (fig. 123) represents a wave upon the surface of a fluid, *a b c* the depression of this wave, *c d e* its elevation, and *e* the surface of a solid body against which the wave impinges, a period will occur at which, as at A I, half the length of the elevation, or one-fourth the length of the entire wave, will have reached the reflecting surface, and the wave will have the position *a b c d*, A I. The first half of the elevation of the wave will then be already reflected, and the half elevation seen in contact with the reflecting surface will consist of a progressive half-wave *c d*, and a reflected half-wave *d′ e′*: it will therefore be higher. After a second similar period of time has elapsed, the wave in its progress towards the surface will have reached the limit between its elevation and depression, and its whole elevation will be reflected, as at A II, where *a b c* is the depression of the wave, *c′ d′ e′* the reflected elevation. The elevation and depression will therefore obliterate each other, and the surface will at this period be even.

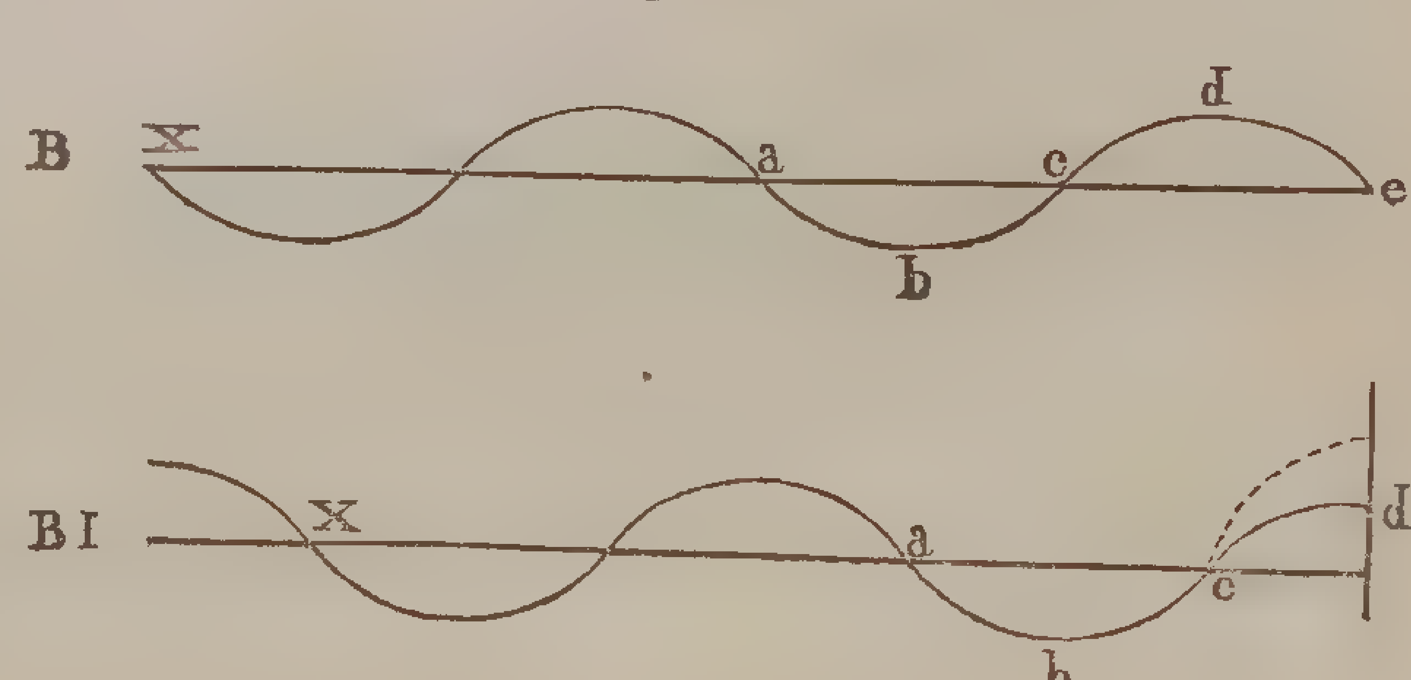
After the lapse of a third period, half the depression of the wave only (*a b*, A III,) remains, the other half will have been reflected, *b′ c′*, and the elevation of the wave previously reflected, *c′ d′ e′*, will have advanced half in length in the retrograde direction. After a fourth similar period has elapsed, the second half of the depression of the wave will also have impinged on the surface and have been reflected, A IV, *a′ b′ c′*, and the reflected elevation *c′ d′ e′* will have reached the distance of its entire length from the reflecting surface. The position of the wave is now therefore the same as at first, only the relative situation of its elevation and depression is reversed; the depression occupies the place of the elevation, and the elevation that of the depression, as shown in the last diagram of the figure.

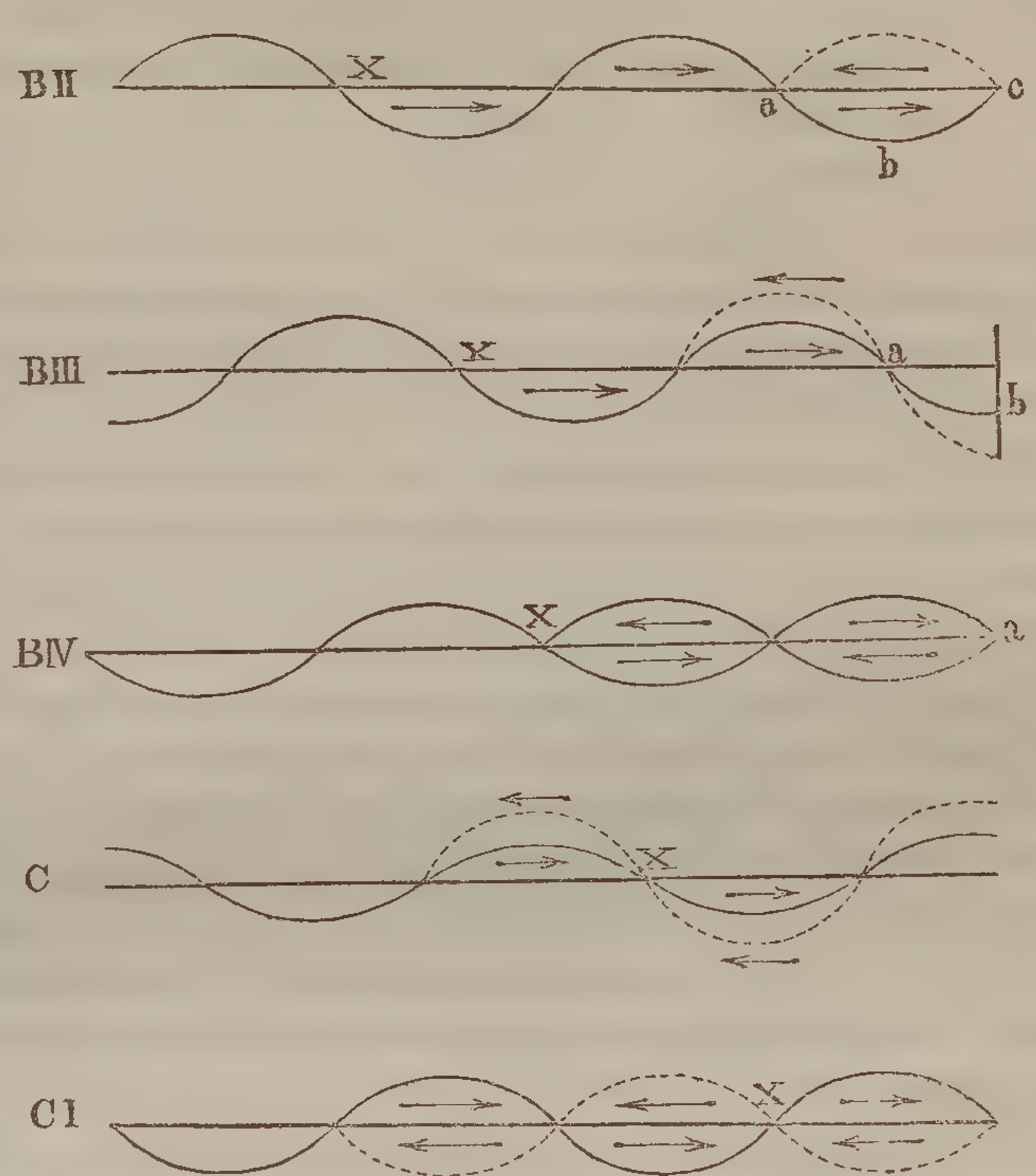
Fig. 124.



If, now, the first wave *a b c d e* (fig. 124, B) is followed by a second *x a*, the position which they will hold after the first period has elapsed, is represented by B I, that which they will have after the second period, by B II; that after the third,

Fig. 125.





by B III. The elevation of the second incident wave, and that of the first reflected wave, are now coincident, and the elevation is consequently more considerable. After the fourth period, the elevation of the second incident wave will coincide with the depression of the first reflected wave, and *vice versâ*, as at B IV. At this moment of time, therefore, the surface will be even. After the next period, each wave, the incident and reflected, will have advanced the extent of one-fourth of its length; or, in other words, the parts of the waves which were before coincident have become separated by half the length of a wave: the form of the surface will therefore be as represented at C, where the depressions are again coincident with each other, and the elevations also producing a deeper depression and a higher elevation. After the following period, the depressions will again coincide with the elevations, as at C I. These waves, recurring at regular intervals, are called stationary waves, or stationary oscillations. Their elevations and depressions do not move in a progressive manner from one part of the surface to another; the movement in the vertical direction only remains. They are alternate vertical elevations and depressions of the surface, resulting from the meeting of progressive waves from opposite directions.

Stationary oscillations or waves are produced in the straight channel by exciting a succession of waves at regular intervals of time, which are then reflected at the opposite extremity of the channel; or, in a circular vessel, by exciting waves from its centre by impulses repeated at regular intervals. The MM. Weber also observed the stationary waves in vessels filled with fluid, and placed upon a drum or a cane chair, when impulses were given to the elastic surface at regular intervals.

B. *Undulations of inflexion or flexion-waves in solid bodies.* — The cause of the undulations of this kind in fluids is the force of gravity; in solid bodies it is the force of cohesion and elasticity. These undulations are much quicker in solid bodies than in water, and in elastic bodies are the cause of sound.

If a stretched cord or string of a musical instrument is struck, not at its middle, but near one extremity, an extension of it is produced at this part, and is communicated as a wave or oscillation to the whole cord, travelling from one end to the other where it is reflected back again like the undulations of fluids.

If the cord or string is struck several times in succession, a regular series of undulations is produced, as upon the surface of water. The reflection of these undulations at the extremity of the cord, and the meeting of the incident and reflected undulations, give rise to the stationary vibrations; and the parts of the cord which remain at rest between these stationary waves or vibrations are the "nodal points."

The simplest stationary vibration of a cord or string is, however, that which results, not from the meeting of progressive undulations, but from the transverse vibration or movement from side to side of the whole cord between its fixed extremities, which here constitute the nodal points. This kind of vibration is induced most readily by striking a string with the finger, or with a violin-bow. The transverse oscillation of solid bodies which do not owe their elasticity to tension, such as metal rods fixed at one extremity only, is also an instance of stationary vibration.

C. *Undulations of condensation in liquids, gases, and solid bodies.* — The undulations of inflexion in water are not attended with any condensation and rarefaction, nor are they necessarily so in a cord or string. If the cord is not extensile, or not elastic, the undulations of inflexion may be produced by the mere displacement, and the striving of the parts of the cord to regain the straight direction. Generally, however, the waves of inflexion in strings are attended with alternations of condensation and rarefaction. The peculiarity of the undulations of inflexion consists in many parts of the body having imparted to them so considerable a movement in the direction perpendicular to its surface, that the form of the surface undergoes a visible change. All bodies become the seat of undulations of condensation, on the contrary, when, by an impulse communicated to them, their most minute constituent parts only are in succession thrown into motion, the impulse being imparted from one particle to another. Hence these undulations are sometimes called undulations of the progressive impulse. By the impulse of the molecules moved upon those in front of them, condensation is produced; and this is necessarily accompanied by a rarefaction behind it. The movement thus propagated from particle to particle is so slight, that no change in the surface of the body is visible; just as an impulse is propagated through a row of solid balls, while these balls themselves retain their original place.

a ———————— *b*

The direction of the movement induced in the particles by the impulse may in a rod or string be different from that in which the undulation is propagated. If, for example, a rod or string, *a*, *b*, is struck at a point near *a*, in a direction perpendicular to its length, the particles immediately set in motion by the impulse induce a similar movement—namely, a movement in a direction perpendicular to the length of the rod *a b*,—in the particles next to them, these again in others next to them, and so on to the other end, *b*, of the rod or string. All the particles of the rod or string between *a* and *b* are, therefore, successively moved, or thrown into a state of condensation in the perpendicular direction;—that is to say, an undulation travels in the direction from *a* to *b*, while the movement of the particles themselves, induced by the impulse, has a totally different direction,—namely, a direction perpendicular to *a b*. If the middle of the rod is struck, the undulation is propagated in two directions; towards *a*, and towards *b*. Similar undulations are produced also in a broad plate, as Savart has shown.*

The propagation of an impulse in bodies occupying a cubic space, as in rocks, or masses of air and water, takes place in all directions. The propagation of sound, in all bodies, is effected by the propagation of the impulse or waves of condensation.

Undulations excited in the air consist of progressive condensations and rarefactions. The part where the condensation exists is analogous to the elevation; that where the rarefaction is, to the depression of an undulation of inflexion. A progressive undulation travelling through a column of air in a tube is reflected at the extremity of the tube if this is closed, and in its retrograde course retains its original properties. The wave is also imperfectly reflected even when the extremity of the tube is open; but, experience has shown that in that case the properties of the un-

* Compare Weber, op. cit. p. 440.

dulation are reversed, its rarefaction taking place where its condensation should be, and *vice versâ*. Undulations in the open air have a spherical form.*

II. *Of the stationary and progressive undulations of sonorous bodies.*

The vibrations of sonorous bodies are either undulations of inflexion, or undulations of condensation. Either of these kinds of undulations, or both simultaneously, may take place in strings and solid bodies which give sound. Columns of air, in yielding sound, are the seat of undulations of condensation only. The undulations of sonorous bodies may be either stationary or progressive. If a tense string is drawn out of the straight line at its middle, and then left to the force of its elasticity, no progressive undulations are observed to take place in it,—at least, not distinctly. On the contrary, the string vibrates from side to side, like a pendulum, in the whole extent of the curve which was given to it, or in its whole length. After being drawn out of the straight line, it strives to resume this line by virtue of its elasticity; but the force by which it is moved carries it beyond the straight line to the opposite side, and this is repeated until it gradually returns to its state of repose or equilibrium. This is a stationary vibration.

The rate of the vibrations of stretched strings, or the number of the impulses which they impart to the air, increases in an inverse ratio with their length, and in a direct ratio with the squares of the extending forces. Thus a string which performs one hundred vibrations in a second of time, if reduced to half the length, will vibrate two hundred times in the same period, the extending force being equal; or, its length remaining the same, if it performs one hundred vibrations with an extending force of one loth [half an ounce], it will vibrate two hundred times when the extending force equals four loth, four hundred times when the extending force is sixteen loth.

Sonorous rods are also susceptible of stationary vibrations, the number of which in a given time will be in a direct ratio with the thickness of the rods or bars, and in an inverse ratio with the squares of their length.

Under certain circumstances a progressive movement of the summit of the undulation is combined with a stationary transverse vibration, without any change in the rapidity of the transverse vibrations being thereby induced: for instance, when a string is struck near one of its fixed points, it not merely performs transverse vibrations, such as it makes when struck at its middle,—that is, transverse vibrations equal in length to the whole length of the string,—but the summit of this stationary undulation travels to and fro from one end of the string to the other, being reflected by each of its fixed points. The number of vibrations of a string thus vibrating is exactly the same as that of a string the summit of whose vibrations remains constantly in the middle; and as the acute or grave character of a sound, or its pitch, always depends on the number of vibrations performed within a certain time, the "pitch" of the note produced is in both cases the same, but the "tone" is somewhat different. This is an important circumstance in relation to the theory of the "tone," or quality of different sounds.

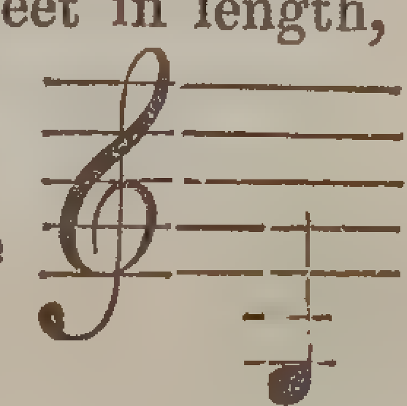
Stationary undulations or vibrations are produced also when, by touching lightly a stretched string, we give rise to a nodal point in that situation, and then strike the part of the string thus isolated. If, for example, the string is touched at its middle, and either its upper or its lower half then struck with the violin-bow, not merely does the half that is struck become the seat of transverse vibrations, but the other half also vibrates from side to side, though in the opposite direction. The number of the vibrations in a given time is in this case twice as great as when the string vibrates in

* Weber, op. cit. § 276.

its whole length, and the sound produced is the octave of the fundamental note of the string. If the string is touched at the point of junction of its first and middle third, a nodal point is formed between its middle and last third also, and the number of the vibrations is three times as great as that of the vibrations of the entire string within the same period. In the same way, by isolating and striking a fourth or fifth of the string, a regular division of the string into four or five vibrating portions, separated by nodal points, is induced. Pieces of paper placed upon these nodal points during the vibration of the string are not thrown off. The sounds resulting from the vibration of a string thus divided by nodal points are called "harmonic notes."

Plates or disks thrown into vibration by means of a violin-bow divide into four, six, or eight segments, which vibrate in opposite directions, and are separated from each other by nodal lines, on which sand strewed over the surface remains at rest. Lightly touching the margin of the plate at any point gives rise to a nodal line there, and this determines the situation of the other nodal lines. The second influential condition is the part at which the margin of the plate is struck with the violin-bow; for this becomes a vibrating portion, and determines the situation of the other vibrating segments. In this way are produced the symmetrical nodal figures of sonorous vibrating surfaces, described by Chladni.

Both stationary and progressive undulations of elastic bodies are adequate to the production of the phenomena of musical sounds, if they are regularly repeated; for even the stationary vibrations become progressive undulations when communicated to conducting media: each stationary vibration excites in the air, in water, or in solid bodies capable of conducting sound, a progressive undulation.

Sounds may be produced in solid bodies, as well as in columns of air in tubes, by progressive undulations of condensation. Rods may be thrown into longitudinal undulations of condensation and rarefaction by friction in the longitudinal direction. These progressive undulations of condensation, without any transverse vibration, may likewise produce sound in a stretched string. The time occupied by the progress of the undulation from one end of the string to the other, and back again, on which depends the number of the undulations excited in the air, is of course determined by the length and tension of the string. These longitudinal undulations do not, however, maintain the requisite strength, and are not of sufficient duration to produce sounds, unless the impulse be constantly repeated. This constant repetition of the impulses is supplied by friction. By a modification of these impulses the rapidity of the longitudinal undulations may, indeed, be influenced. This is exemplified by the longitudinal vibrations which Chladni excited in strings by friction in the longitudinal direction. The sounds yielded by the strings of the Æolian harp appear also to arise from vibrations of this nature: according to Pellisov,* they are attended with no perceptible transverse vibration; and variations in the strength of the current of air give rise to different harmonic notes, without any nodal points being apparently formed. Pellisov has further described a mode of proceeding, by which very different notes may be obtained from a violin-string, of which the tension remains the same, without the developement of nodal points. It consists in laying the bow upon the string (which should be two feet in length, and one-third of a line thick, and tuned to G treble below the line ), close to the bridge, and drawing it across the string, at first as lightly as possible, and with one equable movement. The

* Poggendorf's Annal. xix. 237.

sound produced then varies in pitch entirely in accordance with the strength and rapidity of the stroke of the bow; and not merely can those notes be easily produced which the wind is capable of producing in the Æolian harp,—namely,

G, D, G¹, B¹, D¹, E¹, G², A²,

but also most of those intermediate between them and other higher notes. The undulations in the production of the sounds thus excited travel, according to Pellisov, from the molecules immediately acted on by the bow to the other extremity of the string, and are there reflected. By a particular manipulation of the bow he was able to obtain notes which were lower in pitch than the fundamental notes of the strings, and were, therefore, certainly not due to transverse vibrations.

Pellisov goes still farther; and maintains that, even when the string vibrates in the transverse direction, the sound produced is not due to the transverse vibrations, but to the undulations of condensation and rarefaction (called also molecular vibrations) which travel up and down the string. According to the view generally adopted, these minute undulations, originating at the part of the string which received the impulse, and communicated thence by virtue of the property of elasticity to the whole string, are of importance only so far as they have for their result the transverse vibration of the whole string between its fixed extremities, or between its nodal points. Pellisov maintains that the contrary of this is the fact; that the pitch of the sound depends on the rapidity with which the ultimate particles of the sonorous body, whether string, column of air, rod, or plate, vibrate; and that the vibrations of the string, column of air, or plate, or of their larger segments, contribute to the result in no other way than by determining the rapidity of the molecular vibrations. According to this view, therefore, a string vibrating transversely would produce no sound, unless at the same time its individual constituent molecules were vibrating, — that is to say, unless progressive undulations of condensation were travelling to and fro between the nodal points of the string.*

Though the correctness of the hypothesis of the transverse vibrations of strings being incapable of producing sound cannot be admitted as proved, yet the simultaneous existence of the transverse vibrations, and of the progressive undulations of condensation and rarefaction in sonorous bodies, may serve to give us a very good idea of the mode of production of several different sounds simultaneously by one body. A vibrating string is prone to yield, besides its fundamental note, another fainter sound, a harmonic of the other; as the fifth, or the third of the higher octave. The fainter sounds accompanying the principal sound of a bell are well known.

The column of air in pipes is susceptible of no transverse vibrations, but merely of the progressive undulations of condensation, which travel to and fro along the length of the tube. The blast is continuous; but the effect which it produces is intermittent. The number of undulations within a given time, or, what is the same thing, the length of the undulations, is determined by the length of the column of air.

A gentle blast gives rise to the fundamental note of a covered pipe, in which case the nodal point lies at the extremity of the column of air. The same blast causes the developement of a nodal point in the middle of the column of air in an open pipe, and the note produced is consequently an octave higher. By blowing with greater force, the column of air is made to subdivide itself still further, and higher notes are the result. (See page 978.)

We have lastly to explain the difference which obtains between a mere "noise," a "report," a "continued sound not of musical character," a "musical sound," and "tone." Any impression upon the organ of hearing by an undulation, or

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* Pellisov, loc. cit.—Fechner, Repertor. der Experimental Physik, i. B. p. 256.

several undulations, communicated to it, gives rise to a sound or noise. This sound, when produced by a single impulse, is short in duration; and, if intense, has the character of a "report." The intensity of the sound depends on the extent of the excursions of the vibrating particles. The "quality" may be very various. Wood, pasteboard, and metal produce each a sound of different quality. The quality of the sound appears to depend partly on the form of the undulations, and partly on the simultaneous existence of undulations of different rapidity. One and the same body, if it possess unequal elasticity in different directions, may, on receiving an impulse, become the seat of undulations of different rapidity in different parts, and will communicate these undulations to a conducting medium, not simultaneously, but at more or less distinct periods, producing thus in the latter a compound wave of peculiar form. This compound wave, or sum of waves, is transmitted to the organ of hearing in the same order and form as it was received by the conducting medium, in which all modulations are propagated with equal rapidity.* The circumstance, also, that a body may be affected with a transverse and longitudinal vibration at the same time, has a share in the production of the quality of a sound. A string struck with the finger near one extremity vibrates in the transverse direction in its entire length; but, at the same time, the summit of the undulation travels alternately from one end of the string to the other. Hence the quality of the sound yielded by the same string, though its length and tension remain unaltered, may vary somewhat according to the part at which it is struck. Lastly, the form of the wave is modified, according to Pellisov and Eisenlohr, by the density of the body which is its seat. In a dense body the aberration of the vibration is less considerable than in a body less dense. The particles of air in contact with it receive the impulse from it more simultaneously, and the rarefied space which it leaves by its contraction after giving the impulse is smaller. If the density of the sounding body, in fine, be unequal, the condensations and succeeding rarefactions which it imparts to the air, must also be unequal.

If several undulations succeed each other, a more or less prolonged sound results, which may or may not have a musical quality. A succession of similar or dissimilar short sounds, at unequal intervals, gives rise to various unmusical sounds or noises. A succession of short sounds, even at equal intervals, if the individual sounds are distinguishable, does not produce a musical sound. For the production of a sound of musical character, it is necessary that the succession of separate sounds or impulses be not recognizable. The height or pitch of a musical sound depends on the rapidity with which the separate impulses succeed each other. Savart's experiment with the toothed wheel illustrates the mode of production of musical sounds: as long as the separate strokes of the teeth can be heard, the sound has not a musical character; but acquires it when they are made to succeed each other more rapidly, although the unmusical quality of the sounds resulting from the impulse of the separate teeth is still heard. A continued sound of definite musical value may therefore result, not merely from a regular succession of simple waves or vibrations, but also from a regular succession of very compound undulations, such as separately constitute short unmusical sounds. A full and pure musical sound requires for its production simple undulations of sufficient strength without the irregular intermediate undulations. The quality of "tone," or "timbre," possessed by a musical sound, is dependent on the same causes as the quality of a simple sound not musical; the musical sound differs merely in the undulations which produce it, succeeding each other at regular intervals.

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* Eisenlohr, Lehrbuch d. Physik, p. 151.

III. *Of the undulations by which sound is propagated.*

*Of the progressive undulations engaged in the propagation of sound.**—The propagation of the vibrations of sonorous bodies is effected ordinarily by undulations of condensation and rarefaction, not by undulations of inflexion. Sonorous vibrations are propagated even in water by means of undulations of this kind; by a movement, therefore, very different from the undulations of elevation and depression of the surface of the water.

An impulse in every direction imparted to the air at one point gives rise to a spherical wave of condensed air, of the form of a hollow sphere, which extends equally in all its dimensions, maintaining consequently its spherical form. A spherical body suddenly expanding in the air would excite such a wave. The particles of air which receive the impulse from such a body thus suddenly expanding, acquire at first a motion in a direction corresponding to that of the impulse,—namely, in the direction of the radius of the expanding sphere; and, subsequently, when the expanding body contracts again and produces a rarefaction around it, a motion in the opposite direction. All the particles of the air traversed by the spherical wave, or undulation, experience the same movement. The extent of the forward and retrograde motions of the particles of air, which is to be regarded as the same thing as the height of the elevation of the undulations on the surface of water, decreases with the progress of the wave, while the thickness of the wave remains the same, just as a circular wave excited upon the surface of water becomes lower as it extends itself, though its breadth remains unaltered. The cavity of a spherical wave increases uniformly in diameter; and its circumference consequently increases as the square of its diameter. The elevation of the undulation decreases in the same ratio. This is the cause why the intensity of a sound diminishes, in the open air, in an inverse ratio with the squares of the distance from its origin. In the motion of the air in a tube no cause for the diminution of the intensity of the sound exists.

If the impulse is imparted to the open air by a solid body, not in every direction, as in the case of the spherical body suddenly expanding, but in one direction only, the wave produced is still spherical, just as a wave excited upon the surface of water by a blow in any one direction extends in all directions, and is consequently circular. The height of the elevation of the wave, or the extent of the to and fro movement of the particles of air affected by the undulation, is, however, greater in the direction corresponding to that of the impulse. Hence, if the undulations in a sonorous body, as a vibrating string or column of air, have a determinate direction, the sound will be heard more distinctly and with more intensity in that direction. It appears to me, that in some cases the following circumstances also may contribute to this effect. The wave produced in a medium capable of sonorous undulation by an impulse acting upon it over some extent, may be regarded as compounded of a number of circular undulations of equal diameter lying side by side. To the extent to which the impulse reached, and in lines parallel with the line of its application, these circular undulations coincide with and strengthen each other, but beyond that extent such is not the case. The action of the wave will, therefore, be stronger in the direction perpendicular to the line on which the impulse acted than in other directions.

The intensity with which sounds are conducted depends, *cæteris paribus*, on the relation existing between the sonorous body and the conducting medium. The more the latter resembles in its physical properties the body which yields the sound, the more perfectly will it conduct it, and *vice versâ*. The column of air of a wind instrument, for example, communicates its sonorous vibrations in such perfection to the

* After Weber, op. cit. p. 501.

atmosphere, that the interposition of other media does not tend to increase the intensity of the sound; while to solid bodies, on the contrary, the vibrations of a column of air are not readily communicated. On the other hand, solid bodies impart their vibrations imperfectly only to the air, and in all their intensity to other solid bodies. Moreover, sonorous undulations, in their transition from one medium to another different medium, are, like rays of light, partly reflected. These considerations afford an explanation of the interruption offered by rocks to sounds excited in the air, and of the circumstance that the sonorous vibrations of a solid body, such as a rod, are communicated to the ear with greater intensity by means of a cord than through the intervention of the air. Mr. Wheatstone states,* that by means of a wire the sounds produced by a stringed instrument may be conducted to a resounding body placed at a considerable distance.

Resonance is a means of rendering a sound louder than it is as produced by the sounding body itself. It consists in increasing the extent of surface of a soniferous medium similar in kind to the sounding body. Hence the increase of sound produced by placing a vibrating tuning-fork upon a solid body. The influence of the bridge and sounding-board of stringed instruments is due to the same principle. Greater resonance is, however, produced by an insulated body than by one which has no circumscribed surfaces; for an insulated body reflects back a part of the undulations within it at its borders and surfaces, and, these reflected undulations meeting with the undulations newly excited in it, an increased extent of the excursions of the oscillating particles, answering to the increased height of the elevations of flexion-waves, is produced (see pages 1218 and 1219).†

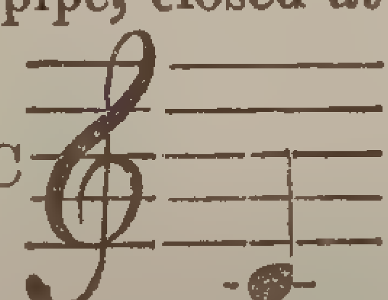
Stationary vibrations in bodies conducting sound.—Stationary vibrations are developed in bodies to which sonorous vibrations are communicated, and which are insulated, and at the same time elastic. We have stated that progressive sonorous undulations in an insulated body are reflected at its borders and angles; and that, in consequence of this, the undulations newly communicated to the body, and those reflected within it, meet and intersect each other. When sonorous undulations are communicated from one body to another, the breadth of the separate undulations in the second resounding body is not determined by this body,—they are not necessarily aliquot parts of it; but their breadth is determined by the body originally producing the sound, in which the undulations always correspond to aliquot parts of itself. An insulated body, to which sonorous vibrations are imparted from another body, may, however, divide into several segments by the developement of nodal points and nodal lines. Savart's experiments have shown, for example, that such nodal lines are formed in tense membranes, while conducting sonorous vibrations, and are seen when a light powder is strewed upon the surface. Metallic or glass laminæ also present the same phenomenon when they are brought, by means of a rod, into connexion with a body emitting sound.‡

The sound of one body may, under certain conditions, excite in another insulated elastic body not merely resonance, but also a new production of sound; the sound emitted by the body thus secondarily thrown into sonorous vibration, being in this case the note peculiar to itself, and different from that produced by the body primarily affected. Stretched strings will reciprocate the sounds of other bodies by the notes for which their degree of tension fits them; for this to occur, it appears to be necessary not merely that the sonorous body secondarily affected be very elastic and bounded by

* Ann. de Chimie et de Phys. t. xxiii. p. 317. † Weber, op. cit. p. 536.

‡ On the difference in the nodal figures produced on bodies in which the vibrations are primarily excited, and on those vibrating by reciprocation, see Weber, op. cit. p. 541.

free surfaces, but also that the number of the vibrations in the note which it is adapted to yield should bear a simple numerical relation to those of the original sound.

Finally, an elastic sonorous body of definite extent may, under certain conditions, even modify the pitch of the sound yielded by the body primarily thrown into sonorous vibration; the vibrations of each reciprocally influencing those of the other, so as to give rise to undulations which differ from those proper to either separately. Thus, the column of air of a tube combined with a reed modifies the pitch of the sound yielded by the latter (see page 985). I have observed another remarkable example of this reciprocal influence of sonorous vibrations of different bodies in a pipe, the open end of which I had closed with a membrane (of pig's bladder). A one-foot mouth- or flute-pipe, closed at one extremity with a plug, has, it is known, for its fundamental note C  ; but when the pipe, instead of being thus closed, had its extremity merely covered with a membrane loosely stretched over it, the note yielded with the feeblest blast was from a "third" to a "fifth" deeper than this C: in proportion as the membrane was made more tense, the note became sharper; and, when it stretched as tightly as possible, it acted like the solid plug.

Fluids capable of propagating sonorous vibrations present, when in immediate contact with bodies emitting sound, peculiar undulations of inflexion on their surface, which ought to be distinguished from the undulations of condensation by which they propagate the sound. Their surface presents small wave-like elevations and depressions very regularly arranged, like stationary undulations or vibrations. These appearances have been described by Oersted, Purkinje, Chladni, W. Soemmering, and Faraday.*

If a tuning-fork, of which one side is covered with a thin layer of water, be held horizontally with this side uppermost, and be allowed to vibrate freely in the air, the water on its surface will be seen to become affected with most beautiful parallel stationary undulations, which generally occupy the entire breadth of the tuning-fork, and are about three-fourths of a line in length. They are, as it were, impressions of the vibrations of the sounding body, produced by the impulses imparted by those vibrations to the particles of water. If the tuning-fork be held with one of its surfaces immersed in a basin of water, the surface of the water at its sides will be seen to become the seat of very regular parallel divisions, just as if the water in contact with the tuning-fork were thrown simultaneously with it into a movement of undulation, and as if its undulations were prolongations of the undulations of the fork. If the broad surface of the tuning-fork, covered with a thin layer of water, be raised above the surface of the water of the basin, and its sides only be immersed, it will become evident that the undulations of the water on the surface of the tuning-fork, and those of the water in the basin, are prolongations of each other. It is a remarkable circumstance, however, that, whichever surface of the fork is immersed in the water, the stationary undulations of the water that are produced, always abut perpendicularly upon the surface of the fork. The only deviation from this law is observed at the angles of the instrument where the lines of the undulations become divergent.

The same phenomenon is observed in musical glasses filled with water: such a vessel being thrown into sonorous vibrations by means of a violin-bow, the surface of the water is seen to divide itself into several compartments (four, six, or

* See Chladni and W. Soemmering, in Kastner's Archiv. für die gesammte Naturlehre, B. 8, p. 91.—Faraday, Philosoph. Transact. 1831. 319.

eight, according to the height of the note produced,) separated by nodal lines, between which, if the stroke of the bow was gentle, stationary undulations are seen directed perpendicularly against the internal surface of the vessel. If the stroke of the bow was stronger, other figures are produced; and, by the decussation of undulations having different directions, rhomboidal stationary undulations are developed. The water, moreover, accumulates in the vibrating segments, and is spirted out of the vessel when the action of the bow is violent. If the glass vessel is thrown into vibration by the friction of the finger upon its margin, the vibrating segments and the nodal lines move round in a circle, following the movement of the finger.

The application of the violin-bow to the border of a lamina of glass, of which the surface is covered with a thin layer of water, gives rise to the same phenomena in a still more marked degree.

If to the parchment of a drum a piece of cork be fastened, and to this a rod of wood terminated at its other extremity by a round or square lamina, and if the drum be so placed that this wooden plate dips lightly into the surface of some water, the vibration of the membrane of the drum will be found to give rise to similar stationary undulations in the water, which have a direction perpendicular to the margin of the wooden plate; so that, when this is of a circular form, a starlike figure is produced on the surface of the fluid. A satisfactory explanation of the phenomenon cannot at present be given.

Dr. Faraday says, in explanation, that the slightest possible difference in any circumstance during the vibration of an elastic plate is adequate to produce an elevation or depression of the fluid, and thus give the first impulse to the phenomena; but I cannot imagine that such regular phenomena can be explained in this way, without reference to a regular division into segments, or to the vibrations of the sounding body, although these considerations do not at present afford us a satisfactory theory.

The undulations on the surface of water, to which we have been just referring, are undulations of elevation or inflexion; but the undulations by which sound is conducted in water, as in the air, are undulations of condensation.

The rapidity with which sound is propagated depends on the density and elasticity of the body. The rapidity in dry air, at a temperature of 32° Fahr. is at the rate of 332·49 metres, or 1022·194 feet (Parisian measure), [or about 1090 feet English measure] in a second. Its rapidity increases with the rise of temperature. Sound is propagated in water with about four times greater velocity than in air; in solid bodies its rapidity of transmission is still greater. Iron propagates sound with ten and a half times, wood with eleven times, greater rapidity than atmospheric air.

Reflection of sound.—In relation to their reflection, the undulations of sound resemble those of light; in passing from one medium into another different one, they are in part reflected, and in part only propagated onwards. The ticking of a watch placed in the focus of a concave mirror may be heard in the focus of another mirror placed so as to receive and concentrate the reflected sonorous undulations. It is owing to sonorous vibrations of air being propagated with more facility in that medium than they are imparted from it to solid bodies, that sounds are transmitted in their full intensity through tubes, just as on the same principle solid rods propagate sonorous vibrations to great distances almost without any loss of intensity. A *speaking-trumpet* represents a parabola, in the focus of which the sound is excited. Being reflected by the parabolic surface, the sonorous undulations are all thrown in a direction parallel to the axis of the parabola (see page 1217). The cause of the increased intensity given to the sound by the *speaking-trumpet* is, for the most part, the coincidence of newly excited undulations with others already reflected, producing undulations with greater condensations and rarefactions. But the resonance of the confined mass of air in the tube also contributes to this effect; for the air of a tube open at both extremities, while it propagates sound, also becomes the seat of resonance.

The *ear-trumpet* becomes narrower towards the ear, and consequently concentrates the sonorous undulations. If its walls have the parabolic form, and the focus of the parabola be at a point near the ear, sonorous undulations coming in a direction parallel with the axis of the parabola will of course be brought to a focus near the ear.* If a reflecting surface is situated so as to throw sonorous undulations upon the ear, and is at such a distance that the reflected undulations reach the ear perceptibly later than the undulations coming direct from the sounding body, an echo results, which is perfect when the difference of time is so great that the two series of undulations strike the ear at perfectly distinct periods.

CHAPTER II.

OF THE DIFFERENT FORMS OF THE AUDITORY APPARATUS, AND OF ITS ACOUSTIC PROPERTIES.

1. *Of the different forms of the organ of hearing.*

In the greater number of invertebrate animals there are no parts known which can be regarded as analogous to the organ of hearing of the higher classes; and in the case of many animals it may be doubted whether they really hear at all; for every reaction of nerves under the influence of vibrations cannot be called the sensation of sound, since the sense of touch is capable of perceiving the same vibrations as a tremour.†

In all cases the first essential of an organ of hearing is the special nerve endowed with the property of perceiving impulses as sound; and, next to this, an apparatus adapted for conducting these impulses to the nerve. Inasmuch, however, as all matters have the property of propagating sonorous vibrations as undulations of condensation, it is evident that a special apparatus for conducting these vibrations may be absent; and this enables us to understand why no special auditory apparatus has been hitherto found in many invertebrate animals. The auditory nerve, if merely in contact with the solid parts of the head, will be as certainly affected by the vibrations communicated to those parts as if it were spread out in a special organ.

The simplest form of the organ of hearing in which a special apparatus is added to the nerve with the specific endowment, is a small sac containing fluid, with the auditory nerve expanded upon it. The sonorous vibrations are communicated to this organ, either through the medium of the hard parts of the head alone, or at the same time by the contigu-

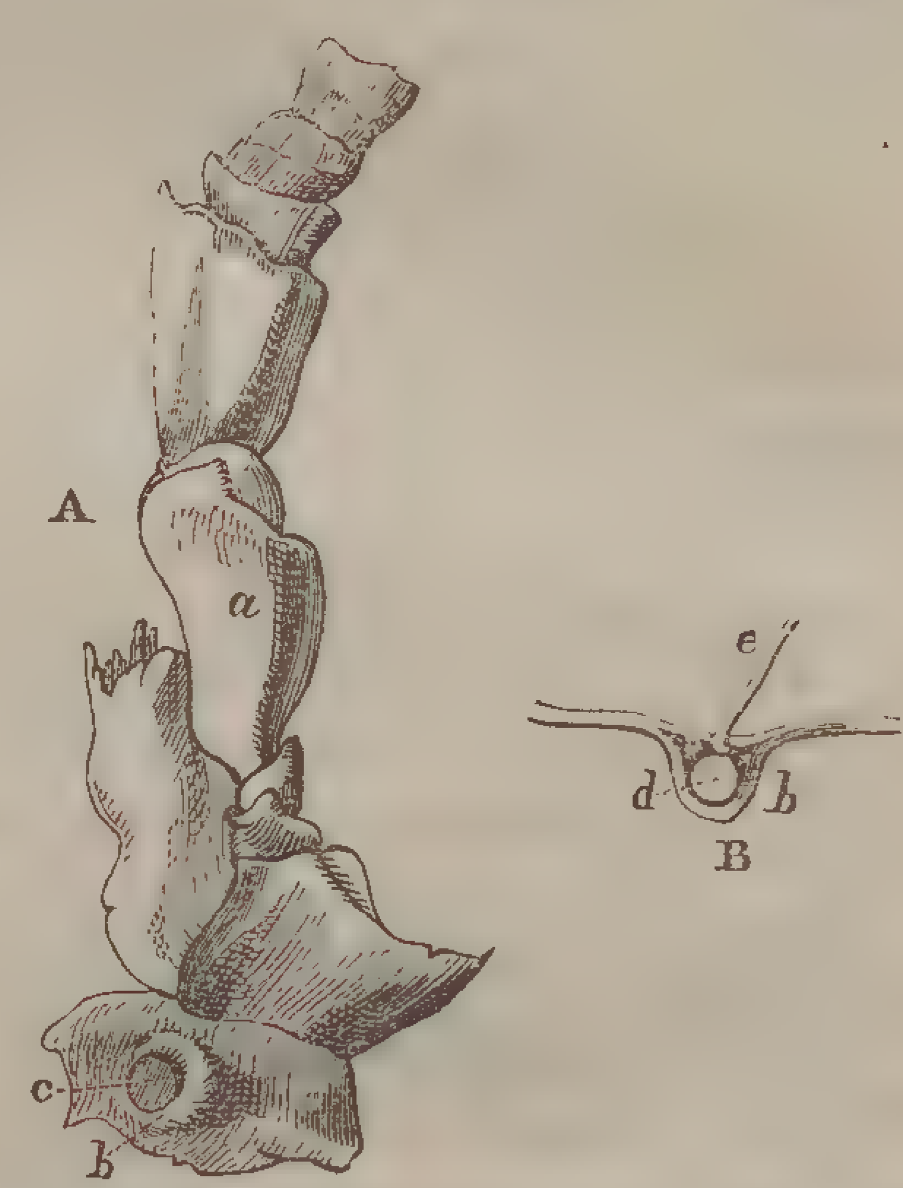
* Eisenlohr, loc. cit. p. 164.

† For an account of the parts regarded as organs of hearing in insects, see Comparetti, Obs. Anat. de Aure Interna Comparata; Patavii, 1789: Treviranus, Ann. d. Wetterauischen Gesellschaft, B. i. 2; Frankfort, 1809, p. 169: Ramdohr, Magazin d. Gesellschaft Naturforschender Freunde; Berlin, 1811, p. 389: J. Müller, Physiol. des Gesichts-sinnes, p. 437.

ous hard parts, and by a membrane lying freely exposed to the surrounding medium. This is the form of the organ of hearing in the Crustacea among the Articulata, and in the Cephalopoda among the Mollusca.

In the Crustacea this organ lies at the inferior surface of the head on each side, in the basilar segment of the outer great antenna. It consists of an osseous vestibulum, the external opening or fenestra of which is closed by a membrane analogous to the membrana tympani secundaria fenestræ rotundæ of the higher animals (fig. 125, A). In the interior of this osseous cavity lies a membranous sac filled with a watery fluid, upon which the auditory nerve is expanded (fig. 125, B).

Fig. 125.*



The Cephalopoda have a cartilaginous vestibule, which is a mere excavation in the cartilage of the head, devoid of fenestra or external tympanum-like membrane. This cavity encloses a membranous sac, over which the auditory nerve distributes itself. In the Octopus the inner surface of the vestibule is smooth; in the Sepia and Loligo it is beset with soft knots or processes, by which the interior vesicle is held suspended. Within the vesicle is a hard concretion or otolite.†

The organ of hearing in the Vertebrata is in no instance so simple as in these invertebrate animals. It was formerly thought that the Petromyzon resembled the Invertebrata in this respect; but my researches have shown that they possess a complicated labyrinth with two semicircular canals. In tracing the organ of hearing from fishes up to Mammalia, we find it present a progressive developement and increasing complexity.‡

In fishes the cochlea and tympanum of the higher Vertebrata do not exist; but they have the membranous labyrinth, — namely, the alveus s. sinus communis canalium semicircularium, (the oblong portion of the membranous vestibule or sacculus oblongus, into which the semicircular

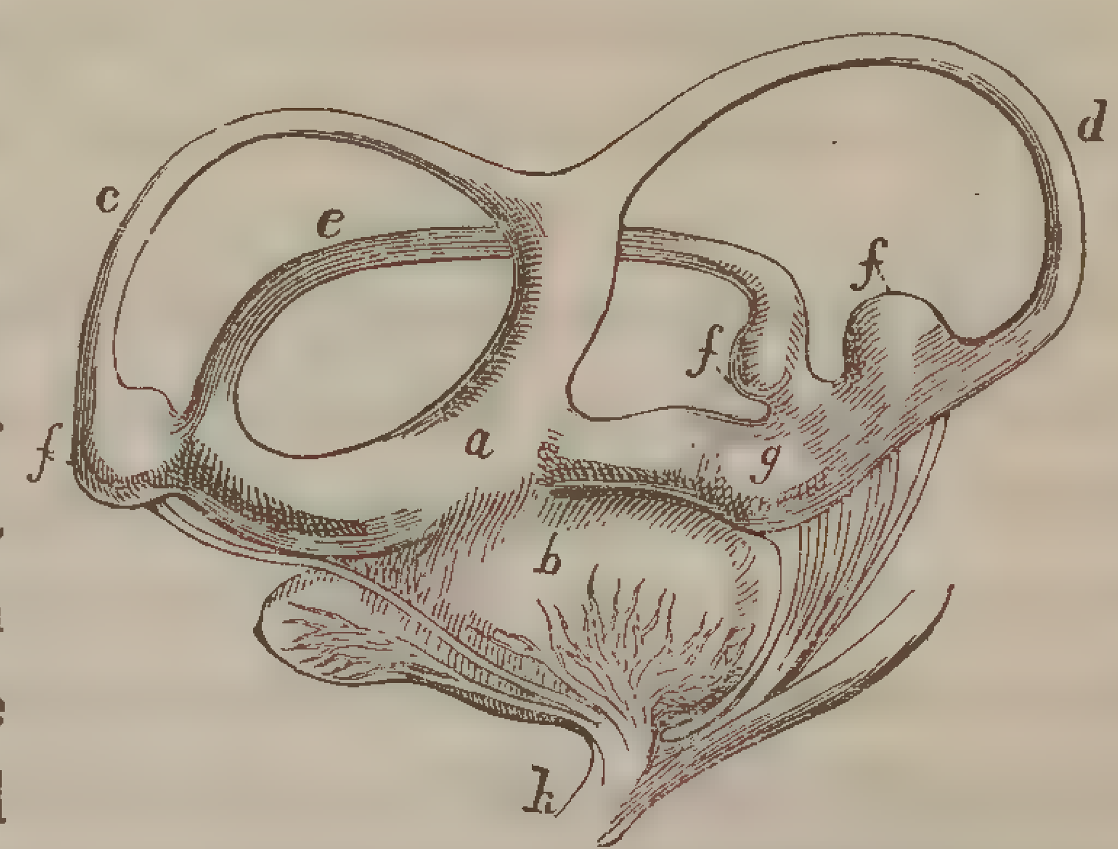
* [Organ of hearing of the Astacus fluviat. after Weber.—*a*. Antenna; *b*. papilla containing the organ of hearing; *c*. membrane of the fenestra; *d*. the membranous sac upon which the nerve, *e*, is distributed.]

† On the organ of hearing of the Astacus fluviatilis and Octopus, see Weber, De Aure et Auditu Hominis et Animalium. Lips. 1820, tab. 1, 2.

‡ The structure of the ear in vertebrate animals and man is fully considered in the works of Scarpa, De Auditu et Olfactu; Ticini, 1789: Weber, op. cit.: and Breschet, Recherches Anat. et Physiol. sur l'Organe de l'Ouie; Paris, 1836.

canals open,)—and generally the round saccular appendage of that part (sacculus rotundus), and the semicircular canals (fig. 126). This membranous labyrinth either is wholly enclosed in the cartilaginous mass of the skull, as in the cartilaginous fishes, — the Cyclostomata and Plagiostomata; or lies partly in the cranial bones, and partly in the cranial cavity between the brain and walls of the cranium, as in the osseous fishes, and the families of the sturgeon and Chimæra.

Fig. 126.*



The following are, however, more important differences relating to the forms of this organ in fishes :—

1. One semicircular canal only, which returns into itself so as to have an annular form, and of which one part,—that namely where the auditory nerve expands itself,—corresponds to the alveus communis of the vestibule. This form exists in the myxinoid fishes (Myxine and Bdellostoma), and was first observed by Retzius in the Myxine.

2. Two semicircular canals, each of which arises from the sinus communis by an ampulla with three elevations. The two canals lying upon the surface of that sac converge towards each other, unite in the form of arches, and at their place of union communicate again by means of a cleft with the sinus communis (or principal sac of the vestibule), which has in addition a sac-like appendage. This is the form of the organ in the Petromyzon and Ammocœtes.†

In these two forms of auditory apparatus no otolite exists in the labyrinth.

3. In the third form there are three semicircular canals issuing as in the higher animals, from a common vestibular sac. With this sac or sinus communis of the semicircular canals is connected a smaller sacculus, which is not analogous to the cochlea of the higher animals and man; for in them also the vestibular alveus communis has a sac-like appendage (the sacculus rotundus). Lying free in the cavity of both these sacs in fishes are either pulverulent concretions, as in

* [Organ of hearing of Lophius piscatorius, after Scarpa.—*a.* Sinus communis; *b.* the sac or sacculus rotundus; *c.* posterior semicircular canal; *d.* anterior semicircular canal; *e.* external semicircular canal; *f.* ampullæ of the canals; *g.* utricule of the sinus communis; *h.* nervous trunk from which branches are given to the sac, utricule and ampullæ.]

† See J. Müller, in the Report on the papers worthy of publication read at the Berlin Academy of Sciences, 1836; Archiv. 1836, lxxxiv.

plagiostomatous fishes; or hard stony bodies,—otolites or lapilli,—as in the osseous fishes.

In the Plagiostomata, (the rays and sharks,) a prolongation of the labyrinth extends to the surface, where it is covered merely by the skin.

In the sharks, the cavity of the cartilaginous vestibule merely is prolonged through the opening in the occipital portion of the skull, and reaches to the inner surface of the skin. In the rays, on the contrary, both the cavity of the cartilaginous vestibule and the membranous part of the labyrinth, are thus extended towards the surface. A hollow or depression in the middle of the occipital portion of the skull, which is covered by thin, or even by dense skin, has four openings, two on the right, and two on the left side: the posterior opening of each side communicates merely with the cartilaginous cavity of the vestibule, and is closed by a membrane; each anterior opening serves to allow the following communication with the membranous labyrinth. Between the two openings in the cranial bones and the skin lie two membranous sacs; the cavity of each of which communicates, by means of a canal which passes through the anterior opening in the cranial bones, with the sinus communis of the membranous labyrinth. This sinus auditorius externus and its canal are filled with carbonate of lime, which also exists in the form of a concretion in the alveus communis. From the part of the sinus auditorius which is united with the skin, three very minute canals pass through the skin to the surface of the body.* In the Chimæra, also, I found an opening in the cranium, and, corresponding with it, two attenuated spots of the skin; but the opening led into the cavity of the cranium, where a portion of the labyrinth is situated.

A communication of the osseous labyrinth with the external surface through the medium of openings in the cranium closed with membrane, is met occasionally in the osseous fishes also, but only as an exception to the ordinary structure, — for instance, in two species of Lepido-leprus, according to Otto,† (not in the Lepido-leprus Norwegicus,) and in Mormyrus cyprinoides, according to Heusinger.‡

Professor E. H. Weber first observed the connexion of the labyrinth with the air-bladder in many fishes.

In several genera,—as, Cyprinus, Silurus, and Cobitis,—this connexion is effected by means of a chain of small moveable bones. In the Cyprini, for example, the two membranous labyrinths, consisting of their alveus s. sinus communis, the semicircular canals, and the sac containing the calcareous body, are connected by continuity of membrane with a sinus impar, which lies concealed in the base of the occipital portion of

* Monro, On Fishes, 1785. — E. H. Weber, op. cit. tab. ix.

† Tiedemann's Zeitschrift für Physiologie, ii. pt. i. p. 86.

‡ Meckel's Archiv. 1826, p. 324.

the cranium: this sinus impar is prolonged backwards on each side into a membranous atrium, which, as it lies upon the surface of the first vertebra, receives a partial osseous covering. In contact with this atrium is the first of the small auditory bones, while with the last of these is connected the anterior extremity of the air-bladder.

In the Sparoid family (as, Boops and Sargus) the anterior extremity of the air-bladder sends forwards two canals, the blind ends of which become attached to special openings of the cranium which are closed with membrane.

In the Clupeæ the air-bladder is prolonged anteriorly into a tube, which then bifurcates. Each branch enters a bony canal in the occipital part of the cranium, and here again bifurcates; each of the small tubes which result from this division dilating at last within an osseous capsule. One of these capsules contains merely the blind extremity of the prolongation of the air-bladder; but in the other a prolongation of the membranous labyrinth comes into contact with that of the air-bladder.

In the genus Myripristis, also, a connexion is stated by Cuvier to exist between the air-bladder and the labyrinth. The cranial cavity is closed inferiorly merely by a membrane to which the air-bladder is attached.

The tympanum and Eustachian tube, and the sinuses communicating with the nostrils in the higher animals, the air-sacs of birds, and the air or swimming bladder of fishes, belong to one class of structures. They are all cavities filled with air and formed originally as diverticula from the respiratory and intestinal mucous tract, though at a subsequent period some of them continue to communicate with those cavities or mucous tracts by ducts or openings, while others become completely insulated from them, as is the case with the air-bladder of many fishes, the original communication of which with the pharynx is closed in the course of developement.

In reptiles and amphibia, as in all Vertebrata higher in the scale than fishes, the labyrinth has one or two external openings closed with a membrane,—fenestræ, which are either simply covered by skin and muscles without having connected with them a tympanic cavity, (a disposition which may be compared to the prolongations of the labyrinth subjacent to the skin in some fishes,) or are in relation with a tympanic cavity containing air. The membranous labyrinth is entirely enclosed within the bones of the cranium. The fluid of the labyrinth rarely contains any lapillus or otolite, though these are found in some instances, —namely, in those Amphibia which most resemble fishes, as Menobranchus: generally, however, there is merely a calcareous pulp composed of microscopic crystals.

The structure of the auditory apparatus presents considerable differences in these classes. Both among the Amphibia and the reptiles there are families in which the tympanic cavity is wholly wanting; but Amphibia are entirely distinguished from reptiles by having only one fenestra and no cochlea.

Amphibia have only the fenestra ovalis s. vestibuli, which is closed by a flat or conical stapes. The fenestra rotunda, or f. cochleæ, is, together with the cochlea, absent.

a. Some Amphibia have no tympanum. The only one of the small bones of the tympanum which they have is the flat plate of the stapes covered by muscles and the skin. The membranous labyrinth consists, as in most fishes, of the sacculus ovalis, or sinus communis of the vestibule, with three semicircular canals opening into it. Such is the structure in the Cæciliæ (Cæcilia and Epicrium), the Derotremata (Amphiuma and Menopoma), the Proteidea (Proteus, Menobranchus, Siren, Axolott, and probably also Lepidosiren), the Salamandrina (Salamandra and Triton), and in the family of Bombinator among the Batrachia or anourous Amphibia.*

b. Other Amphibia possess a tympanum. The membrana tympani here either lies free, or is concealed by the thick skin of the body; there are, besides, two or three ossicula auditus,—namely, the malleus, which is merely a small cartilaginous plate united with the membrana tympani, the bony incus, and the stapes. The Eustachian tube, a diverticulum from the cavity of the fauces, exists here, being always found where a tympanic cavity is present. The Amphibia which present this form of auditory apparatus are all the Batrachia, with the exception of the Bombinator family. These batrachian or anourous Amphibia differ, however, very much amongst themselves in the form of the external part of the auditory apparatus. They may, with reference to these differences, be classed under three heads.

1. Batrachia destitute of tympanic cavity, membrana tympani, and Eustachian tube. These are the Bombinator family, including the genera Bombinator (igneus); Cultripes, Muell. (C. provincialis); and Pelobates, Wagl. (P. fusc. Wagl. the Cultripes minor of Müller).

2. Batrachia with a membrana tympani, which is either visible externally, or is concealed under the skin, a tympanic cavity, which is for the most part membranous, three ossicula auditus, and Eustachian tubes opening into the fauces by distinct orifices. Such are most of the genera of frogs and toads,—for example, Rana, Bufo, Alytes, &c.

3. Frogs with cartilaginous membrana tympani, a tympanic cavity wholly bounded by bony parietes, two ossicula auditus, and Eustachian tubes opening together in the middle of the palate by a single orifice. This form exists only in the genera Pipa and Dactylethra. Of the three ossicula present in the former division of the Batrachia, the first

* See Windischmann, De Penitiori Auris in Amphibiis Structurâ; Bonnæ, 1831.

has here become metamorphosed into the cartilaginous membrana tympani; the second is a very long, bent, styliform body, to which the third is a scarcely perceptible lamella-like appendage closing the fenestra vestibuli.*

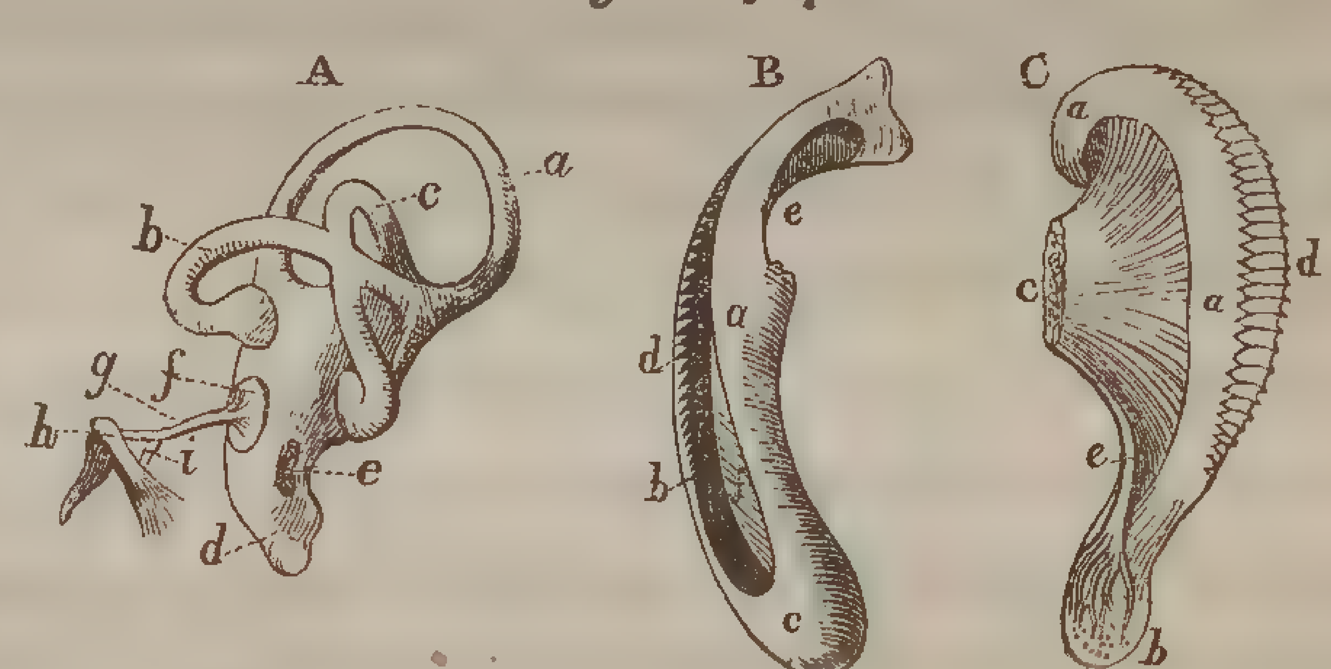
The reptiles have both the fenestra vestibuli and the fenestra cochleæ. The cochlea, except in the Chelonia (turtles and tortoises), has the same form as in birds.

The reptiles without tympanic cavity are the serpents, and also Chirotes, Lepidosternon, and Amphisbœna. The only one of the ossicula existing here is the stapes, which is prolonged into a style-like body of more or less considerable length (the columella). This, together with the fenestra, is covered by the muscles and skin.

The reptiles with tympanum and Eustachian tube are, the Chelonia, Crocodilida, and Lacertæ, as well as the Saurians devoid of extremities, which have eye-lids, — namely, Bipes, Pseudopus, Ophisaurus, Anguis, and Acontias. The columella exists here as in the former group, and is connected with the membrana tympani by means of a fibro-cartilaginous mass.† In most of these reptiles provided with a tympanum the membrana tympani is visible externally; but in some of the last-named genera it is covered by the skin.

In birds the organ of hearing (fig. 127, A) has in most respects — namely in the structure of the tympanum, columella, and cochlea, — the same conformation as in the Crocodilida and Lacertæ. The tympanum communicates with cavities in the cranial bones, which thus become filled with air, and increase the extent of surface, tending by resonance to render sounds more intense. The cochlea (fig. 127, B, C,) is not convoluted, but is a nearly straight canal, closed at its extremity, and divided by a very delicate membranous septum into two passages, the scala tympani, and the scala vestibuli. The septum is extended in a cartilaginous frame, which towards the blind extremity of the cochlea arches over in a pouch-like

Fig. 127.‡



* See J. Müller, in Tiedemann's Zeitschrift, iv. 2; and Müller's Archiv. 1836, lxvii.

† J. Müller, in Tiedemann's Zeitschrift, iv. 2.

‡ [Organ of hearing in birds.—A. General form of the organ of hearing in Corvus corax, magnified (after Breschet). *a*. Anterior semicircular canal; *b*. external canal; *c*. posterior canal (the osseous canals only coalesce as here represented; the membranous canals within are distinct); *d*. the cochlea; *e*. fenestra cochleæ; *f*. fenestra vestibuli closed by the base of the stapes, *g*.; *h*. malleus; *i*. small bone analogous to the incus.—B. Cartilage of the cochlea of the owl (after Huschke). *a*, *b*. The opposite portions of the

form, bearing the same relation to the septum that the upper leather of a slipper bears to the sole (fig. 127, B). The arch of this pouch, or lagena, (Huschke,) is continued along the whole length of the cochlea by a vascular membrane thrown into transverse plicæ (fig. 127, C). These folds are what Treviranus first described as isolated lamellæ, analogous to the keys of a pianoforte. The sacculus ovalis vestibuli, or sinus communis canalium semicircularium, and the flask or pouch-like part of the cochlea, contain a crystalline powder composed of carbonate of lime.*

Mammalia generally have an organ of hearing, which is not essentially different from that of man, and the varieties of form which it presents are not, for the most part, of such physiological importance as to render it necessary for us to describe them. The cochlea is always convoluted, and possesses a spiral lamella, formed partly of bone and partly of membrane, running round the central modiolus: the cochlea of the Ornithorhynchus, and that of the Echidna, are the only exceptions, resembling in all respects the same part in birds. The bony tympanum has in many Mammalia the form of a large osseous pouch, generally resulting from a developement of the os tympanicum. In many animals the cavity of the tympanum extends into other contiguous bones. In some there is also a second superior tympanum, formed by the pouch-like expansion of the os petrosum upwards and backwards; such a cavity exists, for example, in the genera Pedetes, Dipus, and Macroscelides. These are all means for increasing the extent of the cavities for resonance. The Cetacea and the Ornithorhynchus have no external ear; the Eustachian tube in the Delphinus family opens into the nasal cavity; and the external auditory passage of animals living entirely in the water is extremely narrow.

The ultimate distribution of the auditory nerve in the cochlea, and the observations of Treviranus and Gottsche relative to that subject, have been referred to at page 605. Just as the nervous fibres are spread out in the cochlea upon the lamina spiralis for the purpose of being in contact on both sides with the fluid of the labyrinth, so also in the ampullæ of the semicircular canals they are, as Steifensands has shown,† expanded upon a process, which, however, is not carried entirely through the ampulla, but merely projects into it. Into the ampulla of each semi-

cartilage; *c.* flask or lagena of the cartilage; *d.* dentations of the principal branch of the cartilage; *e.* situation of the fenestra ovalis; *f.* fine membrane closing the cleft between the branches of the cartilage.—C. Soft parts of the cochlea of Strix stridula (after Breschet). *a.* Cartilage; *b.* lagena, containing a calcareous pulp; *c.* cochlear nerve, sending through the cartilage numerous filaments, which issue by the dentations of its border, and contribute to form the plicæ of the arched membrane, *d.*; *e.* branch of the nerve going to the lagena.]

* See Windischmann, loc. cit.; Huschke, in Müller's Archiv. 1835, 335; Breschet, Ann. d. Sc. Nat. 1836; Müller's Arch. 1837, lxiv.

† Müller's Archiv. 1835, 171.

circular canal in Mammalia a transverse rounded body projects like an imperfect septum at the part corresponding to the expansion of the nerve on the ampulla.* In birds, a process with a rounded extremity projects upwards from this septum, and another similar one downwards; so that the whole resembles a cross, of which the transverse branches are fixed to the walls of the ampulla, the perpendicular branches free. In the tortoise, the rounded septum of the posterior ampulla has merely one boss-like prominence (umbo) in its centre. The septum of the anterior ampulla is placed transversely upon the parietes of the cavity, and has not this prominence: in the external ampulla only half of the septum exists. In crocodiles and lizards the external ampulla resembles that of the tortoise; the others have the septum of the cruciate form. In fishes the septum is a rounded transverse fold.

All the acoustic contrivances of the organ of hearing are means for conducting the sound, just as the optical apparatus of the eye are media for conducting the light. Since all matter is capable of propagating sonorous vibrations, the simplest conditions must be sufficient for mere hearing, for all substances surrounding the auditory nerve would communicate sound to it. In the eye a certain construction was required for directing the rays or undulations of light in such a manner that they should fall upon the optic nerve with the same relative disposition as that with which they issued from the object. In the sense of hearing this is not requisite. Sonorous vibrations having the most various direction and the most unequal rate of succession, are transmitted by all media without modification, however manifold their decussations; and, wherever these vibrations or undulations fall upon the organ of hearing and the auditory nerves, they must cause the sensation of corresponding sounds. The whole developement of the organ of hearing, therefore, can have for its object merely the rendering more perfect the propagation of the sonorous vibrations and their multiplication by resonance; and, in fact, all the acoustic apparatus of the organ may be shown to have reference to these two principles.

For the mere perception of sounds, therefore, neither membrana tympani, ossicula, cochlea, semicircular canals, nor even the vestibule and fluid of the labyrinth, are essential. Hence all these parts may be absent.

The organ of hearing of invertebrate animals is reduced to a mere sacculus; and in some Invertebrata even this is wanting, and the mere nerve, with the specific endowments, appears here to be all that is required. Every substance is capable of propagating undulations; and the body of an animal, and the parts immediately surrounding the audi-

* [Steifensands' figures of this structure in man will be found copied in Mr. Wharton Jones's art. Organ of Hearing, in the Cyclopæd. of Anat. and Physiology, which may be consulted with reference to the structure of the human ear generally.]

tory nerve, will receive them in the same order in which the conducting medium propagates them: it cannot, therefore, be maintained even that the distinction of the pitch and relative intensity of the sounds requires special apparatus. The distinctness and absolute intensity of the sounds will, however, increase with the acoustic developement of the organ.

The use and mode of action of this apparatus will be best learnt by following them from their simplest forms through the different stages of their developement in which new parts are added. We thus ascertain what parts are independent of others, and what parts necessarily co-exist with each other.

2. *Of the propagation of sound to the labyrinth in aquatic animals.*

In animals living in the atmosphere, and hearing through its medium, the sonorous vibrations of the air are communicated first to the solid parts of the body of the animal and of the organ of hearing, and by them to the fluid of the labyrinth. The intensity with which sounds are heard by these animals must, therefore, depend on the degree in which the solid parts of the organ of hearing are susceptible of the vibrations communicated to them by the air, and on the degree of diminution which the excursions of the vibrating particles suffer in the passage of the vibrations from the air to the solid external parts of the organ of hearing, and further on the degree of facility with which vibrations can be communicated by these external parts of the auditory apparatus to the fluid of the labyrinth. The whole external part of the auditory apparatus is calculated, as we shall see, to render less difficult the communication of sonorous vibrations of the air to solid bodies.

In animals living in the water, and hearing sound through its intervention, the problem is a very different one. The medium by which the sonorous vibrations are conducted to the animal is here the water: it communicates them to the solid parts of the body of the animal, whence they are in turn transmitted to the fluid of the labyrinth. The intensity with which the sound is heard depends, in this case, on the degree in which the solid parts of the organ of hearing, through which the sonorous undulations must first be transmitted, are capable of receiving the undulatory movement from the surrounding water, and of imparting it again to the fluid of the labyrinth, and on the degree in which the excursions of the vibrating particles are diminished in the transition of the vibrations from the one medium to the other. We shall see here also that the whole external portion of the auditory apparatus is calculated to facilitate this transition of the vibrations.

Undulations being communicated from the air to solid bodies, and from water to solid bodies, with very unequal intensity, and their transition from the one medium to the other being facilitated by very different means in the two cases, it has been necessary for nature to employ very different apparatus in forming the external portion of the organ of hearing in animals hearing sounds through the medium of the air, and in those to which water is the conducting medium; while the internal parts of this organ have a much more uniform construction.

The problem to be solved in the case of aquatic animals is in general simpler than that which presents itself in reference to the hearing of animals living in the air. In the former the sound is propagated to the auditory nerve by three media in succession, of which two, however, are of the same nature: 1, the water in which the animal lives; 2, the solid parts of the animal's body, and of the organ of hearing; and 3, the fluid of the labyrinth. In animals living in the atmosphere the sonorous vibrations are communicated by three media in succession, which are all different: namely, the air; the solid parts of the body of the animal, and of the auditory apparatus; and the fluid of the labyrinth. For this, and no other reason, is the organ of hearing generally more complicated in the latter animals. The organ of hearing of aquatic animals, as fishes, being ordinarily wholly enclosed by solid structures, the first question which presents itself respects the transition of sonorous undulations from water to solid bodies, and from these to water (the fluid of the labyrinth). We know that, in the transition of sonorous undulations from air to solid bodies, a considerable diminution of the excursions, or impulses of the vibrating particles, takes place; while the undulations are communicated from air to air, or from one solid body to another, without any diminution of their intensity. The full sound produced by a solid body vibrating, such as a string without a sounding-board, is only heard when it is conducted to the solid parts of the ear by means of a solid medium,—for instance, by a rod interposed between the bridge over which the string is stretched, and the external ear, the meatus of which is filled with a solid substance. If merely the air intervenes between the solid body which is the source of the sonorous vibrations and the ear, the sound heard is feeble; for the communication of the vibrations of a solid body to the air is attended with diminution of the excursions of the vibrating particles, or of the impulse. On the other hand, the sonorous vibrations of a body of air, such as that of a wind-instrument, are propagated and communicated to the ear with their full intensity by the atmosphere; but are imparted with difficulty, and only with a diminution of their force, to solid bodies. Hence the sound of a pipe is not heard better by placing a rod reaching to the vicinity of the sonorous column of air in apposition with the ear plugged with a solid substance. Does the same difficulty prevail in the transition of undulations from water to solid bodies? Is a diminution of their intensity here also the result?

This subject has not hitherto been at all investigated. The imperfect state of the acoustics of the auditory apparatus, which can indeed be scarcely said to have existed hitherto, led me to institute a series of experiments relative to this point, the results of which I shall now state.

I. *Sonorous vibrations excited in water are imparted with considerable intensity to solid bodies.*—This is shown by the following experiment:—A basin of glass, porcelain, or wood, is filled to the brim with water, on the surface of which a shallow vessel is made to float without touching the basin. A sound is produced in the floating vessel by dropping some solid body into it. If the ears are firmly stopped by means of plugs of twisted paper, of which the end that is inserted into the auditory passage has been previously chewed, while the other end projects from the ear, a sound produced by a solid body is heard through the medium of the air very indistinctly; but by the intervention of a rod of wood, or, what is better, a glass tube which is held in contact with both the sounding body and the plug in the ear, with very great distinctness and loudness. If, now, the glass rod still held in contact with the plug in the ear be immersed in the water of the basin while a body is dropped into the vessel floating on its surface, a loud and clear sound, such as a blow applied to that vessel always produces, is heard; and the sound thus heard is much louder than when transmitted to the ear through the medium of the atmosphere only. In this case, the sonorous vibrations are communicated from the floating cup or solid body to the water, and from the water again to the glass rod, and thus to the ear. Two things are here proved, namely, that solid bodies communicate their sonorous vibrations with great intensity to water, and, more than this, that water imparts them again very readily to solid bodies,—for instance, to the rod which conducts the sound to the ear. The result of the experiment is much the same, whether the rod be held in the water, or in contact with the walls of the basin containing it. The sonorous undulations communicated to the water are transmitted by it to the rod either directly or through the intervention of a second solid body. The sound heard may indeed be somewhat louder in the latter case, from the resonant action of the basin coming into play.

II. *Sonorous vibrations of solid bodies are communicated with greater intensity to other solid bodies brought into contact with them, than to water, but with much greater intensity to water than to atmospheric air.*—This may be readily shown by the foregoing experiment. The sound produced by the body falling into the floating vessel is heard with greatest loudness when the rod held in contact with the plug in the ear is lightly applied by its other extremity to the floating vessel itself. The sound is much fainter when the rod is immersed in the surrounding fluid, but it is much more feeble still when transmitted by the air alone to the plugs in the auditory passages.

III. *Sonorous vibrations are communicated from air to water with great difficulty, with very much greater difficulty than they are propagated from one part of the air to another; but their transition from air to water is much facilitated by the intervention of a membrane extended between them.*—That sounds produced in the air are heard in the water is a fact long known; but a new fact which I have observed, namely,—that a membrane extended between water and air, which are in contact with its two surfaces respectively, facilitates in an extraordinary degree the communication of sonorous vibrations from the air to the water,—appears to me to be of great interest. If, while my ears are plugged, I cause a metal or wooden mouth- or flute-pipe one foot in length, and destitute of side openings, to be sounded, the lower end of the pipe being at the time immersed in water, the sound which I hear by means of the rod, also immersed in the water and in contact with the plug of one ear, is very feeble even when the pipe is held perpendicularly in the water, so that the undulations of the air strike upon the fluid in that direction. If, however, a piece of thin membrane, as pig's bladder, is tied over the lower opening of the pipe, not very tensely, the sound which reaches my ear by the same means as before, when the pipe is blown, is very loud; particularly if the rod which conducts the sound to the ear is held in the direction of the undulations, that is, in the line of the pipe. The sounds thus heard are very sonorous. The lowest or fundamental note, or one of the middle notes of the pipe, is best suited for the experiment. The rod used to conduct the sound to the ear is a rod of wood, or, still better, a glass tube six or eight lines in diameter, which is held at right angles in the line of direction of the sonorous vibrations of the water. If the rod, while in contact with the ear by its upper extremity, be moved to and fro in the water, the sound of the pipe will be found to increase in intensity (swells) each time that the rod passes in front of the membrane covering the lower mouth of the pipe. This contrivance is indispensable in all the subsequent experiments on hearing in the water, and on the acoustic properties of the different parts of the organ of hearing; it has been of the greatest use in my researches, and without it I should have arrived at no results. The higher or more acute notes of pipes are heard with but little or no increase of intensity by this means. The experiment proves, at the same time, that the undulations in water, as in air, though in general circular or spherical in form, are nevertheless more intense in the direction corresponding to that of the original impulse.

IV. *Sonorous vibrations are not only imparted from water to solid bodies bounded by definite surfaces which are in contact with the water, but are also returned with increased intensity by these bodies to the water, so that the sound is heard loudly in the vicinity of those bodies in situations where, if it had its origin in the conducting power of the water alone, it* *would be faint.*—In the experiment described in the preceding paragraph, the sound of the pipe, closed at its lower extremity by a membrane, was heard by means of the conducting-rod with great distinctness when water merely was interposed between the end of the pipe and the conductor, this conductor being placed in the line of the direction of the pipe. The sound is also heard with equal, or nearly equal intensity, when a thin lamina of wood is placed between the rod and the pipe; in which case the sonorous undulations have to pass from the water through this septum, and then through water again before they reach the conductor. But not merely is this the case at the part corresponding to the line of direction of the pipe; the sound is also loud in the vicinity of all parts of the surface of the wooden septum, even at a considerable distance from that line, and where it is heard faintly only when the wooden septum is removed. At all parts of this plate of wood the sound is heard louder than elsewhere in the water contained in the basin. If the basin itself be of wood, increased intensity of the sound can be perceived when the conducting rod is brought near its internal surface.

V. *Sonorous undulations propagated through water are partially reflected by the surfaces of solid bodies.*—This fact, which is of assistance in explaining the acoustics of the labyrinth of the ear, may be verified by means of the simple apparatus already frequently described. The ears being plugged as before, the pipe closed at its lower extremity by membrane is immersed in the water of a large basin; a glass cylinder, six inches in length, closed below and filled with water, is also immersed in the water of the basin, and held there by an assistant with both hands in such a manner that it does not touch the basin at any part. The end of the pipe being now introduced into the mouth of the cylinder, and its fundamental note elicited by a feeble blast, while the conductor is held near the mouth of the cylinder, but without coming into contact with it or the pipe, as loud a sound is heard as when the conducting-rod is held opposite the end of the pipe. This intensity of the sound is the result of reflection by the internal surface of the cylinder, and not merely of the resonance of its walls; for the intensity of the sound heard, as above described, is not diminished though the resonant power of the walls of the cylinder be lessened as much as possible by covering its internal surface with a layer of tallow, and by damping the vibrations of its walls externally by embracing it with both hands. Moreover, the sound heard by placing the rod in the water on the exterior of the cylinder is much fainter.

VI. *Thin membranes conduct sound in water without any loss of its intensity, whether they be tense or lax.*—A membrane interposed in the water between the end of the pipe and conducting-rod, which was held in the line of the pipe, caused not the slightest difference in the intensity of the sound; which was loud in this situation, namely, opposite the end of the pipe, but feeble in all other parts. The membranous septum first used was tense, being formed by stretching a piece of pig's bladder over a large ring; but lax membranes, merely suspended in the water, afforded the same result. Even when several, namely, from four to eight layers of the bladder, which had been dried and again soaked, were laid one upon another, and pressed together so as to expel the air, and the septum, thus formed, interposed between the end of the pipe and the conducting-rod, some increased intensity of sound could still be remarked as the rod came opposite the end of the pipe, that is, in the direction of the impulses of the column of air in it. An addition of several thicknesses of the membrane entirely prevented this being perceived. A portion of human skin, and a piece of the wall of a pregnant uterus three lines in thickness, had the same effect; and the sound, as heard behind the screen thus formed, was not louder than in any other part of the water out of the direction of the strongest undulations.

VII. *The paragraphs* III. IV. *and* VI. *afford an explanation of the process by which the sound is conducted to the ear in aquatic animals not breathing atmospheric air.*—When we plug our ears very tightly, and use a rod of wood as a conductor of the sonorous vibrations from the water, we place ourselves entirely in the condition of the fish with respect to the hearing of sounds. Immersion of the head in the water is not necessary, nor is it calculated to allow of an undisturbed observation of the result. The solid conducting-rod forms a prolongation of the solid parts of our body, and brings them into immediate communication with the sonorous undulations of the water, as in the fish. The simple or compound labyrinth of aquatic animals is either wholly enclosed in the bone or cartilage of the cranium, as in the cyclostomatous and osseous fishes and the Sepiæ; or, its cavity being prolonged to the surface of the body, it is there brought into communication with the conducting medium by means of a membrane, besides receiving the vibrations through the medium of the solids of its body, which is the case in the plagiostomatous fishes and in the Crustacea, where the auditory sac is covered at one part merely by a membrane. The cranial bones are also capable of resonance, that is to say, the vibrations communicated to them are increased by reflection within them by their surfaces; and these reflected vibrations, as well as those directly communicated from without, are propagated to the labyrinth. This is illustrated by the facts stated in paragraph IV. In the plagiostomatous fishes (sharks and rays), which have a soft cartilaginous skeleton, this increase of the sound by resonance in the walls of the cranium may possibly be less considerable than in the osseous fishes; and it is on this account, probably, that the prolongation of the labyrinth to the surface of the body in the former was necessary. In the cyclostomatous cartilaginous fishes (as the myxine and lamprey), the auditory sac belongs wholly to the solid parts of the skeleton, and in them it is also covered by muscles which must tend to deaden the sonorous vibrations propagated to it.

VIII. *When sonorous vibrations are communicated from water to air enclosed in membranes or solid bodies, a considerable increase of the intensity of the sound is produced by the resonance of the air thus circumscribed.* The pipe, closed by membrane at its lower extremity and immersed in water, was sounded by an assistant, while I conducted the sonorous vibrations to my ear (stopped as before) by means of a conducting-rod. The air-bladder of a fish (Cyprinus Erythrophthalmus; German Plötze) was now held in the water, between the end of the pipe and the conductor, but so as to be in contact with neither; when, the pipe being sounded again, the sound heard was much louder than before, though the distance of the conducting-rod from the end of the pipe remained the same. This experiment proved, first, that with the intervention of membranes sound is transmitted very readily, and without any loss of intensity, from water to air, and again from air to water; and, secondly, that if the air be enclosed in a membrane surrounded on all sides by water, the resonance of the body of air thus isolated, that is, the partial reflection of the sonorous undulations at the surfaces of the air, and consequent production of stronger undulations, gives rise to a considerable increased intensity of the sound.

IX. *A body of air enclosed in a membrane, and surrounded by water, also increases the intensity of the sound by resonance when the sonorous undulations are communicated to it by a solid body.*—The air-bladder of the same fish was fixed in the cleft of a rod of wood; this rod was held firmly in contact with the walls of a basin filled with water, into which the air-bladder projected; a vibrating tuning-fork was then brought into contact with the edge of the basin, while I applied a conducting rod immersed in the water to one of my ears, which were plugged as in the other experiments. The result was, that the sound heard was very much louder when the rod was brought near the air-bladder, than when it was at any other part of the water equally distant from the source of the sound; it was as loud, indeed, near the air-bladder as it was near the sides of the basin.

According to the laws of the propagation of sound in the atmosphere, this resonance of a body of air should be greater in proportion to the degree of its condensation, since the intensity of sonorous undulations in a gaseous fluid increases in direct ratio with its density, and the sound of a bell in the receiver of an air-pump becomes fainter and fainter as the air is rarefied, until at length it ceases to be heard. In direct experiments, however, condensation of the air in the air-bladder of a fish seems to produce little difference in the degree of resonance. I performed the experiment as before, with the difference only of fixing the air-bladder to the pipe of an air-tight syringe, by which the air in the bladder could be much condensed. The air-bladder, being invested by an external fibrous or tendinous coat, yields scarcely at all to the distending force.

X. *From the foregoing observations we may conclude that the air-bladder of fishes, in addition to other uses, serves the purpose of increasing by resonance the intensity of the sonorous undulations communicated from the water to the body of the fish.*—The sonorous vibrations of the water are communicated to the air of the air-bladder partly through the soft parts of the fish's body, and partly through the medium of the bones, namely, the vertebræ, beneath which it lies; and it becomes the source of sonorous undulations, increased in intensity by resonance, which are in turn imparted from it to the surrounding parts, especially to the bones. It cannot, therefore, be denied that the air-bladder of fishes, even when it is not connected with the auditory apparatus, must contribute in some degree to render the impression of sound on the organ of hearing stronger; but where there exists a connexion of the air-bladder with the labyrinth, either through the medium of a chain of small auditory bones, or by a prolongation of the air-bladder itself, this viscus must have a most intimate relation with the organ of hearing, acting as the multiplicator, condensor, and conductor of the sonorous undulations imparted by the water to the whole body of the fish. In the genus Cobitis this seems to be the chief function of the air-bladder, which is very small,—lies, in greater part surrounded by bone, in a pouch-like excavation of the second vertebra,—and is anteriorly brought into connexion with the labyrinth by the small auditory bones.

The conducting and resonant power of the air in the air-bladder being greater in proportion to its density, the influence of this organ on the perception of sounds will, of course, be greater in deep waters, where the pressure upon it is considerably increased.*

In the Amphibia which live in water, as the Proteidea, the Amphiuma, Menopoma, and Bombinator families, the sonorous undulations are conducted to the labyrinth, not merely through the bones of the head, but also through the medium of a fenestra; which is not, however, merely closed by the skin as in plagiostomatous fishes (sharks and rays), but has a moveable operculum, the lamina of the stapes, which is connected to the margins of the opening by membrane. This fenestra of the labyrinth is, like the bones of the head generally, covered with muscles and skin. The degree in which such a structure will assist hearing in the water may be ascertained by experiment with

* J. Müller, Physiologie des Gesichts-sinnes, 1826, p. 441.—Compare Carus, in the Report of the Proceedings of the Meeting of Naturalists (Bericht über die Versammlung der Naturforscher) in Jena; Weimar, 1837.

a similar artificial contrivance. Its principal use is, however, for hearing in the air, not in the water, as will be shown at a future page; for hearing in the water this structure of the fenestra would not have been required. The Amphibia in which it exists live both in the air and in the water.

3. *Of the propagation of sound to the labyrinth in animals living in the air.*

The propagation of the sonorous vibrations from the surface of the body to the fluid of the labyrinth, requires in an animal living in the air a much more complicated apparatus than in an aquatic animal, in consequence of the transition of the vibrations from air to the solid parts which surround the organ of hearing and the fluid of the labyrinth being attended with much greater difficulty than the transition of the vibrations from water to solid bodies. Accordingly, in most animals living in the air, the labyrinth has two fenestræ, of which one is closed by a membrane, the other by a solid operculum. Most of these animals have also a tympanum and Eustachian tube, and a double means of conducting the sound from the exterior to the labyrinth,—namely, a chain of solid bodies, the ossicula auditus, interposed between the membrana tympani and the fenestra ovalis of the labyrinth; and the air of the tympanum, which conducts the vibrations from the membrana tympani to the membrane of the fenestra rotunda. The dispute which has occupied physiological writers, as to which of these is the true conducting medium of the sound, has no scientific grounds. The air, membranes and small bones of the ear, are all capable of conducting sonorous vibrations, and they do respectively what their physical properties adapt them for. The propagation of the sound in two different ways simultaneously must necessarily strengthen its impression. The laws by which the propagation of sound from the exterior to the labyrinth of animals living in the air are regulated, have not hitherto been determined. We shall, therefore, investigate the subject as fully as we have done that of the process of hearing in aquatic animals.

To learn the acoustic value of each part of the apparatus, it is requisite to study them in the order of their progressive developement.

The propagation of sound to the fluid of the labyrinth in animals destitute of tympanum is seldom left to the conducting power of the cranial bones alone. Sonorous vibrations are imparted too imperfectly from air to solid bodies, for the propagation of sound to the internal ear to be adequately effected by that means. In nearly all animals living in the air, even in those which have no tympanum, the labyrinth has an opening, or fenestra, towards the exterior, which, when the tympanum is absent, is covered by the skin and muscles. In the genera Rhinophis and Typhlops only did I find both fenestra and ossicula auditus wanting.

I. *Sonorous undulations, in passing from air directly into water, suffer a considerable diminution of their strength ; while, on the contrary, if a tense membrane exists between the air and the water, the sonorous undulations are communicated from the former to the latter medium with very great intensity.*—This is the fundamental fact from which we start. The proof of it is contained in the experiment already described in paragraph III, page 1241. We have in this fact at once an explanation of the use of the fenestra rotunda, and of the membrane closing it. They are the means of communicating in full intensity the vibrations of the air to the fluid of the labyrinth, whether the tympanum exist or not. The thin membrane of the fenestra is in serpents not immediately in contact with the atmosphere, but is covered with skin and muscles: but these coverings do not essentially impede the transmission of sound; for, in the experiment just referred to, I found that, when the mouth of the pipe was covered with several layers of the pig's bladder, the fundamental note of the pipe, being sounded, was heard much more distinctly by means of the conducting-rod placed in the water, than when the mouth of the pipe was closed by a solid plug. This peculiar property of membranes is the result, not of their tenuity alone, as will be readily conceived, but of the elasticity and capability of displacement of their particles. In passing from the air into a solid body, sonorous vibrations are at once rendered feeble, whether the solid body itself be thick or thin; for the impediment to the propagation of the vibrations exists at their very transition from the one medium to the other. A membrane cannot therefore, with respect to its influence in communicating sound from air to water, be regarded merely in the light of a very thin body. It is owing to the extensile property of membrane that sonorous undulations are so readily communicated to it from air, as though it were itself air; and that it so readily imparts them again to water, as though it were water.

It is, moreover, not necessary that the membrane be impregnated with moisture; the membrane covering the end of the pipe may be dry, and yet the sound transmitted by it, before it has become softened by the water, will be loud. This fact finds its application in the membrane of the fenestra rotunda in animals provided with a tympanum.

II. *The sonorous vibrations are also communicated without any perceptible loss of intensity from the air to the water, when to the membrane forming the medium of communication there is attached a short solid body, which occupies the greater part of its surface, and is alone in contact with the water.*—This fact elucidates the action of the fenestra ovalis, and of the moveable plate of the stapes which occupies it in animals living in the air, but destitute of tympanum and membrana tympani. To the membrane stretched loosely over the end of the pipe I glued a circular piece of cork half an inch in length, and so broad as to cover the membrane to within a line of its edge. The pipe being now immersed in water, and its fundamental note sounded, I heard by means of the conducting-rod held in the water in the line of the pipe, (my ears being closed by plugs,) a sound which was nearly as loud as when the end of the pipe was closed by the membrane alone. The difference was immediately perceptible if the conductor was moved out of the line of the pipe; the sound heard became then much fainter. If, on the contrary, the lower end of the pipe was completely closed by a plug, no perceptible increase in the intensity of the sound could be perceived when the conducting-rod was brought opposite the mouth of the pipe. Whence it results that the same solid body, when separated from the pipe, and rendered mobile by a narrow portion of membrane left free around it, permits a transmission of sound with considerable intensity, but when firmly fixed in the mouth of the pipe, becomes a direct impediment to the passage of sound.

These observations prove that both fenestræ—that closed by membrane only, and the other with which the moveable stapes is connected—transmit very freely the sonorous vibrations from the air to the fluid of the labyrinth.

Of the animals living in the air, and destitute of tympanum, the Bombinatores, the land Salamanders, and the Cæciliæ have only the fenestra ovalis, or that closed by the osseous operculum. Serpents, on the contrary, have both fenestræ.

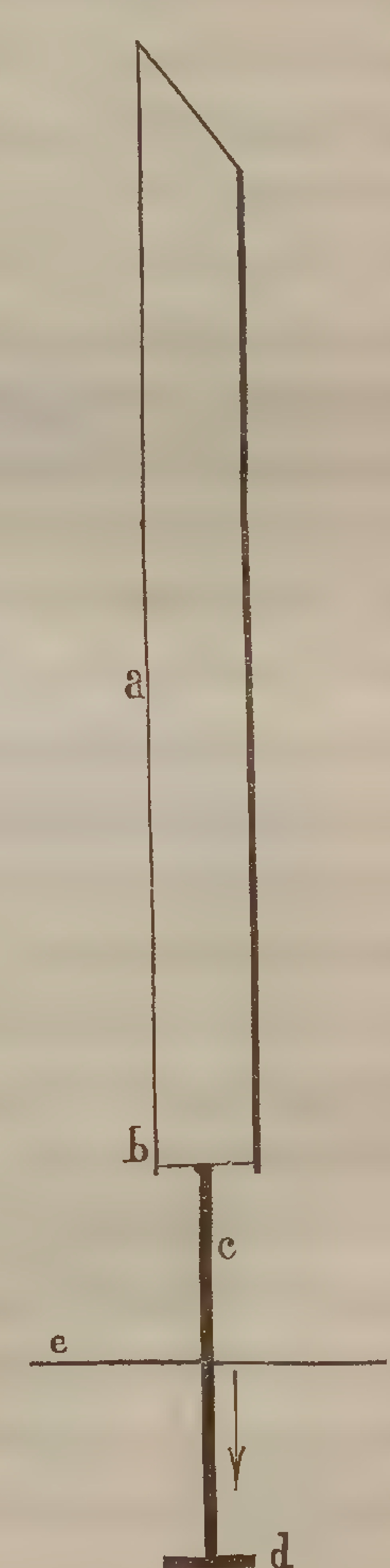
Propagation of sound by the membrana tympani and ossicula auditus.

III. *A small solid body, fixed in an opening by means of a border of membrane, so as to be moveable, communicates sonorous vibrations, from air on one side, to water, or the fluid of the labyrinth, on the other side, much better than solid media not so constructed. But the propagation of sound to the fluid is rendered much more perfect if the solid conductor thus occupying the opening (fenestra of the labyrinth) is by its other end fixed to the middle of a tense membrane which has atmospheric air on both sides.*

Vibrations of the air are communicated to solid bodies with difficulty, and with a considerable diminution of their intensity; but a membrane is readily thrown into motion by them. Savart has shown that membranes of small extent, as the membrana tympani itself, even when made tense, are so affected by sonorous vibrations excited in their vicinity as to cast off sand which is strewed over their surface. It may also be proved by direct experiment, that a tense membrane is a much better conductor of the undulations of air than any other solid bodies bounded by definite surfaces; and, what is equally essential, that the vibrations are also communicated very readily by a tense membrane to solid bodies in contact with them. The membrana tympani has not hitherto been considered under this point of view, namely, as the means of transmitting sound from the air to the chain of auditory bones. To elucidate this part of the subject, I performed the following experiments :—

A very thin membrane (paper) extended over the mouth of a cup, or similar vessel, is thrown into such vibrations when a vibrating tuning-fork is brought near it, that small bodies, such as seeds of Lycopodium, do not rest upon its surface. The vibrations of the air are, however, communicated also with great facility or intensity from the tense membrane to solid bodies which touch it at any point. If, for example, one end of a flat piece of wood be applied to the membrane of a drum while the other end is embraced by the hand, the vibrations or tremors are felt distinctly when the vibrating tuning-fork is held over the membrane without touching it; while the lamina of wood alone, isolated from the membrane, would, under otherwise similar conditions, propagate the vibrations of the air to the hand very feebly. In the following experiment the complication arising from the resonance of the air contained in the drum is avoided. A portion of very thin paper was stretched over a ring, and the ring held in one hand while the tuning-fork was approximated to the paper: the tremors were felt distinctly. The paper being removed, no vibrations could be perceived, even though the tuning-fork was brought very near to the ring.

Fig. 123.

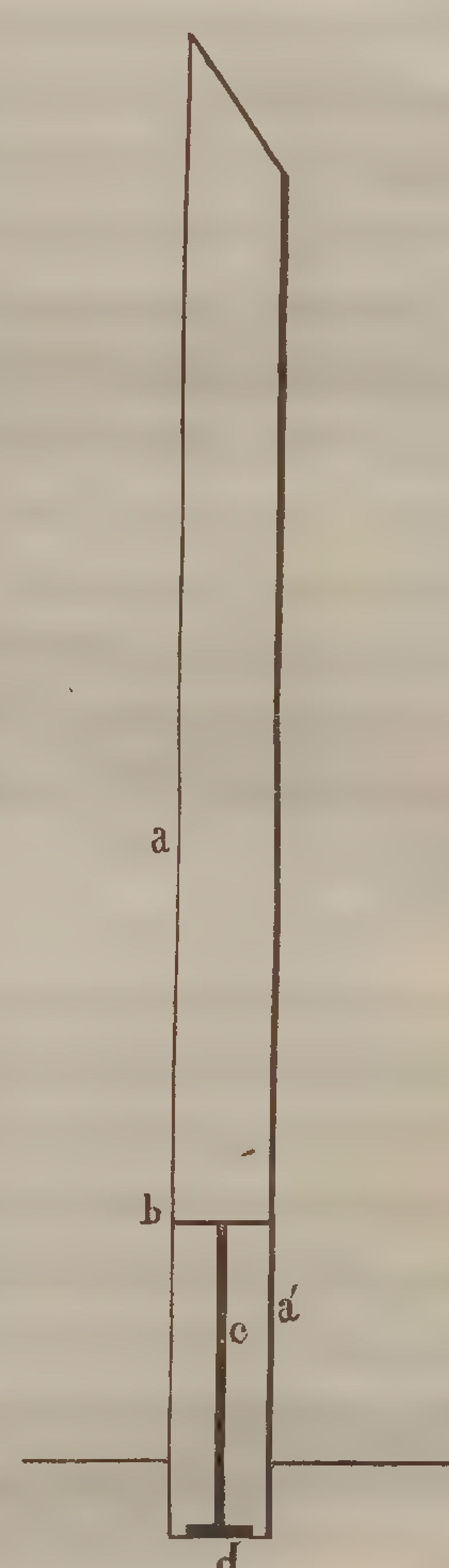


The influence of the membrana tympani in causing the sound to be transmitted with great intensity by the chain of ossicula of the ear, is rendered manifest still more clearly by the following experiment :—

Over the extremity *b*, of a pipe one foot in length (*a*), was stretched a thin dry membrane (pig's bladder). To the middle of the membrane was glued a small piece of cork, which had attached to it a small rod of wood, *c*, while the other end of this rod was fixed in a disk of cork, *d*. The end of the rod was immersed in water (*e*), and the fundamental note, or one of the middle notes of the pipe, sounded. The ears being stopped, as in the experiments before described, and one end of a conducting-rod (a glass tube of the diameter of half an inch) applied to one ear, while the other end was moved about in the water, it was found that in a direction perpendicular to the surface of the lamina of cork, *d*, the sound was extremely loud, but in all other parts of the fluid much fainter.

In this experiment we could also satisfy ourselves that the strongest undulations were propagated in the longitudinal direction of the wooden rod, *c*. For when the glass conductor, still in the water, was brought near the rod, *c*, from the side, the sound heard, although loud, was not near so intense as in a direction perpendicular to the disk of the cork, *d*. If, in place of the membrane covering the end of the pipe, a plug of cork, inserted tightly, is substituted, the rest of the apparatus being the same, the sound is very slightly if at all louder in the direction of the rod,—that is to say, in a direction perpendicular to the plate of cork, *d*, than in other parts of the fluid.

Fig. 129.



The structure of the tympanum may be more exactly imitated on a large scale. Let *a* (fig. 129) be the pipe corresponding to the external meatus. A wooden tube, *a′*, which can be fixed to the end of the pipe, and which has a membrane, *b*, corresponding to the membrana tympani, stretched over that end which is contiguous to the pipe, represents the cavity of the tympanum: a rod, *c*, is fixed by its upper extremity to the membrane, *b*, and by its lower to a disk of cork, *d*, which is glued firmly to a membrane covering the lower end of the tube, *a′*, in such a manner that it is connected with the tube by a border of membrane a line in breadth; this disk of cork, *d*, and the rod, *c*, represent the stapes moveably attached in the fenestra ovalis. The lower end of this apparatus being immersed in water, and the pipe sounded, a conducting rod placed in the water opposite the end of the tube, or opposite the stapes, communicates to the stopped ear a sound as loud as was heard in the previous experiment.

The ossicula of the ear are the better conductors of the sonorous vibrations communicated to them, on account of being isolated by an atmosphere of air, and not continuous with the bones of the cranium; for every solid body thus isolated by a different medium propagates vibrations with more intensity through its own substance than it communicates them to the surrounding medium, which thus prevents a dispersion of the sound, just as the vibrations of the air in the tubes used for conducting the voice from one apartment to another are prevented from being dispersed by the solid walls of the tube. The vibrations of the membrana tympani are transmitted, therefore, by the chain of ossicula to the fenestra ovalis and fluid of the labyrinth, their dispersion in the tympanum being prevented by the difficulty of the transition of vibrations from solid to gaseous bodies. The membrana tympani being a tense solid body bounded by free surfaces, the sonorous undulations will be partially reflected at its surfaces, so as to cause a meeting of undulations from opposite directions within it; it will therefore, by resonance, increase the intensity of the vibrations communicated to it, and the undulations thus rendered more intense will act in their turn upon the chain of auditory bones.

We have now to investigate the nature of the vibrations of the membrana tympani. Are they undulations of inflexion, like the transverse vibrations of strings and membranes? or are they undulations of condensation? An impulse communicated to a string or rod in the direction of its length gives rise merely to progressive waves of condensation, not to vibrations of the string or rod from side to side. But if a sufficiently thin body, as a string or membrane, receives an impulse in a direction perpendicular to its length or to its surface, undulations of inflexion are also produced. If the impulse affects one point only of the string or membrane, the flexion-waves are propagated from this point to the extreme limits of the body, and then reflected back again like undulations on the surface of water; if the body is displaced in its whole extent by the impulse, transverse vibrations of inflexion of the entire body are the result. The question to be decided then is, whether such vibrations of inflexion are produced in membranes propagating sonorous undulations, when they are affected by an impulse acting perpendicularly upon their surface; or whether undulations of condensation merely result? It is certain that sand and powder of Lycopodium, placed upon thin plates or membranes while these are the subject of sonorous undulations, are thrown into motion; Savart has indeed shown that this is the case with the membrana tympani itself when very loud sounds are produced in its vicinity. It must not, however, be thence inferred that the body upon which small particles are thrown into motion is necessarily affected with undulations of inflexion, for even undulations of condensation might excite motion in such light particles of matter by acting as an impulse upon them, and the particles of air affected with undulations of condensation communicated to them from the solid body may carry light substances with them. Even the nodal lines developed upon thin plates, to which sonorous vibrations are communicated, are no proof that the undulations of these plates are undulations of inflexion, for nodal points may be developed in a body whose vibrations consist of condensations and rarefactions of its particles, such as the column of air in musical pipes. Strings, which reciprocate the sound of another string vibrating in their close vicinity, give to the eye at least no evidence of being affected with transverse vibrations or undulations of inflexion; though this is, on the other hand, no proof that they are not the seat of such vibrations, since, when the excursions are not great, transverse vibrations are not visible. The drum, however, affords us distinct proof that membranes propagating sound may vibrate in this manner. If one membrane of a drum is struck so as to be thrown into vibration, the membrane of the opposite side is seen to vibrate transversely, and with excursions of considerable extent. The panes of a window also bend, and may even break, during the undulation of the air produced by the report of a cannon. It depends, therefore, entirely on the intensity of the impulse imparted to it by the sonorous vibration, whether a body extended in the form of a membrane, and capable of conducting sound, shall be thrown into undulations of inflexion or not. The possibility, therefore, of such undulations being excited in the membrana tympani cannot be denied; although, on account of its limited size, the extent of its oscillations must be very small, even when they are produced by the loudest sounds. Accurately speaking, the membrana tympani will become the seat of transverse oscillations whenever the space through which its particles move in the undulations excited by sonorous vibrations of the air exceeds the thickness of the whole membrane; and, when the impulses of the air have a certain degree of intensity, this must occur. The articulation and relative position of the small bones of the ear being such as to allow an approximation of the two extremities of the chain which they form, the oscillations of the membrana tympani are not impeded by them. Even where only one of the ossicula exists, as in birds and reptiles, its outer extremity, which is connected with the membrana tympani, is mobile. We may from these considerations infer that the articulation of the small bones of the ear has not a relation merely to the action of muscles upon them,—which, indeed, is sufficiently proved by reference to comparative anatomy, for they have moveable articulations in the frog as in man, though they have there no muscles attached to them.

On examining, however, more closely the conditions of the propagation of sonorous undulations in the atmosphere, we find that only the most intense sounds can possibly give rise to oscillations of the membrana tympani as a whole. If the extent of oscillation of the particles of a body emitting sound, or the intensity of an impulse, be so great that the rate of motion of the particles giving the impulse is equal to the velocity of sound in the air, the extent of oscillation of all the particles of air affected by the undulation will be equal to the extent of oscillation of the particles of the body communicating the impulse to the air, provided the air thus affected be confined in a tube. If the velocity of the particles communicating the impulse be only half as great as the velocity of sound in air, the extent of oscillation of the particles of the air (in a tube) will be only half as great as the extent of oscillation of the particles communicating the impulse to them. All the particles of air in a tube will oscillate through the same space when the undulation reaches them.* Vibrations of the membrana tympani, as a whole, will therefore be most prone to occur when the sound of a body oscillating with great intensity is transmitted to the ear through a tube; but the propagation of sound through an unconfined body of air is attended with a progressive diminution of the intensity of the undulations, or of the extent through which the oscillating particles of air move. For while the length of the waves — that is, the distance from the commencement of one wave to the commencement of the next,—remains the same during the propagation of spherical undulations of constantly increasing extent from one point in the atmosphere, the extent of oscillation of the particles affected by these waves diminishes in the ratio of the squares of their distance from their centre or source.† If, for example, the extent of the oscillations of the particles of air in the immediate vicinity of a sounding body, or of a body communicating an impulse to it, were an inch, the extent of their oscillation at the distance of two feet would be a quarter of an inch, at the distance of three feet $\frac{1}{9}$th, at four feet $\frac{1}{16}$th, and at ten feet $\frac{1}{100}$th of an inch, which is less than the thickness of the membrana tympani.

In calculating the effect of sonorous undulations on the membrana tympani, we must, moreover, take into account the difference in the velocity with which sound is propagated by it and by the air, and also the resistance offered by its attachments, which, even though the extent of the oscillation of the particles of air striking it exceeded the thickness of membrane, would cause the extent of its movement to be much less considerable.

The oscillations of the membrana tympani as a whole, produced by very intense sounds, will, if the undulations of the air fall upon the membrane in a perpendicular direction, occupy its whole extent at once; but if the undulations of the air fall upon it obliquely, so as to strike one part of it before the rest, the movement of the membrane will commence at this point, and will thence extend to the other parts, like the oscillation which is excited near one extremity of a cord or musical string, or at one limited part of the membrane of a drum. These oscillations, being reflected at the borders of the membrane, will traverse it to and fro. In consequence of the oblique position of the membrana tympani, this must always occur when the sonorous undulations enter the ear in the direction of the meatus auditorius externus,—that is, in a direction parallel with its axis. When the sonorous undulations enter the meatus in any other direction, they will be reflected back-

* Weber, Wellenlehre, p. 503. † Ibid. p. 504.

wards and forwards by the walls of the passage; and it will depend on the angles at which they are reflected, in what manner, and at what point, they shall first strike upon the membrana tympani.

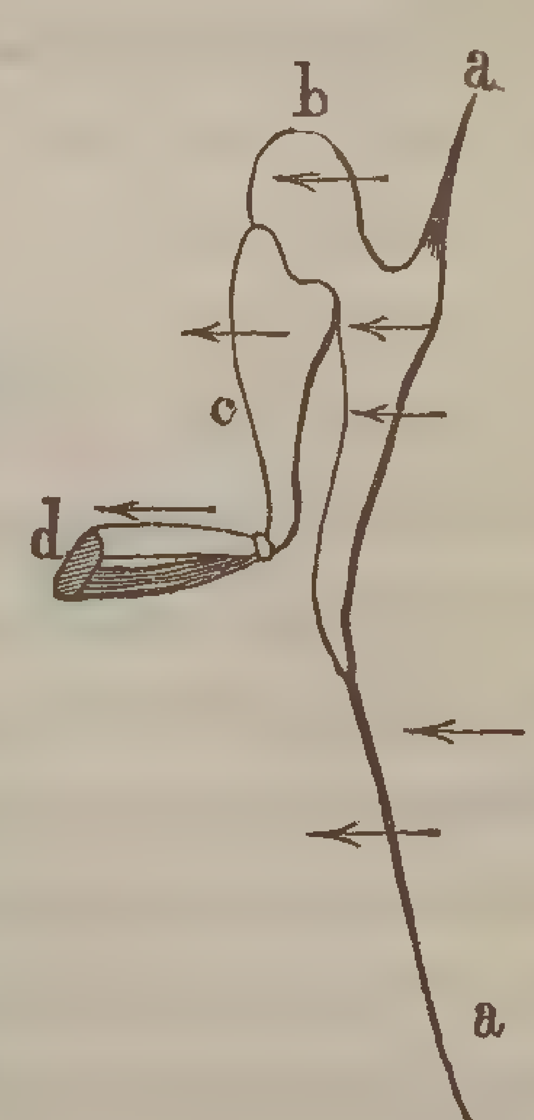
The propagation of the undulations of condensation and rarefaction, in which the smaller particles merely of the membrane move, is also modified in the same way by the mode in which undulations of the air strike it. The undulations of the air either strike every part of its surface simultaneously, or one point of it before the rest: in the latter case, the undulations communicated to the membrane are propagated in it in a determinate direction as far as its border, and then reflected back, so as to give rise to the crossing of undulations in the membrane. All sonorous undulations communicated to the membrana tympani by the solid parts of the head,—such as the cartilage of the outer ear, the walls of the external meatus, and the cranial bones,—are, of course, undulations of condensation and rarefaction of the particles. The undulations thus communicated to it are condensed and rendered more intense by the membrane.

If the undulation of the air be compound, so that during its progressive movement the most condensed part changes its relative position in the entire undulation, (in the same way that, while a string struck near one end vibrates transversely, the summit of its wave travels to and fro from one end to the other,) the membrana tympani will become the seat of undulations of the same character, and will give rise to the perception of a sound of the tone or timbre which that form of undulation is calculated to produce. If the undulations of the membrana tympani were in this case of the nature of transverse oscillations, the form of these oscillations would be, for example, similar to those described as being presented by a string struck near one extremity. If they were undulations of condensation and rarefaction of the particles of the membrane, they would have a direct progressive movement through the thickness of the membrane, with, at the same time, a lateral movement to and fro of the maximum of condensation and rarefaction in each wave. It will be readily conceived that such compound undulations are necessarily propagated unchanged through the chain of ossicula in the tympanum.

The necessity for the presence of air on the inner side of the membrana tympani,—in other words, the necessity for the existence of the tympanic cavity,—to enable the membrana tympani and ossicula auditus to fulfil the objects which we have described, is obvious. Without this provision, neither would the vibrations of the membrane be free, nor the chain of bones isolated, so as to propagate the sonorous undulalations with concentration of their intensity. But while the oscillations of the membrana tympani are readily communicated to the air in the cavity of the tympanum, those of the solid ossicula will not be conducted away by the air, but will be propagated to the labyrinth without being dispersed in the tympanum. Equally necessary is the communication of the air in the tympanum with the external air through the medium of the Eustachian tube for the maintenance of the equilibrium of pressure and temperature between them.

The propagation of sound through the ossicula of the tympanum to the labyrinth must be effected by undulations of condensation and rarefaction of their particles only, not by oscillations of the entire bones, even in cases where the entire membrana tympani oscillates; for, if the stapes were in its vibrations alternately more nearly approximated and removed from the labyrinth, the fluid of the latter cavity must necessarily be very compressible. The extent through which the individual particles affected by the undulations oscillate equal very minute fractions only of the length of the stapes.

Fig. 130.

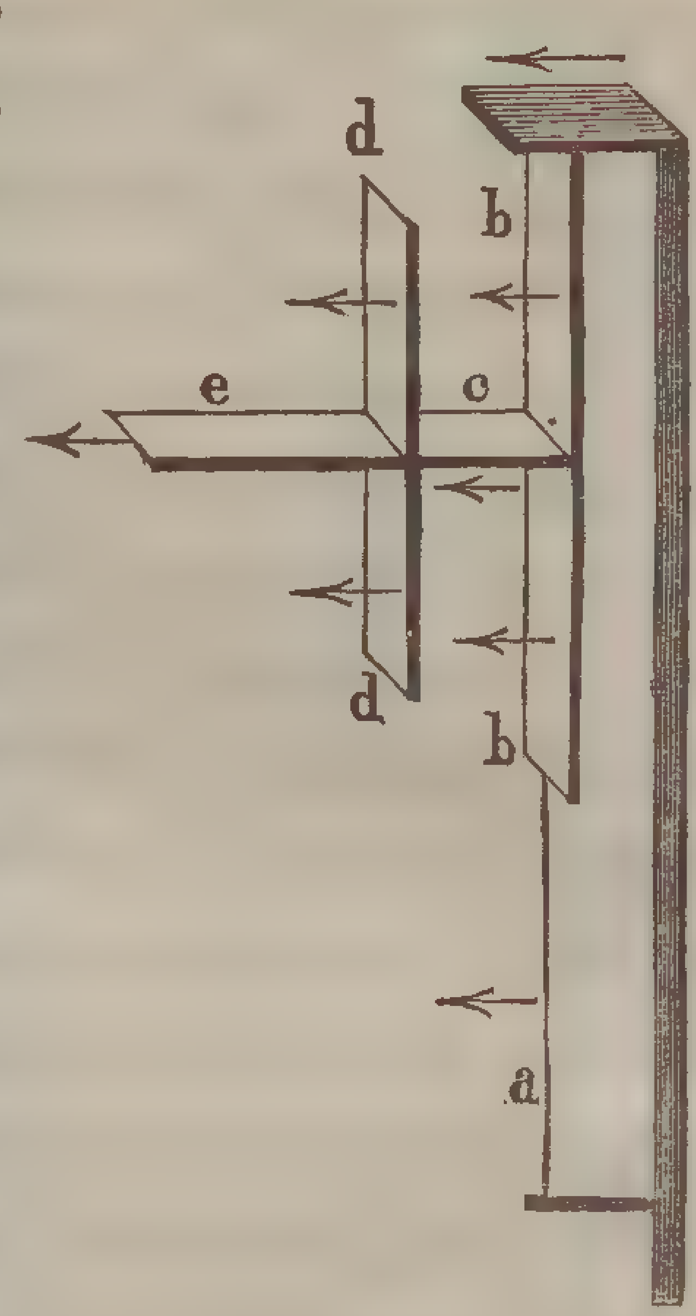


The long process of the malleus, *b* (fig. 130), receives the undulations of the membrana tympani (*a*, *a*) and of the air in a direction nearly perpendicular to itself. The undulations maintain this direction through the whole chain of ossicula quite independently of its direction, and of that of the individual bones forming it. From the long process of the malleus the undulations are propagated to its head, which projects from it at an angle; thence into the incus (*c*), the long process of which has a direction parallel with the long process of the malleus. From the long process of the incus the undulations are communicated to the stapes (*d*), which is united to it at right angles. All these changes in the direction of the chain of bones have no influence on that of the impulse, which remains the same as it was in the meatus externus and long process of the malleus, so that the undulations are communicated by the stapes to the fenestra ovalis in a perpendicular direction. The proof of this statement is contained in M. Savart's experiments on the propagation of sound in solid plates united to each other at right angles.* The plate *b* (fig. 131) is so connected with the support to which the string *a* is attached, that, when the string is made to vibrate transversely, the same kind of vibrations are communicated to it. Another lamina, *c*, connected with the former at right angles, vibrates in the longitudinal direction, the vibrations communicated to it maintaining their original course. The lamina *d*, having a direction perpendicular to that of the former lamina *c*, again vibrates

* Ann. de Chim. et de phys. t. xxv. p. 12, 138, and 225.

transversely, and the plate *e* longitudinally. The direction of the vibrations in the different plates was shown by the direction in which the dust was thrown from their surface. It is indicated in the figure by arrows. The analogy between the vibrations of the plates in M. Savart's experiment, and that of the bones of the ear, is manifest. The string *a* in M. Savart's figure may be compared to the membrana tympani. The plate *b*, which is fixed to the support of the string, is analogous to the long process of the malleus, which, being the means of making tense the membrane, may also be regarded as its bridge or support. The plate *c* answers to the head of the malleus; the plate *d*, to the long process of the incus; and the plate *e*, to the stapes.

Fig. 131.



Tension of the membrana tympani.

IV. *A membrane of small extent propagates sound better in the lax condition than when made very tense.*

The inquiry respecting the capability of the membrana tympani to conduct sound better in its lax or in its tense condition, may be made to embrace membranes generally. We must, however, distinguish here between reciprocation of sonorous vibrations, resonance, and conducting power. The reciprocation of sounds is a phenomenon which bodies rendered elastic by tension are not capable of manifesting in their lax condition. A string made tense is capable of reciprocation, however, only under certain conditions; of resonance under all conditions. The sound excited by a vibrating tuning-fork is much louder when the fork is held near the tense membrane of a drum than when it is held in the vicinity of a perfectly lax membrane; but, in order that a body shall reciprocate a sound in its own proper fundamental note, it is necessary that its fundamental note should be in unison with the original sound, or that it should at least bear a simple relation to it; otherwise, it will merely render the original sound louder by resonance.

The degree of resonant action of a body, however, also depends, *cæteris paribus*, on the pitch of its fundamental note, and on the relation which it bears to the original sound.

If a vibrating tuning-fork be held over the mouth of tubes of pasteboard of different lengths, the resonance of their column of air will be less marked in proportion as the fundamental note which it is calculated to give is more distant in the musical scale from the note emitted by the tuning-fork: there will, therefore, be one length of tube in which the resonance will be loudest. If the length of the tube be such that the fundamental note of its column of air is in unison with the original sound, it will reciprocate that sound. The resonance of a column of air will, according to Mr. Wheatstone, be loud also when its length is a multiple of the column of air in unison with the tuning-fork, nodal points being in this case developed. A glass vessel may, by a greater or less quantity of water being poured into it, be tuned so as to increase the intensity of the sound of a tuning-fork in a great or a very slight degree. These principles being applied to strings and membranes, a membrane perfectly lax will not increase the intensity of a sound by resonance, or, at least, will do so in a much less degree than a tense membrane; but the resonance will, of course, not increase in intensity, *pari passu*, with the degree of tension of the membrane. On the contrary, it will be greatest when the tension of the body (supposing its mass to remain the same) is such that its fundamental note is in unison with the original sound.

A more particular application of these principles to membranes of so small extent as the membrana tympani is scarcely possible. It is of much more importance here to inquire whether increasing tension of the membrana tympani increases or diminishes the facility of transition of sonorous undulations from the air to it.

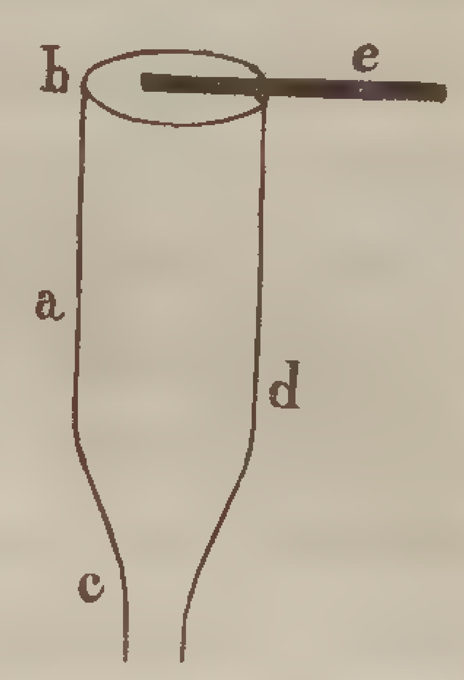
M. Savart was the first, and has hitherto been the only physiologist, who has endeavoured to elucidate this problem by experiment. He observed that the dry membrana tympani, on the approach of a body emitting a loud sound, rejected particles of sand strewn upon it more strongly when lax than when very tense; and inferred, therefore, that hearing is rendered less acute by increasing the tension of the membrana tympani.* M. Savart obtained a similar result when he produced increased tension of an extended membrane by means of a lever applied to it. Repeating M. Savart's experiment, with very thin paper extended over the mouth of a drinking-glass, I obtained the same result. The more forcible agitation of the grains of sand does not, however, justify our concluding with certainty that the sonorous undulations of the membrane are more intense. Muncke† remarks, that the agitation of the sand may arise from the greater extent (amplitudo) of the undulations, and not depend on their intensity; and that the pressure of the lever by which the tension is increased may give rise to the developement of a nodal line, by which the extent of the vibrating parts would be limited. Fechner, also, questions the correctness of Savart's conclusions. Under these circumstances, it appeared to me that direct experiments upon the relative capability of membranes of small ex-

* Ann. d. Chim. et Phys. t. 26. p. 25.

† Gehler's Physikal. Wörterbuch, iv. 2, p. 1210; 8, p. 501.

tent, in the relaxed and in the tense conditions, to transmit sound, the ear itself being employed as the measure, would be of considerable interest.

Fig. 132.



A wooden tube, *a* (fig. 132), was employed, the diameter of whose lumen was eight lines, and length four inches, and which at one end diminished to a smaller neck, *c*, so that it could be inserted deeply and firmly into the external auditory passage. This smaller end was open; the other (*b*) was covered with a membrane which was not tightly stretched. Upon the membrane, a small rod, *e*, two lines broad, was glued, its extremity reaching a little further than the middle of the membrane, while the larger part of the rod projected far beyond the edge of the tube, to which it was firmly tied. Hence, when the outer end of the rod, *e*, was raised, the inner end was depressed, and the membrane consequently pressed inwards and made tense. The apparatus thus resembled, to a certain extent, the natural structure of the membrana tympani, the rod representing the malleus. The narrow end of the tube being now inserted into one ear, while the other was closely stopped with a plug of chewed paper, it was easy to compare the strength of the sound transmitted by it in different states of tension and relaxation. By the addition of a small opening in the side of the tube, at *d*, the influence of the Eustachian tube may be imitated, the air in the interior of the tube being thus enabled to maintain its equilibrium with the air without. But this produces no essential difference in the result; and it is better that the opening should not exist, since it would admit sonorous undulations to the ear, which had not passed through the membrane on the mouth of the tube. The result was in all my experiments the same. The sound was transmitted with much greater intensity through the lax membrane than through the membrane made tense by raising the outer extremity of the rod. A watch may be used as the source of the sound in these experiments. But every noise is heard louder when the membrane is lax; and its intensity diminishes in proportion as the tension of the membrane is increased.

The membrana tympani in one's own person may, however, be rendered tense so as to produce this influence on the intensity of sounds at will. In the dead subject, the membrana tympani may be rendered more tense in two ways besides by the retraction of the malleus; namely, by exhausting the air in the tympanum by sucking through the Eustachian tube, and by forcing more air into the tympanum through the same canal. In the first case, the membrana tympani is pressed inwards. In the second case, it is forced outwards; the long process of the malleus, however, not being displaced by the pressure of the air within the tympanum, the centre of the membrane is prevented from changing its position, while the rest of it is protruded.

Both these modes of tension of the membrana tympani may be practised in the living body also, and in the experiment on our own persons, namely, by a strong and continued effort of expiration while the mouth and nostrils are closed, or by a strong and long-continued effort of inspiration under the same circumstances. In the first case, the compressed air is forced with a whizzing sound into the tympanum, and immediately hearing becomes indistinct. The same temporary imperfection of hearing is produced by rendering the membrana tympani tense, and convex towards the interior, by the effort of inspiration; a fact first noticed by Dr. Wollaston.* The imperfection of hearing, produced by the last-mentioned method, continues even after the mouth is opened, in consequence of the previous effort at inspiration having induced collapse of the walls of the Eustachian tubes, which prevents the restoration of equilibrium of pressure between the air within the tympanum and that without; hence we have the opportunity of observing that even our own voice is heard with less intensity when the tension of the membrana tympani is great. If I have produced increased tension of the membrane by forcing air through the Eustachian tube into the tympanum, the equilibrium of the air within and without the tympanum is usually restored, and hearing regained immediately upon the mouth or nostrils being opened; sometimes, though rarely, the natural condition is only gradually regained. On the contrary, when I have produced the tension of the membrana tympani by rarefying the air in the tympanum, the partial deafness usually lasts for some time, and during this period I feel very distinctly a sensation of tension in the membrane of the tympanum. In either case, if the imperfection of hearing and sensible tension of the membrana tympani do not cease spontaneously on the mouth being opened, I can remove them by a voluntary movement in the ear, which I shall presently show to be produced by a voluntary contraction of the tensor tympani muscle. The re-opening of the Eustachian tube, or the separation of its collapsed walls, is probably effected by the slight pressure of the air in the tympanum, when the tensor tympani acts so as to draw inwards the membrane. Persons who are not able to execute this voluntary movement of the tensor tympani muscle may still dispel the deafness by the contrary proceeding to that which produced it. If, for example, the imperfection of hearing had been induced by forcing outwards the membrana tympani, they should make a strong effort at inspiration while the mouth and nostrils are closed, and *vice versâ*.

If the pressure of the external air or atmosphere be very great, while,

* Philos. Transact. 1820.

on account of collapse of the walls of the Eustachian tubes, the air in the interior of the tympanum fails to exert an equal counter-pressure, the membrana tympani will of course be forced inwards, and imperfect deafness be produced. It is thus, in my opinion, that we must explain the singular observation of M. Colladon, that in the diving-bell both the voices of his companions and his own voice sounded faintly. The fact cannot be owing, as has been supposed by some writers, to the bad conducting power of the condensed air, since air conducts sound better in proportion to its density.

The effect of the increased tension of the membrana tympani is not to render both grave and acute sounds equally fainter than before. On the contrary, it was observed by Dr. Wollaston, that, when he had rendered his membrana tympani tense by exhausting the cavity of the tympanum, he was deaf to grave sounds only. By striking the table with the ends of his finger he produced a deep dull note; striking it with his nail, he gave rise to a sharp sound. When he had exhausted the tympanum by the effort of inspiration, he could hear the latter sound only; the former deeper note was inaudible. The heavy rumbling sound produced by the movement of a carriage was not heard in the same condition of the membrana tympani, while the rattling of a chain or loose screw about the vehicle was perceived quite distinctly. These observations are perfectly correct, and will, I believe, be confirmed by every one who has had the necessary practice in such experiments. The effect of forcing air into the tympanum is exactly the same as that of exhausting it, with reference to the perception of grave and acute sounds. Thus the dull rumbling sound of carriages passing over a bridge, or of the firing of cannon, near my house, and the beating of drums at a distance cease to be heard immediately on tension of the membrana tympani being induced in either of the ways above mentioned. But the treading of horses upon the stone pavement, the more shrill creaking of carriages, and the rattling of paper, I hear very distinctly while my membrana tympani remains tense. The character of the deafness is very strikingly shown by the fact, that the ticking of a watch is heard at the distance of eight feet quite as distinctly when the membrana tympani is rendered tense as in the natural state, perhaps even more distinctly, while all dull grave noises in the street cease to be heard.

This difference in the loudness of acute and grave sounds, under the conditions here stated, is easily explicable according to the principles stated at page 1256. The greater the tension to which the membrana tympani is subjected, the more acute will become its fundamental note, and all the harmonic notes also which it is capable of emitting when divided by nodal lines into separate vibrating segments; and in the same ratio will its property of repeating perfectly the vibrations proper to the deeper notes diminish. The nearer a sound approaches to the fundamental note proper to the tense membrana tympani, the more distinctly it will be heard when the membrane is in this tense condition.

These facts admit of a practical application in pathology. It is not very rare to meet with persons who are deaf to the more grave sounds only, while they still hear distinctly acute sounds, even though they be not loud. One of my colleagues, who is deaf, hears acute better than grave sounds. In such cases it is very probable that the membrana tympani is in a state of too great tension. In the present state of obscurity of the diagnosis of diseases of the ear, this hint may be of some use. Such unnatural tension of the membrana tympani may, of course, be produced by several different causes. It may arise from occlusion of the Eustachian tube; in which case the air in the tympanum may either be expanded by the heat of the body, and so force outwards the membrana tympani, or it may be partially absorbed, when the membrane would be pressed inwards by the air without. Another cause may be a contracted state of the tensor tympani muscle. In my colleague the Eustachian tube is free, for he can force air into the tympanum. When the Eustachian tube is closed, and the tension of the membrana tympani is the consequence of the expansion or partial absorption of the air in the cavity of the tympanum, the operation of puncturing the membrane, or the mastoid process, may be easily conceived to be beneficial; but when the too great tension of the membrana tympani, and consequent deafness, are owing to a contracted state of the tensor tympani muscle, the operation must be useless. This may in part account for the various results obtained from it.

The influence of the musculus tensor tympani in modifying hearing may now be estimated.

If we admit, as a very probable supposition, that the tensor tympani may through reflex nervous action be excited to contraction by a very loud sound, just as the iris and orbicularis palpebrarum muscle are by a very intense light, the impression being conveyed by the sensitive nerve to the brain, and thence reflected upon the motor fibres; then it is manifest that a very intense sound would, by exciting a reflex action of this muscle, induce a deadening or muffling of the ears. A loud sound excites by reflection nervous action, winking of the eye-lids, and, in persons of irritable nervous system, a sudden contraction of many muscles. The above supposition has, therefore, great probability in its favour.* Increased tension of the membrana tympani by the tensor

* A very loud noise, such as that of a cannon, if near, may, by forcing in the membrana tympani, give rise to the production of a new sound by that membrane itself; at least, I think, I have observed this in my own person. At the time of the report of a cannon I perceived a cracking or jerking sound, similar to that which is heard

tympani muscle, by whatever cause excited, must moreover cause the graver sounds, rather than the more acute, to be heard faintly.

We have now to inquire whether the tensor tympani is subject to voluntary influence. Like the stapedius, it presents under the microscope, according to my observations, the characters common to all muscles of animal life; its primitive fasciculi are regularly marked with the cross striæ. The so-named laxatores tympani are, on the contrary, not muscles. In the musculus mallei externus I could recognise none of the characters of muscle which are so evident in the tensor tympani; it is a mere ligament. The two real muscles of the ossicula, however, belong without doubt to the system of animal muscles. It is true, that the muscles of the vascular system, the heart, and lymphatic hearts, have likewise primitive fasciculi marked with transverse striæ; — that this character is not confined to the muscles of the parts developed in the external serous layer of the germinal membrane, but also prevails in those formed from the middle vascular layer. But the primitive fasciculi of the organic muscular fibres of internal viscera are constantly devoid of the transverse striæ.* Moreover, the small muscles of the external ear are subject to the will; (I can move them, more especially the m. antitragicus, distinctly;) there can therefore be no reason to deny a similar subjection of the muscles of the tympanum to the will. As a circumstance in favour of such a voluntary influence over these muscles existing, may be noticed the origin of the nerve of the tensor tympani from the third branch of the fifth,—namely, from the internal pterygoid nerve; and the origin of the nerve of the stapedius muscle from the facial.

The opinion that the tensor tympani muscle is subject to the influence of the will was held by Fabricius ab Aquapendente, who maintained that he had himself voluntary power over it, he being able to produce a peculiar noise in his ears at will. Fabricius could perform the movement only on both sides simultaneously. Mayer was acquainted with a gentleman who had such power over the motions of the small bones of his ear that another person could distinctly hear the sound thus produced when their ears were applied to each other.† I have the same power of producing at will a sound in either ear, more particularly in the left, in which I can excite it without causing it on the other side. The sound is of a snapping character, like that emitted by the electric spark, or that produced when the end of the finger, rendered adhesive, is pressed upon paper and then suddenly

when the movement of inspiration is suddenly performed while both the nostrils and mouth are closed, so as to draw inwards, and thus render tense, the membrana tympani.

* [See explanation of plate II. fig. 9.]

† Compare Lincke, Handbuch der Ohrenheilkunde; Leipz. 1837; 1, p. 472.

removed. Another person can hear this knacking or snapping sound by interposing a conducting rod between my ear and his own, both his meatus having been previously closed by plugs: he can also hear it when he places his ear, not stopped, near mine, or even at the distance of one or two feet from it. One person distinguished the snapping sound in my ear at the distance of three feet, our ears being placed directly opposite to each other. Each time that I made the movement in my ear he declared that he heard the sound.

We have now to adduce the arguments in favour of this sound being really caused by contraction of the tensor tympani muscle, and its action on the membrana tympani, which it draws inwards, and thus influences in the same manner as an impulse from without. A circumstance favourable to this view is the occurrence of the same sound at the moment of allowing the air to escape, and the membrana tympani therefore to resume its natural position after it has been pressed outwards, by forcing air into the tympanum from the throat while the mouth and nostrils were closed; the sound then heard is quite distinct from the buzzing of the air rushing against the membrana tympani, and is audible to a second person. On observing the condition of the fauces by means of a mirror during the production of the snapping sound in the ear, I found that the soft palate was raised at the same moment. This naturally suggests the notion that a current of air may be forced into the Eustachian tube by the elevation of the velum palati. But this idea is at once shown to be incorrect by the fact that the soft palate may be raised with great force without the sound in question being produced in the ears. Thus, while singing with the mouth wide open before a mirror, I can perceive that during the production of the high falsetto notes, even with a low voice, the palate is very much elevated, without the snapping sound in the ears being induced; though, by a voluntary effort, it may be caused at the same time. This observation also proves that the phenomenon in question cannot arise from the upper palatine muscles, which arise partly from the cartilage of the Eustachian tube, acting, during their contraction, upon this tube so as to produce a sound which is transmitted to the ear. Such an opinion is, indeed, sufficiently refuted by the fact that the snapping sound produced in my ear is heard by other persons at the distance of several feet. Its cause appears therefore to me to be a voluntary contraction of the tensor tympani muscle.*

Among the movements which induce the snapping sound by asso-

* On more mature consideration it appears to me that the reasons above given for the dependence of the snapping sound on a voluntary action of the musculus tensor tympani do not amount to an absolute proof. [Note in the Addenda of the original work.]

ciation, deglutition must be mentioned; but it is not a constant and necessary attendant on the movement of deglutition. Besides the snapping sound above described, I am able to produce at will another different noise in the ear, and upon both sides simultaneously. It is of a humming or buzzing character, and can be prolonged for the space of a second or more. Its production is likewise accompanied by elevation of the soft palate, and appears to be owing to the contraction of the palatine muscles. This humming or buzzing sound occurs sometimes during yawning and eructation, even when this movement is voluntarily induced.

During the production of the snapping sound my hearing for other sounds is not perceptibly affected, but the humming sound just referred to interferes with hearing.*

An involuntary contraction of the tensor tympani muscle, like its action under the influence of the will, must produce a sound. Many persons will have observed noises in their ear from this cause.†

The influence of the stapedius muscle in hearing is unknown. It acts upon the stapes in such a manner as to make it rest obliquely in the fenestra ovalis, depressing that side of it on which it acts, and elevating the other side to the same extent. The only effect which, it appears to me, could be ascribed to it, would be to render tense the membrane by which the base of the stapes is connected with the margin of the fenestra.

* The snapping sound may occur simultaneously with the humming or buzzing sound described above, but it may also be produced separately. If I perform the movements necessary for causing both these sounds, and immediately afterwards emit a humming vocal tone while my mouth is either closed or only slightly open, this tone has an extraordinary resonance; and it is evident that the movements just mentioned have effected some change, in consequence of which a part, which previously had only very slight or no effect on the intensity of sounds, acquires a great influence on them. The sound of one's own voice by this means acquires the intensity of the tones of an organ. The movement which produces the buzzing sound in the ear, and not that which produces the snapping sound, appears to be the cause of the increased resonance; for I can give rise to the latter separately without influencing the resonance of the voice. I am able also to confine the resonance to either ear. I cannot explain these phenomena. Another circumstance connected with the resonant action of the ear deserves mention. The experiment just described does not readily succeed with every person; this fact, on the contrary, may be easily verified. If, while the mouth is held closed, any vocal sound be produced in a singing or humming manner, and the external meatus of the ears be closed by the fingers lightly introduced, but not firmly pressed into them, the sound of the voice is heard much louder than before, but with a peculiar dull resonance in the ears, like the tone of an organ. If the fingers are pressed strongly into the ears, the resonance ceases. The resonance may be heard in one ear only, if the finger be applied to the meatus only of one ear. The resonance of the voice produced in this manner is of a similar character to that experienced in the former experiment, but of much less intensity.

† Compare Lincke, op. cit. p. 481.

The fenestræ, ovalis and rotunda.

The existence of two fenestræ for the transmission of sound to the labyrinth is not a necessary condition for hearing in animals living in the air, which are furnished with a tympanum; for, as the experiments already detailed prove, both a tense membrane, (such as the membrana tympani secondaria, or membrane of the fenestra rotunda,) and a moveable solid body connected with a tense membrane, are capable of conducting sound with considerable intensity to water. Comparative anatomy also furnishes proofs of the truth of this statement; for frogs in which a tympanic cavity otherwise perfect exists, have no second fenestra, or fenestra rotunda, the chain of auditory ossicula being in them the only means of conducting the sound to the labyrinth. In this case the air in the tympanum can scarcely be regarded as an auxiliary, since its sonorous vibrations cannot be communicated in any intensity to the solid parts of the organ. Its principal use must here be to insulate the small bones of the ear and the membrana tympani.

When both fenestræ exist together with a tympanum, the sound is transmitted to the fluid of the internal ear in two ways,—namely, by solid bodies and by membrane; by both of which conducting media sonorous vibrations are, as my experiments have shown, communicated to water with considerable intensity. The sound being conducted to the labyrinth by two paths will, of course, produce so much the stronger impression; for undulations will be thus excited in the fluid of the labyrinth from two different though contiguous points, and by the crossing of these undulations stationary waves of increased intensity will be produced in the fluid.

It is natural to inquire here by which of the paths above indicated the sounds are conducted with most intensity from the membrana tympani to the labyrinth; whether through the chain of bones and the fenestra ovalis, or through the air of the tympanum and the membrane of the fenestra rotunda.

This question has hitherto been answered for the most part in an arbitrary manner. By some writers the conducting power of the chain of ossicula has been denied, on the ground of hearing having been retained after the loss of those bones, as in the cases observed by Sir A. Cooper,* and previously by Caldani and Cheselden. While others again have denied that sound is transmitted by the fenestra rotunda, because in numerous cases deafness has been the result of destruction and loss of the ossicula.† It would, however, be incorrect to ascribe the propagation of sound to either path exclusively, since each part of the apparatus capable of propagating sonorous undulations must con-

* Philos. Transact. 1801.

† See Haller, Element. Physiol. t. v. 285.—Compare Lincke, loc. cit. 465.

tribute to the result in a degree determined by physical laws. The relative conducting power of the different parts is, therefore, all that we have to determine. Muncke* has reviewed the various opinions relative to this question, and the arguments on which they are founded. He himself decides in favour of the chain of ossicula being the principal means of conducting the sound. If we suppose, he says, that any one held two watches, which beat with equal loudness, at the same distance from the ear, one of them, however, being connected with it by means of a rod of bone, the other suspended freely in the air, it is evident that he would hear the first distinctly, the second not at all. Again: We need, he says, only consider the common experiment in which the sound of a spoon, which would not be audible if transmitted by the air only, is heard very loudly in consequence of being suspended by a thread, and connected by this with the ear, in order to come to the conclusion that the sound must be conducted to the labyrinth principally by the ossicula auditus. But the analogy is here not perfect. Sonorous undulations emitted primarily by a solid body are, it is true, conducted to the ear with very great intensity by a solid rod, and very feebly by the air; but, in the same way, sonorous undulations excited in the air are conducted by air much better than by a solid body. The question which we have to determine is, whether sonorous undulations excited in the air, or communicated to it, are transmitted by the membrana tympani most readily to the ossicula or to the air of the tympanum; and whether they are transmitted most readily by the ossicula to the fluid of the labyrinth, or from the air of the tympanum to the same fluid through the membrane closing the fenestra rotunda.

We may express the problem to be decided in other words, thus: By which succession of media is the intensity of sonorous undulations least diminished?—by air, a tense membrane, an insulated and moveable solid body, and water; or by air, a tense membrane, air, another tense membrane, and then watery fluid? The experiments which I have instituted prove very clearly that

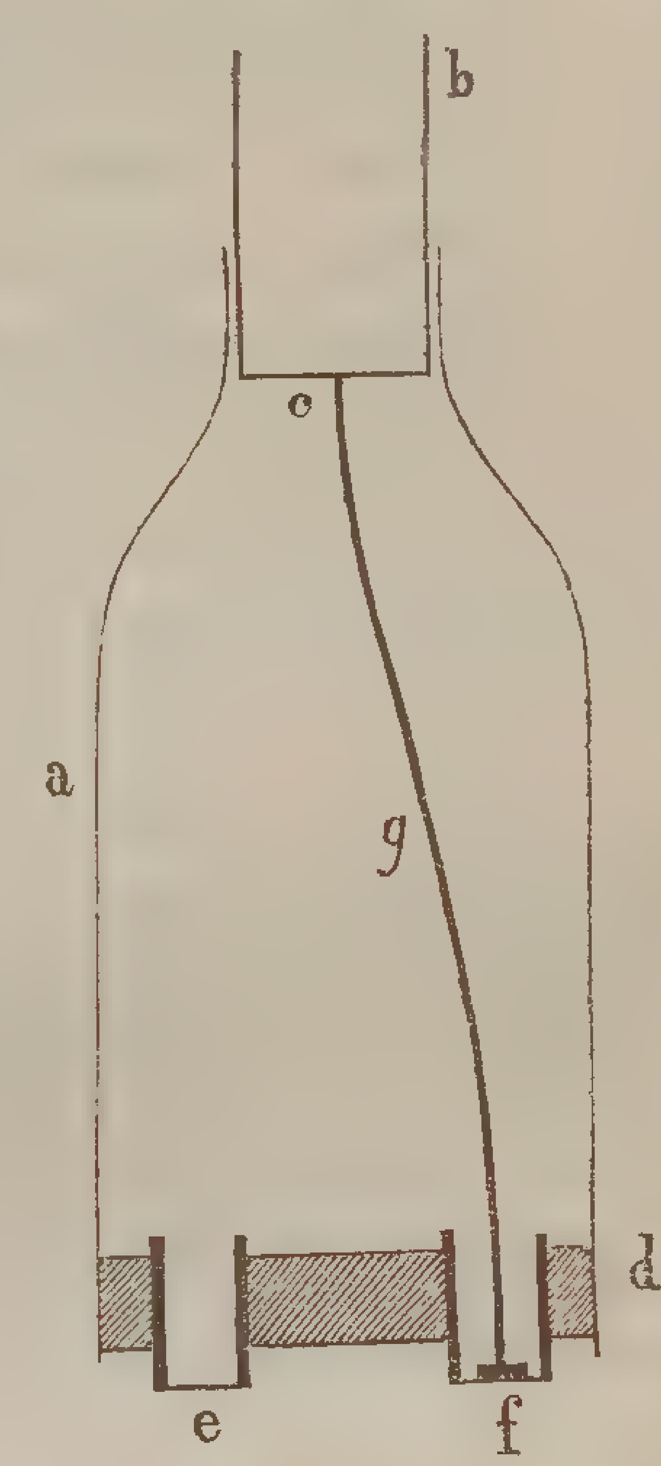
V. *Vibrations are transmitted with very much greater intensity to water when a tense membrane, a chain of insulated solid bodies capable of free movement, are successively the conducting media, than when the media of communication between the vibrating air and the water are the same tense membrane, air, and then a second membrane;* or, to apply this fact to the organ of hearing, that *the same vibrations of the air act upon the fluid of the labyrinth with much greater intensity through the medium of the chain of auditory bones and the fenestra ovalis, than through the medium of the air of the tympanum and the membrane closing the fenestra rotunda.*

I imitated the structure of the tympanum in the following manner.

* Kastner's Archiv. für d. ges. Naturlehre, 7, 1.

To the neck of a glass cylinder, two inches and one-third in diameter and six inches long, *a* (fig. 133), I fixed tightly a wooden tube, *b*, the diameter of whose lumen was eight lines. The upper end of this tube, *b*, was adapted to the mouth of the metal flute-pipe one-foot in length; its lower extremity was covered with a tense membrane (of pig's bladder), *c*, which represented the membrana tympani; while the tube itself corresponded to the external meatus, and the cavity of the glass cylinder, *a*, to the tympanum. The lower wide extremity of the glass cylinder was closed by a thick lamina of cork, *d*, in which there were two openings, equally distant from the walls of the cylinder, for the reception of short wooden tubes from three to four lines in diameter. The outer opening of each of these tubes was covered with membrane. The membrane of the tube *f* was brought into connexion with the upper membrane *c*, by a wooden rod *g*, which was in contact with the upper membrane at its middle only, but was connected with the lower membrane *f*, through the medium of a broad plate of wood occupying nearly the entire surface of the membrane. The rod *g* was of such length as to keep both the membranes with which it was connected somewhat tense; it represented the chain of ossicula extending between the membrana tympani *c*, and the fenestra ovalis *f*. The fenestra rotunda was represented by the other short tube, and its membrane *e*. The lower part of the apparatus being immersed in water, and the musical pipe fitted to the tube *b* and sounded, the conditions for the propagation of the sound to the water were the same as in the natural ear for the transmission of sounds to the fluid of the labyrinth. And if, in addition, a space be left at one point between the edge of the lamina of cork *d*, and the glass cylinder, and if this part of the cylinder be raised out of the water during the experiment, while the mouths of the tubes *e* and *f* remained immersed, the air in the interior of the cylinder *a* will be brought into communication with the external air, just as the air of the tympanum is by means of the Eustachian tube. The presence or absence of this communication, however, makes no difference in the result of the experiment.

Fig. 133.



My ears being stopped by plugs, I could, by means of a conducting-rod held in connexion with one ear, ascertain the relative intensity of the sonorous vibrations communicated to the water through the two openings *e* and *f*, corresponding to the fenestra rotunda and the fenestra ovalis, while another person sounded the pipe. The difference was very striking. The sound transmitted by the wooden rod to the opening *f* was in a remarkable degree louder than that propagated through the air of the cavity and the membrane of the opening *e*. The loud sound issuing from the opening *f* was heard even opposite the opening *e;* hence, to ascertain the strength of the sound issuing from the latter separately, it was necessary to remove the rod from the apparatus, and to close completely the opening *f*, corresponding to the fenestra ovalis, by means of a solid plug. It was then found that the sound was transmitted by the membrane *e* (the fenestra rotunda), with but little more intensity than by the solid lamina of cork itself. The same sound may possibly be communicated to the labyrinth by the two fenestræ, not only with a different intensity, but also with a somewhat different quality or " timbre." The undulations transmitted by the fenestra rotunda are undulations of air up to the point of their reaching the membrane of this fenestra. Those transmitted by the fenestra ovalis are, on the contrary, undulations of solid bodies,—the ossicula auditus. Now, it is well known that one and the same sound may be modified in " timbre" by the resonance of different bodies. What a different character, for example, has the sound produced by a vibrating tuning-fork, according as it is held free over a bowl containing air only, or approximated to the walls of the same vessel! How differently does a bell rung in water sound, according as its sound is conducted to the ear by a solid rod, or only by the air! In the first case the sound is loud and full, in the second it is feeble. It is difficult to ascertain by direct experiment how far the sounds transmitted by the two fenestræ in the above described apparatus differ in " timbre;" since, to compare sounds in this respect, they should be of equal intensity. The experiments which I have instituted were, however, favourable to the opinion of such a difference in " timbre" existing, rather than opposed to it.

The undulations transmitted by the fenestra ovalis act primarily upon the vestibule and the semicircular canals; those transmitted by the fenestra rotunda, upon the cochlea: but those communicated immediately to the fluid of the vestibule, inasmuch as they extend as circular waves in the fluid, must ultimately reach the cochlea; and the relation of the fenestra rotunda to the cochlea is by no means constant, since in chelonian reptiles (tortoises and turtles) both fenestræ exist, though there is no proper cochlea.

The Eustachian tube.

The Eustachian tube is never absent when the tympanum exists. Its great importance in rendering hearing perfect is proved by the circumstance of the occlusion of it, as a consequence of disease, being always attended with deafness and tinnitus. But it cannot, from these cases of disease, be determined whether the Eustachian tube is itself essential to the hearing of sounds with distinctness and intensity, or whether its occlusion affects hearing only indirectly.

It may be easily conceived that the ill effect of obstruction of this passage would be equally great whether its office were merely to prevent the production of too great tension of the membrana tympani by expansion or condensation of the air in the tympanum, or to carry off the mucus generated in that cavity by the ciliary motion of its mucous lining. All the provisions by which the tympanum has been adapted to the better propagation of sound would be rendered unavailing if it were to become filled with mucus.

The different offices which might be, and have been, attributed to the Eustachian tube are the following: we shall consider them in succession.

1. Some writers have imagined that a body of air inclosed on all sides is not adapted for the transmission of sonorous vibrations. Thus Saunders* says, that when the Eustachian tube is obstructed, "the included air, incapable of yielding in any other way than by condensation, counterbalances the pulses excited by sounding bodies." This supposition is, as Muncke remarks, directly contradictory to the laws of physics; for no displacement of the air is necessary in the propagation of an impulse.

2. According to the laws of physics, the very opposite of the foregoing view would be more probable; for if the conducting chain of ossicula be left out of consideration, and the cavity of the external meatus and tympanum be compared to that of a tube used for conducting the voice to a distance, in which the sonorous undulations, on account of the column of air propagating them being insulated, are transmitted with their full intensity, the presence of an opening from the exterior into the cavity of the tympanum ought to cause a partial dispersion of the undulations, as a similar opening into such a tube would, and therefore, in the case of a violent impression of sound, render their effect, as far as it is felt by the fenestra rotunda, less intense.

3. Other authors, among whom is Muncke,† imagine that unequal density of the air within, and of that without the tympanum, would be an impediment to hearing. To this opinion also I cannot subscribe. Sound, in passing through strata of air of different densities, appears certainly to lose somewhat of its intensity; but by the mere presence of a membrane, such as the membrana tympani, between two bodies of air even of equal density, the medium of transmission is already rendered threefold. The undulation has to be communicated from air to the membrane, and from the membrane to air again; and the

* Anatomy of the Human Ear; London, 1806.—Second edition, 1817, p. 79.

† Op. cit. 26.

important circumstance is not the degree of difference between the one body of air and the other, but the degree of capability of the second body of air (the air within the tympanum) to become affected with undulatory motion communicated to it by the membrane.

4. According to another view, the Eustachian tube is destined to prevent the resonance of the air in the tympanum. This opinion is, however, least of all tenable; for a body of air is capable of resonance, whether the cavity containing it be opēn at one or both ends. Simple resonance, so as to increase the intensity of the sound, would be rather an advantage than the contrary. It is only the sympathetic vibration of a body of air in its own proper note which would disturb the integrity of hearing. With reference to this sympathetic vibration of a body of air, it is to be observed, that the column of air of an open tube is to be regarded as equal to that of a closed tube of half the length.

5. A fifth view would regard the Eustachian tube as destined to increase the resonance of sounds in the ear. Thus Henle* compares it to the apertures in the sounding-board or belly of a violin, which are so necessary to give the instrument strength and fulness of tone, by causing the air contained in the body of the violin, as well as the mere sounding-board, to reinforce the sound by resonance. Henle supposes that the air of the cavity of the mouth and nose are in like manner enabled, through the medium of the Eustachian tube, to increase by resonance the intensity of sounds entering the ear through the external meatus. The possibility of such a mode of action cannot be denied. Direct experiments upon the influence of a side tube communicating with a short main tube, in rendering the resonance greater, are favourable to the view in question. The sound of a tuning-fork held over the mouth of a short tube (four inches long and one inch wide) seemed to me to be louder when a second longer tube (two feet in length) was connected with it at an opening in its side, than when this side opening existed and no second tube was connected with it. If the opening between the tubes was very small, no difference in the sound was perceived.

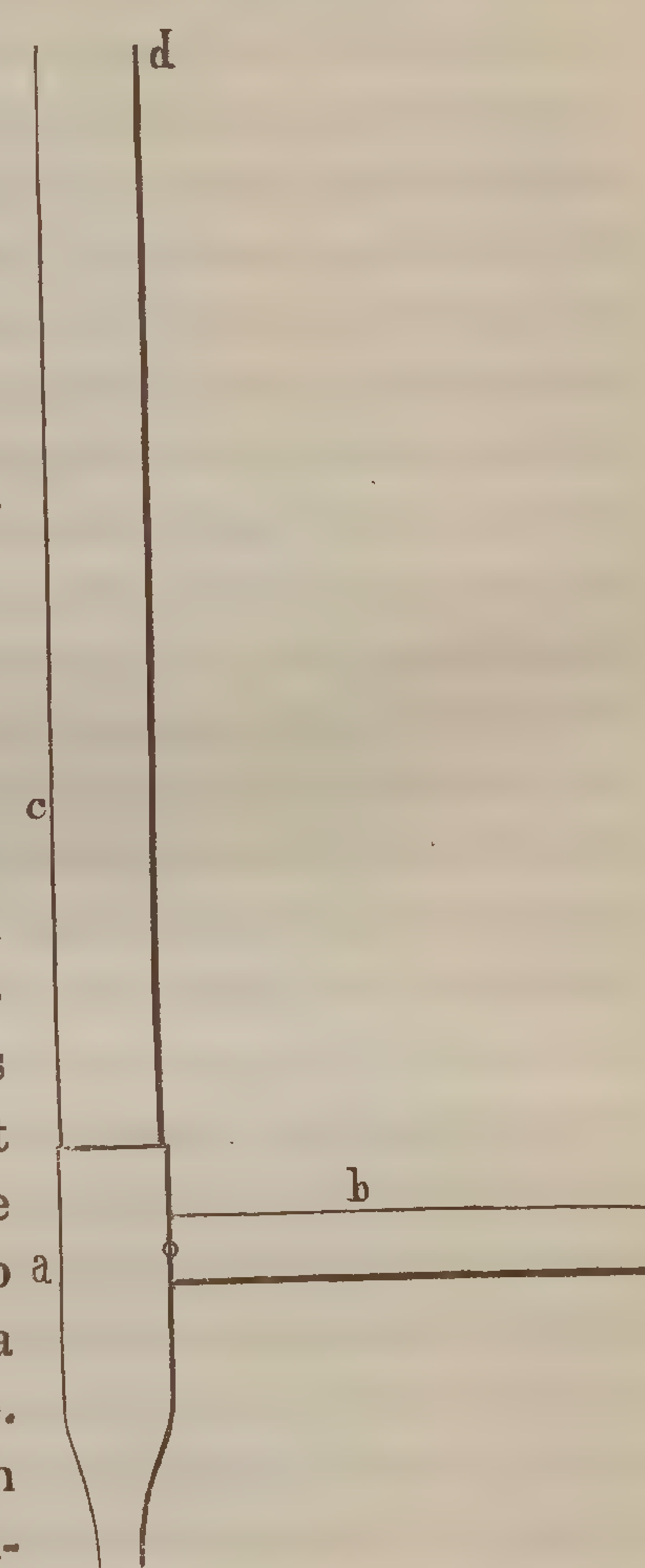
Direct experiments are capable of being instituted to determine whether the resonant influence of side cavities is not for the most part rendered null, when the opening of communication is so small as that of the Eustachian tube. A rough model of the tympanum, with the Eustachian tube, may be constructed in the following manner:—

A wooden tube, *a*, measuring eight lines in diameter, and three inches in length, and contracted towards one extremity, so that it may be inserted deep into the external meatus, is closed at its wider extremity by a membrane. In the side of this tube, which

* Encyclop. Wörterbuch der Medic. Wissensch. art. Gehör.

represents the cavity of the tympanum, is a very small opening; and at this point a second tube, *b*, can be connected with it. The tube *c*, which serves the purpose of the external auditory passage, receives, by its lower extremity, the large end of the tube *a*, which is fitted tightly into it.

Fig. 134.



The sound, by means of which the influence of this apparatus is to be estimated, must not be excited in the free space of the surrounding air, for then it would reach the ear through the tube *b*, or, when this is removed, through the small opening in the tube *a*, as well as through the pipe *c*, which represents the external auditory passage. It must be produced within the tube *c*, in such a manner as to extend but little beyond it. The best mode of fulfilling this condition I found to be, to cause an assistant to apply his lips closely to the mouth of the pipe *d*, and, while he closed his nostrils, to strike his teeth together so as to produce a noise, which was imparted to the air in the tube. The contact of the soft parts of the lips with the tube *c* prevents the sound from being communicated to the walls of that tube; while, by the air of the tube, it is conducted to the membrane, and to the air of the tube *a*, which represents the tympanum. The narrow part of the tube *a* being fixed firmly in my ear, I compare the differences of the sounds transmitted to it when the side opening in the tube *a*, or tympanum, is closed, when it is open, and when the side tube *b* is affixed. The sound I find is duller when the side opening which represents the opening of the Eustachian tube into the tympanum, is closed than when it is open; but there is little or no difference in its intensity. The difference is much less between the sound heard when the side tube is affixed, and that heard when the orifice is merely open without the side tube being placed over it; the "timbre" is here in both cases the same, and there is no perceptible difference in intensity,—at least, no decided difference. When, therefore, the opening between a cavity representing the tympanum, and a side cavity, *b*, is very small, the latter cavity loses all, or nearly all, its influence by resonance upon a sound which is not communicated directly to it.

6. The most generally adopted view of the office of the Eustachian tube is, that it does away with an impediment which a body of air con-

fined on every side in the tympanum would offer to the propagation of sound, by diminishing either the original vibrations of the membrana tympani itself, or the resonance of that membrane, and of the air of the tympanic cavity. Itard illustrated this view by reference to the soldier's drum, which yields only a dull and faint sound when the opening in its side is closed. This example, however, bears little analogy to the case it is intended to elucidate; for, if the sound of a drum were louder when it has a side opening, this would be owing to the vibrations of the air within the drum being communicated better to the atmosphere and ear by air itself, than by the solid walls of the drum and its membranes (parchment heads). Moreover, I find the difference between the sound of a small drum, when its side hole is open, and when it is closed, very slight, amounting to a scarcely perceptible difference in "timbre." No increase in the intensity of sounds can be supposed to be produced by the sonorous undulations entering the mouth and nostrils being transmitted to the tympanum through the Eustachian tube; for a person whose organs are perfectly healthy hears as well when his mouth and nostrils are closed as when they are open.

Several experiments which I have instituted are not favourable to the opinion, that the presence of the Eustachian tube renders the sounds transmitted through the membrana tympani more intense. A short tube, with a side opening like the portion *a*, in fig. 134, was inserted deep into the ear, and a sound excited upon the membrane closing its outer extremity, while the other ear was stopped with a plug of chewed paper. A sound produced in the surrounding atmosphere could not, of course, be made the subject of comparison, since it would be transmitted through the side opening of the tube to the air in its interior with greater intensity than through the membrane at its extremity. It was found, however, that a sound excited in the membrane itself by striking or rubbing it with the finger, was always heard with a dull tone when the side opening of the tube was closed, and with a clear, and, as it were, sharp character, when the same orifice was open. But there was no difference in its intensity; on the contrary, when the membrane was moistened, the dull sound heard with the side orifice closed seemed to me to be louder than the clear sound heard with it open. The result was the same when the experiment was performed with the apparatus represented by fig. 134, in the manner before described. The sound heard when an assistant applied his lips to the mouth of the tube *d*, and struck his teeth together while his nostrils were closed, (the end of the tube *a* being fixed in the experimentor's ear, and the side tube *b* removed,) had a duller character when the side orifice was closed than when it was open; but it did not differ perceptibly in intensity.

We may, therefore, admit that a certain degree of dulness, which the sound might acquire from the resonance of the apparatus of the tympanum, is avoided by the presence of the Eustachian tube; but that this tube tends to increase the intensity of the sound, as the above-mentioned hypothesis supposes, cannot be conceded. Some other experiments, also, on the organ of hearing itself, in which the Eustachian tube is closed or left open, tend to confirm the above conclusion, at which we have arrived. The most certain method of ascertaining the function of the Eustachian tube would undoubtedly be to close the Eustachian itself artificially, but in such a way that the pressure of the air in the tympanum should not thereby be increased, and greater tension of the membrana tympani produced. But this is scarcely possible; and, besides, the experimentor who allowed his Eustachian tube to be catheterized, could never be perfectly sure whether or not the instrument was really in the canal. This idea may, therefore, be at once renounced, as little calculated to advance physiology. Pathological observations, again, have hitherto afforded but little aid in solving the difficulty. The injection of water into the Eustachian tube was observed by Cheselden to produce immediate deafness. Saunders, on the contrary, states that this operation on a person labouring under deafness was followed by an improvement of hearing, which lasted as long as the fluid was retained in the ear. This discrepancy in the results seems to have another cause than the mere occlusion and opening of the Eustachian tube. More importance was probably due in these cases to the state of tension of the membrana tympani, which might have been increased by the operation; or if the pressure of the air within the tympanum had previously been less than natural, so that the membrana tympani was pressed inwards, diminution of its tension might be produced by the injection of the water increasing the pressure of the air within. There is, however, a means of producing at will either occlusion or dilatation of the Eustachian tube, with equal though increased tension of the membrana tympani. By making an effort at inspiration, while the mouth and nostrils are closed, the air in the tympanum is rarefied, and at the same time the sides of the Eustachian tube collapse, which is known by the sensation due to the tension of the membrana tympani continuing after the cessation of the movement of inspiration until voluntarily removed by an effort in the ear (see page 1259). On the other hand, by a strong effort of expiration, the mouth and nostrils being closed as before, the Eustachian tube may be dilated beyond its ordinary size; here, also, the membrana tympani is rendered tense: the conditions of the tympanum are, therefore, with the exception of the state of density of the air, nearly the same in both cases. In both the membrana tympani is more tense than natural; but in one the tuba Eustachii is dilated, in the other it is closed. Hearing, however, is equally impaired in both states.

7. The opinion that the Eustachian tube is destined for the transmission of the sound of the individual's own voice to his ear, would seem to be sufficiently refuted by the experiment performed long since by Schellhammer. He introduced a vibrating tuning-fork into the interior of his mouth, and found that its sound was in that situation scarcely heard. Held in front of the mouth moderately open, it sounds very loudly, in consequence of the resonance of the air in the cavity, just as the air of a bottle renders the sound of a tuning-fork held near its mouth much louder. But in this case, also, the sound is conveyed to the tympanum principally through the medium of the external ear. The ticking of a watch also held in the mouth, in such a manner that it does not touch the teeth or tongue, is scarcely heard. Schellhammer's experiment is not, however, conclusive; for the sound of the tuning-fork, like all sonorous vibrations of solid bodies, is not readily imparted to the air; while the vibrations of the vocal cords, like those of all reed-instruments, excite regular sympathetic vibrations of the air itself. There is another method, however, by which we may satisfy ourselves that the influence of the Eustachian tube in rendering the individual's voice audible to himself, is very slight. The Eustachian tubes may, as we have already described, be closed or opened at will by the aid of certain movements of inspiration. The tubes being closed by an effort of inspiration, or opened by an effort of expiration, we have merely, while the mouth and nostrils are still held closed, to produce a vocal sound, (which can be effected at least with the character of a short humming sound,) when we shall perceive that in either case we hear our voice quite distinctly. The difference in the sound is very trifling, its intensity being in a slight degree greater when the Eustachian tubes are wide open than when they are closed. It is certain, therefore, that these tubes are not the principal route by which our own voice is conducted to our ears. Our voice is heard partly through the medium of the external meatus; it spreads forth from the mouth in circular waves, the hinder portions of which fall upon the concha, and are reflected by it towards the tragus, and thence into the external meatus.

The concha of the external ear appears to me, indeed, to have the very position best adapted for reflecting towards the meatus the sonorous undulations issuing from the mouth. The sound of our voice is, however, communicated from the air in our nostrils and mouth to the walls of these cavities, and thus also through the cranial bones to the ear, and again, in a still more direct path, by a chain of solid parts from the vocal cords to the labyrinth. The great share which this mode of propagation must have in conducting the sound of our voice to the ear may be inferred from the distinctness with which we hear sounds produced in situations wholly surrounded by the solid parts of our body, such as borborygmi in the intestines. A still better conception of the propagation of the sound of our voice to our ear through solid parts may be obtained by closing both ears with plugs, and interposing a conducting-rod between one ear and the larynx of another person while he speaks. His voice is then heard just as we hear our own. Autenrieth* and Lincke† have observed that, when the Eustachian tubes are obstructed in consequence of diseased action, external sounds are rendered indistinct, but that the patient hears his own voice well.

8. That the Eustachian tube has the office of conveying away mucus secreted in the cavity of the tympanum by means of cilia vibrating on its surface, cannot be doubted; and the deafness consequent on occlusion of the tube is in part explicable by the tympanum becoming then filled with mucus. But this cannot be the sole office of the passage.

9. The principal object for the fulfilment of which the Eustachian tube exists, wherever there is a tympanum, appears to me to be the maintenance of the equilibrium between the air within the tympanum and the external air, so as to prevent inordinate tension of the membrana tympani, which would be produced by too great or too little pressure on either side, and the effect of which would be imperfection of hearing. It is not the increased or diminished density of the air on either side of the membrane which is of the chief importance, but the tension of the membrana tympani which they necessarily produce, and which always interferes with the integrity of hearing.

It is on this principle that we must explain the good effect of catheterizing the Eustachian tube, or of perforating the membrana tympani, or mastoid process of the temporal bone, in many cases of deafness caused by chronic occlusion of the tube. While, however, I maintain that this is the principal office of the Eustachian canal, I do not deny that it has other uses, of which the next in importance appear to me to be the modification of the sound so as to render it more clear, the supplying the tympanum with air, and the discharge of the secretion of that cavity.

When the Eustachian tubes are sufficiently wide, the density of the air within the tympanum will be kept constantly equal to that of the external air; and, when the latter rapidly increases in density, the air within the tympanum will immediately acquire the same density, so as to balance the increased external pressure upon the membrana tympani, without our being conscious of any change. In proof, however, that in other cases the balance of the pressure within the tympanum and upon its exterior may be disturbed, the observations of persons who have descended in the diving-bell (see page 1260) may be adduced.‡ Carus§

* Reil's Archiv. ix. 321.

† Op. cit. p. 502.

‡ [See also Dr. Todd's observations in the Cyclopædia of Anât. and Physiol. art. Hearing, p. 575.]

§ Bericht über die Versammlung der Naturforscher in Jena.

also, in ascending high mountains, perceived a sensation of tension in the ears; and, after a certain height was attained, a snapping sound, which was repeated at elevations differing about six hundred feet from each other. Whether these sensations be perceived or not by others, will, of course, depend in part on differences of individual conformation. I do not myself recollect to have experienced anything of the kind. Before, however, the state of disturbed balance of pressure had reached its maximum, I should remove it by a voluntary action of the tensor tympani (see page 1262), which is also attended in me with a snapping sound.

Muncke supposes that the membrane of the fenestra rotunda serves by its elasticity to moderate the effects of a violent impulse communicated to the fluid of the labyrinth. An opening in the side of a tube filled with air and conducting sound, is certainly calculated to divert the sonorous vibrations which are otherwise kept insulated within the tube on account of the difficulty with which undulations are communicated from air to solid bodies; but undulations of condensation and rarefaction produced by an impulse in water are imparted with facility to solids.

The external auditory passage.

The meatus auditorius externus influences the propagation of sound to the tympanum in three ways: 1, inasmuch as the sonorous undulations entering directly from the atmosphere are transmitted by the air in the tube immediately to the membrana tympani, and are prevented from being dispersed; 2, by the walls of the passage conducting the sonorous undulations imparted to the external ear itself by the shortest path to the place of attachment of the membrana tympani, and so to this membrane; 3, by the resonance of the column of air contained within the passage.

As a conductor of undulations of air, it receives the direct undulations of the atmosphere, of which those which enter in the direction of the axis of the canal must produce the strongest impression. The undulations which enter the passage obliquely will be reflected by its parietes, and will thus by reflexion reach the membrana tympani. By reflexion, also, the external meatus receives the undulations which impinge upon the concha of the external ear, when their angle of inflexion is such that they are thrown towards the tragus. Other sonorous undulations again, which could enter the meatus from the external air neither directly nor by reflexion, may still be brought into it by "inflexion;" undulations, for instance, whose direction is that of the long axis of the head, and which pass over the surface of the ear, must, in accordance with the laws of "inflexion," be bent into the external meatus by its margins. The action of those undulations will, however, be most intense which enter the meatus directly, neither by reflexion nor inflexion. Hence we are enabled to judge of the point whence sound comes, by turning one ear in different directions.

We have next to consider the walls of the meatus as solid conductors of sound; for those vibrations which are communicated to the cartilage of the external ear, and not reflected from it, are propagated by the shortest path through the parietes of the auditory passage to the membrana tympani. Hence both ears being close stopped, the sound of a pipe is heard more distinctly when its lower extremity covered with a membrane, is applied to the cartilage of the external ear itself, than when it is placed in contact with the surface of the head.

Lastly, the external auditory tube is important, inasmuch as the air which it contains, like all insulated masses of air, increases the intensity of sounds by resonance. To convince ourselves of its really having this influence, we need merely lengthen the passage by affixing to it another tube. Every sound that is heard, even the sound of our own voice, is then much increased in intensity. If tubes of considerable length are used, and their length is adapted to the sound, the column of air in them will reciprocate it by their own fundamental notes, as the MM. Weber have shown. Shorter columns of air do not thus reciprocate sounds, but merely increase their intensity by resonance.*

Cartilage of the external ear.

The action of the external ear upon sonorous vibrations is partly to reflect them, and partly to condense and conduct them to the parietes of the meatus externus. With respect to its reflecting action, the excavation called the concha is the most important part, since it directs the reflected undulations towards the tragus, whence they are thrown into the auditory passage. The other inequalities of the external ear do not promote hearing by reflexion;† and, if the conducting power of the cartilage of the ear were left out of consideration, they might be regarded as destined for no particular use; but, receiving the impulses of the air, the cartilage of the external ear, while it reflects a part of them, propagates within itself and condenses the rest, as all other solid and elastic bodies would do. This action of the cartilages of the external ear is with justice insisted on by M. Savart. The sonorous vibrations which it receives by an extended surface are conducted by it to its place of attachment. The mode of propagation of the impulses in the cartilage of the ear may be illustrated by reference to Savart's investigations concerning the propagation of undulations in bodies formed of branches having different directions, the results of which I applied to the explanation of the propagation of sound by the ossicula auditus. The undulations

* See note to page 1264. [The resonant action of the meatus, particularly when lightly closed, was pointed out by Mr. Wheatstone, in the Journal of Science and Arts for 1827, vol. ii. New Series.]

† See Esser, in Kastner's Archiv. xii.

communicated to the cartilaginous external ear will not follow its various curves, but will traverse it in their own original direction, causing the neighbouring parts of the cartilage also, whatever their position, to be thrown into a vibratory movement which has exactly the same direction. This propagation of the movement is continued from particle to particle even to the interior of the ear, the membrana tympani, and the bones of the head. In consequence of the connexion of the parietes of the auditory passage with the solid parts of the whole head, some dispersion of the undulations will result; but the points of attachment of the membrana tympani will receive them by the shortest path, and will as certainly communicate them to that membrane, as the solid sides of a drum communicate sonorous undulations to the parchment head, or the bridge of a musical string its vibrations to the string.

Regarding the cartilage of the external ear, therefore, as a conductor of sonorous vibrations, all its inequalities, elevations and depressions, which are useless with relation to reflexion, become of evident importance; for those elevations and depressions upon which the undulations fall perpendicularly, will be affected by them in the most intense degree; and, in consequence of the various form and position of these inequalities, sonorous undulations, in whatever direction they may come, must fall perpendicularly upon the tangent of some one of them. This affords an explanation of the extraordinary form given to this part.

The external ear of many animals is in every respect comparable to an ear-trumpet capable of being directed different ways at will, in which the undulations of the air are propagated onwards and concentrated at the same time, and whose parietes also are capable of transmitting the sonorous vibrations communicated to them. Moreover, this form of ear, like the ear-trumpet, lengthens the column of air of the auditory passage, and increases the influence which its resonance has in rendering the sound more intense.*

Solid bodies and masses of air in the neighbourhood of the labyrinth influencing sounds by their resonance.

In this light we must regard, not merely the cranial bones, but all cartilages and membranes in the vicinity of the organ of hearing.

By the resonance of bodies of air occupying cavities within the head our voice is rendered more audible, not merely to others, but also to ourselves. Any mass of air bounded by a different medium is excited to resonance by a sound produced near it. If a vibrating tuning-fork is held over the mouth of an apothecary's phial, the air within it gives great increased loudness to the sound by resonance; while, if the tuning-fork is merely

* The great influence of the insulated column of air in increasing the intensity of the sounds is frequently overlooked in the case both of the ear-trumpet and of the speaking-trumpet.

brought near the side of the phial, the resonance is much less marked. The resonance of the column of air in a tube open at one or both extremities, is very strong. So, also, if a tuning-fork is held, while vibrating, close in front of the mouth, great resonance is produced, which is heard as well by the experimentor as by a bystander.* Whereas, if it is introduced quite into the interior of the mouth while this is held wide open, the sound heard is remarkably faint, not only to the ear of other persons, but to that of the individual himself. The circumstance of persons whose hearing is bad holding their mouth open while listening, appears to have some connexion with the resonant power of the air in the mouth: it cannot have reference to the transmission of the sound through the Eustachian tubes, since a tuning-fork vibrating even at the back of the mouth is heard but faintly. The habit of holding the mouth open in persons whose hearing is imperfect, may, however, have for its object more particularly to dilate the cartilaginous portion of the auditory passage, which, as Elliot remarks, is effected by opening the mouth.

At all events, the intensity which the voice of another person acquires when he speaks through a tube placed in front of our mouth or nostrils, must depend in part on the resonance of the cavities containing air which lie in our head.

Even the air in the external auditory passage and in the tympanum has an action of resonance. This is perceived when we simply elongate the auditory passage by inserting a tube into it. We then hear not merely the sound of the circulation in the ear, and of the slight movements of the air apparently at rest, which, without being necessarily sonorous undulations, produce a sound in the tube, just as a sound is produced in a musical pipe by a blast of wind; but every sound, as well that of our own voice as of external bodies, is accompanied by a distinct resonance. The same influence of the air of the meatus auditorius in increasing the intensity of sounds by resonance may be shown by shortening the column of air in the meatus by means of a plug inserted deeply, as well as by lengthening it; for, when the external auditory passages are thus plugged, not only are all external sounds rendered indistinct in consequence of the propagation of the undulations of the air to the membrana tympani being interrupted, but also the sound of our own voice is heard indistinctly and feebly. This cannot be wholly owing to the sonorous undulations issuing from our mouth being no longer admitted into the external meatus; for, though the undulations

* The sound thus produced resembles the sound of the letter *u broad*, or *oo*, when the opening of the mouth is small, and that of *a broad* when it is wider. The sound produced by holding a vibrating tuning-fork over a tube three and a half inches in length, and eight lines in diameter throughout, which is set upon a table, is likewise similar to that of the vowel *u* when the opening of the tube is narrowed by the hand, and more similar to *a broad* when the opening is left entirely free.

spreading out in circles from our lips do in the natural condition partly reach the external auditory meatus by reflexion from the concha towards the tragus, and by inflexion, yet their entrance into the auditory passage may be entirely prevented by holding the flat hands close in front of both ears, and our voice will still sound loudly to us if the whole meatus be full of air, so as to reinforce the sound by resonance. The want of the resonant body of air in the meatus must therefore be in part the cause of the indistinctness and faintness of our own voice when our ears are plugged.

The propagation of sound to the labyrinth through the cranial bones compared with that through the tympanum.

By the apparatus of the tympanum sonorous vibrations are communicated to the labyrinth on its external side, through the medium of the fenestræ, whence they spread in all directions through the perilymph or aqua Cotunnii.

The cranial bones, which in the osseous fishes are the only medium through which sound can reach the labyrinth, communicate the sonorous vibrations to it with equal facility on every side. Sound is conducted to the labyrinth in this way in animals living in the air also, but with very little intensity, on account of the difficulty with which vibrations of the air are communicated to the solid parts of the head. We have no means of ascertaining the degree of intensity with which sounds would be heard through the medium of our cranial bones alone; for, even when our ears are close stopped, the cartilage of the external ear still conducts the sound better than the cranial bones, and the insulated ossicula in the tympanum make a stronger impression on the labyrinth than the cranial bones, which are not thus insulated. The reinforcing power of the chain of small bones of the ear may come into play even when the sonorous undulations of the air are communicated primarily to the bones of the cranium; for, even in this case, the undulations are conducted by the latter bones to the membrana tympani and the ossicula, and are reinforced by the resonance of the apparatus of the tympanum. The same is the case with the sonorous undulations of our own voice, which, being communicated to the parts surrounding the mouth, throat, and nostrils, excite resonance of the acoustic apparatus of the tympanum. Undulations imparted to the bones of the head by solid bodies also are reinforced by resonance in the tympanum. A vibrating tuning-fork applied to the head, while both ears are stopped, is heard most faintly at the vertex, more loudly when placed upon the temple, and with more and more intensity the nearer it is brought to the meatus externus of the ear, and not merely in proportion to its approximation to the labyrinth.

For sounds to be heard through the medium of the cranial bones alone, it would be necessary for the apparatus of the tympanum to be absent, as well as the external meatus closed. It is probable that sounds propagated by the air would then either be inaudible, or be heard with excessive faintness; while the sonorous vibrations of solid bodies conducted by solid media to the head would still be audible if the labyrinth were free from lesion. This test might be employed in cases of deafness, to ascertain whether the labyrinth and auditory nerve are sound.

A deaf person, who is unable to hear any sound through the medium of the atmosphere, is nevertheless sometimes able to perceive the sound of strong blows upon the ground or floor, owing to the vibrations being conducted to his ear through the solid parts of his body. There is here a difficulty, however, in distinguishing between the perception of vibrations by the sense of touch and by the sense of hearing. All grave sounds act readily upon the nerves of touch; the sonorous vibrations are felt distinctly as tremors when the hand is applied to the thorax while speaking, or when a solid body emitting a sound is held in the hand. The sonorous vibrations excited in water by means of a musical pipe are not sensible to the touch when the hand is dipped in the water, but are perceived distinctly if a solid body held in the hand is partially immersed in it. This perception of sonorous vibrations by the sense of touch has given rise to the false notion that other nerves than the auditory nerve are capable of the sensation of sound.

Of the propagation of sound to the ear by different media.

1. *By the air.*—Sounds are most frequently heard through the medium of undulations of the air, whether these are primarily excited in it, or imparted to it by other bodies. Sonorous undulations are communicated to the ear with much greater intensity if originally produced in the air, and not merely conducted by it from other bodies; for, in the transition of sonorous vibrations from other media into air, they suffer a diminution of their force. Hence the feeble sound heard when strings or a tuning-fork vibrate without being connected with a sounding-board, by a bridge or other means; while wind-instruments, in which the air is the original seat of the vibrations, require no sounding-board. The only body which could increase the intensity of sonorous vibrations generated in air would be an insulated mass of the same medium. All solid bodies would contribute but little to the strengthening of the sound, on account of the loss of intensity which the vibrations would suffer in their transition from the air originally sounding to the solid body, and from this again to the air.

On account of the difficulty attending the transition of sonorous undulations from water, as from solid bodies, into the air, a sound produced in the water, and transmitted to the ear by the atmosphere, is always heard faintly; and, if the direction of the sonorous undulations with regard to the surface of the water and air is very oblique, it is not even audible; just as rays of light under the same conditions do not reach the eye. This difficulty was experienced by M. Colladon in his experiments on the velocity of the propagation of sound in water. A tube immersed in the water and applied to the ear afforded him no aid, until a solid plate for the reception of the sonorous undulations of the water was placed at the lower end of the tube. To render sounds in water distinctly audible while the ear is surrounded by an atmosphere of air, the sonorous undulations must not merely be received by a solid rod and conducted by this to the ear, but this rod must be brought into contact with a solid plug occupying the meatus externus, so that the intervention of air as a conducting medium may be avoided as much as possible. This is the only method by which the full sound of a small bell immersed in water can be made audible.*

The obstruction to the sound is still greater when it has to pass first from air into water, and then again from the water into air, before reaching the organ of hearing; hence persons in the diving-bell hear nothing of sounds generated in the atmosphere above.†

The loudness of sounds heard through the medium of the air is, moreover, influenced by its density and degree of dryness. The velocity of sound increases with the diminution of the density of the air, but its intensity decreases. The sound of a bell vibrating in the exhausted receiver of an air-pump is scarcely audible; though this strictly proves nothing more than that sonorous vibrations are very much diminished in intensity in passing from the bell to the rarefied air, and from this to the walls of the receiver. Scarcely any experiments have been instituted to determine the difference in the impression produced on the ear by undulations of air of very different densities, when these undulations pass immediately to the tympanum, without the intervention of any solid bodies: there is merely the observation of Dr. Saussure, that, in the rarefied stratum of air on the summit of Mont Blanc, the discharge of a pistol caused a sound not louder than that ordinarily produced by a small rocket.

2. Direct propagation of sound to the ear (that is, to the membrana tympani) by water, may be observed in bathing. All sounds generated

* The fact observed by M. Colladon, that the sound of a bell in the water is not transmitted thence to the ear, but that merely a short impulse is perceived, might depend on the distance of the sounding body, or on the imperfect conducting power of the media; for the sound of a bell made to vibrate in water near the ear is, according to my experiments, always heard, unless it has to pass through a stratum of air to reach the labyrinth instead of being conducted by a chain of solid bodies.

† See Gehler's Physic. Wörterb. viii. p. 449.

in the water itself are then heard very distinctly. This fact, which was proved by the experiments of Nollet and Monro, is known to every bather. Sounds produced in the air, and merely transmitted from it to the ear by the water, are, on the contrary, not heard well, on account of the considerable diminution of intensity which sonorous undulations undergo in their transition from air to water.

3. Direct propagation of sound to the organ of hearing by solid bodies.—Sonorous undulations, excited primarily in the air, are conducted to the tympanum best by that medium; and, in the same manner, solid bodies form the best conducting medium for sounds emitted by solid bodies. The sound produced by striking a piece of wood or metal is feeble when communicated to the ear by the atmosphere only; while it is very intense if a cord attached to the sounding body is held between the teeth, or brought into contact with both ears previously plugged. Thus Herhold and Rafn were enabled to conduct the sonorous vibrations produced by striking a spoon so perfectly, by means of a cord fixed to it, that at the distance of three hundred yards it still sounded like a bell. All parts of the head, soft or hard, are capable of conducting to the organ of hearing the sonorous vibrations of solid bodies brought into contact with them, but the soft parts less perfectly than the hard.* The sound conducted by a rod which is in contact with the sounding body, is heard most loudly when the rod is applied to the head at parts where the bones are but thinly covered, or, still better, where they are bare, as at the teeth. The ticking of a watch is heard very distinctly when it is made to touch the teeth, particularly those of the upper jaw, from which the sound is conducted to the ear by hard parts only. The sound is fainter when the watch is applied to the tongue, and still more so when it is held free in the cavity of the mouth. The sound of the watch is conducted with equal and even greater intensity to the ear by the solid parietes of the meatus auditorius externus, this passage being stopped, and a rod interposed between the watch and the plug, or the part of the ear very near the plug. The sonorous undulations in this case, instead of being propagated by the bones of the cranium directly to the labyrinth, are conducted by the solid walls of the external auditory passage to the membrana tympani and ossicula auditus. The use of the

* According to the experiments of Perier and Larrey, on persons in whom the trephine had been used, one should believe that sonorous undulations are communicated from the air to the auditory nerves more readily by the mere soft parts than by the cranial bones covered with skin. It is stated that, when the ears of such individuals were stopped, sounds were heard most perfectly if the sounding body was brought over the cicatrix of the part where the cranial bone had been removed. This result, which appears to require confirmation, was obtained, it is said, only when the opening made by the trephine was situated at the fore part of the head.—(Larrey, Clinique Chirurgicale; Paris, 1836, p. 33.)

ear-trumpet consists partly in the undulations of the air being conducted to the ear with undiminished intensity, and partly upon the resonance of the column of air contained in the trumpet; but its effect is also increased by the vibrations of the resounding walls of the tube being communicated immediately to the solid parietes of the meatus auditorius. Of this we may easily convince ourselves by holding the ear-trumpet by the side between our teeth while our ears are stopped, and then causing another person to speak into the mouth of the tube: the condensation of the undulations of the air in the tube can here have no influence; and, nevertheless, an extremely loud sound is heard, which is due to the resonance of the tube itself, but which, if conducted to the ear by the atmosphere only, would be scarcely heard.

The immediate propagation of sound by solid parts to the organ of hearing comes into play also when the ear is applied to the surface of the ground for the purpose of listening. The sounds are heard still better if the ear is stopped, and the plug touches the ground. Those sounds only, of course, are heard with any intensity which are either produced primarily in the ground itself, or communicated to it by solid media from other solid bodies in which they were originally generated: thus, the treading of men and horses is heard distinctly; while sounds produced primarily in the air, being with difficulty imparted from it to the solid ground, are not heard well in this manner.

The stethoscope again affords us an example of the propagation of sounds from solids, through other solid bodies, to the solid parts surrounding the organ of hearing. The use of the stethoscope has but little advantage over the application of the bare ear, except as far as the sound is increased in intensity by the resonance of the tube. With its ordinary construction, the stethoscope conducts sounds to the ear in two ways,—namely, by its solid portion, which receives the sonorous undulations from the solid body yielding the sound, and transmits them to the solid parts of the head around the organ of hearing; and by the column of air in its interior, which receives the sound also from the solid body, but transmits them through the air of the meatus externus to the membrana tympani. The interior column of air is a much less effective conducting medium than the wooden tube around, on account of the difficulty attending the transition of sonorous vibrations from solids to air, but it is of use by its resonance. Hence a simple solid rod does not answer the purpose of a stethoscope. Sounds may be heard, however, very distinctly by means of a mere rod, if the ear be stopped by a plug of chewed paper, and the one end of the rod be applied, not to the plug itself, on account of the sound of friction which would be produced, but to the external ear near it. Here the sonorous undulations are communicated more completely to the walls of the external meatus by means of the plug, and are thence propagated to the membrana tympani.

In cases of deafness, where the undulations of the air do not make sufficient impression even with the aid of an ear-trumpet, it is sometimes of use to convert the undulations of the air into undulations of solid bodies, and conduct these to the organ of hearing by solid media. This is best effected, when the object is to hear the voice of another person, by causing him to direct his voice into a basin, whence it is conducted to the ear by a rod held between the teeth, or applied to a plug inserted into the meatus auditorius of the deaf person.*

3. *Acoustic properties of the labyrinth.*

The fluid of the labyrinth, aquula Cotunnii, or perilymph, first claims our attention as the most general and constant of the acoustic provisions of the labyrinth. In all forms of organs of hearing, the sonorous vibrations affect the auditory nerve through the medium of a fluid. Why is it that nature has, in most animals, provided against the communication of sound to the auditory nerve directly from the bones of the cranium without the intervention of a fluid? In the case of animals living in the air, the reason might be supposed to be, that sonorous undulations are communicated with so much more facility from air to fluids, through the intervention of a tense membrane, which is either in direct contact with the water, or acts on it through the medium of a moveable and insulated solid body, than from air to solid bodies. But this explanation will not apply to aquatic animals: for vibrations are imparted very readily from water to solid bodies, and therefore would be so to the cranial bones, as, for example, in the osseous fishes; and, nevertheless, here also the sonorous vibrations of the cranial bones become undulations of the fluid of the labyrinth before acting on the auditory nerve. There must, therefore, be some more general reason for this provision. It is probably to be found in the following circumstances. The ultimate purpose of the organ of hearing is to impart, as perfectly as possible, the impulses of the sonorous vibrations to the fibres of the auditory nerve. This nerve being soft, and impregnated with water, like all nerves, sonorous undulations, in being communicated to it from solid parts, would be partly converted into undulations of a fluid, before producing their impression on the fibres. Besides, however, the impregnation of the nervous fibres with water, on which their softness depends, all the interspaces between the fibres are, as in all soft tissues, filled with fluid matters, either blood or the fluid of cellular membrane. Hence the auditory nerve, in receiving the sonorous undulations through the medium of the fluid of the labyrinth, receives it from a medium of the same kind as that

* All the experiments of this kind on the hearing of deaf persons by means of solid conductors, are collected in the works of Chladni, (Akustik, p. 262. 286,) and Lincke (op. cit. p. 530).

which occupies all the porosities and interstices of the nervous fibres themselves. On this account, the vibration of the particles in the nerve itself will probably be much more uniform in character than if merely the surfaces of the nerve had been in contact with solid parts; in which case, the more internal particles of the nerve, being distant from the surface of the solid bone, would be acted on in a different manner from the more superficial particles. Muncke* remarks, with reference to the fluid of the labyrinth, that water, although ill-adapted for the generation of sound, is nevertheless an excellent conductor of it, even a better one than air. This I cannot admit; it can be true only with respect to the velocity of the propagation of sound; for the undulations of air are conducted with least loss of intensity by air, those of water by water.

The passages called aqueducts appear to me to merit no consideration in relation to the physiology of hearing. They contain neither membranous canals nor fluid, nor even venous trunks, but merely serve to bring the periosteum of the cranial bones and dura mater into connexion with the internal periosteum of the labyrinth.†

There are three grades of developement of the labyrinth: 1, a mere vestibule with a sacculus; 2, a vestibule with semicircular canals, and a membranous labyrinth of correspondent form; 3, the preceding parts with the cochlea.

Vestibule, semicircular canals.—The function usually ascribed to the semicircular canals is that which Scarpa attributed to them; namely, the collecting of the sonorous undulations from the bones of the cranium. Canals generally influence sound by the resonance of their contents, by the condensed propagation of the sonorous undulations in their interior, and by the resonance of their walls.

No influence can be attributed to the canals of the labyrinth as resulting from the resonance of their contents; for water bounded by solid bodies is capable of perhaps no perceptible resonance, its undulations not being reflected by its surfaces when thus bounded. Water seems to be little adapted, also, for collecting sonorous undulations from surrounding solid bodies. I poured water into the canals on the surface of a dissecting table, which communicate with each other at several points, and then applied a vibrating tuning-fork to the end of the table, while I immersed a conducting-rod in the water only, and brought its other extremity into contact with my ear; but I did not in this way hear the sound at all more distinctly than when the rod was merely brought into contact with a small quantity of water dropped upon the surface of the table. Again, I caused canals to be bored in a thick plate of wood, and parallel with the surface of the wood, which could be inserted into the side of a wooden bowl, in such a manner that

* Gehler's Physic. Wörterb. iv. 2, p. 1211.

† Müller's Archiv. 1834; p. 22.

the openings of the canals in the wood communicated with the cavity of the bowl. The bowl and canals being now filled with water, and sonorous undulations excited in the water of the bowl by means of the musical pipe covered at its lower extremity with membrane, the sound, conveyed to the ear by a conducting-rod, was as distinct when the openings from the bowl into the canals of the wood were closed with plugs as when they were open.

The extent to which a tube filled with water may be compared to a communicating-pipe filled with air, is the next subject of inquiry. In pipes filled with air, sound may, as is well known, be conveyed to a considerable distance with scarcely any loss of intensity, in consequence of the difficulty with which undulations are communicated from air to the solid walls of the tube, and also owing to their being reflected at the curvatures. It is quite otherwise with a tube filled with water; sonorous undulations are reflected to a certain extent even in water, but the undulations pass into solid bodies much more readily from water than from air, and the strength of an impulse propagated in a determinate direction is maintained in its integrity only for a very short distance when transmitted through a tube filled with water. This may be illustrated by an experiment. The one-foot musical pipe was by its lower extremity, which was covered with membrane, connected with a tube four inches long, and eight lines in diameter, and this tube, and lower end of the pipe, were then immersed in water, which came into contact with the entire surface of the membrane above mentioned; the sound could then be heard, by means of a conducting-rod, much louder at the extremity of the tube than elsewhere in the water,—louder than on the exterior of the conducting tube, and than at the same distance from the end of the musical pipe when no tube was subjoined to it. But if the tube was a foot instead of four inches in length, no difference in the intensity of the sound could be detected at the end of the tube, and in the water at other parts of the vessel. Again, I connected two bowls filled with water by means of a glass tube six feet in length, also filled with water, but could not observe any signs of the tube with water exerting a conducting power similar to that of tubes filled with air. A sound excited at one extremity of the tube was not heard with any greater intensity or distinctness in the water at the other extremity, than in the vicinity of the resounding walls of the second bowl.

It may therefore be inferred, that though the semicircular canals have probably in some degree the power of conducting sounds in the direction of their curve, yet this conducting power is in them much less perfect than in tubes containing air. Some slight increase of intensity of the impression on the nerve of hearing, will result from the circumstance that the same undulation which enters one extremity of a semicircular canal from the vestibule will return with a part of its force by the other extremity. Dr. Young has ascribed some importance to this circumstance.

This degree of reinforcement of the impression of hearing by means of the semicircular canals, will take place even when the impulse is communicated to the labyrinth, not through the fenestræ, but by the cranial bones, as in fishes, and partly in man.

The resonance of the bony walls of the semicircular canals, excited by sonorous undulations in their fluid contents, comes next under consideration. It is found that when sonorous vibrations are imparted to solid surfaces in contact with water, the sound is, *cæteris paribus,* always heard with greater intensity near these surfaces than in other parts of the fluid; in an experiment to verify this fact, the conducting-rod of course must not actually touch the solid surface. If two such resounding surfaces are situated very near to each other, the sonorous undulations of the water between them have necessarily greater intensity. This I had an opportunity of observing in the experiment above mentioned with the piece of wood bored with canals which communicated with the cavity of a basin filled with water. The sound of a tuning-fork applied to the wooden plate was heard rather louder when the conducting-rod was introduced from the basin into the cavity of one of the canals, than when it was held near the walls of the basin at the same distance from the tuning-fork. That the comparison may be accurate, the extent to which the conducting-rod is immersed in the water must in this experiment be always the same; for, the greater the length of rod covered by the water, the louder is the sound.

If, then, we admit that the membranous semicircular canals have the conditions requisite for collecting the sonorous undulations of the cranial bones in their fluid contents, and for conducting them through their curved cavity more readily than they are carried off by the surrounding hard parts in the original direction of the undulations or impulses, the increased intensity of the sonorous vibrations thus attained will be of advantage in acting on the auditory nerve where it is expanded in the ampullæ of the canals, and in the sinus communis. Where the membranous canals are in contact with the solid parietes of the tubes, this action must be much more intense. But the membranous semicircular canals must have a function independent of the surrounding hard parts; for in the Petromyzon they are not separately enclosed in solid substance, but lie in one common cavity with the sinus communis, —a fact of great physiological importance.*

Autenrieth and Kerner imagined that the different canals had the

* [Mr. Pilcher (in his work on the Structure and Diseases of the Ear) has collected accounts of numerous cases of congenital deafness, in which malformations of the internal ear, particularly of the semicircular canals, were found to exist.]

power of making us acquainted with the direction whence sound comes. But we do not appear to have any perception of the direction of sound, except as far as we can judge from its acting more strongly on one ear than on the other, or from the difference in its intensity according as the direction of the external ear and concha is varied. Even supposing we were able to distinguish the direction of the impulse of the vibrating particles acting upon our auditory nerve, this direction would always be two-fold; for, after giving the impulse, the particles vibrate in the opposite direction, and this alternation of movement is regularly repeated in the production of a musical sound.

The *otolites* or *calcareous lapilli** found in the labyrinth of fishes and fish-like Amphibia, and the *crystalline pulverulent masses* which supply their place in other animals, would necessarily reinforce the sonorous vibrations by their resonance, even if they did not actually touch the membranes upon which the nerves are expanded; but, inasmuch as these bodies lie in contact with the membranous parts of the labyrinth, they communicate to these membranes and the nerves vibratory impulses of greater intensity than the aquula Cotunnii can impart. Sonorous undulations in water are not perceived by the hand itself immersed in the water, but are felt distinctly through the medium of a rod held in the hand.

This appears to me to be the real office of the lapilli and crystalline pulpy masses in the labyrinth. The opinion that the crystalline particles of these masses are, during the action of sonorous undulations on the ear, thrown off from the internal surface of the membranous labyrinth in the same way that dust or sand is thrown into motion upon vibrating solid laminæ and membranes, is not confirmed by experiment; for the dust floating on water does not present the slightest appearance of movement during the passage of sonorous undulations.

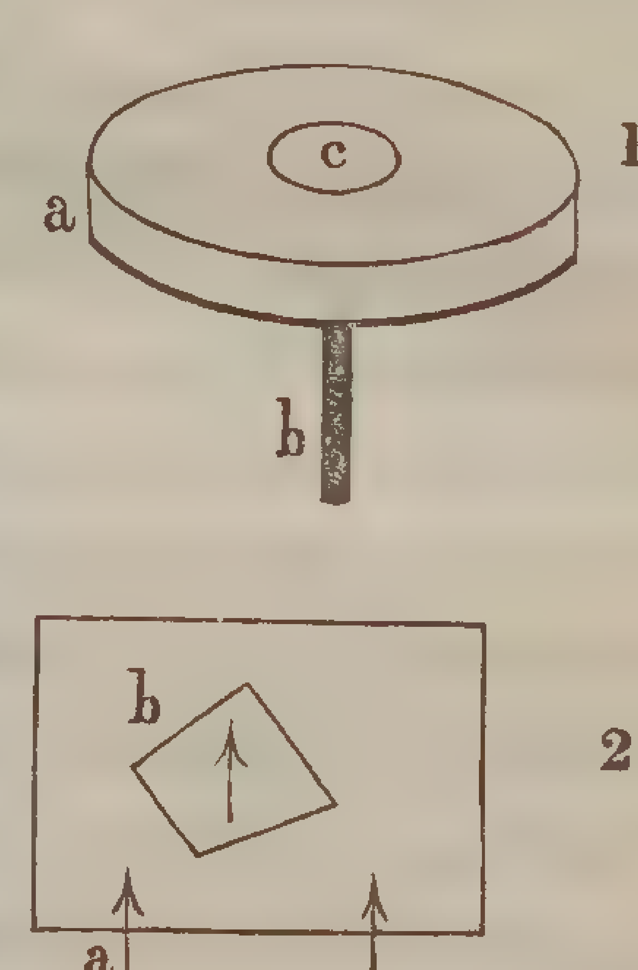
To illustrate further the use of these parts by experiment is difficult. I put some sand and water into a small sac, formed of a portion of softened pig's bladder, pressed this sac flat, and placed it in water, imitating the membranous labyrinth with the crystalline pulverulent mass; I then compared the intensity of the sound of a musical pipe in the water transmitted to the ear by means of a conducting-rod, when the sac with its contents was interposed between the pipe and rod without touching either, and when it was removed: the sound was certainly louder, *cæteris paribus,* when the sac was present. I found,

* The otolites of the osseous fishes have a structure similar to that of the enamel of teeth. Those of the zander (Perca lucioperca), for example, are formed of laminæ with a zone-like arrangement, in which a regular fibrous structure is at once evident. If laminæ of these bodies ground thin be treated with muriatic acid, they are seen to be constituted of acuminated bodies, exactly like those which I have described as existing in the enamel before it has become hardened. (Poggendorf's Annal. 38.)

however, that the same flattened sac merely filled with water, without any sand, had the same effect of increasing the intensity of the sound (by resonance). On what this resonance of membranes in water depends, I have not satisfied myself. The humerus of a bird, deprived of its earthy matter, when placed in contact both by its outer and inner surface with water, presented scarcely any sign of resonance: the same was the case with a portion of calf's intestine. A sound excited in the water without the sac, and transmitted to the ear by a conducting-rod, had exactly the same intensity, whether the portion of intestine immersed in water to which the rod was applied was long or short, provided the distance of the rod from the point of origin of the sound was the same.

The cochlea.—In investigating the acoustic properties of the labyrinth, it becomes necessary that we should inquire the direction in which impulses and undulations are propagated in the solid parts and fluid of the apparatus. Savart's investigations relative to the propagation of impulses from solid bodies to water, and from water to solid bodies, from which he obtained the result that impulses are communicated from one of these media to the other, without any change of direction, afford us data for this inquiry. If, to the bottom of a vessel filled with water, *a*, (fig. 135, 1,) a rod, *b*, is fixed, longitudinal vibrations excited in this rod are transmitted through the water to a lamina of wood, *c*, floating upon its surface, without change of direction, as is proved by the movement of the particles of sand strewed upon the surface of the lamina *c*. Again, if vibrations are excited by means of a violin bow in a vessel filled with water, *a*, (fig. 135, 2,) and they have the direction indicated by the arrows, they are propagated in the same direction through the water, and also through a lamina of wood, *b*, floating upon its surface, of which the margins are directed obliquely with regard to the sides of the vessel and to the direction of the undulations; the oblique direction of the borders of the plate with relation to the impulse does not modify the direction in which it is propagated. In both these cases, then, the sonorous vibrations are propagated in the same direction as if in the one instance the rod *b* were connected immediately with the plate *c*, and as if in the second the side of the vessel *a* were connected with the plate *b*, which is placed perpendicularly to it, by a solid conducting medium. Hence we may apply the laws of the propagation of impulses through plates united to each other at right angles to the case of the labyrinth.

Fig. 135.



We have already shown (page 1255) that when undulations are communicated to laminæ united at right angles, and their direction in the plate *a* (fig. 136) is that indicated by the arrows, they are also propagated through the perpendicular plate *b d*, and the second horizontal plate *c c′*, in the same direction. Now, the perpendicular plate *b d*, in this experiment, may be compared to the modiolus of the cochlea, and the horizontal plates to the lamina spiralis of the same part, and the resemblance becomes more evident when the figure is modified, as in fig. 137. In whatever direction, therefore, sonorous undulations are ex-

Fig. 136.

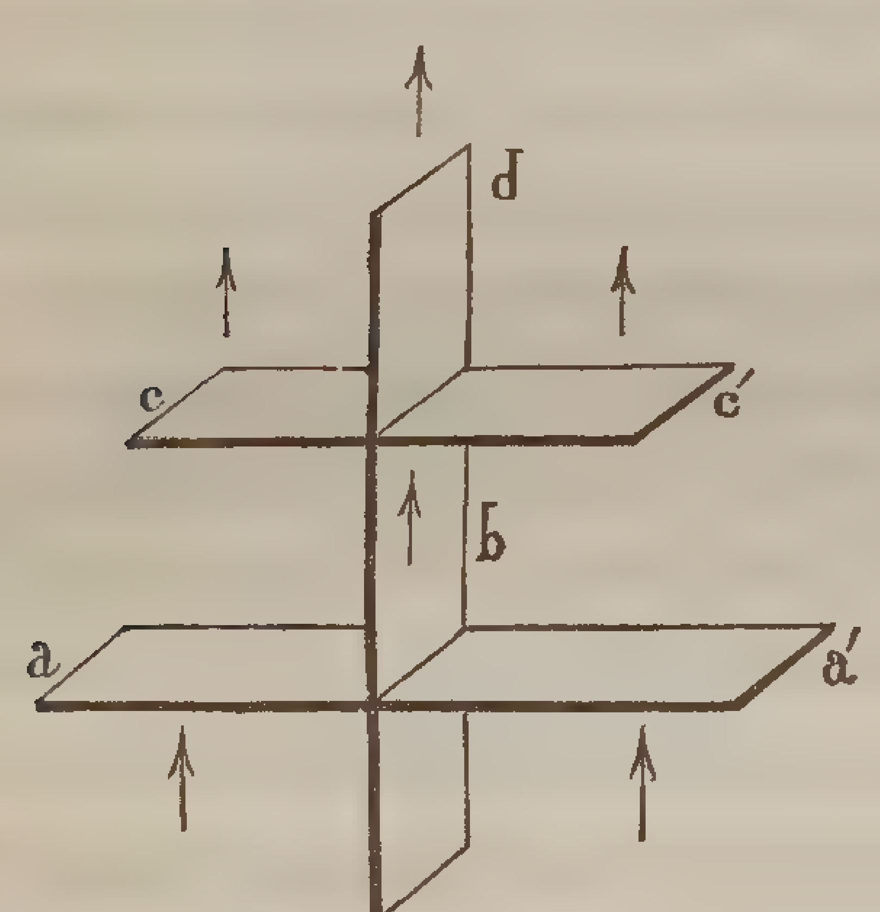
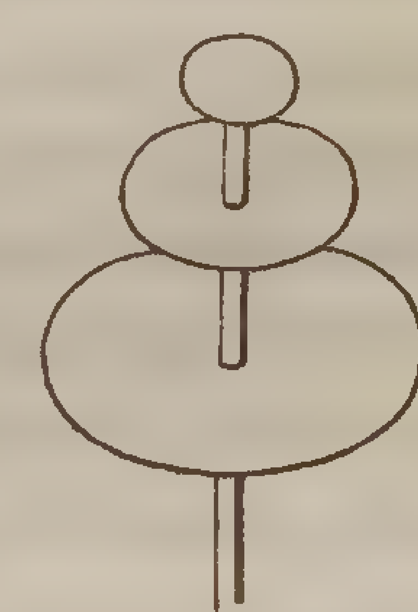


Fig. 137.



cited, either in the modiolus, or in the spiral lamina, they will be propagated with the same direction through all parts of the cochlea, whether the impulse be communicated primarily from the cranial bones to the modiolus, or to the external wall of the cochlea, and thence to the spiral lamina, or from the fluid of the labyrinth to either of these parts. With respect to the undulations communicated to the cochlea through the medium of the fluid of the labyrinth, it is to be observed, that the direction of the fenestra ovalis is such, that a line perpendicular to its area would be nearly parallel to the modiolus of the cochlea; consequently, impulses originating at this fenestra will probably excite in the solid parts of the cochlea undulations having the same direction as the modiolus,—that is to say, the lamina spiralis will in its whole extent become the seat of vibrations having a direction nearly perpendicular to its surface. I am able to ascertain easily the direction of an impulse in solid plates which communicate sound to each other in water by means of a conducting-rod, the sound being always heard with greatest intensity when the rod is applied to the plate in the direction in which the impulse travels.

Thus far we have supposed the different parts of the cochlea to be affected by the impulse simultaneously, or nearly so. The question now suggests itself, whether the sonorous pulses may not possibly be propagated gradually along the windings of the cochlea, for example, from the fenestra rotunda to the cupola, either through the medium of the fluid occupying the scalæ, or by following the turns of the lamina spiralis itself. Since the winding canal of the cochlea and the lamina spiralis are of considerable length, namely, from eighteen to nineteen lines at the outer border of their convolutions, the use of the cochlea — if such a successive propagation of the impulses along its windings were possible — might be to prolong the impression of sounds. The truth of this hypothesis is, however, very doubtful. Sounds would certainly be conducted in that manner through a winding-tube filled with air; but sonorous undulations or impulses are communicated so readily from water to solid bodies, that they will not be propagated simply along the windings of a canal filled with water, but will be transmitted from the commencement of the spire, through the modiolus, so as to intersect the canal at another part of its convolutions. The spiral lamina also can scarcely be supposed to conduct sound merely in the course of its windings; for, being continuous with the solid exterior parietes of the cochlea, and with the modiolus, it will communicate the vibrations to them as readily as to the prolongation of itself, and the impulses thus imparted to the modiolus and walls of the cochlea will be transmitted to other parts of the spiral lamina, without regularly following its windings. A regular propagation of the sonorous undulations along its course would require that the canal, instead of being spirally convoluted, were extended in a straight line in the direction of the impulse.

It is certain, therefore, that this hypothesis of the undisturbed progression of the impulse along the water of the scalæ, or in the spiral lamina, is untenable. Such a gradual affection of the nervous fibres along a course more than $1\frac{1}{2}$ inch in length, would also rather diminish than increase the distinctness of perception; for along the tract there would at the same time be particles of the nerve affected by the maximum of the impulse and the succeeding rarefaction, while in others the maximum could not yet be attained, so that the effect of echo would be produced. The cochlea, however, instead of giving rise to this inconvenience, really provides against its occurrence by the winding of its canal being confined within a small space.

The spiral lamina of the cochlea must therefore be regarded as a surface upon which all the fibres of the cochlear nerve are spread out, so as to be nearly simultaneously exposed to the impulse of the sonorous undulation, and simultaneously thrown into the maximum state of condensation, and again into the maximum state of rarefaction. According to this view of the use of the cochlea, it would make no essential difference if the nervous fibres were spread out upon several distinct circular plates surrounding the modiolus, instead of a continuous spirally wound lamina; but the latter form employed by nature has this advantage, that all parts of the spiral lamina are so connected with each other, that an impulse to one part is communicated more readily to the others.

The convoluted form of the cochlea serves also the purpose of affording in a small space a considerable extent of surface required for the expansion of the nervous fibres.

The object which nature has sought to attain in the cochlea seems to be the spreading out of the nervous fibres upon a solid lamina which should communicate with the solid walls of the labyrinth and cranium, at the same time that it is in contact with the fluid of the labyrinth; and which, besides exposing the nervous fibres to the influence of sonorous undulations by two media, should be itself insulated by fluid on either side. In accordance with this view, we can explain all the acoustic provisions of the cochlea.

The connexion of the lamina spiralis with the solid walls of the labyrinth adapts the cochlea for the perception of the sonorous undulations propagated by the solid parts of the head and the walls of the labyrinth. This use of the cochlea has been previously pointed out by Professor E. H. Weber.* The membranous labyrinth of the vestibule and semicircular canals is suspended free in the liquor Cotunnii, and is evidently destined more particularly for the perception of sounds through the medium of that fluid, whether the sonorous undulations are imparted to the fluid by the intervention of the cranial bones, as in fishes and in man, when sounding bodies are brought into communication with his head or teeth, or through the fenestræ. The membranous labyrinth is certainly exposed to the influence of the resonance of the bony parietes of the labyrinthic cavity; for sonorous undulations in water are, as I have shown, heard with greatest intensity in the vicinity of solid walls; but yet it remains strictly true that the membranous labyrinth is acted on immediately only by the undulations of a fluid. The spiral lamina on which the nervous fibres are expanded in the cochlea is, on the contrary, continuous with the solid walls of the labyrinth, and receives directly from them the impulses which they transmit. This is an important advantage; for the impulses imparted by solid bodies have, *cæteris paribus*, a greater absolute intensity than those communicated by water.

The greater intensity of the undulations of solid bodies than of liquids, has been sufficiently proved in the course of the preceding inquiries. If it be wished to compare the intensity of the sonorous impulses imparted by solid bodies and by water, the experiment must not be performed by placing the conductor in the one case directly in contact with the solid body, and in the other in the water; it will not thus yield a fair result; for the undulations of solid bodies are communicated without any loss of intensity to other solid bodies in contact with them, while in their transition from water to a solid body undulations lose much of their force: but if the conductor be placed in the water,

* Annot. Anatomicæ et Physiologicæ. Lips. 1834.

not in contact with the solid body, but very near it, and again in the water at a distance from it, but at the same distance from the source of the sound, the conditions for the comparison are the same in both cases. The undulations are then in both instances undulations of water before they are communicated to the conducting-rod. And thus it is found that, even when a sound is excited in the water, the sonorous undulations are more intense in the water near the surface of the vessel containing it than in other parts of the water equally distant from the point of origin of the sound; hence we may conclude that, *cæteris paribus*, the sonorous undulations of solid bodies act with greater intensity than those of water. Hence we perceive at once an important use of the cochlea.

This is not, however, the sole office of the cochlea; the spiral lamina, as well as the membranous labyrinth, receives sonorous impulses through the medium of the fluid of the labyrinth from the cavity of the vestibule and from the fenestra rotunda. The lamina spiralis of man and Mammalia is indeed much better calculated to render the action of these undulations upon the auditory nerve efficient than the membranous labyrinth; for, as a solid body insulated by a different medium, it is capable of resonance. That this is the case, may be rendered evident by experiment. A thin lamina of wood tightly fixed in the interior of a thick wooden bowl filled with water increases by resonance the intensity of sonorous undulations excited in the water more than the thick walls of the bowl. The musical pipe closed at its lower extremity with membrane being sounded in the water while directed perpendicularly against the firmly fixed lamina of wood, but without touching it, the conducting-rod placed near the lamina at all parts of it, even at a distance from the source of the sonorous undulations, conveys to the ear a loud sound. If the pipe is directed towards the inner surface of the bowl, and at the same distance from it as it was before from the lamina of wood, the sound is heard distinctly by means of a conductor placed in the water near the walls of the bowl, but it is not so loud as in the former case. It is immaterial whether the lamina be fixed at one edge or both, provided its surfaces be free and in contact with the water.

Lastly, it may be observed that the object of the fibres of the nerve being spread out singly upon the lamina spiralis is evident. In the first place, it insures a more complete participation of the fibres in the impulses communicated by the solid parts of the cochlea; and, secondly, the intensity with which the sonorous undulations are communicated to a body is proportionate to the extent of surface over which they can act on it. Thus, when a sound is excited in water, and is conducted to the stopped ears by means of a rod, the intensity of the sound heard increases with the depth to which the rod is immersed in the water, or with the extent in which it is in contact with the surface of the water.

CHAPTER III.

OF THE ACTION OF SONOROUS UNDULATIONS UPON THE AUDITORY NERVE, AND OF THE ACTIONS OF THIS NERVE ITSELF.

1. *Mode of action of sonorous undulations upon the auditory nerve.*

The investigation of this part of our subject must be based on a knowledge of the properties of the undulations which reach the fluid of the labyrinth.

The distinct properties of the undulations excited by a sounding body, and propagated to the labyrinth, are:—

1. Their thickness or length, and the duration of their impression.
2. Their breadth.
3. Their intensity, or the extent through which the particles affected by them vibrate.

The *thickness or length* of an undulation is its extent in the direction in which it is moving. The length of the undulation in any conducting medium is regulated partly by the time occupied in the production of one entire vibration by the sounding body, and partly by the conducting power of the medium. The column of air of the 32-feet organ-pipe performs 32 double vibrations, or gives 16 impulses in one direction in the course of a second. One part of the double vibration produces the condensation of the medium, analogous to the elevations of the wave on the surface of water; the other returning part of the vibration produces the rarefaction of the medium, or the depression of the wave. Now, since the velocity of sound in the air is about 1022 feet in a second [1124 feet English measure, at 62° Fahr.], the distance between the commencement and termination of one undulation, or its length, in the air, will be $\frac{1022}{16}$, or about 64 feet, when the musical value of the sound is that of the lowest C of the organ produced by the 32-feet pipe.

The fundamental note of the 16-feet organ-pipe, C^1, is produced by 64 half vibrations, or 32 pulses; and the length of corresponding undulations in the air is $\frac{1022}{32}$, or nearly 32 feet.

The length of each of the 64 undulations which, occurring within the space of a second, produce the note C^2 of the 8-feet organ-pipe, is in the air $\frac{1022}{64}$, or nearly 16 feet.

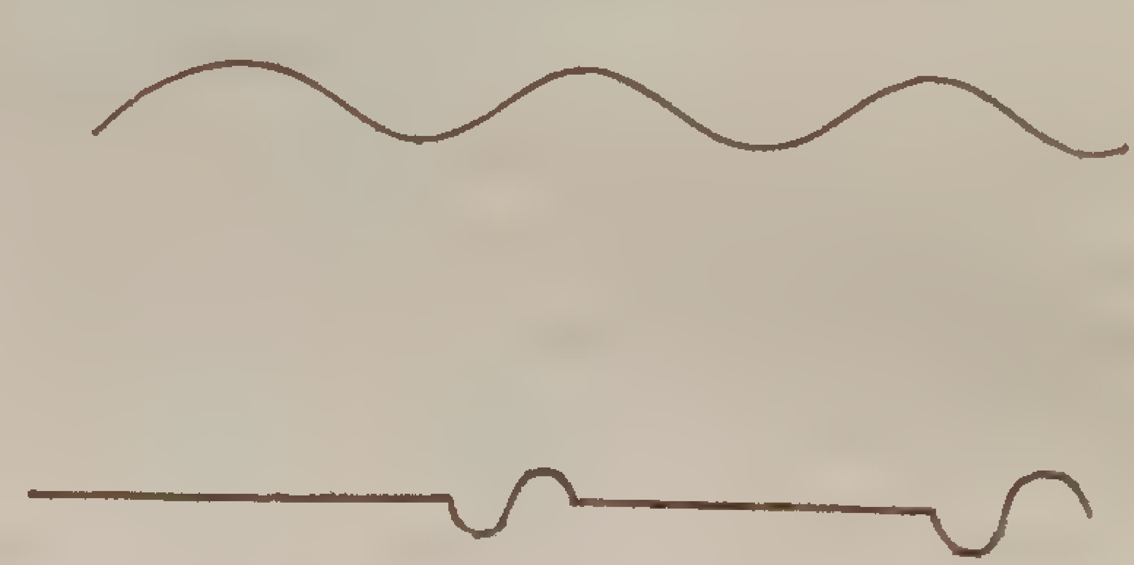
The length of the waves in the air for the note C^3 is eight feet; for the note C^4, two feet; and for C^5, one foot.

The velocity of sound in water is four times greater than in air, being as much as 4090 feet in a second [4708 English feet, according to M. Colladon's experiments]. The length of the undulations in water is therefore greater in the same proportion: thus, the length of the undulations for the lowest C of the organ, that of the 32-feet pipe, is 256 feet; for C^1, 128 feet; for C^2, 64 feet; for C^3, 32 feet; for C^4, 16 feet; for C^5, 8 feet; and for C^6, 4 feet. Such is the length of the undulations, therefore, which traverse the fluid of the labyrinth; and we may hence perceive that, even in the production of the highest notes, several undulations cannot occupy the small space of the labyrinth at the same time, but rather that, as a general rule, the summit or most condensed part of one wave will have left the labyrinth before the most condensed part of a second wave reaches it.

The duration of the impression which an undulation produces in its passage through any one particle of the labyrinth depends on the duration of each vibration of the body emitting the sound; for the lowest C of the organ, the duration of each vibration is $\frac{1}{16}$ of a second; for C^6, $\frac{1}{1024}$ of a second.

It becomes necessary in some instances to distinguish between the length of undulations and their distance from each other. If the sound is generated by a body vibrating to and fro, the distance between the undulations is 0; they succeed each other uninterruptedly, as is represented in the upper line of fig. 138, where the curves must be supposed to have the place of condensations and rarefactions. But if the sound is excited by impulses between which moments of repose occur, the conducting medium will have returned to a state of rest after the passage of one undulation, before a second undulation reaches the same point, as is represented in the lower line, fig. 138. This mode of succession of sonorous undulations can be produced by means of the toothed wheel used by M. Savart, and by the siren. It appears then, that, under certain conditions, the duration of the impression, or the period occupied by the transition of the separate undulations through a given point of the labyrinth, may be shorter than the interval between the passage of the *maxima* of two undulations.

Fig. 138.



Throughout the whole length of each wave, from its commencement to its end, the degree of condensation presents different gradations. The condensation gradually increases up to the end of the first fourth, when it arrives at its maximum; towards the middle of its length the density diminishes again. The latter half of the undulation is the seat of the rarefaction; here the particles previously compressed together repel, and strive to separate from, each other. The rarefaction increases as far as the commencement of the last fourth, and then decreases.

During the transition of the sonorous undulation through the fluid of the labyrinth, all the particles of this fluid in succession must pass through these grades of condensation and rarefaction.

The condensation in an undulation being dependent on the greater approximation of the molecules; the rarefaction, on their repulsion or greater separation from each other; all the particles in the wave will simultaneously move through a certain extent of the course of the impulse. The extent of the motion of the particles is at the commencement of the undulation slight; for, the more distant the particles lie from the immediate seat of the impulse, the less is their motion. In the posterior part of the undulation the particles move in the retrograde direction; and in the extent of their motion there is the same difference. During the passage of the undulation through a given point of the medium, the particles occupying this point become affected with an increasing, then with a diminishing state of condensation, and lastly, in the posterior half of the wave, with a state of rarefaction. The velocity also with which particles of the medium at this point are moved, becomes successively greater, reaches its maximum, and then becomes again retarded. During the passage of the posterior half of the undulation through this same point, the particles in their returning vibration move first with increasing, and then with diminishing velocity. All this is capable of application to the action of undulations on the auditory nerve.

The length of the undulations remains the same, whatever their distance from the source of the sound; but the extent of oscillation of the particles affected by them diminishes in a direct ratio with the square of the distance. It is, however, on the extent of oscillation of the particles that the intensity or loudness of the sound depends.

The undulations in air extend in a spherical form; a portion only of this sphere, however, which may be called the breadth or superficial extent of the undulations, strikes the ear. The breadth of the undulation employed in hearing depends on the extent to which the auditory nerve is acted on by it. Those undulations which enter the labyrinth from the tympanum have only the superficial extent of the fenestræ, ovalis and rotunda; but from these points they spread themselves out in the fluid of the labyrinth.

2. *Of the distinction of different sounds.*

A single impulse communicated to the auditory nerve seems to be sufficient to excite the sensation of sound; of this we have an example in the sound produced by an explosion or the sudden division of the air, by the coming together of two previously separated bodies of air, as in cracking a whip, &c. There is at all events nothing to refute this opinion, and M. Chladni is inclined to adopt it; although it must be admitted that a single shock to the air will very readily excite a succession of undulations. Most frequently, certainly, several undulations or impulses on the nerve concur in the production of the impression of sound. But it may be asked whether each of the impulses, a series of which produce a given sound, must not itself be of such intensity that it would singly excite the sensation of the auditory nerve; and whether a succession of impulses, so feeble that each alone would produce no impression upon the sense of hearing, would not be inaudible. The solution of this question has not hitherto been attempted, and it does not at present seem possible.

By the rapid succession of several impulses at unequal intervals a noise or rattle is produced; from a rapid succession of several impulses at equal intervals, a musical sound results, the height or acuteness of which increases with the number of the impulses communicated to the ear within a given time. This admits of demonstration by means of the siren of M. Cagniard Latour, or of the toothed wheel of M. Savart. A sound of definite musical value is also produced when each of the impulses, succeeding each other thus at regular intervals, is itself compounded of several undulations, in such a way that it would alone give the impression of an unmusical sound; that is to say, by a sufficiently rapid succession of short unmusical sounds at regular intervals a musical sound is generated. This is, in fact, exactly what takes place in the use of the above-mentioned instruments. Each individual impulse which they produce is a compound unmusical sound, which is readily distinguished, even while, by the quick succession of several such sounds, the impression of a musical note of definite pitch is produced.

The number of successive impulses required to produce a definite note is the next point of inquiry. It would appear, from M. Savart's researches, that two impulses which are equivalent to four single or half vibrations are sufficient. The note produced by the shocks of the teeth of a revolving wheel at regular intervals upon a solid body is still heard when the teeth of the wheel are removed in succession until two only are left; the sound produced by the impulses of these two teeth has still the same definite value in the scale of music. If a wheel with two thousand teeth, and revolving once in a second, is deprived of its teeth in half its circumference, so that only one thousand teeth are left, the length of the intervals between the impulses produced by these remaining teeth remains of course the same; but all the teeth, except two contiguous to each other, may be removed, and the sound resulting from the successive strokes of these two teeth, if the rate of revolution of the wheel be the same, namely, once in a second, will still be capable of comparison with the note of a musical instrument, so that its value may be determined.

If, however, only one tooth be left on the wheel, the definite musical note will no longer be heard, but only a rattling noise produced by the strokes of the single tooth, unless the wheel be made to revolve so rapidly that the interval between the separate strokes of the tooth is not greater than is required to elapse between the successive impulses for the production of a determinate note.

Where sounds are excited by vibrations or undulations, of which, when one has ceased, the next immediately commences, it may be matter of doubt whether the pitch of the resulting note may not depend on the length or some other property of the individual undulations. But experiments with the toothed wheel have shown that the acuteness or pitch of musical notes is not in any way dependent on the nature of the undulations; for, in the case of the different notes produced by the revolving wheel, the separate impulses which the solid body struck by the teeth of the wheel imparts to the air are constantly the same, whether the wheel revolves quickly or slowly; it is only the length of the intervals between them which varies.

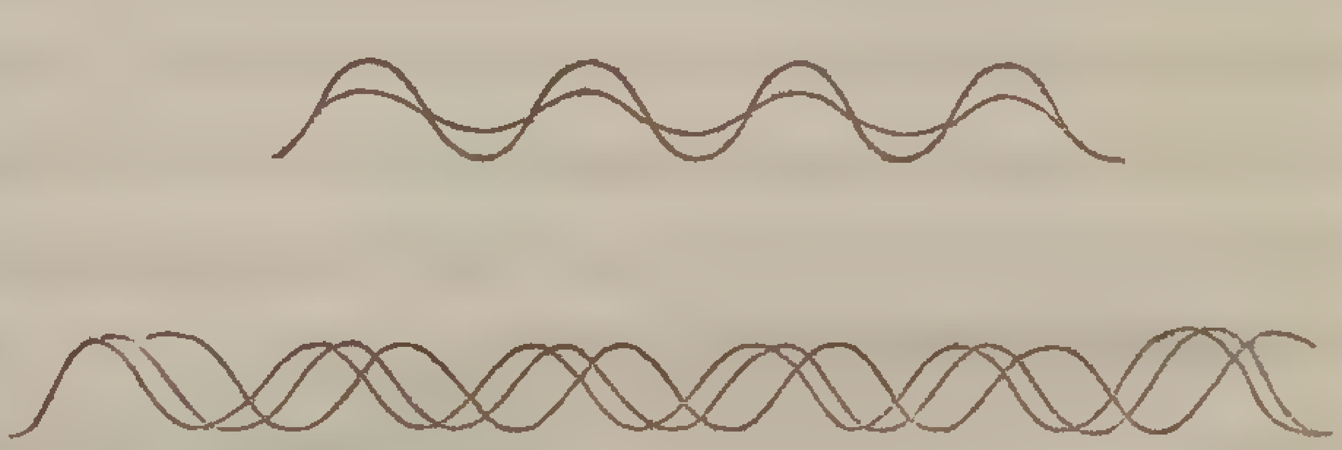
The maximum and minimum of the intervals of successive pulses still appreciable by the ear as determinate sounds, have also been determined by M. Savart, more satisfactorily and more accurately than had previously been done. If their intensity is sufficiently great, sounds are still audible which result from the succession of 48,000 half vibrations, or 24,000 impulses, in a second; and this, probably, is not the extreme limit in acuteness of sounds perceptible by the ear. Again, the sound resulting from thirty-two half vibrations, or sixteen impulses, in a second, is not, as has been supposed, the lowest appreciable note; on the contrary, M. Savart has succeeded in rendering sounds audible which were produced by only fourteen or eighteen half vibrations, or seven or eight impulses, in a second; and sounds still deeper might probably be heard if the individual pulses could be sufficiently prolonged. For the duration which an impulse must have in order to be heard is shorter in proportion to the height or acuteness of the note produced, the interval between every two impulses becoming less in proportion as the notes are higher in the scale: in the deeper notes, therefore, the duration of the impulses must be longer in proportion to the depth of the note. To give a greater duration to the impulses in very deep notes, M. Savart made use of a wheel with two or four free spokes or bars, which during the revolution of the wheel passed close to the edge of a thin board, without touching it, and, by the compression and rarefaction of the air thus induced, gave rise to single audible pulses. The succession of these pulses with sufficient rapidity afforded the impression of a deep note. The apparatus was furnished with a register, by means of which the rate of revolution could be accurately ascertained.

By removin gone or several teeth from the toothed wheel before mentioned, M. Savart was also enabled to satisfy himself of the fact, that in the case of the auditory nerve, as in the nerve of vision, the duration of the sensation is longer than that of the impression which causes it; for the removal of a tooth from the wheel produced no interruption of the sound. The gradual cessation of the sensation of sound renders it difficult, however, to determine its exact duration beyond that of the impression of the sonorous pulses.*

3. *Of the simultaneous impression of several different sounds.*

The simplest case of this kind is that where two sounds in unison with each other are heard at the same time. Here the intervals of the pulses are equal; while the maxima of the undulations may or may not be coincident. In the first case, the condensations of the undulations and the impulses are increased in intensity, as represented in the upper figure (fig. 139); in the second, the maxima of the two or more unisonant series of vibrations follow each other, as in the lower figure, so as to form a compound series of which the aliquot portions are similar, and the intervals equal. This can in no way disturb the impression on the ear. The accompanying figures may also serve to represent the combination of undulations resulting from resonance with the undulations of the primary sound, since they, like two or more unisons, are equal in their number and intervals. "Timbre" or tone results from the decussation of the waves which determine the height of the sound with other accessory waves. These figures (fig. 139) may illustrate also the change in the "tone" or "timbre" of an instrument produced by resonance. The slightest change in the conditions of a resounding body causes an alteration of tone probably by influencing the order in which the undulations are thrown off from it. Since, therefore, the mode of decussation of the primary undulations with those due to resonance may be extremely various, the varieties of tone resulting must also be very numerous.

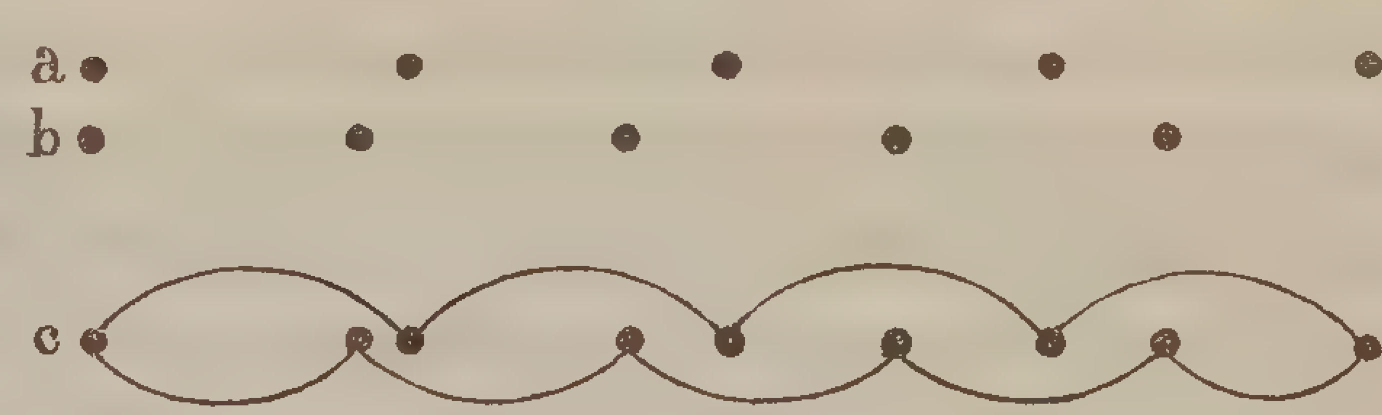
Fig. 139.



The perception of two sounds falling simultaneously on the ear, of which the number of the vibrations is different, must be attended with more difficulty than the perception of a single sound; for the circumstance of the maxima of the one series of vibrations intervening between those of the other must render the comparison of their intervals less easy. If, for example, two sounds, *a* and *b*, (fig. 140,) with the intervals marked by the dots, fall simultaneously on the ear, a compound series, as at *c*, will be produced. If the two sounds in such a case are

* Ann. de Chimie et de Physique, xliv. 337; xlvii. 69.—Poggendorf's Annal. xx. 290.—Fechner's Report, i. 335.

Fig. 140.



excited by two wheels with similarly formed teeth, the separate pulses individually must all be similar; and the nature of the impulses, therefore, cannot be the cause of the two sounds being distinguished from each other, which nevertheless is possible, as I have satisfied myself by experiment. The discrimination of the sounds must, therefore, be due to the perception of the intervals of each in the compound series of pulses. In distinguishing the undulations *a* from the undulations *b*, though the two series are intermingled, the ear must recognise the constant recurrence of the maxima of each series after certain intervals. To the smaller intervals resulting from the intervention of the maxima of one series between those of the other the attention is not directed owing to their not returning regularly, and being very dissimilar according to their position. This discriminating power of the sense of hearing is analogous to the faculty of vision, by virtue of which different parts of a complicated figure are in turn seen with greater distinctness than the rest (see page 1179); for, in the same way, we are able to distinguish the separate tones of one instrument amongst those of an entire orchestra. This power is, of course, much facilitated by the circumstance of different instruments having different tones; the principal vibrations of the sounds of each being attended by other accessory vibrations.

Fig. 141.

Great interest attaches to the case where two bodies giving sound simultaneously are nearly, but not quite, in unison; one vibrating, for example, one hundred times, the other one hundred and one times in a second. Here the vibrations or pulses of the one sound gradually gain on those of the other (see fig. 141), with which they become coincident again at the end of every second. The maxima of the undulations in the two series will be furthest removed from each other at the middle of each second, the maximum of the one being then, in fact, coincident with the minimum of the other, so that each is destroyed; but at the end of each second the maxima will coincide, and form one wave of double intensity. From the commencement to the middle of each second the intensity of the sound will diminish, because thus far the maxima of the one series of undulations will tend more and more to coincide with the minima of the other series of undulations (see fig. 141), until they quite neutralize each other:

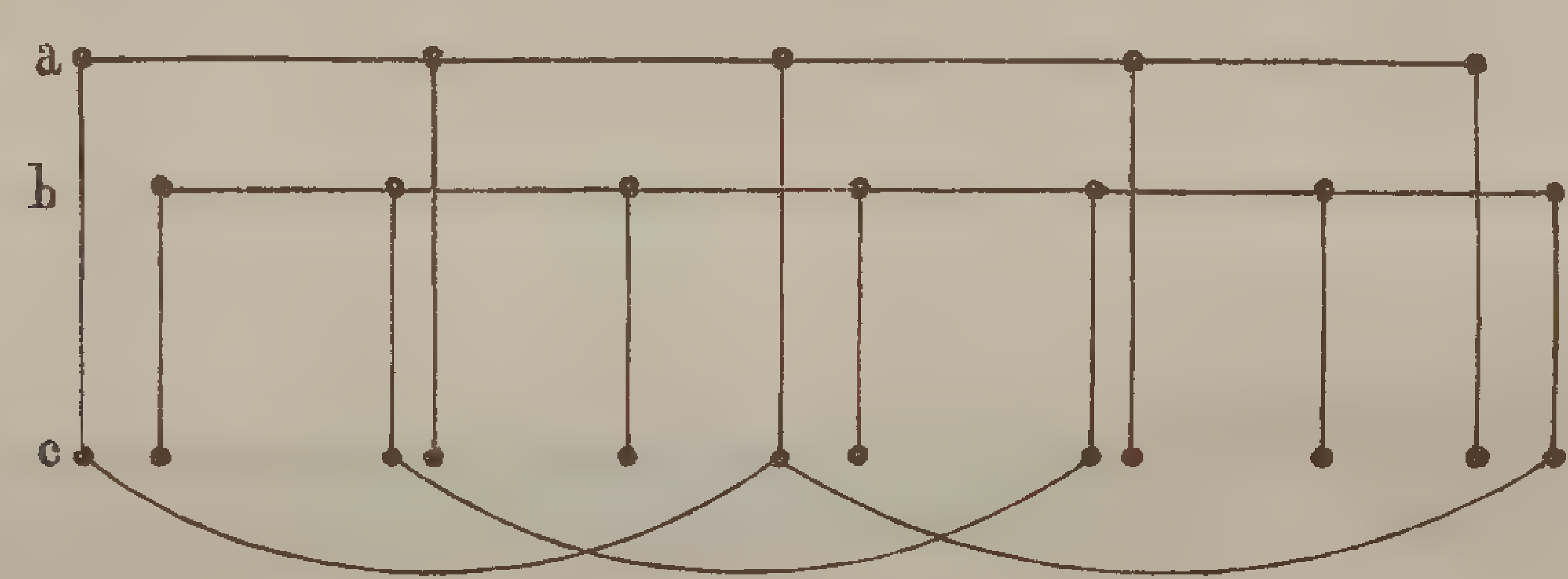
but from that point the maxima of the one series of undulations will become more and more distant from the minima of the other, and the sound will proportionally increase in loudness, until at the termination of the second it will be doubly as loud as would be produced by either series separately, the maxima of their undulations here coinciding. At the middle point of each second there should be a moment of complete absence of sound. No such interruption of the sound, however, is heard, but merely a greater faintness of the sound at that point of time; we may, therefore, regard this as a new proof that sensations of the auditory nerves are of longer duration than the action of the exciting cause. The alternate decrease and increase of intensity of the sound when two instruments nearly, but not entirely, in unison, are vibrating simultaneously, are called "beats." The phenomenon is easily produced by striking two musical strings which are not quite in unison.

When two sounds, of which the vibrations stand in a simple ratio to each other, as of 2 to 3, 3 to 4, or 4 to 5, and in which the coincidence of two impulses or undulations recurs with sufficient frequency, a third sound is produced by this coincidence of the undulations of the two sounds at regular intervals. If, for example, in one sound, *a*, (fig. 142,) two vibrations are produced, while three are taking place in the other, *b*, a coincidence of their vibrations will occur at every second undulation of the one and at every third of the other, provided they have originally commenced at the same moment; and this return of undulations of double intensity, *c*, at regular though longer intervals, will give rise to a new sound, which was first observed by the celebrated musician Tartini. It must be remarked that the dots in the figure do not represent the pulses themselves, but merely their maxima, and that intermediate between them the minima, or points of greatest rarefaction, must be imagined to be situated. The third note resulting from the coincidence of certain vibrations of two other notes may be produced by means of strings as well as by pipes, provided the primary sounds be sufficiently intense and prolonged. If the D string of a violin be tuned to E, and sounded by a long stroke of the bow together with the A string, the lower octave of A is heard. If the C of the A string be sounded with the E above it, the lower octave of C is heard as a third sound: if the first B above the lines be struck with the D above it, G of the second octave below them is heard also. Under certain circumstances, as might be expected, and as M. Blein has observed, two additional sounds are heard.

Fig. 142.

In the foregoing instance it was presupposed that the first pulse of the two sounds occurred at the same moment. But this may not be the case; and then, instead of a perfect coincidence of the undulations, there will be only an approximation to coincidence at certain intervals, as in figure 143, where the series of sonorous pulses *a* and *b* have

Fig. 143.



the same relation to each other as in the former figure; that is to say, two pulses occur in *a* in the space of time occupied by three in *b*. They give rise to the compound series of pulses *c*, in which the approximation to coincidence of the maxima of the two series of pulses at certain intervals is sufficient to be perceived, and to give rise to the accessory note; although this will not be so loud and distinct as in the former case. The greater the approximation to coincidence of the maxima of the two series of pulses or undulations, the louder and more distinct will be the new note produced. From this consideration we may infer the cause of the uncertainty in the occurrence of this phenomenon, and the reason why it can never be calculated on in music.

The accessory sounds of Tartini thus produced, which are always deeper than the primary notes, must be distinguished from the higher accidental notes of strings, bells, &c. which are sometimes heard associated with the fundamental tone, and which belong to the system of harmonics. The latter have a physical cause in the action of the instrument itself; the former have not.

Of the harmony of sounds.—The relation which the notes of the scale of music universally adopted bear to each other, is determined partly by the degree in which the power of discriminating the general impressions produced by different numbers of vibrations is possessed by the sense of hearing, and partly by the circumstance that a pleasing effect is produced upon the sense by the succession of sounds of which the vibrations bear a simple numerical relation to each other.

The ratio most easily recognised by the ear is that of 1 : 2 : 4 : 8, &c. that, namely, of the fundamental note to its octaves. Sounds, of which the vibrations in the same period are in the proportion of 1 to 2, are so similar that they act on the ear only as repetitions of one another; hence the relation between two sounds is not essentially altered by raising or lowering one of them the extent of one or two octaves. Other proportions which are easily recognisable, and agreeable to the ear, are that of 2 to 3, or of the fundamental note to the "fifth;" and that of 4 to 5, or of the fundamental note to the "third." If the fundamental note be designated as 4, the proportional number for the "third" will be 5, that for the "fifth" 6, and that for the octave 8. Or, taking the fundamental note C at 1, the relative numbers for the vibrations of the "third," "fifth," and "octave" will be as follows:

C	E	G	C[1]
1	$\frac{5}{4}$	$\frac{3}{2}$	2
Fund. note.	Third.	Fifth.	Octave.

These four notes together form the simplest and most effective combination of sounds: the first three constitute a triad, or chord of three notes, which is very agreeable to the ear. Music has, however, not stopped here; there are, as might readily be conceived, other intervals which are capable of being combined so as to produce an agreeable impression on the sense of hearing. The sound to which the octave 2 would stand in the ratio of a "fifth," or of 3 to 2, bears an equally simple proportion to the fundamental note, namely that of $\frac{4}{3}$ to 1; it is the note F of the musical scale. The "third" of the note G again, or B, bears the proportion of $\frac{15}{8}$ to the fundamental note, this being 1. Further, between C and E lies another note, which stands in the relation of a "fifth" to the G of the lower octave, and bears the proportion of $\frac{9}{8}$ to the fundamental note C, or 1; it is named D. Lastly, there is between G and B a note which bears the same proportion in the number of vibrations to B, as C does to D; it is A, the proportional number of which, compared with the fundamental note, is $\frac{15}{8}$.

Thus we have the musical scale:

$$\begin{array}{cccccccc} C, & D, & E, & F, & G, & A, & B, & C^1. \\ 1, & \frac{9}{8}, & \frac{5}{4}, & \frac{4}{3}, & \frac{3}{2}, & \frac{5}{3}, & \frac{15}{8}, & 2. \end{array}$$

The relation of the different notes in this series to each other is as follows:

$$\begin{aligned} C, D, &= 1 : \tfrac{9}{8} \\ D, E, &= 1 : \tfrac{10}{9} \\ E, F, &= 1 : \tfrac{16}{15} \\ F, G, &= 1 : \tfrac{9}{8} \\ G, A, &= 1 : \tfrac{10}{9} \\ A, B, &= 1 : \tfrac{9}{8} \\ B, C^1 &= 1 : \tfrac{16}{15} \end{aligned}$$

The intervals $1 : \frac{9}{8}$ and $1 : \frac{10}{9}$ are called entire tones; the interval $1 : \frac{16}{15}$, a semitone. Where notes are separated by an entire tone, we distinguish other intermediate sounds or semitones.

It will be perceived that the raising of one note a semitone, or the interval of $1 : \frac{16}{15}$, is not identical with the lowering of the following note the same extent; C♯ is therefore a different sound from D♭. The interval $1:\frac{5}{4}$, or C : E, is called the major third; the interval $1:\frac{6}{5}$, or C : E♭ the minor third.

To form a harmonious combination of several sounds, or a chord, it is necessary that the different sounds should bear a simple relation to the fundamental note, and also to each other. The notes C, E, G, produce a harmonious triad, or chord of three; for the number of the vibrations of E and G, as compared with C, is in the ratio of 5 to 4, and of 3 to 2; and E and G themselves also are concords, their proportions being as 1 to $\frac{6}{5}$. The notes C, E♭, E♮, on the contrary, of which the ratio is $1:\frac{6}{5}:\frac{5}{4}$, do not form a chord. For though C with E♭, and C with E♮, are concords, the combination of E♭ with E♮ is discordant, their ratio being as $\frac{6}{5}:\frac{5}{4}$, or as $1:\frac{25}{24}$. The cause of harmony is, therefore, the simple relation between the sounds in regard to the number of their vibrations.

The combination of the fundamental note with the major third and the fifth,—namely, C, E, G, of which the ratio is $1:\frac{5}{4}:\frac{3}{2}$,—is called the perfect major chord; the combination of the fundamental note with the minor third and the fifth, or C, E♭, and G, of which the ratio is $1:\frac{6}{5}:\frac{3}{2}$, is called the perfect minor chord. They both consist of the intervals of a major third and a minor third, namely, $\frac{5}{4}$ and $\frac{6}{5}$, which together form a fifth. In the perfect major chord the major third precedes the minor; in the perfect minor chord the minor third precedes the major. These two chords produce different impressions on the ear. The harmony is more pleasing in the major chord.

Discords also are rendered agreeable to the ear when they form the transition to concords, by which the dissonance is resolved. A dissonant chord contains, besides concordant intervals, an additional discord. Thus, the octave would be concordant with the fundamental note, the third, and the fifth; but the seventh forms a discord. The chord of the seventh is formed by the combination of the fundamental note with the third, fifth, and seventh; it is a dissonant chord. A dissonance is resolved by a concord which contains a concordant in place of the discordant note, or which forms a concord with this note. This neutralization of discords is similar to the effect which the intervention of a third colour between two disharmonious colours, with one of which it harmonizes, while towards the other it is indifferent, has in removing the impression of the want of harmony. Thus the want of harmony between blue and red is removed by the intervention of green, which harmonizes with red, and is indifferent towards blue. Orange has the same effect, it being the complementary colour of blue, and indifferent towards red. The influence of discords as well as concords upon the sense of hearing has been very well set forth by Descartes in the passage pointed out by Chladni : "Inter objecta sensus illud non animo gratissimum est, quod facilè sensu percipitur, neque etiam facillimè ; sed quod non tam facilè, ut naturale desiderium, quo sensus feruntur in objecta, planè non impleat; neque etiam tam difficulter ut sensus fatiguet." The harmony of octaves is too simple to be pleasing; and even dissonance becomes pleasing when the difficulty attending the perception of the discordant intervals is relieved by a succeeding concord.

In a long succession of notes the relation of the intervals cannot be preserved in arithmetical perfection, such as is otherwise required by the ear, as is shown by the following example adduced by Chladni. When the intervals G, C, F, D, G, C, are executed continuously and accurately, the C, when it occurs the second time, will not have the same value as at first; and the same is the case with the G. The accurate ratio of the notes or the intervals is as follows:

$$G : C = 3 : 2$$
$$C : F = 3 : 4$$
$$F : D = 6 : 5$$
$$D : G = 3 : 4$$
$$G : C = 3 : 2;$$

or the relation of the notes in the series $G : C : F : D : G : C = 243 : 162 : 216 : 180 : 240 : 160$. G, therefore, has at first the value 243; the second time, 240: C values the first time 162; the second time, 160. If further repeated, the notes would vary more and more from their original value. This inconvenience is remedied by giving to them such a slight deviation from their true ratio, as is not perceptible to the ear; this is called "temperament." When the deviation from the true musical ratio is distributed equally among all the notes, the "temperament" is "even;" when unequally, it is "uneven." The first has been found the most generally applicable in music; while the attempt to maintain certain notes in the different octaves in theoretical purity has only rendered the other notes more imperfect. The defects in the intervals incident to the even temperament are not perceptible by the ear, any more than other slight deviations from the accurate tuning of an instrument. If the ear detected such small deviations from the true musical intervals, the attainment of these intervals upon instruments would be impossible; since, as it is, the perfect tuning of an instrument for practical purposes is attended with very great difficulty.*

Influence of the mind in hearing. — The perception of the direction of sounds is not a faculty of the sense of hearing itself, but is an act of judgment which founds it on experience previously acquired. From the modifications which the sensation of sound undergoes according to the direction in which the sound reaches us, the mind infers the position of the sounding body. The only true guide for this inference is the

* Full information with regard to the musical intervals will be found in Chladni's Akustik.

more intense action of the sound upon one than upon the other ear. But even here there is room for much deception by the influence of reflexion, or resonance, and by the propagation of sound from a distance without loss of intensity through curved conducting-tubes filled with air. By means of such tubes, or of solid conductors which convey the sonorous vibrations from their source to a distant resonant body, sounds may be made to originate apparently in a new situation.

The direction of sound may also be judged of by means of one ear only; the position of the ear and head being varied, so that the sonorous undulations at one moment fall upon the ear in a perpendicular direction, at another moment obliquely.

When neither of these circumstances can guide us in distinguishing the direction of sound, as when it falls equally upon both ears, its source being, for example, either directly in front or behind us, it becomes impossible to determine whence the sound comes: this, which has been demonstrated by Venturini's experiments,* is a necessary consequence of physical laws. Undulations give not merely the impulses of condensation in one direction, but that of rarefaction in the opposite; and, when several undulations succeed one another, these impulses in opposite directions regularly alternate. If, therefore, the nerves were capable of distinguishing the direction of impulses, no means would thus be afforded for determining whether a sound came in one direction or in the opposite.

Ventriloquists take advantage of the difficulty with which the direction of sounds is recognised, and also of the influence of the imagination over our judgment, when they direct their voice in a certain direction, and at the same time pretend themselves to hear the sounds coming from thence.

The distance of the source of sounds is not recognised by the sense itself, but it is inferred from their intensity. The sound itself is always seated but in one place, namely, in our ear; but it is interpreted as coming from an exterior soniferous body. When the intensity of the voice is modified in imitation of the effect of distance, it excites the idea of its originating at a distance; and this also is taken advantage of by ventriloquists.

The mind has, however, the power of influencing the act of sensation itself,—of voluntarily increasing its intensity, as in "listening." By the faculty of attention we can distinguish one sound out of several or many others,—can follow the tones of one instrument in a full orchestra.

When two persons address their speech to our opposite ears simultaneously, the two impressions conveyed to the sensorium become mixed; and it is only by great exertion of the attention, and by the aid of a dif-

* Voigt's Magazin, Bd. 2.

ference of tone of the two voices, that we are enabled to follow the sounds of one exclusively, disregarding those of the other, which are then heard as a more or less indistinct murmur. When the activity of the sensorium is not directed to the impressions communicated to it by the auditory nerves, sounds that exist are not heard; or, what frequently happens, a sound may be so faint, that, on account of the mind being directed to other objects, it is for a moment disregarded, but is heard as soon as the attention is recalled to it. Similar phenomena are observed to occur in the case of the other senses.

Permanence of the sensation of sound.—The experiments of Savart, already referred to (see page 1299), prove that the effect of the action of sonorous undulations upon the nerve of hearing endures somewhat longer than the period during which the undulations are passing through the ear. If, however, the impression of the same sound be very long continued, or constantly repeated for a long time, then the sensation produced may continue for a very long time, more than twelve or twenty-four hours even, after the original cause of the sound has ceased. This must have been experienced by every one who has travelled several days continuously in a heavy public vehicle, for some time after which the rattling noises are heard when the ear is not acted on by other sounds.

We have here a proof that the perception of sound as sound, is not essentially connected with the existence of undulatory pulses; and that the sensation of sound is a state of the auditory nerve, which, though it may be excited by a succession of impulses, may also be produced by other causes. The sensations of the retina remaining after the external impression of light had ceased, have been attributed by some persons to a retention of some of the matter of light for a certain time by the retina, as in the absorption of light by dark bodies; but, in the case of the sense of hearing, such an hypothesis is evidently untenable. No irritating matter and no impulse can be here retained; and, even if it be supposed that undulations excited by the impulse are kept up in the auditory nerve for a certain time, they must be undulations of the nervous principle itself, which, being excited, continue until the equilibrium is restored.

Double hearing.—Corresponding to the double vision of the same object with the two eyes, is the double hearing with the two ears; and analogous to the double vision with one eye, dependent on unequal refraction, is the double hearing of a single sound with one ear, owing to the sound coming to the ear through media of unequal conducting power. The first kind of double hearing is very rare; instances of it are recorded, however, by Sauvages and Itard. In one of the two cases related by Sauvages, the octave was heard with the fundamental note, which, if the observation was correct, would be difficult to explain. In

Itard's case, the sound heard by the two ears differed in height. Such cases may possibly be found to be more frequent than is supposed, when attention is more directed to the subject: I was myself once troubled by a kind of echo of higher pitch which accompanied sounds of moderate intensity, such as the human voice. This phenomenon was, however, very transient, and has never recurred; moreover, I do not know that it arose from unequal action of the two ears.

The second kind of double hearing, which depends on the unequal conducting power of two media through which the same sound is transmitted to the ear, may easily be experienced. If a small bell be sounded in water, while the ears are closed by plugs and a solid conductor is interposed between the water and the ear, two sounds will be heard differing in intensity and tone; one being conveyed to the ear through the medium of the atmosphere, the other through the conducting rod. In like manner, if, while both ears are plugged, the pipe closed by membrane at its lower extremity be dipped into the water and sounded by another person, its note may be propagated to the ear with two different characters at the same time, by the atmospheric air, and by the solid rod immersed in the water.

Acuteness of hearing. — The sense of vision may vary in its degree of perfection as regards either the faculty of adjustment to different distances, the power of distinguishing accurately the particles of the retina affected, sensibility to light and darkness, or the perception of the different shades of colours. In the sense of hearing there is no parallel to the faculty by which the eye is accommodated to distance, nor to the perception of the particular part of the nerve affected; but just as one person sees distinctly only in a bright light, and another only in a moderate light, so in different individuals the sense of hearing is more perfect for sounds of different pitch: and just as a person, whose vision for the forms of objects, &c. is acute, nevertheless distinguishes colours with difficulty, and has no perception of the harmony and disharmony of colours, so one, whose hearing is good as far as regards the sensibility to feeble sounds, is sometimes deficient in the power of recognising the musical relation of sounds, and in the sense of harmony and discord; while another individual, whose hearing is in other respects imperfect, has these endowments.

Many persons, whose hearing is good, are incapable of perceiving very high or acute tones; Dr. Wollaston observed several instances of this kind: while deaf persons sometimes hear shrill sounds very well. Among the causes of this latter condition is, as we have before remarked, a state of too great tension of the membrana tympani, in whatever way produced. Many deaf people hear sounds, which are not very intense, better when a loud noise prevails at the same time. Of this condition, *paracusis Willisiana*, two instances are described by Willis:

one was that of a person who could only maintain a conversation when a drum was beat near him; in the other case, the individual could hear only while a bell was ringing. Similar cases have been observed by Holder, Bachmann, and Fielitz;* they are, perhaps, to be attributed to a state of torpor of the auditory nerve, which requires to be roused before it can exercise its functions. Sometimes, however, the circumstance of a deaf person hearing particular sounds during a great noise as well as other people who are not deaf, may arise from his being much less disturbed by the noise than they. It is thus that the deaf person mentioned at page 1261 explains the fact that, when travelling in a closed carriage, he can take a part very well in conversation. His companions, he says, do not then hear each other's voices better than he, because the noise of the carriage is heard much more loudly by them. Excessive acuteness of hearing, *hyperacusis*, arises from a state of too great excitability of the auditory nerve, and corresponds to the photophobia of vision.

The causes on which the defect of a musical ear depends, are unknown. A person who is deficient in the sense of musical intervals, harmonies, and discords, will be a bad singer, though he have a good voice.

Subjective sounds—sounds independent of sonorous vibrations.—These are the result of a state of irritation or excitement of the auditory nerve produced by other causes than sonorous impulses. A state of excitement of this nerve, however induced, gives rise to the sensation of sound. Hence the ringing and buzzing in the ears heard by persons of irritable and exhausted nervous system, and by patients with cerebral disease, or disease of the auditory nerve itself; hence also the noise in the ears heard for some time after a long journey in a rattling noisy vehicle. Ritter found that electricity also excites a sound in the ears (see page 1063). From the above truly subjective sounds we must distinguish those dependent, not on a state of the auditory nerve itself merely, but on sonorous vibrations excited in the auditory apparatus. Such are buzzing sounds attendant on vascular congestion of the head and ear, or on aneurismal dilatation of the vessels. Frequently, even the simple pulsatory circulation of the blood in the ear is heard. To the sounds of this class belong also the snapping sound in the ear produced by a voluntary effort, and the buzz or hum heard during the contraction of the palatine muscles in the act of yawning; when air is forced into the tympanum, so as to make tense the membrana tympani; and in the act of blowing the nose, as well as during the forcible depression of the lower jaw.

The buzzing in the ears which attends obstruction of the Eustachian tube does not at present admit of a satisfactory explanation.

In Dr. Henle the peculiar circumstance presents itself, that gently

* See Muncke, in Gehler's Physic. Wörterbuch, iv. 2, p. 1220.

passing the finger over the cheek excites a sound in the ear. This may be owing to a reflex transmission of the impression made upon the facial nerve to the acoustic nerve through the medium of the brain, or it may be produced by a movement of the muscles of the ossicula auditus excited by reflex nervous action.

Sympathies of the auditory nerve. — Irritation or excitement of the auditory nerve is capable of giving rise to movements in the body, and to sensations in other organs of sense. In both cases it is probable that the laws of reflection through the medium of the brain come into play. An intense and sudden noise excites in every person closure of the eyelids, and in nervous individuals a start of the whole body. The secondary sensations induced by impressions on the sense of hearing are principally seated in the nerves of touch, or common sensation. A sudden noise excites in persons of excitable nervous system an unpleasant sensation, like that produced by an electric shock, throughout the body, and sometimes a particular feeling in the external ear. Various kinds of sounds, such as the friction of paper, or scratching of glass, cause in many people a disagreeable feeling in the teeth, or, indeed, a sensation of cold trickling through the body. Intense sounds are said to make the saliva collect in the mouth in some people.*

The sense of hearing may in its turn be affected by impressions on many other parts of the body; but this is observed especially in diseases of abdominal viscera, and in febrile affections. Here, also, it is probable that the central organs of the nervous system are the media through which the impression is transmitted.

The cases in which sensitive impressions of other kinds affect the sense of hearing by sympathy are very rare. The observation of Dr. Henle, related above, affords an instance of such sympathy. It has been maintained by many writers that even the nerves of touch are capable of audition, or at least of affording a very easy path for the transmission of the sonorous undulations to the seat of the sense of hearing. That they have such a conducting power is by no means probable; but that an impression on a nerve of touch may by reflection exert an influence upon the auditory nerve is very likely, since a similar relation of mutual action is observed to exist between other senses; and an impression on the nerve of hearing itself is capable of exciting sensations in the nerves of touch. But the instances in which an impression on the latter nerve excites the sensibility of the auditory nerve are extremely rare.

The chorda tympani and nervus facialis have no share in the sense of hearing, and are incapable of influencing it, except by such a reflex action as we last referred to.

* Many other examples of sympathy of this kind have been collected by Tiedemann, (Zeitschrift f. Physiol. B. i. H. 2,) and Lincke (op. cit. p. 567).

SECTION III.

Of the sense of Smell.

CHAPTER I.

OF THE PHYSICAL CONDITIONS FOR THE PERCEPTION OF ODOURS.

The sense of smell ordinarily requires for its excitement to a state of activity the action of external matters, which produce certain changes in the olfactory nerve; and this nerve, like that of taste, is susceptible of an infinite variety of states dependent on the nature of the external stimulus.

The first condition essential to the sense of smell is the existence of a special nerve, the changes in whose condition are perceived as sensations of odour; for no other nerve is capable of these sensations, even though acted on by the same causes. The same substance which excites the sensation of smell in the olfactory nerves causes a peculiar taste in the nerve of taste, and may produce an acrid and burning sensation in the nerves of touch. The opinion of Kant, that smell is distant taste, appears to me to be incorrect.

The second condition of smell is a peculiar condition of the olfactory nerve, or a peculiar change produced in it by the stimulus or odorous substance.

The material causes of odours are, in the case of animals living in the air, substances suspended in a state of extremely fine division in the atmosphere; or gaseous exhalations, often of so subtile a nature that they can be detected by no other re-agent than the sense of smell itself. In fishes the odorous matters are contained in the water; but in what form,—whether dissolved in the same manner as the gases absorbed by water,—is uncertain. The solution of these matters in water is clearly no reason for denying the sense of smell to fishes, or for placing the sense of taste in their nares; for the essential characteristic of the sense of smell consists, not in the gaseous nature of the odours, but in the special sensibility of certain nerves, and in its difference from the sensibility with which the nerves of taste are endued. The matters of odours, also, must in all cases be dissolved in the mucus of the mucous membrane before they can affect the olfactory nerves, and their state in the mucus must be the same as that in which they are contained in water. On the other hand, the nerve of taste is not acted on solely by liquid and solid matters; gaseous substances also are sometimes tasted, when, like sulphurous acid, and many other gaseous bodies, they are capable of being dissolved in the fluid covering the tongue. It may, therefore, be easily conceived that the very same principle will produce different sensations in the organs of smell and taste; in the former the sensation of a particular odour, in the latter that of a peculiar taste. The observation of Treviranus, that in animals living in the air the organ of smell is comparable to a lung, in fishes to a gill or branchia, is, to a certain extent, correct and ingenious; but it would be as erroneous to suppose that the odorous matters dissolved in water must be converted into the gaseous state before acting on the olfactory nerve, as that the gases absorbed and dissolved in the water must be restored to the form of gases in the branchiæ before being taken up into the blood. The state in which these gases are contained in the blood is, indeed, the same as that in which they exist in the water. Lastly, it is to be observed that the olfactory nerves of fishes are identical with the olfactory nerves of all other animals; they arise from the same parts of the brain, the lobi olfactorii, which, even in Mammalia, exist in the form of the olfactory bulb.

A further condition necessary for the perception of odours is, that the mucous membrane of the nasal cavity be moist; for, as we have already observed, the moisture of the mucous surface is the vehicle through the medium of which the odorous matters are more immediately applied to the nerves. When the Schneiderian membrane is dry, the sense of smell is lost; thus, in the first stage of catarrh, when the secretion of mucus within the nostrils is lessened, the faculty of perceiving odours is either lost, or rendered very imperfect.

In animals living in the air, it is also requisite that the odorous matters should be transmitted in a current through the nostrils. This is effected by the respiratory movements: hence we have voluntary influence over the sense of smell; for by interrupting respiration we prevent the perception of odours, and by repeated inspirations render their impression more intense.

In aquatic animals this influence over the sense by voluntary movement does not exist; for in them the nostrils are generally closed posteriorly, and do not communicate directly with the respiratory organs. Yet even here the effect which the current through the nostrils would produce is attained in another way,—namely, by the constant current into the mouth, and from the branchial apertures, which is maintained by the movements of the branchial operculum.

CHAPTER II.

OF THE ORGAN OF SMELL.

The organ of smell is but little known in invertebrate animals, though the perception of odours is very acute in many of them, as in the common meat or blue fly (Musca vomitoria), which deposits its ova in putrefying animal substances, and is sometimes deceived by the odour of the Stapelia hirsuta.*

The principle determining the form of the organ of smell, and its varieties, is that of obtaining a large sentient surface within a small space. In this respect the organ of smell, and respiratory organs, are much allied.

In fishes, and, as Rusconi has shown, in the Proteus among the Amphibia, the increase of surface is attained by means of folds of mucous membrane, which either are arranged side by side, as in the Cyclostomata (Lamprey, Myxine, &c.); radiate from a central point, as in the Sturgeon; or project as parallel laminæ from the two sides of a median band. The laminæ are frequently subdivided, in a tuft-like or arborescent form.

In most fishes the nasal cavities are superficial depressions, not extending through the palate. In the Lophius piscatorius they are bell-shaped organs, supported upon a pedicle, and having folds of membrane at the fundus of their cavity. In the Cyclostomata the nasal cavities are united into one, from which a tubular canal extends to the surface of the head, as in the Petromyzon and Ammocœtes; or to the extremity of the muzzle, as in the Myxine. This nasal tube is, in the myxinoid fishes, very long, and provided with cartilaginous rings just like the trachea. In the cyclostomatous fishes the nasal cavity is not a blind sac; a canal extends from it, at least, through the bony palate. In the Petromyzon, however, there is no opening in the soft palate; the palatine canal from the nasal cavity ends as a blind tube between the bones of the cranium and the membrane lining the cavity of the fauces. In the Ammocœtes, also, the palatine nasal canal terminates by a cæcal extremity. It serves, therefore, in these fishes merely to give the power of forcing water out of the nasal cavity, and of taking fresh water in. In the myxinoid Cyclostomata, on the contrary, both the soft and hard palate are pierced by the nasal tube; and behind its palatine opening there is merely a membranous valve directed backwards, which appears to serve the purpose of keeping in motion and renewing the water contained in the nasal cavity.

The apparatus for forcing the water out of the nasal cavity in the Petromyzon, and the moveable valve in the myxinoid fishes, seem to be provisions rendered necessary by the organization of these animals. A necessary condition for the perception of odours is the movement of the medium in contact with the sentient surface. In man it is necessary that a current of air should be maintained through his nose. In most aquatic animals the renewal of the strata of the odoriferous medium around the head is attained by the respiratory movements, which pro-

* The different facts which have been observed relative to the sense of smell in the Articulata will be found in Wagner's Vergleichende Anatomie, 1834; B. i. p. 467.

duce an inward current at the oral aperture, and an outward one at the branchial clefts. But in the cyclostomatous fishes the renewal of the fluid in the nostrils cannot be effected in this manner while their mouth is used in suction.

In reptiles and Amphibia the nasal cavity is always perforate. In some of the Proteidea the palatine extremity of the nasal canal does not pass through the bones, but merely through the upper lip, in consequence of the rudimentary condition of the superior maxillary bone, which lies free in the soft parts: this is, however, not a general character of the Proteidea, for in the Axolotl the palatine opening of the nares is bounded by bone, as in other Amphibia. The Proteus has, also, plicæ of the mucous membrane in the nasal cavity, like those in the nasal cavity of fishes; in the other genera of the Proteidea these plicæ are absent.

In reptiles and birds the turbinated processes for the increase of surface first make their appearance.

In Mammalia the nasal apparatus includes the labyrinth of the ethmoid bone, the turbinated bones, and the accessory sinuses opening into the nasal cavity. The developement of surface in the inferior turbinated bone is very remarkable. The most peculiar forms are presented on the one hand by the Ruminantia, Solidungula, &c.; on the other, by the Carnivora. In the former orders, the inferior turbinate bone is, at its line of attachment, a simple lamina, which afterwards divides into an upper and a lower lamella, of which the first is rolled upwards like a scroll of paper, the other downwards in the same form. In Carnivora the lamina divides into branches, which give off side branches, much in the manner of the arbor vitæ of the cerebellum. Compared with these states of developement, the condition of the turbinated bones in the human subject appears quite rudimentary. The organs discovered by Stenson maintain a communication between the nasal cavity and mouth at the situation of the foramen incisivum in many Mammalia. These canals must not be confounded with the partly membranous, partly cartilaginous, tube observed by Jacobson, which lies on the floor of the nostrils, between the vomer and the mucous membrane, and communicates with the canals of Stenson. The function of these parts is not known.*

I believe [illegible]

The accessory cavities or sinuses communicating with the nostrils seem to have no relation to the sense of smell. Air impregnated with the vapour of camphor was injected by Deschamp into the frontal sinus through a fistulous opening, and Richerand injected odorous substances into the antrum of Highmore; but in neither case was any odour perceived by the patient. Nature seems to attain nearly the same object

* See Rosenthal in Tiedemann's Zeitschrift f. Physiol. ii. p. 289. With reference to the pretended absence of olfactory nerves in the Cetacea, see page 767.

whether she fills the cavities of bones with air or with fat; in either way she renders the bones lighter than they would be were they solid throughout. In birds many bones are filled with air; those of the trunk through the medium of the lungs, those of the head through the Eustachian tube: in man certain bones of the head only contain air, namely, the mastoid process of the temporal bone, and the bones bounding the nasal cavity. The mucous membrane both of the nares, and of the sinuses opening into them, presents the ciliary motion in all animals.

The process by which the stimulus is conveyed to the nerve, in the senses hitherto considered so complex, is here very simple. The odorous matters suspended in the air in the form of vapour, or sometimes, perhaps, of a very fine powder, are brought into contact with the sentient mucous surfaces by the current to which the respiratory movements give rise. A current of air from within outwards sometimes excites the sensation of odour, as in the case of odorous substances being developed in the respiratory organs, or when such matters developed in the digestive organs are expelled upwards by eructation.

It only remains for us here to consider the mode in which the perception of odours may be rendered more acute or prevented. We are able to avoid the perception of unpleasant odours, by interrupting inspiration through the nose. By inspiring the odorous vapours through the nostrils with greater force, or by repeating the inspiration frequently, we can render their impression greater. In tracking by the scent, animals seek the part of the atmosphere containing the odorous matters by making rapidly-repeated inspirations in different directions, and then follow the scent to its source by the same means. The perception of the odorous matters also may be favoured by the wind. In this way ruminant animals, without tracking the scent, are believed frequently to perceive odours developed at a distance.

Besides the sense of smell, the nasal cavities are also endowed with common sensibility by the nasal twigs of the first and second divisions of the fifth nerve. Hence the sensations of cold, heat, itching, tickling, and pain; and the sensation of tension or pressure in the nostrils. That these nerves cannot perform the function of the olfactory nerves is proved by the cases in which the sense of smell is lost; while the mucous membrane of the nose remains susceptible of the various modifications of common sensation or touch. (See the observations on this subject at page 768.) It is often difficult to distinguish the sensation of smell from that of mere feeling, and to ascertain what belongs to each separately. This is the case particularly with the sensations excited in the nose by acrid vapours, as of ammonia, horse-radish, and mustard, &c. which resemble much the sensations of the nerves of touch; and the difficulty is the more apparent when it is remembered that these acrid vapours have nearly the same action upon the mucous membrane of the eyelids.

CHAPTER III.

OF THE ACTION OF THE OLFACTORY NERVES.

Animals do not all equally perceive the same odours; the odours perceived by a herbivorous animal and by a carnivorous animal are different. The cause of this difference must lie in the endowments of the central parts of the olfactory apparatus. The Carnivora have the power of detecting most accurately by the smell the special peculiarities of animal matters, and of tracking other animals by the scent; but have apparently no sensibility to the odours of plants and flowers. Man is far inferior to carnivorous animals in respect of the acuteness of smell, but his sphere of susceptibility to odours is more uniform and extended.

Opposed to the sensation of an agreeable odour is that of a disagreeable or disgusting odour, which corresponds to the sensations of pain, dazzling and disharmony of colours, and dissonance, in the other senses. The cause of this difference in the effect of different odours is unknown; but thus much is certain, that odours are pleasant or offensive in a relative sense only, for many animals pass their existence in the midst of odours which to us are highly disagreeable. A great difference in this respect is, indeed, observed amongst men. Many odours generally thought agreeable are to some persons intolerable: the smell of burnt horn is to many persons unpleasant; to others, who are not at all fanciful, agreeable. To many individuals mignonette does not smell very sweet; but rather herb-like, as Blumenbach observes, and as I experience in my own person. We have no exact proof that a relation of harmony and disharmony exists between odours, as between colours and sounds; though it is probable that such is the case, since it certainly is with regard to the sense of taste. It is also not certain that sensations of odours continue after the impression of the odorous matter has ceased, though we can scarcely imagine that such is not the case. It is difficult to ascertain this point by direct observation: the cadaverous odour, which is frequently retained in the nose very long after post-mortem examinations, cannot be regarded as a proof, since it probably arises from some of the odorous matter remaining dissolved in the mucus of the nostrils.

The sensations of the olfactory nerves, independent of the external application of odorous substances, have hitherto been little studied. It has been found that solutions of inodorous substances, such as salts, excite no sensation of odour when injected into the nostrils. The friction of the electrical machine is, however, known to produce a smell like that of phosphorus. Ritter, too, has observed, that when galvanism is applied to the organ of smell, besides the impulse to sneeze, and the tickling sensation, a smell like that of ammonia was excited by the negative pole, and an acid odour by the positive pole; whichever of these sensations was produced, it remained constant as long as the circle was closed, and changed to the other at the moment of the circle being opened. Frequently a person smells something which is not present, and which other persons cannot smell; this is very frequent with nervous people, but it occasionally happens to every one. In a man who was constantly conscious of a bad odour, the arachnoid was found after death, by MM. Cullerier and Maignault, to be beset with deposits of bone; and in the middle of the cerebral hemispheres were scrofulous cysts in the state of suppuration. Dubois was acquainted with a man who, ever after a fall from his horse, which occurred several years before his death, believed that he smelt a bad odour.

Whether substances which have a strong odour would, when introduced into the circulation, excite the olfactory nerve to the perception of the odour, has not been ascertained experimentally.

No senses are so intimately connected with the instinctive operations of the animal economy, as are smell and taste. Odours excite powerfully the sexual impulse of animals, and, by their influence on the brain and spinal cord, give rise to the actions connected with that impulse.*

SECTION IV.

Of the sense of taste.

CHAPTER I.

OF THE PHYSICAL CONDITIONS FOR TASTE.

THE conditions for the perception of taste are:—1, the presence of the nerve with special endowments; 2, the irritation of this nerve by the sapid matters; 3, the solution of these matters in the secretions of the organ of taste. The mode of action of the substances which excite taste can hardly be mechanical, any more than that of odorous matters; but must rather consist in the production of a change in the internal condition or material composition of the nerve by matters in solution; and, according to the difference of these matters, an infinite variety of changes of condition, and consequently of tastes, may be induced in the nerve. It cannot, however, be affirmed that the excitement of taste by a mechanical impression on the nerve of taste is absolutely impossible. Pressure, traction, pricking, and friction excite in the tongue only varieties of common sensation, it is true; but Henle has observed that

* An account of the facts known with regard to the sense of smell was published by H. Cloquet at Paris, in 1821, under the title of "Osphresiologie."

a small current of air directed upon the tongue gives rise to a cool saline taste, like that of saltpetre, and the mechanical irritation of the fauces and palate produces the sensation of nausea, which has no affinity to the various modifications of touch or common sensation, but is so allied to taste that it cannot be separated from it.* Electricity is the only imponderable principle which excites taste.

As a general rule, the matters to be tasted must either be in solution or be soluble in the moisture covering the tongue; insoluble substances produce merely sensations of touch. It is a matter of doubt whether the mere contact of a moist animal substance used as food with the vital organ of taste can excite its specific sensation independently of the matters contained in solution within the mass of food. Some gases, however, as sulphurous acid gas, are capable of exciting the sense of taste.

For a perfect action of a sapid, as of an odorous substance, it is necessary that the sentient surface should be moist. There are no other means for conducting the stimulus to the nerve in this sense than the mucous secretion of the tongue. Hence the investigation here, as in the case of the sense of smell, is rendered very simple.

CHAPTER II.

OF THE ORGAN OF TASTE.

The sense of taste has its seat in the fauces, but more especially in the tongue, which, nevertheless, is in many animals more important as an organ of deglutition. On account of this latter circumstance, the numerous varieties of form presented by the tongue in the animal series have little interest with reference to the sense of taste, and need not here engage our attention. The circumstance of the tongue being devoid of soft parts and stiff, as in fishes and many birds, (the parrots, ducks, geese, and some other birds are excepted,) must not lead us to infer that the sense of taste is absent; for this sense is a property of the whole fauces,—not of a special limited organ, but of the mucous membrane lining the cavity just mentioned. It is only where animals swallow their prey entire and covered with hair and feathers, as is the case with serpents, that the sensation of taste may be supposed not to exist; the mode in which the food is taken itself rendering taste impossible. The same may be said with regard to the insectivorous and granivorous birds. The peculiar organ in the palate of the Cyprinus family, which was regarded by many as an organ of taste, has been

* [The translator has shown, at page 1062, that a distinct sensation of taste, similar to that caused by electricity, may be produced by a mechanical stimulus applied to the papillæ of the tongue.]

shown by M. E. H. Weber to be a contractile organ, and is, in my opinion, destined to aid deglutition.

In man, the contact of the finger or any solid body with the soft palate excites the sensation of nausea, which might certainly be explained by supposing it to result from the impression being reflected upon the nerves of taste; but the sensibility of the palate to sapid substances is proved by the experiments of Dumas, Autenrieth, Horn, Lenhossec, Treviranus, and Bischoff; and, when I rub upon the velum palati a small piece of Swiss cheese, I perceive distinctly its taste in the palate. It has been demonstrated by the experiments of Dupuytren, Mayo, and myself, that the ninth, or hypoglossal, is the motor nerve of the tongue, and the lingual branch of the fifth the sensitive nerve; for these experiments have proved that irritating the hypoglossal nerve by galvanism, or mechanically, excites muscular contractions in the tongue, while division of the lingual nerve gives rise to violent pain. Experiments made to ascertain whether the lingual branch of the fifth nerve has any motor power require to be performed with the same precautions as experiments upon the roots of the spinal nerves. The nerve must first be divided, and the peripheral portion thus cut off from its communication with the central organs of the nervous system alone irritated. If the lingual branch of the fifth nerve be subjected to irritation, while yet in connexion with the brain and spinal cord, muscular contractions may be excited in the tongue and other parts by reflection, as I have myself once recently observed.

With respect to the controversy as to whether the lingual branch of the fifth, or the glossopharygeal, nerve be the nerve of taste; we have already stated the principal arguments (see page 769).* Professor R. Wagner † has adopted Panizza's view, on the ground of physiological as well as anatomical facts; Valentin and Bruns also have arrived at a similar conclusion from the results of their experiments; while those of Kornfeld, Gurlt, and myself favour the opposite opinion,—namely, that the lingual branch of the fifth is the principal nerve of taste.‡ I cannot regard Valentin's experiments as conclusive proofs of the sense of taste residing in the glossopharyngeal nerve, since a fortnight after the division of the nerve the animal is stated to have begun to taste again. This period is so short as even to render it probable that taste was never lost. Dr. Alcock's experiments § have not decided the question. The perception of bitter substances was [not] lost after division of the glossopharyngeal nerve; it was lost at the anterior part of the tongue only, when the lingual nerve was divided. He believes the sense of

* See also Bischoff, in the Encyclop. Wörterbuch der Med. Wissenschaft.

† Froriep's Notiz. 1837, n. 75.

‡ See Müller's Archiv. 1838, p. cxxxiv; and Valentin's Report, 1837, p. 221.

§ Med. Gaz. 1836, Nov.; and Dublin, vol. x. p. 260.

taste to be seated not only in the glossopharyngeal nerve and the lingual branch of the fifth, but also in the palatine branches of the fifth; the experiments with respect to the latter nerves were not decisive.

The pathological observations, showing loss of taste accompanying lesion of the fifth nerve, as in the cases detailed by Parry, Bishop, and Romberg, are very important. In Mr. Bishop's case, the pressure of a swelling upon the divisions of the fifth nerve was productive of loss of taste in the corresponding half of the tongue.* The case related by M. Romberg† is that of a person in whom taste and common sensibility were lost in one half of the tongue; and here, also, the commencement of the third branch of the fifth nerve was found acted on by a small tumour, while the glossopharyngeal nerve was healthy.

It appears to me certain, both from the experiments of Magendie, Gurlt, Kornfeld, and myself, as well as from the pathological observations of Parry, Bishop, and Romberg, that the lingual branch of the fifth is the principal nerve of taste of the tongue; but I do not regard it as proved that the glossopharyngeal nerve has no share in the perception of taste at the posterior part of the tongue and in the fauces. M. Romberg ascribes to it the sense of nausea, by which the entrance into the digestive organs is guarded.

CHAPTER III.

OF THE SENSATIONS OF TASTE AND THE ACTIONS OF THE GUSTATORY NERVES.

It is quite impossible to explain the various sensations of taste. The nature of the essential quality of taste, by which it is distinguished from smell, common sensation, sight, and the sensation of sound, is, like the nature of every other sensation, quite inexplicable. Of the essential quality of blue, for example, we can form no further conception; it can only be perceived as a sensation; and we must remain contented with the knowledge that the different nerves of sense enjoy special properties, one perceiving colours,—blue, for example; another sounds, a third odours, and so on. But the causes on which the differences in the various sensations of one and the same nerve depend may possibly be ascertained, and in the cases of vision and hearing they are already known. We know that one sound differs from another in proportion to the difference in the number of undulations producing them; and that the number of undulations of the imponderable ether of light, within a given time, is different for each colour. In the cases of the senses of taste and smell, however, we are far from having such a

* Med. Gaz. 1833; and Müller's Archiv. 1834, p. 132.

† Müller's Archiv. 1838; Heft iii.

theory to explain the varieties of sensations. Bellini tried to elucidate the great variety in the sensations of taste by means of the old hypothesis of the different form of the ultimate molecules of bodies,—a theory which cannot be refuted, but which is quite as incapable of proof. At the period when everything was accounted for by chemical polarities, it was customary to make application of this hypothesis also to explain the phenomena of taste.

Besides the sense of taste, the tongue is endued with a very delicate and accurate touch, which renders it sensible of the impressions of heat and cold, itching, pain, and mechanical pressure, and consequently of the form of surfaces.

The tongue may lose its common sensibility, and still retain the sense of taste, and *vice versâ*.* This fact renders it probable that the nervous conductors for these two different sensations are distinct, just as the nerves for smell and common sensibility in the nostrils are distinct. It will be easily conceived that the same nervous trunk may contain fibres differing very essentially in their specific properties. Facts detailed at a previous page prove that the lingual branch of the fifth nerve is the seat of sensations of taste; but it is also certain, from the marked manifestations of pain to which its division in animals gives rise, that it is a nerve of common sensibility. The hypoglossal, or ninth nerve, also is endowed with sensibility in addition to its motor power (see page 657).

Many substances having odour as well as taste, their simultaneous action upon the two senses gives rise to a more or less mixed sensation. The sensation of taste may, however, in such a case be isolated from that of smell by closing the nostrils. Many fine wines lose much of their apparent excellence if the nostrils are held close while they are drunk.

It would appear, from the experiments of Horn,† that some substances excite a different taste, according as they are applied to different papillæ of the tongue; an observation which would seem to afford an explanation of the difference often perceived between the flavour first excited by some substances, and those which they leave behind them upon the tongue. Horn instituted experiments with a great number of substances, and found that a part of them tasted the same in all regions of the tongue's surface; while others had very different tastes, according as they were applied in the neighbourhood of the papillæ filiformes, or of the papillæ vallatæ.

Very distinct sensations of taste are frequently left after the substances which excited them have ceased to act on the nerve; and such sensations often endure for a long time, and modify the taste of other

* Müller's Archiv. 1835, p. 139.—Medical Gazette, Oct. 1834.

† Über den Geschmacks-sinn des Menschen. Heidelberg, 1835.

substances applied to the tongue afterwards. After I have chewed a piece of the root of sweet flag (acorus calamus), milk and coffee have to me a sourish taste; the taste of sweet substances spoils the flavour of wine, the taste of cheese improves it. There appears, therefore, to exist the same relation between tastes as between colours, of which those that are opposed or complementary render each other more vivid, though no general principles governing this relation have been discovered in the case of tastes. In the art of cooking, however, attention has at all times been paid to the consonance or harmony of flavours in their combination or order of succession, just as in painting and music the fundamental principles of harmony have been employed empyrically while the theoretical laws were unknown.

Frequent and continued repetition of the same taste renders the perception of it less and less distinct, in the same way that a colour becomes more and more dull and indistinct, the longer the eye is fixed upon it. Red and white wine can at first be distinguished by their flavour when the eyes are bound; but, after frequently tasting first one and then the other, it soon becomes impossible to discriminate between them.

The simple contact of a sapid substance with the surface of the gustatory organ gives rise frequently to a very indistinct sensation of taste, and sometimes to none at all. The sensation is, on the contrary, very much heightened by the compression, friction, and motion of the substance to be tasted between the tongue and palate. The cause of this may be either that the impression is rendered more intense when combined with a mechanical impetus, as is the case in the perception of odours; or that the excitability of the sentient points of the tongue's surface soon becomes exhausted, so that motion is necessary to bring the foreign substance into relation with fresh parts of the nerve. The hypothesis recently proposed by Raspail that a reciprocal action is here excited between the two living surfaces brought into contact with each other is very improbable, since the friction of the substance to be tasted upon the tongue by any other means, without the contact of the tongue and palate, has the same effect.

Sensations of taste, independent of the application of sapid substances, have been hitherto little observed. We have instances of these sensations, however, in the nausea produced by mechanical irritation of the root of the tongue and soft palate; in the saline taste observed by Henle to be excited by the impression of a small current of air; and in the acid and alkaline tastes to which the application of galvanism by means of two plates of different metals to the tongue give rise. Reasons which render impropable the opinion that this last phenomenon is due to decomposition of the salts of the saliva are stated at page 623; [moreover, the same tastes can be excited by a mechanical stimulus.]

The re-action of the sense of taste seems capable of being excited also through the medium of the blood, in the same way that the sense of vision is affected so as to produce flickering before the eyes, &c. by the presence of narcotic substance in the circulation. M. Magendie has observed that dogs, into whose veins milk has been injected, lick their lips with their tongue as if they tasted. It is probable that the sense of taste is sometimes modified, and peculiar sensations of taste excited, by internal changes in the condition of the nerves; but it is difficult to distinguish such phenomena from the effects of external causes, such as changes in the nature of the secretions of the mouth.

SECTION V.

Of the sense of Touch.

The sense of touch is not confined to particular parts of the body of small extent, like the other senses; on the contrary, all parts capable of perceiving the presence of a stimulus by a sensation of mere touch, or a modification of the sensations of pain or pleasurable feeling, or of heat or cold, are the seat of this sense. The external causes exciting these sensations are mechanical, chemical, or electrical influences, and changes of temperature. The sense of touch, or common sensibility, extends throughout the whole animal and organic system, though its acuteness varies exceedingly in different parts. Even the special organs of the other senses are endowed with common sensibility, and hence are supplied with other nerves besides that of the particular sense peculiar to them. The nerves of touch are the posterior ganglionic roots of the nerves of the vertebral or spinal system, which includes some of the cerebral, and all the spinal nerves. The sensitive fibres contained in these posterior ganglionic roots go, for the most part, to compose with other fibres the nerves of animal life; but a smaller part of them assist in forming the nerves of organic life, endowing the latter nerves with their obtuse sensibility, the former with their vivid sense of touch. The so-named common feeling (cœnæsthesis) is not a peculiar sense, but merely the common sensibility of the internal parts of the body, which is capable of endless modifications, from the feeling of fatigue to that of pain in disease, and from the feeling of ease to that of pleasurable sensations and tickling in the state of health.

Parts endowed with the sense of touch and common sensibility. Organs of touch.—Touch, in its more limited sense, does not differ essentially from the sensibility more generally enjoyed by the textures of the body: its peculiarity depends solely on the relation of the sensitive organ to the external world. Every part of the surface endowed with sensibility has the sense of touch, inasmuch as it is capable of perceiving the contact of external bodies. It becomes especially an organ of touch, when its sensibility is very delicate and it is endowed with motion. The organs of touch are therefore the whole extent of the skin, but more especially the hands, the tongue, the lips, (particularly in feline animals, and seals and walruses, where they are provided with vibrissæ, the pulps of which are very sensitive, and plentifully supplied with nerves,) the proboscis and mouth of some animals, the tentacles of the Mollusca, the antennæ and palpi of insects, and the finger-like processes of the pectoral fins of the Triglæ, the nerves of which arise from a series of special lobes or enlargements of the spinal cord. The part developed for the purpose of touch in the skin is the corpus papillare, consisting of small elevations of the surface of the cutis, visible by the aid of a lens, which are invested by a sheath of the rete Malpighii, and contain the terminations of the nerves.*

The minute description of the organs of touch in different animals belongs to comparative anatomy.

The parts of the body in which the sense of touch or common sensibility has its special seat, are certain regions of the central organs of the nervous system, and the vertebral or spinal system of nerves; and by these it is imparted to most organs of the body.

There are parts of the nervous centres which appear to be perfectly insensible; for example, the surface of the hemispheres, which, there have been frequent occasions to observe, both in man and animals, may be wounded without the production of any pain. In cases where, after injuries to the head, it has been necessary to remove partially destroyed and projecting portions of brain, while the patient was in a state of consciousness, the operation has never caused pain, or even been felt.

Other parts of the nervous centres, on the contrary, are very sensible; but the sensations of which they are susceptible are not uniformly the same. When the parts of the central organs connected with the sense of vision are irritated, appearances of light are perceived. It is an old observation, that pressure upon the brain in the human subject gives rise to the perception of luminous appearances and flashes like lightning. But there are other parts of the brain which are susceptible of the varieties of common sensation; for although pain in the head is in many instances seated merely in the nerves of the exterior investments of the brain, yet the possibility of such sensations, as of tension or pain, being seated in the brain itself, is shown by cases of chronic affections of that organ, where the patient has had a more or less distinct consciousness from his sensations of the seat of the disease.†

The spinal portion of the encephalon and the spinal cord are susceptible only of the modifications of common sensation, which are perceived both at the situation where they are excited, namely in the middle line of the back, and in the external parts to which the spinal nerves are distributed, having there the character either of pain or of the creeping of insects,

* See Breschet and Roussel de Vauzème, Ann. d. Sc. Nat. 1834. t. i. p. 167.

† See Nasse, über Geschwülste im Gehirn, p. 26; and Abercrombie, on Diseases of the Brain, translated into German by De Blois. Bonn, 1821.

"formicatio." The local sensations in the back are sometimes unattended with those in the peripheral parts, and *vice versâ*. The cause of these remarkable differences is unknown.

The laws regulating the production of sensation in nerves by irritation applied to themselves, have been fully considered in the book on the physiology of the nerves. It only remains for us, therefore, here to speak of the sensations caused by stimuli applied to their peripheral extremities.

The horny tissue and teeth are perfectly destitute of sensibility, though their matrix or pulp is supplied with nerves as well as with vessels. The sensation in the teeth produced by the contact of acids must therefore be regarded as an affection of their pulp; and it is easy to conceive how the acid may be conducted to that part by the capillary dental tubes, whether we suppose it to act first on the ivory of the tooth where it is uncovered, or to reach the ivory through the clefts which are so frequent in the enamel.

Tendons, cartilages, and bones are in the healthy state void of sensibility, as Haller proved by numerous experiments. Haller's experiments also seemed to show that the periosteum is insensible. The dura mater, however, appears to constitute an exception; it is at least certain that it is supplied with nerves. (See p. 776.) In the state of disease, however, the bones, like the viscera of the chylopoetic system supplied by the sympathetic, become the seat of severe pain.*

The sensibility of the muscles is much less than that of the skin, a fact which is evident in the operation of acupuncture. The skin itself varies very much in different parts in the degree of its sensibility, which is probably proportionate to the number of nervous fibres distributed in it. An account of Professor E. H. Weber's observations relative to this subject has been given at page 700. At the same parts of the surface, where two small bodies applied at a very little distance from each other were recognised as separate bodies, the differences of temperature, and the weight of bodies applied, were also, according to Professor Weber's observations, most accurately recognised. The weight of bodies produced a greater impression at these parts; a body placed upon the volar surface of a finger seemed heavier, its pressure was perceived with greater intensity, than when it was laid upon the skin of the forehead.

The sensibility of the mucous membranes is very great in the respiratory apparatus, in the organs of sense, and in the generative organs, where they are supplied by nerves of animal life; while in the intestinal canal the sensibility of the analogous membrane is very slight in the normal condition, though in disease it may be exaggerated to great intensity. The external and internal tegumentary system differ from each other, moreover, in the circumstance that the tingling sensation, or "formication,"

* For an account of the numerous experiments which have been instituted relative to this question, see Haller's Element. Physiol. iv. p. 271—289.

which is frequently excited in the skin by internal causes, and particularly by affections of the spinal cord, appears to be never felt in the mucous membranes.

Various modifications of common sensation.—The sensations of the common sensitive nerves have as peculiar a character as those of any other organ of sense. The sense of touch renders us conscious of the presence of a stimulus, from the slightest to the most intense degree of its action, neither by sound, nor by light, nor by colour, but by that indescribable something which we call feeling, or common sensation, the modifications of which often depend on the extent of the parts affected. The sensation of pricking, for example, informs us that the sensitive particles are intensely affected in a small extent; the sensation of pressure indicates a slighter affection of the parts in a greater extent, and to a greater depth. It is by the depth to which the parts are affected, that the feeling of pressure is distinguished from that of mere contact.

The sensation of a blow or shock arises from a sudden change being produced in the state of the nerves by an external or internal influence,—namely, by the mechanical influence of a solid body, or by an electric discharge. A sudden discharge of nervous principle from the brain also, as at the moment of fright, is sometimes productive of the sensation of a shock or blow. The peculiarity of this sensation, therefore, depends in no way upon the mechanical action of the foreign body.

In some other senses, a rapid succession of impulses produces peculiar sensations, which vary in their quality according to the number of the impulses communicated to the nerve within a given time, — such, at least, is the case with the sense of hearing, and, perhaps, also with that of vision, — while on the senses of taste and smell this mode of excitement has no such effect. How is it with the sense of touch?

A rapid succession of equal impulses, such as produces the sensation of sound in the organ of hearing, is felt by the nerves of touch as a thrill or tremour. If the impression of the vibrations be more intense, and the part which is the seat of it very sensible, — such as the surface of the lips, — it may give rise to the sensation of tickling; this sensation is produced, for example, by bringing a vibrating tuning-fork very close to the lips; it is also very readily excited in the tongue. It might be imagined that the sensation of tickling when arising from other causes—such as the slight contact of another body, and the sensation of sensual pleasure so nearly allied to it, are both dependent on vibrations of the nervous principle itself with a determinate rapidity within the nerves. The sensation of tickling, or the allied pleasurable sensations, may be produced in all parts endowed with common sensibility; but they are experienced with greatest intensity in the generative organs; less strongly in the female breast, in the lips, in the skin generally, and in the muscles.

The sensation of pain seems to depend on the violence with which the nerves of touch are irritated.

The feelings of warmth and cold are most frequently caused by changes produced in the condition of the organized tissues by the imponderable physical agent, caloric; but they are frequently present when no variation of temperature can be detected by the thermometer, being then produced by some internal change in the condition of the nerves. Moreover, the sudden sensation of very great cold, and that of burning heat, appear to be very similar.

In comparing the temperature of different media by means of the sense of feeling, the degree of capability of the media for conducting caloric must be taken into consideration. The same heat acts with much greater intensity upon our skin, and produces the sensation of much greater warmth, when the medium by which it is communicated to our sense is water, than when it is air. Cold water also feels much colder to us than air of the same temperature, because water conducts away the caloric of our body more rapidly.

Reciprocal influence of the mind and the sense of touch.—When the activity of the sensorium is directed to a sensation, it is perceived; while, if the mind does not thus co-operate, the organic conditions for the sensation may be fulfilled, but it remains unperceived. The distinctness and intensity of a sensation in the nerves of touch, or common sensibility, depends on the mind's co-operating for its perception. A painful sensation becomes more intolerable the more the attention is directed to it. A sensation in itself inconsiderable, as an itching in a very small spot of the skin, is thus rendered very troublesome and enduring. When a person speaking to us spirts particles of saliva in our faces, the idea attached to the saliva causes the sensation it produces to be much increased in intensity and duration.

By the co-operation of the mind, and the application of experience previously gained, we attain the faculty of referring sensations at one time to our own body, and at another to external objects. Strictly speaking, we can feel only the present condition of our nerves, whether this condition be excited by internal or external causes. When we apply our hand to an external object, we do not feel the object itself, but only the hand which touches it; the mind, however, having already a conception of the external body, refers the sensation to it, and we say that we feel it. We have explained, at page 1080, how the idea of external objects, as distinguished from our own body, is first obtained. The ideas which we obtain of different objects by the touch have their source in the knowledge of the natural relation of the different parts of our body which is implanted in our sensorium; a faculty which is rendered more acute and accurate by the exercise of the sense of touch, and in the adult attains such a degree of developement, that, when our limbs are out of their natural position, if our attention is not directed to this circumstance, we deduce from sensations excited in them the same ideas that we should do had they their natural relation to each other. Hence, in the experiment, mentioned by Aristotle, of rolling a globular body between two fingers of one hand which are crossed over each other, the sensation obtained is that of two convex surfaces opposed to each, and apparently belonging to two separate spheres.

A sensation in a part endowed with touch appears to the sensorium to be, *cæteris paribus,* more intense when it is excited in a large extent of surface than when it is confined to a small space. The temperature of water, into which he dipped his whole hand, appeared to Professor Weber to be warmer than water of really higher temperature, in which he had immersed only one finger of the other hand. Similar observations may be made by persons bathing in warm or cold water.

As every sensation is attended with an idea, and leaves behind it an idea in the mind which can be reproduced at will, we are enabled to compare the idea of a past sensation with another sensation really present. Thus we can compare the weight of one body with another which we have previously felt, of which the idea is retained in our mind. Professor E. H. Weber was, indeed, able to distinguish in this manner between temperatures experienced one after the other better than between temperatures to which the two hands were simultaneously subjected. This power of comparing present with past sensations diminishes, however, in proportion to the time which has elapsed between them.

Sensations connected with muscular motion.—The muscles are endowed with a certain degree of sensibility, and, in spasmodic affections of their nerves, become the seat of intense sensations. These sensations are not, however, always proportionate to the degree of the muscular contraction; which renders it probable that the motion and sensation of the muscles are not due to the same nervous fibres. Thus, for example, the sensation of cramp in the muscles of the calf may be very severe, though the extent of muscular motion attending it is very slight. The same circumstance is sometimes observed in cramp of the digastric muscle of the lower jaw, which, when there is a disposition to repeated yawning, occasionally follows a violent movement of that kind: the pain then felt in the anterior belly of the digastric muscle is often extremely severe, though the movement of yawning has ceased, and the spasmodic action of the muscles has much diminished.

The sensation which informs us of the contraction of muscles enables us to estimate the degree of force exerted in resisting pressure or in raising weights. The perception of weight is more accurate than that of mere pressure, according to Professor Weber, who states that a difference between two weights may be detected when one is only one-twentieth or one-fifteenth less than the other. It is not the absolute, but the relative amount of the difference of weight which we have thus the faculty of perceiving.

It is not, however, certain that our idea of the amount of muscular force used is derived solely from sensation in the muscles. We have the power of estimating very accurately beforehand, and of regulating, the amount of nervous influence which it is necessary to emit from the brain for the production of a certain degree of movement. When we raise a vessel, with the contents of which we are not acquainted, the force we employ is determined by the idea we have conceived of its weight. If it should happen to contain some very heavy substance, as quicksilver, we shall probably let it fall; the amount of muscular action, or of nervous energy, which we had exerted, being insufficient. The same thing occurs sometimes to a person descending stairs in the dark; he makes the movement for the descent of a step which does not exist. It is possible that in the same way the idea of weight and pressure in raising bodies, or in resisting forces, may in part arise from a consciousness of the amount of nervous energy transmitted from the brain, rather than from a sensation in the muscles themselves. The mental conviction of the inability longer to support a weight must also be distinguished from the actual sensation of fatigue in the muscles.

So, with regard to the ideas derived from sensations of touch combined with movements, it is doubtful how far the consciousness of the extent of muscular movement is obtained from sensations in the muscles themselves. The sensation of movement attending the motions of the hand is very slight; and persons who do not know that the action of particular muscles is necessary for the production of given movements do not suspect that the movement of the fingers, for example, depends on an action in the forearm. The mind has, nevertheless, a very definite knowledge of the changes of position produced by movements; and it is on this that the ideas which it conceives of the extension and form of a body are in great measure founded. The sensorium may possibly derive this knowledge, independently of sensations in the muscles, from the consciousness of the groups of nervous fibres to which it directs the current of nervous energy. The accuracy with which the muscular movements are regulated and proportioned to their object, or the manifestation of the muscular sense, is most remarkable in all those movements by which the equilibrium of our own body, or of other bodies supported by us, when the base of support is small, is maintained; and also in the preservation of our balance during voluntary and involuntary movements of our whole body.

Touch, in its more limited sense, or the act of examining a body by the touch, consists merely in a voluntary employment of this sense combined with movement, and stands in the same relation to the sense of touch or common sensibility, generally, as the act of seeking, following, or examining odours does to the sense of smell. Every sensitive part of the body which can, by means of movement, be brought into different relations of contact with external bodies, is an organ of "touch." No one part, consequently, has exclusively this function. The hand certainly is best adapted for it by reason of its peculiarities of structure, — namely, its capability of pronation and supination, which enables it, by the movement of rotation, to examine the whole circumference of a body; the power of opposing the thumb to the rest of the hand, and the relative mobility of the fingers. Other conditions for the exercise of the sense of touch in great perfection are, great sensibility of the part, and a distinct perception of impressions on separate points of the sentient surface. The regular grooving of the skin of the palm, with the arrangement of the papillæ in regular series, must increase the delicacy of touch, inasmuch as the inequalities of the skin will more readily detect the inequalities of the bodies touched, and are better adapted for receiving distinct impressions from them.

In forming a conception of the figure and extent of a surface, the mind multiplies the size of the hand or fingers used in the inquiry by the number of times which it is contained in the surface traversed; and, by repeating this process with regard to the different dimensions of a solid body, acquires a notion of its cubical extent.

Sensations left after impressions;—modification of sensations by contrast.—The after-sensations left by impressions on nerves of common sensibility or touch are very vivid and durable. As long as the condition into which the stimulus has thrown the organ endures, the sensation also remains, though the exciting cause should have long ceased to act. Both painful and pleasurable sensations afford many examples of this fact.

The law of contrast, which we have shown to modify the sensations of vision, prevails here also. After the body has been exposed to a warm atmosphere, a degree of temperature very little lower, which would under other circumstances be warm, produces the sensation of cold; a sudden change to the extent of a few degrees from a warmer temperature, which has been of long duration, will produce the sensation of extreme cold. Hence the facility with which catarrhs are contracted even in the warmest climates. Heat and cold are relative terms. A particular state of the sentient organ causes what would otherwise be warmth to appear cold. A diminution in the intensity of a long-continued pain gives pleasure, even though the degree of pain that remains would in the healthy state have seemed intolerable.

Sensations dependent on internal causes are in no sense more frequent than in the sense of touch. All the sensations of pleasure and pain, of heat and cold, of lightness and weight, of fatigue, &c. may be produced by internal causes. Neuralgic pains, the sensation of rigor, formication, or the creeping of ants, and the states of the sexual organs occurring during sleep, afford striking examples of subjective sensations. The increased force of the current of blood synchronous with the heart's contraction excites sensations in almost all the organs of sense; in the retina the periodic appearance of a luminous spectrum, in the ear a periodic buzzing sound, in the nerves of touch a feeling of pulsation. There are mechanical causes for this sensation of pulsation, but it may be induced by a particular condition of the nerves; thus, it is often experienced in parts to which the blood is not sent with increased force.

The mind also has a remarkable power of exciting sensations in the nerves of common sensibility; just as the thought of the nauseous excites sometimes the sensation of nausea, so the idea of pain gives rise to the actual sensation of pain in a part predisposed to it. The thought of anything horrid excites the sensation of shuddering; the feelings of eager expectation, of pathetic emotion, of enthusiasm, excite in some persons a sensation of "concentration" at the top of the head, and of cold trickling through the body; fright causes sensations to be felt in many parts of the body; and even the thought of tickling excites that sensation in individuals very susceptible of it, when they are threatened with it by the movements of another person.

These sensations from internal causes are most frequent in persons of excitable nervous systems, such as the hypochondriacal and the hysterical, of whom it is usual to say that their pains are imaginary. If by this is meant that their pains exist in their imagination merely, it is certain quite incorrect. Pain is never imaginary in this sense; but is as truly pain when arising from internal as when from external causes; the idea of pain only can be unattended with sensation, but of the mere idea no one will complain. Still, it is quite certain that the imagination can render pain that already exists more intense, and can excite it when there is a disposition to it.

The sympathies of the sense of touch with the other senses, and with muscular movements, are dependent on reflex nervous action; they have been discussed in the Chapter on Nervous Reflexions in the Book on the Physiology of the Nerves, where the sympathy between the secretions and sensitive impressions has also been considered.

BOOK THE SIXTH.

Of the Mind.

SECTION I.

Of the nature of the mind generally considered.

CHAPTER I.

OF THE RELATION OF THE MIND TO ORGANISATION AND MATTER.

A. *Results of observation and experiment.*

In the introductory portion of this work, which treated of general physiology, a comparison was drawn between an independent organised body or organism, and a piece of mechanism, the component parts of which are combined for the fulfilment of a determinate purpose, and depend for their individual action on the harmony of the whole. In this comparison we met with more points of dissimilarity than of resemblance. The organism and the piece of artificial mechanism resemble each other in the well-adapted combination of their several parts for the production of a general result; but the organic body is distinguished by the power of reproducing the mechanism of its own organs, in the form of germ, and of thus propagating itself. Again, not merely does the action of organic bodies depend on the harmony of their component organs, but this harmony itself is an action of the organism; while the cause to which each part of the organised system owes its state and properties resides not in itself, but in the cause which produces and maintains the whole. A piece of mechanism is formed in accordance with an idea held in view by the artificer, this idea being the purpose for which it is intended. An "idea" also regulates the structure of every organism, and of each of its component organs. In the former case, however, the ruling idea exists external to the artificial mechanism, namely, in the mind of the artificer; while the idea, which is the cause of the harmony of organic bodies, is in action in the organism itself, exerting in it a formative power unconsciously, and in obedience to determinate laws.

The cause which produces an organism being constrained to work out a predetermined plan, or pre-existent idea, necessarily maintains the form and endowments of one organism distinct from those of another, which is constructed according to a different idea. But, although this is the case, yet the different organic forms are connected by a more general principle of construction, which arranges them in classes, orders, families, genera, and species. The genus exists only in the different species which are quite independent of each other, and not as a distinct organism producing these species. Everywhere in the animal, as well as in the vegetable kingdom, we see manifested a perfect unity in the general plan, together with all logical modifications in the realisation of it: yet each of the various species which constitute a genus, cannot depart from its own specific type of structure and mode of action; so that the species ceases to exist as soon as all living individuals belonging to it and their germs have perished. Except in this sense, the species is immortal; since the vital force or principle which creates and maintains its organisation is successively imparted by the perishing, parent organisms, to the new beings which they produce.

The action of the vital principle which forms organic beings in conformity with determinate ideas, is known to us only by its effects *in* organic beings. If organic forms were produced spontaneously and independently of organisms already existing, we should have the phenomenon of a vital force operating in conformity with determinate ideas, elsewhere than in living organic beings. But the doctrine of the generatio æquivoca is constantly losing ground before the advances of strict investigation, and preserves merely the form of an hypothesis alike destitute of proof and incapable of demonstration.

It is in no way probable that the vital principle which produces the definite compound structure of an organism is itself a compound of distinct parts; and the same may be said of the sentient mental principle of animals. That which owes its integrity to its compound structure, must be rendered imperfect by division; but the organising principle of a plant or animal may be divided at the same time with the plant or animal in which it resides, and yet retain all its organising power. Thus the parts of a divided polype or planaria become, or are from the moment of their division, independent organic beings endowed with the power of producing the proper organisation of their species. So it is likewise with the sentient and thinking principle of animals; if indeed that principle is distinct from the vital principle. It cannot be a compound of different parts; for if it were, the division of an animal would necessarily destroy its integrity; and we know that an animal may be divided, and yet the mental principle in each portion remain perfect, manifesting sensation, volition, and desires. Whatever is true with regard to the mental principle of other animals, may be predicated of the mind of man; for everything which feels and moves voluntarily in accordance with its desires, is endowed with a mind. Such, indeed, was the remark of Aristotle, who, in his Essay on the Mind, says: "As soon as they feel, they must have thoughts and desires; for where there is sensation, there must be pain and pleasure; and where these exist, desires must exist likewise."

The vital principle and the mind or mental principle of animals resemble each other, therefore, in this respect: they exist throughout the mass of the organism which they animate; but, unlike it, are not composed of separate parts, and when divided together with the organism, do not suffer any diminution or change of their powers.

In a former part of this work, it has been proved that the vital principle has not its special seat in any one organ. The facts adduced in support of this position were the following: — First, the presence and activity of the vital principle in the germ before any organs are developed, and in anencephalous and acephalous monsters; secondly, the persistence of life in separated fragments of animals and plants, and the development of these fragments into perfect organisms; and, lastly, the phenomenon of the spontaneous organisation of the germ of the higher animals and man after its separation from the parent system. The separation of the germ from the parent is an instance of true division of an organism; the part separated in this case merely differing from the sprout cut from a plant, or the fragment of a divided animal in its possessing only the organising power, but not the already organised structure. The same force is in action in both cases. The circumstance of the stimulus to organisation being afforded to the germ by fructification, and the existence of distinct male and female sexes, are not valid objections to this proposition; since the influence of a fructifying matter is not necessary for the preservation of life in parts already organised when they are separated from the parent system; and even the dualism of the sexes may be reduced to a mere dualism of the sexual organs in one individual, as we see exemplified in plants and hermaphrodite animals, some of which latter are capable of self-impregnation.

It was also shown at the same time that the mental principle, or cause of the mental phenomena, viz. the conception of ideas, thought, &c. cannot be confined to the brain; but that it exists, though in a latent state, in every part of the organism. In proof of this was adduced the manifestation of mind, by sensations, volition, and desires, in new animals, developed from the germ and semen, from the buds of animals propagating by gemmation, or from the separated portions of those which divide spontaneously, as soon as the organs necessary for mental action are formed.

At the same time, however, a difference between the vital and the mental principle was pointed out in the dependence of the latter for its manifestation, as a conscious mind, on one organ—the brain. The mental principle exists only in a potential state in the germ, and is totally unable to manifest itself by perception, will, ideas, or thought, until the whole organisation of the brain is perfected by the plastic vital force.

The development of the germ is dependent on certain external conditions. The vital principle resident in it is unable to effect the organisation of its component matter until this matter is exposed to certain external influences, such as warmth and air. Without these aids the germ cannot assimilate the surrounding nutriment, owing to the unfitness of the latter to combine with the substance of the germ, so as to preserve its necessary chemical properties and composition. The vital principle, therefore, may itself exist in a latent or merely potential state in the germ, just as the mental principle has that condition in all parts of the fully developed organism except the brain. From these latter remarks, we may clearly infer the points of dissimilarity, as well as those of agreement, between the vital principle and the sentient mental principle. Both are simple, not composed of dissimilar parts, and therefore are divisible, together with the organic substance which they animate; and both are capable of existing in a latent state. But the vital principle requires for the manifestation of its organising powers only the chemical co-operation of certain external influences; while for the action of the conscious mind the presence of matter already organised with the structure of the brain is essential.

The germ and young animal are not distinguished from the fully developed organism merely by the imperfection of their organisation, and the smaller size of those organs which are developed in the young animal. A more essential difference between the germ and the organism in which the whole structure is perfected, and which is capable of generation and of producing offspring, consists in the latter being a multiple of the germ. Hence only can we explain the fact that a part of the fully organised or "multiple" animal may separate itself and become a new animal, while the rest of the parent organism loses nothing of its power of further organisation.

The development of the multiples of the germ by the process of growth will, in the Section on Generation, be demonstrated to take place both in plants and in the Coralline Polypifera, Naides, Vorticellinæ Polygastrica, Planariæ, and Hydræ. Here we shall see the multiplication of the original organism manifested by the formation of buds, and by spontaneous division, while the multiple character of some others will be rendered evident by the persistence of life in portions separated by artificial division.

The portions of a divided Hydra have not at first the whole structure of a perfect animal, but they soon develop that structure within themselves. This fact shows us that the multiplication of an individual does not necessarily consist in the increase of analogous forms with analogous endowments, but may take place only virtually, in such a way that the forms produced are unlike the original, though their virtual endowments are the same. And thus we are led to understand the process subsisting in the higher animals, which, though capable neither of propagation by spontaneous division, nor of living after artificial division, yet are virtually a multiple of the germ from which they were developed. Here a part of the multiple animal can separate from the rest in a state capable of continued life and development only when it has become isolated in the form of an undeveloped germ. Now, in all the modes of propagation to which we have alluded, those of spontaneous or artificial division, germination, and sexual generation, both the vital principle and the mental principle, as we have before shown, undergo division.

The questions next present themselves, how is it possible for the growth of an organic being to cause a multiplication of its organising force? and how is the divisibility of the mental principle acquired at the same time, to be explained or understood? Is it a peculiarity belonging to the nature of the vital principle, and also of the mental principle, as a potential essence, that their extension through a large mass of matter, and their subdivision, is incapable of diminishing their intensity? or does the mere assimilation of new matter by a growing organism give rise to an increase of those principles, in consequence of their being contained in the nutritive matter itself in a latent state, though they are incapable of manifesting themselves until the matter is assimilated by an organic body?

The supposition last proposed necessarily involves a second, namely, that the principles of life and mind exist in a latent state in all matter; for although animals are capable of assimilating merely vegetable matters, plants, on the other hand, increase their substance from inorganic materials: indeed, unless there were such a new formation of organic matter from the inorganic elements, organic beings must at length perish, owing to the great destruction of organic substances by putrefaction and combustion.

The alternative contained in the two questions proposed above, is the farthest limit which our actual knowledge enables us to reach in the investigation of the relation subsisting between the vital and mental principles on the one hand, and organisation and matter on the other. At this point the inquirer is constrained to leave the field of empirical physiology, and to enter that of hypothetical speculation and philosophy. In the remarks which I have made in the foregoing pages, I have carefully avoided all considerations of the latter kind, my object having been, by a careful induction from facts, to develop those views which have the greatest semblance of truth in their favour. Moreover, as it appears to me very unadvisable to adopt any other mode of inquiry in our science, or arbitrarily to exchange the strictly inductive method for that of mere speculation, I shall, in the following pages confine myself to a simple exposition of the theories contained in the two questions already alluded to, without supporting either the one or the other. I shall not follow exclusively any special form of philosophy, but shall explain both systems without mixing up with them the consideration of physiological facts, though at the same time I shall endeavour to make their bearing on those facts as evident as possible.

B. *Cosmological Systems.*

I. *Hypothesis of the dependence of organisation and the mental phenomena on active innate "ideas" or spiritual essences implanted in organic bodies.*

This hypothesis admits that in every part of the universe ideas of the Divine Spirit are being carried into operation; but supposes that in organic beings alone are implanted such ideas as are capable of constantly reproducing their kind, and of developing in matter the mechanism proper for the actions of organic bodies. The active "idea" of an organic body is, therefore, an emanation of divinity, living in that body and its products from the period of creation downwards. This "idea" is the only part of the organic body which is permanent, for the matter of the body is constantly leaving it, while new matter is as constantly being subjected to the influence of the innate spirit. In matter itself is neither soul nor life, even in a latent or potential state. All the vital and mental phenomena presented by matter after its assimilation by an organic body, are due to the idea which exists in and rules the organism. This is the doctrine taught in a mythical manner in the Timæus of Plato;* and is indeed the view most generally adopted respecting the relation in which the vital and mental principles stand to the body. According to this theory, the vital idea, or spirit, may after death dissolve its connection with the body, and may return to the divine source whence, at the creation of animated beings, it had emanated. The soul, therefore, is essentially independent of matter, and is connected with it only by a bond capable of solution. The proper endowments of matter are wholly of a physical nature. The various fables respecting the condition of the soul after death, the doctrines of the Pythagoreans and Plato, concerning the fate of spirits after death, and the notions of the New Platonists and Mystics, with respect to the soul freeing itself from the bonds of matter even in this life, as well as the practical application made of these views, are all modifications of the same fundamental cosmological theory, the main propositions of which we have just stated,—to wit, that the soul is independent of the body; is not a property of it or of matter in any form; and is only united with

* [The article on Plato's writings and philosophy in the Encyclopædia Brittanica, contains a full exposition of the theory of "innate ideas."]

matter in living organic bodies. The belief in this doctrine is strengthened and confirmed by the interest which the "self" of each individual feels in his continued personal existence; and by the hope in the duration of this existence even beyond the grave. For few are they who are content to merge their personal being in that of the universal spirit, and, with Fichte, to regard the mental existence, even in this world, as the mere striving after infinity and eternity.

Now life and mind, or the animating "idea," not being latent properties of all matter, the increase and division of animated organic beings, and the simultaneous division of the vital and mental principles cannot, according to this view, be ascribed to the assimilation of new matter in the process of nutrition, but must be regarded as due to a property of the vital and mental principles themselves, which contrary to every attribute of matter, renders them capable of division, *ad infinitum,* without any diminution of their power or intensity. Such a property it is certainly difficult for the mind to conceive. But this fundamental hypothesis of the animating ideas of organic bodies being independent of their material substance, and emanations from the Divine Spirit, renders it more easy to understand how the different individual organisms, and their classes, orders, families, genera, and species can have a distinct and independent existence; while, at the same time, they manifest such distinct signs of the original influence of one ruling idea. This general idea is so logically followed out in all the modifications presented by the genera of one family, that zoologists, from the knowledge of the characters of a family, and of some of the genera belonging to it, can frequently predetermine the existence of the other genera and their peculiarities. The hypothesis of original innate spirits or ideas agrees also with the known law of creation, that if in either of the organic kingdoms all the individuals of a species perish, the form is not restored by any general life of nature; and the original identity of structure of the germ of the most various organic beings, constituted, as it always is, of a cell with a nucleus, seems to prove that the cause of the variety of classes, families, genera, and species of animals and plants developed from the germ resides not in the structure or chemical property of the germ, but in the idea or spirit implanted in it at its creation.

II. *Pantheistic view of a universal spirit, and its relation to matter.*

Directly opposed to the foregoing theory is the doctrine that the principle of life is inherent in all matter; that so far from being something superadded, it is in fact a property of matter itself, although it manifests itself in the various forms of organic nature, only under certain conditions, and when the matter has a determinate composition and structure. As soon as matter is assimilated by an organic being, it falls under the influence of conditions which compel the vital principle latent in it to manifest itself in the definite form of the organic body. According to this view, the multiplication of the organic force during the growth of a living being, and the capability of division which organisms possess, are intelligible. When organic beings die, moreover, merely the conditions necessary for the manifestation of life in their definite forms are lost; the matter returns to the general lap of nature, still endowed with the vital principle, and still capable of manifesting life.

The doctrine of pantheism, and at the same time of materialism, is here expressed in general terms, without reference to historical peculiarities, and in the form best adapted for illustrating the problems alluded to in the preceding inquiry. Cosmological theories of this kind are contained in a more or less varied form in the writings of the philosophers of ancient Greece, Heraclitus, Anaxagoras, &c. Anaxagoras taught that all might originate in all; and that "the spirit" was the soul of all things, and the universal form of all things. According to Heraclitus, animated beings receive the spiritual principle of the universe through the medium of their respiration and their senses. But by no philosopher has this theory of the world been more clearly laid down than by Giordano Bruno in his "Dialoghi de la Causa, principio et uno." *

The following passages from the speculative treatise of Bruno, will afford the reader some insight into the nature of this system of cosmology, which has been reproduced, and more fully developed in the writings of modern philosophers.

"The soul of the universe fills and illumines the whole world, and instructs Nature in the production of the genera and species of things in their proper form. This creative universal intellect stands in the same relation to the production of all the objects of Nature as our intellect does to our conceptions of genera and species."—Loc. cit. p. 4.

"The final cause which the great first cause, the creative soul of the universe, has in view, is universal perfection; and this consists in the development of all possible forms in the different parts and masses of matter,—an object in which the universal intellect takes such delight that it never rests from evoking all varieties of forms from the womb matter."—P. 45.

* See the translation of this work in Rixner and Siber's "Leben und Lehrmeinungen berühmter Physiker am Ende des 16. und Anfang des 17. Jahrhunderts, als Beiträge zur Geschcihte der Physiologie."—v. Heft. Jordanus Brunus, Salzbach, 1824. [An account of the writings and speculative doctrines of Giordano Bruno, with some extracts from his works, will be found in Mr. Hallam's "Literature of Europe during the Fifteenth, Sixteenth, and Seventeeth Centuries," vol. ii. p. 146.]

"The universal cause of all things must be one soul, that soul, namely, which presides over all matter throughout the universe, and which being unity in itself, produces from matter, according to its faculty of receiving various forms, and according to its different active properties, the different objects of Nature with their different qualities. Thus some of these created things live devoid of sensibility, on account of their spiritual endowments, being either through their own feebleness (?) or other causes, oppressed by the preponderating matter."—P. 56.

"Although the heavenly bodies and nature generally do not possess the human faculty of thought or memory, it can by no means be inferred that they form their products without any intelligence or design; for even perfectly educated musicians and penmen, though they are little or not at all observant of that which they execute, do it with perfect regularity."—P. 48.

"I say, therefore, that a table as a table, a coat as a coat, leather as leather, and glass as glass, are not animated; but, as products of Nature and compound things, they have matter and form. How small and inconsiderable soever a thing is, it has always a part of the spiritual substance within it, which, if it finds a fit subject or basis, is ready to become a plant, or an animal.* In short, there is one spirit in all things, and no body is so small that it does not contain a portion of the Divine essence by which it is animated."—P. 53.

According to this theory, then, organisms are products of the first of all causes, — bodies endowed with life, in which the vital and spiritual phenomena are manifested in a determinate form through the medium of a definite structure and chemical composition. This structure also has not arisen accidentally; for it has emanated from the creative spirit of God: and the ideal connection of all organic beings in their relation of classes, families, genera, and species, precludes the notion of their being the result of accident. As soon, however, as the so-called dead matter is brought within the sphere of action of the already existing organism, receives from it the same structure, and becomes subject to its vital principle, the capability of life, as yet latent in this matter, begins to manifest itself in a determinate form, which is included in that of the existing organised system. In this way the assimilation of new matter by an organic being gives rise to an increase of its organic force; and with this is combined the capability of multiplication by division. Phenomena, analogous to such a conditional mani-

* [In the German version, this sentence stands thus: — "Be a thing ever so small and insignificant, it always possesses a part of the spiritual and animating substance, *which is always a fit basis, from which* anything may be formed, as a plant or an animal." This appears to be an incorrect version, which mars the sense of the passage. The translator has therefore followed the Italian words, and the translation given by Mr. Hallam, op. cit. p. 149.]

festation of a principle of vitality latent in all matter, are known in physical science. Forces, or principles, such as electricity and light, for example, which are present in a latent state in bodies, are manifested when these bodies are subjected to certain conditions.

The doctrines of pantheistic cosmology are here merely sketched in a general manner. The elucidation of the different forms in which the philosophical systems of this school have been presented, is foreign to the design of this work. The only object held in view has been to offer for consideration the two principal hypotheses which take up the inquiry into the connection of life and mind with matter at the point where it passes beyond the domain of empirical physiology.

CHAPTER II.

OF THE MIND CONSIDERED IN A MORE LIMITED SENSE.

Distinction between the Mind and Life.

The most general operations of life in organic beings are beyond the sphere of consciousness, and consist in the development and maintenance of the well-contrived organisation of those beings, and the reproduction of similar organisms. These operations of life take place alike in plants and animals. In both kingdoms of organic nature the germ receives from the parent organism, as the foundation-stone of its structure, a cell with the nucleus attached to its wall; this is, in animals, the germinal vesicle with the germinal spot. The first steps in the process of organisation consist in the development of new cells of the same kind from similar nuclei. The germinal membrane of the animal ovum, according to Schwann's observations,* is constituted of an aggregation of cells, and the tissues of the fœtus are at first, according to the same observer, formed of cells, similar both in form and mode of origin to those of vegetable cellular tissue, having generally attached to their walls a nucleus around which they are developed. It is only when these cells become transformed into the permanent tissues that animal and vegetable structures assume their distinctive characters.

If we compare the mental phenomena, which animals and the human species alone present, with the operations of organisation common to them and plants, we find points both of resemblance and of difference. In both we see an accordance with design and with the demands of reason; but in the operations of the organising power this is effected

* Froriep's Notiz. 1838. N. S. No. 3. [See also Schwann's Mikroscopische Untersuchungen über die Uebereinstimmung in der Struktur und dem Wachsthum der Thiere und Pflanzen. Berlin, 1839. p. 63, and the analysis of this work in No. 18 of the British and Foreign Medical Review.]

without consciousness, while in the mental actions it is attended with consciousness and perception. Hence in the vegetative operations of vitality the manifestation of design is the result of necessity, not of choice; one fixed end only can be attained, and that is, the production of the special form and properties of the particular plant or animal. Everything which does not contribute to this end is disregarded, while all that is calculated to aid in its accomplishment is appropriated to that use. The "idea" of the particular species of plant is the sole theme which is again and again worked out. Just as in the formation of a piece of art by a well-practised artificer the rules for its construction are never deviated from, so it is in the organisation of a plant in accordance with the fundamental "idea" of the species.

In the mental phenomena, on the contrary, a much greater scope for arbitrary variety in action is allowed.

The various objects of the external world give rise to the perception of images which are reproduced and combined. The general quality of many such images is conceived, and an image of this is retained, and is called a general idea: these ideas, also, are combined with one another, and with other images; the act of doing which is thought. Here the creative action follows no model, but obeys merely the necessity of combining the different images, and of forming from them general or abstract ideas. The materials for these images may be supplied by the whole of nature, as far as it is cognisable by our senses. The mind may therefore be likened to an instrument which effects a most manifold reflection of the numerous things external to the organism, and within it, but yet in accordance with a simple law of combination. In organisation and life, on the other hand, like always reproduces like; the vital force creating the definite form of the species, with its peculiar properties, from the matter subjected to its action, while it takes no cognizance of external objects. If there is any similarity between the two processes, it lies merely in the images which form the material of mental action being disposed of according to an innate law of combination, just as matter and its principal properties are applied by the vital force, in obedience to the innate law of organisation.

The products, also, of mental action and of vitality are different: for, although it is possible for the mind to reproduce the objects of nature in the form of mental images, which are, as it were, signs of the things themselves, yet the whole process is one of mere consciousness; — from a mental image merely a mental image is produced;—from a sign merely a sign. The organising force, or vital principle, on the contrary, realises the type of its operations in a material form. Again, amidst the general ideas conceived in the mind, the particular images or details can be separately produced; just as from the germinal membrane, which includes the general vitality of the animal, there are generated the specialities of structure which are essential to the developed organism; but in the former case the products exist only in the consciousness of the individual, while in the latter instance a material tissue or organ is created. While, however, there are these differences between the processes of mental action and that of organisation, both the mental and vital principles, in their relation to matter, present, as we have before seen, in most points the same properties (page 1335).

There is one class of phenomena in which the creative vital power of the animal organism takes a part in the operations of the mind, directing them, producing series of thoughts, like dreams, and determining the animal to certain acts which are called "instinctive." The bee is obliged to realise the cells of wax according to the type presented as a dream to its sensorium; each animal of a species must construct its habitation or its web on the same plan as those which have preceded it, or must sing as they have done, perform the same migrations, and protect its offspring while under the rule of passions which take their rise in the business of generation. The originator of all these ideas, which though obeyed and worked out by the mind of the animal, are not conceived by it, is the organising force, — the first cause of the organism, which reproduces like from like, and forms all the organs of the animal body in accordance with design. It is this power which determines animals to the act of sexual union, which enables the young to maintain their equilibrium without previous education, and leads the young ducks to seek the water, the mole to burrow, and the sloth to climb, in accordance with the structure of its limbs, which are adapted for that movement, and not for leaping. In these phenomena we see a power at work which has the attributes of the unconscious vital principle, and not those of the mind: but this power merely gives the theme of the instincts; their realisation is effected by an act of the mind itself. The cells of the bee, and the electric organs of the electric rays, therefore, owe their origin primarily to the same cause, but the immediate agents engaged in their construction are different, — the mind coming into play in the case of the bee's cells, and acting on the mediate agent in the realisation of that structure out of the body of the animal, which the vital force within it has determined.*

It is evident, therefore, that the vital force or principle may exert a direct influence on the formation of internal mental perceptions, and on the action of the mind; but it is, nevertheless, capable neither of proof nor of refutation that the primary cause of organisation and that of the mental phenomena are the same. It must consequently remain a

* The description of the instinctive acts of animals does not come within the plan and purpose of this work, but belongs to natural history. For information on the subject I refer the reader to Kirby and Spence's Entomology, and to Darwin's Zoonomia. The nature of the instinctive movements has already been discussed. See page 946.

matter of doubt whether the presence of the organising action alone in plants is owing merely to the want in them of the structure necessary for the manifestation of the mind, or whether it is the result of an original difference in the innate "ideas" implanted in them, as organic beings.

Action of the brain in the production of mental phenomena.—The peculiar quality of the mind is "consciousness," a something of which no further definition can be given, and which admits of description as little as the states or properties called sound, blue, red, and bitter. Just as it is the property of a specific nerve connected with the sensorium to have sensibility, so it is the property of the brain to have consciousness. The conception of ideas, thought, and emotion, or the affections, are modes of consciousness. There is no sufficient reason for admitting the existence of special organs or regions set apart in the brain for the different acts of the mind, or for regarding these as distinct powers or functions.* They are, in fact, as we shall presently show, merely different modes of action of the same power. Moreover, although the clearness of the ideas conceived, and of the thoughts, and the intensity of the emotions are affected by structural changes of the brain; and although the integrity of that organ is quite essential to consciousness, yet the action of the mind cannot be explained as the result of material processes, but must rather be regarded as in its essence independent of all material relations, though influenced in its clearness and intensity by the condition of the organ which is its seat. It is true that the mind is rendered conscious of external impressions only through the medium of the nerves of sense, and their action on the brain: but the retention and reproduction of the mental images of external objects of sense, exclude altogether the notion of particular orders of ideas being fixed in particular parts of the brain; for example, in the ganglionic corpuscules of the grey substance. For the thoughts accumulated in the mind become associated in the most various manners, in a chronological succession, according to the relation of simultaneous occurrence, or according to their similarity or contrariety; and these relations of the ideas or thoughts to each other change every moment. It is certainly correct that structural changes of the brain are sometimes followed by partial loss of memory; facts relating to certain periods of time, or certain kinds of names, substantives, or adjectives being forgotten. But the occurrence of partial loss of memory of the first kind could only be used as an argument for impressions being successively fixed in the order of time in stratified parts of the brain,—a supposition which cannot be for a moment entertained. And if the perception of mental impressions and thought were ascribed in a general way to the ganglionic corpuscules; if the direction of the mind from individualities to general ideas, or from general ideas to individual-

* See p. 835* of the second edition of the first volume of this work, or p. 837 of the first edition.

ities, were supposed to depend on the relative exaltation of action of the peripheral part of a ganglionic corpuscule above its nucleus, or of the nucleus above the peripheral part; if the combination of ideas in an act of thought, or a proposition, for which the conception of object, predicata and copula, at the same time is necessary, were explained by a reciprocal reaction of ganglionic corpuscules through the medium of intermediate processes acting as copulæ; or, lastly, if the association of ideas successively in the order of their first conception, or simultaneously according to their previous existence were admitted to be attended with a successive action of certain united corpuscules, or a simultaneous action of several corpuscules,—if all these suppositions were adopted, we should be merely indulging in vague and groundless hypotheses.

It is best, therefore, to limit ourselves to the supposition that the clearness and distinctness of our ideas depend on the intensity of the organic actions of the grey globules or nucleated corpuscules of the brain.

Primitive ideas and abstract notions.- Philosophers of all ages have been led to inquire whether the correspondence observed to subsist between our thoughts and the relations of external objects, has its origin entirely in the evidence of our senses and the experience obtained through them, or whether it is also in part due to a pre-established harmony between the world of phenomena, the macrocosm, and the mind, the thinking microcosm; being the result of the action of laws necessary alike to the connection of the phenomena of nature and to the connection of the thoughts of the mind. According to those who adopt the former view, *nihil est in intellectu, quod non erat in seusu.* Those, on the contrary, who prefer the latter opinion, admit the existence of *a priori* abstract notions innate in the mind, the categories of Aristotle, such as the notions of quality, quantity, relation and modality. These abstract notions are supposed to constitute the whole material of *a priori* thought, which, though excited by the experience of the senses, yet exerts a ruling influence over the impressions thus received. These notions, therefore, are not deduced from experiments or observation, but are illustrated by it. Locke, in his analysis of the human understanding, arrived at the conclusion that the mind has no such original notions or ideas implanted in it, but derives all its purely abstract notions from experience, being unable either to create or to change them. But since the impressions on the senses are not themselves abstract ideas, the latter expressing rather the relation of the sensations, it becomes again a question how far the understanding can conceive anything, which, even if present, yet does not act on the senses; and whether the combination of sensations into a general idea is dependent on the existence of original ideas, or abstract notions of the mind, or on a necessity arising merely out of habit. The latter explanation was maintained by David Hume. According to his view, the combination of ideas is owing to the frequency of their association, in consequence of which this association becomes a matter of subjective necessity; the association of cause and effect, for example, resulting from our being accustomed to see them succeed each other. Now, since we are entirely dependent on this habituated combination of our ideas, we can, according to Hume, have no "objective" knowledge.

Kant denied the truth of this doctrine, on the ground that the reality of *a priori* science, such as the pure mathematics, proves the existence of *a priori* ideas. Kant's pure ideas of the understanding are, 1. The category of quantity (comprehending unity, plurality, and totality). 2. That of quality (including reality, negation, and limitation). 3. That of relation (essence and accident, causality and reciprocation). 4. Modality (possibility, existence, necessity). These constitute the material of abstract thought, while, according to Kant, the ideas of space and time are the primitive forms of conception for the impressions of the senses,—the forms of all phenomena. We have, however, according to this philosopher, no knowledge of external things except that which we gain by the application of these principles to the results of experience, and to the recognition of what corresponds with the above categories.

That innate ideas may exist, cannot in the slightest degree be denied: it is, indeed, a fact. All the ideas of animals, which are induced by instinct, are innate and immediate; something presented to the mind, a desire to attain which is at the same time given. The new-born lamb and foal have such innate ideas, which lead them to follow their mother and suck the teats. Is it not in some measure the same with the intellectual ideas of man?

I believe that this question respecting the operations of the human mind can be answered in a way favourable neither to the hypothesis of Hume nor to that of Kant. From the frequent combination of two things in the mind, no other result can necessarily follow than that when the one is conceived, the other must also be associated with it; or that when an idea returns which had previously produced a pleasant or an unpleasant impression, this same impression may again be expected with certainty. In this way the dog connects the idea of blows with the perception of the stick, the association of the stick and blows having become through habit a thing of necessary occurrence. But to form an abstract conception of this association as of something common to many other combinations of ideas, under the notion of cause and effect, is a perfect impossibility, both to the dog and to every other brute animal. Brutes form no general notions. The cause of this difference between man and beasts does not lie in the comparative lucidity or obscurity of the impressions made on their minds respectively; for in this respect there is assuredly no superiority in the human mind. I am therefore of opinion that the human mind also would never derive from the mere experience afforded by the senses, and from habit, the general abstract idea of causality, unless it had a certain power of abstraction,—a power, namely, of forming a mental something out of the returning combinations of two things, of which one requires the succession of the other.

On the other hand, I do not adopt the opinion that the mind is originally occupied by the primitive ideas of Kant, or the categories of Aristotle; these appear to be the fruit of experience and of the power of abstraction. But the original power by which the different categories are first acquired, from the observation of external nature, is the faculty of extracting the general property from many specialities or separate perceptions, in other words the power of forming an abstract notion, λόγος. When this faculty is present, the frequent experience that a particular external influence is necessarily followed by a change in one's-self, becomes connected with the observation of a similar relation between other facts, and produces in the mind the idea of "causality," or of the necessity of the change of one object by another; and in the same way all the general abstract ideas are produced by the mind rising from mere simple facts communicated directly by the senses to their general quality.

When an object perceived through the medium of vision no longer presents the same appearance as before, and the same fact is perceived with regard to numerous other objects, the distinct individual perceptions remain uncombined in the mind of an animal; but in the human mind the notion of "change" arises. This abstract notion includes merely that in which all the changing phenomena agree, but takes no cognizance of what is peculiar to the different phenomena. If the change is attended with an alteration of locality, the notion of "motion" is obtained. In phenomena which undergo changes, the different acts of the change agree only in the circumstance of their succeeding each other. This being conceived of many different phenomena, gives origin to the notion of "succession."

The faculty of forming a general idea or notion is not, however, a distinct power of the mind acting on the simple perceptions; but it consists in the mutual reaction of allied perceptions amongst themselves. The human intellect has such a degree of development that many distinct perceptions or simple ideas may exist in it simultaneously, and react on each other. If many allied perceptions are present, which in one respect differ, while in another they agree, the points of difference amongst the mass of ideas become obscured, while only that which the different ideas have in common remains distinct. General ideas, or abstract notions thus obtained, are the more stringent in proportion as the application of which they are capable is more general.* The abstract notion of "causality" is more stringent than

* Herbart, Lehrbuch der Psychologie, p. 143.

that of "weight," because it finds its application in the relations both of mental and physical facts. If the notion of weight acquired by experience were capable of as extended application as that of causality, it would seem equally binding as the so-named primitive ideas.

The most general abstract notions formed in the manner above described are those of change, essence, infinity, finiteness, form, size, quality, space, time, motion, power, matter, object, subject, self, causality, existence, nonentity. Some of these may be conceived of all things material as well as immaterial. Such are the principal abstract notions which are called categories. Other general notions have been deduced solely from the perceptions of physical objects — "*phenomena*;" or solely from conceptions of the intellectual world — "*noumena*." Such are the notions of "matter," "force," "motion," "object," "subject," "self," &c.

The next question which presents itself for solution, respects the degree in which the conceptions of the mind correspond to their objects, and the possibility of their amounting to an absolute or complete knowledge of things. The great development and extension given to mental philosophy by some speculative writers,—as Bruno, Spinoza, Schelling, and Hegel, — led to the doctrine that this absolute knowledge of things was possible, and that the purely mental thought by the analysis of itself could produce thoughts entirely according with natural objects. The origin of this axiom is to be found in a passage from Bruno's writings, which we have already cited, where he says, — "This creative universal intellect stands in the same relation to the production of all the objects of Nature as our intellect does to our conceptions of genera and species." To a limited extent the power of reproducing in thoughts the properties of objects, is certainly possessed by the human mind; and that intellect which, by virtue of a talent for speculative inquiry, is capable of distinguishing and comprehending what is general and essential amidst the variable and accidental, or of discovering laws and general facts from which many phenomena may be deduced, has such a power in the greatest degree: but this can scarcely be called an absolute knowledge of things. Setting out with the notion of infinite existence, it has not yet been possible, even with the aid of experience (as Hegel understands that word), to give an absolute definition of light, of electricity, or of life; for this requires the previous knowledge of a different kind of absolute infinity from that on which philosophy is obliged to found her speculations. The analysis of a philosophical idea, even by the greatest philosopher, can, therefore, be merely a more or less successful exercise of the speculative talent according to a method which is not strictly conclusive.

When the properties of a thing have such a simple and necessary connection, that from its definition *all* its unknown properties may be deduced, a complete knowledge of it is possible; as, for example, in the case of the simple relations of form and size. In the expressions of a triangle, circle, cone, &c. all their properties are given. Pure geometry, consequently, is an absolute science; but there are many other things in Nature of which it is impossible to give any such definition or notion as will involve the knowledge of all their properties. In these things, it is true, certain properties may be discovered which render it possible to deduce many other properties; but still, in natural objects, when the properties detected by the senses and those deduced by reason (λόγος) are known, the greatest part of them still remains undiscovered. Science does not here attain to the absolute discovery of the essence of things. It is only so far absolute as certain consequences follow with absolute necessity from a given axiom, whether this be a thesis or a deduction from observation; although here only a certain series of phenomena or relations is explained. All sciences, when they have attained a certain degree of perfection, are susceptible of this mathematical mode of study. Speculative philosophy was treated in this manner by Spinoza. In the natural sciences, the object is to discover general facts from which, as from a fundamental principle, many others may be deduced. Those sciences, indeed, make the most rapid progress, which follow most closely the mathematical mode of investigation. The law of gravitation affords data for the deduction of the laws of motion of the planetary system; but the essence of gravitation remains a mystery. So, likewise, in electricity laws are known, from which the electro-magnetic phenomena may be deduced, as geometrical truths are deduced from their axioms; but we are still quite ignorant of the essential nature of electricity. The phenomena of the mind, also, may, like physical phenomena, be made the subject of observation. Psychology in all respects, indeed, resembles one of the physical sciences; the deduction of mental phenomena from known principles is quite possible; but we do not thereby advance a step towards the discovery of the real nature of the mind.

From these considerations we may infer the method of inquiry which must be most fruitful in the natural sciences. The most important truths in those sciences have been discovered neither solely by the analysis of philosophical notions, nor solely by mere observation, but by a combination of reflection with observation; that which was essential being distinguished from the accidental in the facts observed, and fundamental principles thus discovered from which many other phenomena might be deduced. This is more than mere empirical observation; it is philosophical observation.

There are general notions or ideas belonging to all sciences: they are the general truths which are not tangible by the senses, but are abstracted by the mind. These abstract notions are obtained, however, only by the analysis of observations. In the natural sciences, phenomena are analysed for the sake of forming general notions from them, and of ascertaining the relations of the simple ideas suggested by things. Abstract mental notions, and their relations to each other, are peculiarly the proper subjects of philosophy; and hence this science draws its material from all other sciences, and forms the bond of their union. Although so nearly allied to the philosophical study of some other sciences, yet philosophy is itself a distinct one; since it has to do with abstract notions, which form the basis, not of one science only, but of many, — such as the notions of existence, essence, accident, change, cause, quantity, quality, space, time, matter, spirit, &c. Many general notions,—such as those of force and matter, motion and weight,—belong chiefly to particular sciences; but every science is philosophical as far as it embraces general notions from which phenomena may be deduced.

The mind of man and that of animals compared.—The mental phenomena presented by animals, and by man, agree in several points; while in others they differ. In the minds of both, ideas or mental perceptions are formed from the impressions on the senses, are retained, and are reproduced, and in both association or mutual attraction of ideas, according to definite laws, takes place: but only the human mind is able, from the contemplation of several distinct phenomena, to form a general idea which does not correspond to any one of the single impressions on the sensorium, yet represents the common property of all. Man alone can conceive abstract notions. The only general idea which an animal can conceive, is an image comprehending the most frequent and unchangeable characters of an object of the senses. The difference, therefore, between the human and brute mind may be expressed by saying that the latter is wholly devoid of the λόγος; while on the possession of this depends the entire creative power of the human mind and the faculty of speech. The mental operations of animals do not consist of more than the conception of simple ideas, the manifestation of desire, and the association of those ideas, which result immediately from impressions on the senses.

Ideas produced by impressions on the senses are associated both in man and animals, according to the principles of resemblance, forming simultaneous existence in the mind and succession. But the human mind associates general notions also with the simple ideas or conceptions; passing from the general notion to its particular examples in objects of sense, and from these again to another general notion to which the particular object last conceived belongs.

Animals can, it is true, readily combine two ideas; but, notwithstanding all that has been said concerning their reasoning powers, they are wholly incapable of conceiving a general notion. In these remarks, we, of course, except all the instinctive phenomena. A dog will gradually become accustomed to perceive that hats and caps of various forms are put upon the head, but will never form the abstract idea of a covering for the head. Something analogous to the conception of abstract notions certainly takes place, as Herbart has remarked, in the case of the simple conception of objects of sense; since the mind does not retain an image of all the details of an object, but merely an undefined image involving its most constant characteristics. In this sense, an animal also may have general ideas. A dog will recognise its master, whether he wear this or that covering on his head, or none at all,—whether he is naked or clothed; in fact, the dog recognises the same object despite its variations in detail, because some main points remain unaltered. Sticks of very various form and appearance will be known by a dog to be sticks, and the idea of blows will be associated with them: but, nevertheless, brutes are incapable of conceiving the higher abstract notions, which are not mere reflections of impressions on the senses, but depend on the reciprocal action of groups of ideas on each other. The dog recognises the same object in spite of its minor variations; but the abstract notions of identity, of the essential, of constancy, as opposed to accident, of difference and of variableness, are beyond the limits of its mental faculties.

The compound mental phenomena of animals may appear well adapted to the desired object, without being attended by any general notions, or being anything more than an association of impressions made on the sensorium through the medium of the senses. A cat, finding the door of the room which contains its human companions closed, lies down before it until it is opened, and emits its instinctive cry. On several former occasions the door had been opened under these circumstances, and the cat associates the series of acts in its mind; until at length that which is required by the association of ideas really takes place. A keeper of animals has one of his monkeys upon a pole: he wishes to draw it down by means of a string which hangs from it; but the monkey, seeing what his master is about to do, and not wishing to descend, draws up the string with its fore-paws. This act, however, is also the result of previous associations of ideas, just as is the running away of a dog when the stick with which it has been beaten is shown to it; or the sneaking, shamed demeanour of a dog caught in an act which has before been followed by unpleasant consequences.

The association of ideas in the human mind is not a combination merely of simple ideas derived from external impressions according to their resemblance, previous order of succession, or simultaneous occurrence; but with these simple ideas abstract notions become mixed up. From the idea of "blue" there is a transition of the mind to the art of "painting;" from this to "Raphael;" then to the abstract idea of "beauty;" and next to a particular "beautiful object;" and so on, from the general to the special, and thence to other general notions and other specialities. In the ordinary association of ideas this process takes place unconsciously or indistinctly; but in the act of thought, the general notions, and particular ideas belonging to them, are compared with each other, and applied to the elucidation of each other, the whole being a conscious act.

The desires and passions also exist both in the mind of man and in that of animals, in equal intensity; but the passions of animals have never reference to abstract ideas, but merely to external objects of the senses. The attachment and fidelity of animals are founded in the association of former pleasing impressions with the image of the person whom they follow. Both man and brutes seek what is pleasing, and avoid that which is unpleasant; but men only are affected agreeably and painfully by abstract ideas and thoughts.

From the foregoing considerations it may be inferred that the mind of man and that of other animals are distinguished not by the mere obscurity or lucidity of their conceptions, but by the degree of simplicity or complexity of their ideas, and their reciprocal reaction. The inferior class of conceptions, in which no general notions are formed, may in fact be very distinct; while so far is the formation of an abstract general notion from being merely the very lucid conception of an idea, that, in the act of abstraction, those particulars in a group of ideas which do not agree, seem to obscure or neutralize each other, so as to leave merely the common property as the general notion. The formation of general notions, and the act of thought, are highly complex processes; and hence in sleep and fever, where the brain is not in its normal state, the conception of simple ideas, and their association after the manner of the brute mind, can take place, but the higher faculty of thought is never exercised.

SECTION II.

Of the Mental Phenomena.

The whole action of the mind consists of the conception of ideas and of emotions; and all the mental phenomena are either ideas or emotions. These, however, differ in themselves, being sometimes simple and sometimes complex; they differ also in their mode of combination, and in their connection with the actions of the body. The conception of ideas, their association and reaction on each other, constitute what is called the "intellect," or "understanding;" the emotions, both simple and combined, are also termed the "affections," or "passions."

CHAPTER I.

OF THE CONCEPTION OF IDEAS.—THE UNDERSTANDING.

An idea or conception is that which is excited in the mind by impressions on the senses, or by those actions of our own body which are communicated to the sensorium. When once excited, the idea remains in the mind for a certain time. It is something corresponding to a distinct impression on an organ of sense, or to the general quality of several such impressions; and it may be regarded as a definite mode of reaction of the mind under the influence of a determinate stimulus. All our ideas belong either to impressions on the senses, and particular states of our body, or to the general notions deduced from the ideas thus obtained, and the relations subsisting between them. The simple conceptions, or ideas of the first kind, are exemplified by the ideas of a blue spot, a particular sound, a known tune, a certain painting, or a particular tree. We have examples of conceptions of the second kind in the general notions of colour, sound, taste, smell, virtue, power, &c. We may therefore make a distinction between simple ideas suggested by impressions on the senses, and the general abstract notions. There are other ideas which are compounded of both these: for instance, it is possible to form the conception of " a man in a particular state of mind."

1. *Simple Ideas suggested by impressions on the Senses.*

What relation does the mental conception, the idea, in these cases, bear to the sensation ?— in what relation, for example, does the idea of blue stand to the sensation of blue, — or the idea of a tune to the sensation of hearing it ? We know that all impressions on the senses leave an after-sensation frequently of long duration. May not the idea induced by a sensation, and afterwards recalled by memory, be the remains of this after-sensation, merely rendered feeble and indistinct ? On this supposition the idea of blue would differ from the sensation of blue only in intensity. But this cannot be : we can easily distinguish the very vivid idea of a colour from the last glimmering remains of the actual sensation; and while gazing at a yellow surface, we can form the idea of a blue one. It appears, therefore, that the conception of an idea is very different from the mere perception of a quality through the medium of an organ of sense. An idea is rather a sign standing for the sensation, but a sign which is suggested only by a particular object, and which consequently varies altogether with the sensation.

This view receives still more support from the fact of our being able to conceive ideas which cannot possibly be the remains of mere sensation, since they represent only the general quality of many sensations, as is the case with the general ideas of "colour" or "sensation." It cannot be said, in reply to this, that no such general ideas of sensations exist, and that in all cases some definite colour, something special, is present to the mind; for in reasoning, and in the act of thought generally, we certainly do distinguish between the abstract notion of colour generally, and the idea of a determinate colour: without this distinction, indeed, it would not be possible to institute any comparison between the general ideas or abstract notions, and that which is comprehended in them.

The idea of an object of sense is, therefore, different in quality from the corresponding sensation; it is something merely conceived in the sensorium; while the sensation is not only presented to the mind, but also perceived in the peculiar quality or "energy" of the organ of sense: the idea is, in fact, as we have already said, merely the sign of the sensation. That ideas can excite the production of images in the organs of sense, is certainly true; this, however, is a complex phenomenon. The idea and the sensation bear about the same relation to one another as a word to the thing it signifies, or as the notes of a tune to the tune itself.

The recognition of an object on its being again presented to an organ of sense by means of the corresponding idea, which has been retained in the mind, and the consequent belief in its identity, prove not merely the similarity of the idea to the sensation produced by the same object, but further, that each sensation always excites a determinate idea, and that the same sensation invariably produces the same idea. If, therefore, the sensation be not preserved, but the idea retained, each renewal of the sensation will be attended with the reappearance in the same manner of an idea, which, on account of its complete similarity to that excited by the previous sensation, will be regarded as identical with it. And thus written characters call up ideas, although they have not really in themselves anything similar to the object of those ideas.

It is not necessary that the idea of an object having extension in space shall itself have that property. On the contrary, the idea may have the same relation to the object of sense as the expression of a figure in an algebraic equation has to the figure itself, or as the infinitesimals in the differential calculus have to the integrals. Notwithstanding the uncertainty which involves the question whether objects of vision are perceived in the optical apparatus, or in the brain (see page 1163), it may yet be supposed that the ideas of objects of sense are always formed in the organ of sense, on which the impressions were originally made, and consequently have the same properties of extension as those impressions. This view is proposed and illustrated by Henle in a paper "On the Phenomena of Memory in the Senses."* He has founded his remarks principally on the images which present themselves apparently in a visible form, and with the distinctness of reality, when the eyes have some time previously been long engaged in the contemplation of the same objects. These images are different from the mere after-sensations which are left for a certain period of time by a long continued impression on nerves of sense. An anatomist, who during an entire day has been occupied in dissecting the same structures, and has fixed them in his eye, frequently experiences, after the interval of days differently employed, a sudden reappearance before his eyes of those same structures, with distinct outlines, though destitute of light and colour. These appearances will be treated of more fully at a future page. The difference between the sensation produced by an impression on the senses, and the resulting idea, which has not the peculiar quality of the sensation, appears to be, that in the sensation peculiar states of the nerves, — for example, of small points of the retina, — produce simultaneous impressions on the sensorium; and thus exert on the mental image a modifying influence, which does not come into action in the simple conceived idea.

If the idea of an object of sense has been frequently associated with that of a certain sign, however arbitrary and void of analogy, these two ideas will subsequently suggest each other reciprocally, in accordance with the laws of the association of ideas, which will presently be explained: the idea of the object of sense will be always excited whenever the idea of the sign connected with it arises in the mind, and vice versâ. On this depends the use of speech, of the written characters of music, &c. where series of signs suggest innumerable successive ideas of objects of sense.

2. *General ideas or abstract notions.*

These are ideas of a general quality, contained in, or involving several simple ideas. Some ideas of this kind are so little removed from individualities, that they admit of more accurate definition only by reference to the actual sensations; such are the ideas of blueness and redness, which are the abstract ideas deduced from the perception of many red and blue objects, and the idea of colour, which can only be defined as the common quality of many different sensations. These general abstract notions, also, like the simple ideas, become connected with signs, and are suggested by them. It often happens with respect to these general notions, that the ideas popularly associated with their signs are not really those which correspond to their true import. Hence it is that many persons are said to think with words instead of

* In the Wochenschrift für die gesammte Heilkunde, 1838. 18.

ideas; and that in some languages there is frequently great difficulty in rendering by correct signs certain abstract and correctly conceived notions.

3. *Process of the conception of ideas. Association of ideas.*

Every idea which arises in the mind retains its distinctness only for a definite and very short space of time. It is quickly supplanted by other ideas, which surpass it in intensity, but which in their turn experience the same fate. When an idea is supplanted in this manner, the mind ceases to be conscious of it; and in no case, indeed, can more than one idea, or several combined together, be present to consciousness at the same time. Something similar to this is observed with respect to the impressions on the senses. When several impressions are made on different senses at the same time, frequently that only is perceived by the sensorium to which the mind is especially directed, and sometimes, in fact, all external impressions cease to be perceived, when the mind is occupied with an idea which has no reference to them.

Ideas, however, which have been once conceived are not wholly lost, though the mind ceases to be conscious of them, but under certain conditions return with all their former intensity, and become again present to the mind.

It may be asked, whether the consciousness which conceives the idea is something distinct from the idea itself; whether it illumines the ideas, as it were; and then leaves them in obscurity, when they cease to be manifest to the mind; or, in other words, whether a vivid idea is merely one towards which consciousness is directed. It is, however, difficult to conceive of a consciousness free from ideas; even the state of self-consciousness is really the consciousness of an idea. The contrary supposition, namely, that consciousness is merely the presence of a very vivid, that is, an actual idea, appears adequate to explain the phenomena. According to this view, the process of the conception of ideas becomes a more simple one; for we have merely to study the laws according to which ideas become vivid, present to the consciousness, or "actual," by evolution from the chaos of "potential" ideas; while, on the supposition of a consciousness existing distinct from the ideas, there still remains something behind these ideas which requires explanation.* The ideas which are present in the mind, but are not manifest to the consciousness, which, in other words, are potential, but not actual, may, therefore, be regarded as latent or quiescent ideas, which mutually restrain and balance each other; while the "actual" idea of which the mind is conscious may be looked upon as a free active idea, or an idea manifesting itself.

* See Herbart, Lehrbuch der Psychologie, p. 12, and Stiedenroth, Psychologie, p. 50.

When one active idea succeeds another in the mind, the second must either resemble the first; or, if this is not the case, it must have succeeded it in a similar manner on a former occasion, so as to have become combined with it in a more general idea. All these relations resemble each other in an affinity existing between the ideas that are associated. Like attracts like, and so also similar ideas attract each other.* It is a correct and graphic expression, that the motion of ideas is propagated through the connections of resemblance, succession, or previous co-existence, or through the still more simple bond of previous combination.

The active state of an idea consists of an increase in its intensity or lucidity, and a subsequent fading. While this is taking place, the active idea exerts an influence on the mass of latent intelligence, and disturbs its balance, drawing into action those ideas which have an affinity with itself, or, in other words, communicating to them its state of motion or action. The primary idea is itself not persistent; it may be displaced, as soon as a new impression is made on the senses, by the new idea thus excited. If no relation exists between the new idea and sensual impression and the former ones, while the new idea is very distinct, as is always the case with those suggested by impressions on the senses, then the previous idea fades from the mind in proportion as the other becomes more distinct. But even though no new impressions on the senses should excite new mental conceptions, the mind does not remain long occupied by the same idea. For since each active idea exerts an attractive influence on allied ideas which were latent, a series of thoughts soon pass through the mind. From the idea of a tree, for example, I find my mind quickly passing to that of a forest. This, again, suggests the idea of wood, which calls up that of a building; and then the ideas of a marble temple, and a statue, successively pass through the mind. Each link in this chain of conceptions is allied to that which precedes it, as well as to the succeeding one, although the last has no resemblance to the first,—the idea of a marble statue has no affinity to that of a tree. Each new idea, in fact, acts as a new centre of attraction on the mass of latent ideas, while those which preceded it in the state of action are now passive. For an idea to have any permanence in the mind, it is necessary that it should exert its attractive power on the ideas which are still allied to the original idea; as, for example, when the mind passes from the idea of the "whole" to that of a "part," from this to another "part," to the relation of "parts" to each other, and from time to time to the original idea of "the whole." Two similar ideas mutually strengthen each other; while two dissimilar ideas weaken or neutralize each other. Thus a melancholy thought is

* See Hegel, Encyclopædie, p. 422. Compare Beneke, Psychologie, pp. 32. 72.

rendered more intense by the accession of another similar thought; but a melancholy thought and a cheerful one meeting in the mind neutralize each other's action; or if one is in a very active state, so as to call up similar ideas in the mind, then the idea which is opposed to it is reduced to a latent condition.

It is evident, however, that the attraction of ideas is far from explaining the whole process of mental action; for it by no means renders intelligible why, during the rise into activity of the new or attracted idea, the preceding or attracting idea should become latent. If the whole action of ideas consisted in a kind of attraction, they would form aggregates; and each new attraction would be the action, not of the idea last excited only, but of the whole aggregate of similar ideas already called up in the mind. If the attempt is made of fixing an idea in the mind while light and sound, and all impressions on the senses are excluded, it will be found quite impossible to do so. In spite of the greatest effort to keep the idea "bird" fixed in the mind, another allied idea—such as that of "Pegasus"—will soon present itself: then perhaps the idea of "poetry" will follow, and in succession those of "Homer," "Achilles," "tendo Achillis," "Myology," "Albinus," and so on. It appears, therefore, that besides the attraction of similar ideas, there is something in the action of the mind which causes the active state of each idea to cease after a period, just as in the progressive undulations or vibrations of bodies, the motion ceases in the body which excited the progressive undulations in other bodies, even before it has passed through the conducting chain with which it is continuous. In the motion of undulations, the force which induces the state of rest is the tendency to the physical equilibrium. No such physical agency can be supposed to limit the duration of ideas in the mind. It appears, however, that there is an analogous tendency to equilibrium in the latent ideas of the mind; in consequence of which, the disturbance, produced by the tension of a single idea, is soon restored. The duration of the active state of an idea accordingly depends on the time required for its reduction to a state of equilibrium. The motion of the idea which was in the state of tension has, in the mean time, extended to another idea which was inactive, but which is now thrown into tension. The duration of an idea depends therefore on the intensity of its motion.

The association of ideas may then be compared to a progressive motion; the state of tension passes over the ideas which were in a state of rest or equilibrium; and the different ideas are successively thrown, like the particles of matter affected by a wave, from a minimum into a maximum, and again into a minimum of motion. This, of course, is intended merely as a figurative description derived from physical phenomena. The progressive tension of different ideas is the wave; and the ideas which successively arise in the mind, and disappear from it, are compared to the different particles which are in turn affected by the vibrations of the wave, and left at rest behind it.

Allied ideas alone succeed each other in the mind, or become successively thrown into the state of tension. All those latent ideas which are dissimilar to the present active idea, or are indifferent in relation to it, remain unaffected. Each succeeding idea is, however, neither absolutely identical, nor absolutely different from that which precedes it: the two are, in some respects, similar, in others dissimilar; as, for example, are the ideas of a "leaf" and a "tree," those of "genus" and "species," those of "Achilles" and "tendo Achillis," or those of "sea" and "fish." The ideas which succeed each other are allied in their purport, or in part similar; or if, in themselves, quite dissimilar, they are allied in the relation of coexistence in a previous impression on the senses, or in that of previous succession.

The ideas of objects existing in the same landscape mutually suggest each other; and in the same way the successive occurrences of a former journey are easily recalled to mind. Even contrasted ideas are not excluded from mental association; for they are in some measure allied. The ideas of very small and very large things are readily associated in the mind; for they are relative ideas. The ideas of great and small, and of light and dark, are, in fact, so nearly allied, that it is often impossible to distinguish between that which is great and that which is small, or between that which is light, and that which is dark, when they are not actually compared.

Since each idea is allied to many others, and yet is followed in the act of association by one only of these allied ideas, we must seek the cause determining the particular idea which is excited, in the different degrees of disposition to tension of the different allied ideas which are latent. Ideas which were in an active state on the previous day, and have frequently been so, are roused again to activity by a less strong affinity than ideas rarely present to the mind, and long undisturbed. Hence it appears that even latent ideas cannot be regarded as in a state of complete equilibrium. In fact, they do not merely form the latent materials of the understanding, from which the active ideas are derived, and to which they are again reduced by the tendency to equilibrium; but undergo even in this latent state slight and indistinct movements. Though not drawn into the field of actual thought, they yet are so far affected by the tension of other active ideas as to be themselves thrown into a disposition to tension when those ideas are allied to themselves. Sometimes, indeed, we can perceive that an indistinct shadowy idea accompanies other vivid ideas, and seems to be striving to become active and manifest. We have indistinct remembrances of persons and things.

From the foregoing considerations, we may safely affirm that every idea in the state of activity, — that is, in the state of freedom or development from the general equilibrium, — is capable of throwing another allied idea into the same state of activity; but that, while it does this, it becomes itself inactive or latent. The return of an active idea to its latent state is completed very gradually, and not until a long series of other ideas have passed through the mind. The proof of this lies in the fact of our being able to recall very readily ideas which have a short time previously been present to our consciousness. Whether the current of our ideas ever entirely ceases for a period during the waking state, is doubtful. We sometimes, indeed, seem to be in so passive a condition as to have no ideas present in the mind: but even here there may be one idea in the active state; namely, that of our freedom from thought. There is, however, nothing unreasonable in the supposition that during sleep, when all external impressions are excluded, a completely inactive state of all our ideas may ensue for a certain period. There is a difference, too, in the rapidity with which ideas succeed each other, not only in the minds of different persons, but also in the mind of the same person under different circumstances. Exercise of the intellect, and many states of the body, fever, nervous irritation, a certain stage of narcotism, and wakefulness, make the succession of ideas more rapid; while the taking of food, or spirituous liquors in excess, inactivity of body, and sleep, render the current of the thoughts perceptibly sluggish.

In the lower grade of intellectual operations, of which even animals are capable, the act of association is confined to ideas of objects which have formerly been presented to the senses at the same time, or of which the ideas have previously succeeded each other: but abstract notions are also ideas, and are also associated with other ideas, even with those of particular objects. An individual thing which has undergone a change, may give rise to the association of the general notion of change, and this to the general notion of motion, which bears to that of change the relation of species to a genus. A large object calls to mind the general notion of size; the idea of a very large object excites that of infinite size; the idea of a small object that of infinite minuteness; the permanence of one quality, while many others are varying, suggests the general notion of something essential, and this the contrary one of an accidental quality, and so on. In this association of general notions, the relations of succession as to time, and coexistence as to place, remain quite subordinate. The interchange of ideas here consists rather in a constant expansion and contraction of the conception; the mind being alternately occupied by a particular idea, and by the general notion to which it belongs, — as, for example,

× In the case of the Dog [illegible] — [illegible] or abstracting [illegible] that freedom [illegible] [illegible] — but simple [illegible] —

in the following series:—Narcissus, flowers, plant, organic being, animal, elephant, ivory, art, painting, brush, hair, horn, wart, cicatrix, inflammation, and so on.

In reading, two series of ideas accompany each other,—namely, the ideas of the signs, and those of the things indicated by the signs,—the ideas of each series being associated more closely with each other than with those of the other series. When that which is read is also spoken aloud at the same time, a third series of ideas accompanies the others; and the same is the case in the execution of music from notes. In such a complicated mechanism as this, where ideas of signs are constantly alternating with general notions and ideas of particularities, the act of connecting the ideas with each other must naturally be rendered difficult in proportion to the frequency with which the ideas of the signs interrupt the chain of the ideas indicated. Hence, in reading, we frequently find ourselves associating with perfect correctness the ideas with the signs, though without any comprehension of the connection of the ideas amongst themselves.

When the idea of anything is reduced to equilibrium with the other latent ideas of the mind, the thing is "forgotten." The "recollection" of it depends on the idea being again called into an active state from its state of equilibrium. It results from the foregoing considerations that there is no special faculty of "memory." No idea is ever lost; and every act of the mind, by which latent ideas are rendered active by association, is memory.

In proportion as an individual loses the power of vivid association of ideas, he loses his memory. The kind of memory which a person possesses is therefore different, according to his capability of associating merely the simple ideas corresponding to impressions on the senses, or the higher abstract general notions. Many persons have a great memory for words, sentences, language, for the succession and coexistence of particular things and circumstances, without having, in a perfect degree, the faculty of remembering general notions and their connections, and without possessing great intellectual powers. This arises from their minds being chiefly active in the association of particularities. In other persons all ideas are prone to call up general notions which draw their minds away from the series of successive or coexistent particularities, and lead them to abstract speculations. These persons, consequently, are deficient in the memory of individualities, but may have in perfection the power of recollecting the relations of ideas according to general notions.

We are able to give a determinate direction to the association of our ideas, and thus to direct our memory. When I call to mind the occurrences of a journey, I can at will cause the ideas of past circumstances to succeed each other in the retrograde course, from the close of the journey to its commencement. In this case the association is subject to a distinct predominant idea, that of the reversed succession. The direction of the association is, therefore, properly the result of necessity, not of volition; for the main ruling idea being given, the rest must follow in accordance with it. The direction thus determined remains the same, until the ruling idea is reduced to the state of equilibrium. Thus I can determine my own mind to the conception, during a certain period of time, of a number of opposites, such as white and black, essence and accident, infinite and finite, small and great, internal and external, and so on. In this way, also, we endeavour to recollect a particular thing. Frequently we do not succeed, because the idea which we seek—for example, the word corresponding to an abstract notion—does not lie in the direction of the idea taken as the guide to it. Sometimes, also, the idea which is sought presents itself very obscurely to the mind, and we perceive that it is very near but cannot obtain perfect distinctness; or we perceive that the word that is sought exists in the mind although it is defective from a part of its sound or letters being kept in a latent condition, or state of equilibrium, by a contrary idea. Sometimes we succeed better in recollecting what we desire by talking or thinking of indifferent things, amongst which an idea may occur adapted to suggest the one which is sought. Even when it is determined to retain something in the memory, and to execute it at a particular time, the ideas are placed under the rule of a leading idea, and led back from time to time, even though by long circuits, to the original theme.

Imagination, or the production of new ideas, differs from the ordinary reproductive association in its free metamorphosis of the images or ideas called up into the mind, beyond the limits prescribed in mere recollection. This productive, Protean property of the active idea may be best observed in the dark of evening. In bright daylight the strict normal character of the impressions on the senses interferes with the creative action of the mind. But if in the dark we picture to ourselves a face, it generally does not long retain its original form, but undergoes various transformations, often with fearful distinctness; and the forms which are thus produced are by no means such as have previously been presented to the mind through the medium of the senses, but are new and surprising combinations. It has often been a subject of dispute whether the fancy is able to form anything entirely new. That the elements of all the images of fancy are derived from ideas obtained by experience is certain; but the modification and combination of these elements into new products, appears to be wholly in the power of the imagination. In the unilluminated field of vision, the imagination traces all varieties of outlines; and as forms are determined by their outlines, such forms are of course in this way produced as never really existed. A mind which is less imaginative will merely combine images previously presented to the mind by the senses; thus it will unite the wing of a bird to the shoulder of a horse, or the tail of a fish with the body of a quadruped. But the more creative mind will not only combine the images previously derived from without, but will also modify these, expand them, and transform them. When Goethe with closed eyes pictured to himself a flower, this image, as he himself relates, underwent the most remarkable changes: new leaves of new forms were developed from it, and it metamorphosed itself into the most various figures, though with a certain regularity and symmetry.

4. *Thought or reasoning.*

The first step in the process of thought is the formation of general notions, or the act of abstraction. The mere association of ideas and their replacement one by another, is a much more simple process than that of their mutual reaction on each other; and hence the act of imaginative association is less difficult than that of forming abstract ideas. When two or more different ideas are present together in the mind, they neutralize each other in those respects in which they differ, and there remains only that part of them in which they agree. But this, their common quality, acquires an increased intensity; for similar things strengthen each other. From this kind of abstraction to the act of reasoning there is but a step; and reasoning is only a higher grade of intellectual association. The conceptions are here not mere simple ideas alternating with each other and with general notions, but ideas of relation. Thoughts are ideas of relation subsisting between two or more ideas. The action of the mind in its most simple form consists merely in the constant transition from one thing to another. In this simple association the ideas succeed each other like the series a, b, c, d, e, without the relation which they bear to each other becoming the subject of consciousness; but in thought the mutual relation of the ideas, as a : b : c : d : e : is perceived by the mind as well as the ideas themselves. Even a chain of associated ideas, in which general notions mingle themselves with simple ideas, such as the succession of candle, light, blue, optics, acoustics, waves, sea, depth, infinity, does not amount to thought. For here the copula of the simple ideas and general notions, namely, the law of the attraction of like for like, passes through the mind unperceived; and only the copulate or associated ideas are the subjects of consciousness: for we do not in such a train of ideas have the distinct conception that blue *is* light, and that the sea *is* deep. But in the process of reasoning, the copula, *is*, becomes itself a conscious conception of the mind. Every thought, therefore, involves at least three ideas, two of which are united by the third, or the idea of the copula.

The simplest copula is the idea of identity or similarity, and is expressed by the word *is*. The purport of the one idea either is entirely the same as that of the other, or is equal to only a part of it. In either case the copula is expressed by *is*.

The first case may be represented by $A=A$. A particular thing is identical with itself; or two things, a and b, are so similar, that they must be regarded as identical, which may be expressed thus: $a=b$, or $a:b=a:a$.

In the second case just referred to, one idea is only a part of the other, as *ultramarine is blue, sounds are vibrations.* All vibrations are not sounds: this thought is, therefore, not correctly expressed by the sign $a=a$; on the contrary, the thought, *sounds are vibrations*, corresponds exactly to the thought, *in* 4, $\frac{1}{4}$ *or* $\frac{1}{a}$ *is contained.* If we represent sounds by a, and vibrations by b, the formula for the proposition will be, $a=b+x$, or *sounds are equal to vibrations and something besides*, or $a=b\times y$, or $\frac{a}{y}=b$, by which we express that the one idea comprehends only a part of that which the other involves.

In most thoughts *is*, or the idea of entire or partial identity, forms the copula. But any idea of relation may serve to connect the two other ideas. Combinations of simple ideas with general abstract ideas by means of another abstract idea, as in the foregoing examples, are *propositions.* But when two such thoughts or propositions are placed in the same relation to each other by the recognition of identity, or by the idea of partial similarity, as the two principal ideas in each simple proposition, they constitute a *conclusion* or *syllogism*, the formula of which is, $x=a$, and $y=x$, consequently $y=a$.

Besides these most general forms of thought, there are a number of abstract notions which enter as accessory ideas into our propositions and conclusions, and which in language are expressed by the particles. They serve to indicate the modality of the propositions and conclusions, their connection and relations.

5. *Self-consciousness.*

In addition to the conceptions of the relations existing between ideas, our mind conceives ideas of the external world and of the subject or self which is the seat of the mental conceptions. These ideas have their source in our organic appetites for external things which seem to supply that in which we are deficient; but they are rendered more defined and distinct by our experience of the difference between our sentient body and the external world, which is the cause of its sensations, and which reacts against its actions. The circumstance also of the different parts of our own body being constantly present to our senses amidst all the changes of the external world, leads us to recognise this object, which remains constantly the same, as our own body; for we perceive that it varies only according to our will, while all other objects change independently of us. Our spontaneous actions, which are attended with sensations, also leave ideas in our mind, and we learn to distinguish the ideas of these actions from the mass of ideas of other things. Thus arises the idea of independent life. The abstract notion of all which belongs to this independent life is the "Ego," or "self." This is the idea of that general point of resemblance in all our different actions, which remains when their various differences have neutralised each other. The conception of our "self" being the source of ideas, or the conception of ideas being qualities or particular states of our "self," is what is called "self-consciousness." This is evidently an acquired, not a primary or original idea. Moreover, it is at first impossible to distinguish whether the sensations and ideas, when originally produced, belong to the absolutely external object, or to the object which we learn to recognise as our own body.

6. *Feelings.*

The significations of the word "feelings" are so manifold, both in ordinary language and in psychology, that it is unsafe to employ it. By the feelings are sometimes meant the painful and pleasing, and other allied emotions of the mind; sometimes states of the mind wholly devoid of the character of passion or emotion, such as the feeling of truth, and the feeling of presentiment, which are rather ideas only indistinctly conceived; at other times, again, the same word is applied to express certain ruling or predominant ideas, such as the feeling or sense of honour, moral feeling, and the feeling of propriety.

Some psychologists confound all these different states of the mind, although all pleasurable and painful feelings are merely particular states of the "subject" or "self" and of its "strivings"; while the moral feeling, the æsthetic feeling, &c. have reference to true "objective" relations. Most states of the mind belong to the category of ideas. It is very desirable to distinguish particular relations of these ideas to each other by particular names. The words *thought*, *abstract notion*, and *proposition*, serve this purpose; and the word "feeling," also, might be applied to a particular mode or relation of conceived ideas, had it not unfortunately been employed to designate totally different states.

The painful and pleasurable feelings, and the numerous allied states of the mind, will come under consideration in the next chapter, for they are conscious states of desire.

Those "feelings" which are really ruling predominant ideas, notions, or propositions acquired by education, such as the moral feeling, feeling of honour, the æsthetic feeling, the feeling of propriety, &c. and the erroneous modifications of those ideas which are called prejudices, differ from other ideas, abstract notions, and propositions, only in their capability of a practical application to the relations of mankind, and consequent adoption as a standard of right. The majority of numerous other so called "feelings," are nothing more than unconnected, and consequently indistinct, masses of ideas which float before the mind, such as the feelings of "presentiment" or "misgiving."

CHAPTER II.

OF THE PASSIONS, AND OF THE DISPOSITION.

Many ideas are accompanied by a state of the mind which is something distinct from the idea itself, and is what we call emotion. If pain is felt, and the idea of it is conceived in the mind, it excites an adverse mental emotion or striving against the idea. Even the mere idea of pain or pleasure gives rise to emotion. Everything opposed to this striving of the mind excites painful feelings; everything which favours it, feelings of pleasure. The mind, therefore, is susceptible of another state besides the conception of ideas; and the exaltation of this state does not produce an increased lucidity and distinctness of an idea, but the aggravation of an emotion. The object of these emotions or strivings of the mind is not merely to avoid pain, and the ideas of pain, and to obtain pleasure, and ideas of pleasure, but also to maintain a certain power of individual existence, and to resist a diminution of that power. The striving of the mind in its most general sense is the effort to maintain the existence of self, and to extend its power of action. Everything which opposes or restricts this power, gives pain; everything which favours or extends it, causes pleasure. The objects may vary, but the mental striving remains. That which is conceived to be opposed to the striving of the mind to-day, will on the morrow be indifferent to it, or even favourable. The objects of the mental emotion are, therefore, different at different times; but they are always those which at the time are adequate to restore the natural condition of the mind, or to increase its power.

Emotion is constantly combined with ideas. The emotion itself, and the sensations and actions which it causes in the body, are conceived by the mind, as well as the things which are the objects of the emotion. The idea of self, and of individual existence, is the fundamental theme of all the ideas combined with emotions; but the idea of self, and of a change suffered by it, does not, without the state of striving in the mind, constitute passion. Thus the idea of the present state of self, as compared with the former state, when it is A—a, does not constitute sadness; and when it is A + a, does not amount to joy. In order to produce a passion of the mind, the state of emotion or of striving against ideas which oppose it, or with ideas which favour it, is required.

On the other hand, however, only such ideas as have reference to self are capable of exciting passion.

As long as the changes which are the subjects of our contemplation have no reference to ourselves, nor to other beings allied to our feeling of self, the ideas which they suggest pass through our mind unaccompanied by passion; they are not unpleasant to us, and excite neither sadness nor desires. But as soon as the idea of self, of the restriction or extension of the power of our self by the conceived idea, comes into play, then the passion of sadness or joy, or the striving for the preservation of self, or for the increase of its power, arises in the mind; there is then a striving to restore the integrity of self which the mind has conceived to be subjected to diminution or subtraction of power. The feeling of self is, therefore, an element of all passions. It is true, we enter into passionate disputes concerning mere opinions when the *meum* and *tuum* are not directly indicated; but even in this case, the opinions concerning which we differ, have by habit, education, or accident, become identified with ourselves, and in the mind constitute, as it were, a part of ourselves. We also become the subject of passions on account of others, and of accidents which occur to others; but this happens only when our feeling of self is interested, in consequence of the resemblance of others to ourselves and of our own self being implicated in their fate. A controversy concerning opinions loses all its character of passion and restricts itself to the mere objects of dispute as soon as we are able to contemplate those objects without any reference to our individual self. If, when we are engaged in a particular inquiry, we have long followed one opinion, and then meet with a fact which proves the falsity of this opinion which we have long cherished, we experience an unpleasant or painful feeling, because the opinion thus refuted has already begun to form a part of our own self. Regarded in itself, an opinion not expressed, but silently conceived and silently relinquished, should leave us indifferent to it, and truth indeed ought alone to be pleasing to us; but yet it is universally experienced that an opinion which has long been cherished, when found to be erroneous, becomes a cause of sadness. It is not until the new fact, which proves the incorrectness of the previous opinion, has been frequently contemplated, and has in its turn become, as it were, a part of our self, that the equilibrium of our feelings is restored.

All our passions may be referred to pleasure, to pain or unpleasant feeling, or to desire. In all may be recognised, as elements, the idea of self or individual existence; the idea of the power opposed to self, limiting its power of action or increasing it; the striving to maintain the integrity of self; and the power opposing or favouring that striving of the mind.

In considering the relation subsisting between the passions on the one hand, and organisation and the brain on the other, the first thing to be observed is, the fact (which I have already many times insisted on), that the process of organisation is antecedent to mental action, and is the means of rendering possible the manifestation of the mind by producing the peculiar structure of the brain. The conception of ideas, and the affections or emotions, do not, however, stand in the same relation to the brain. There is an unconscious striving of the organism which has not its seat solely in the brain. In all organic bodies there is a tendency towards the exterior, and an effort to preserve their own integrity. Even plants are the subject of such a striving during their growth; and in the same sense has the striving even in man a much wider basis than the brain, and is an action manifesting itself throughout the whole organism, and determining the process of organisation. In animals, however, this organic *appetitus* is reflected in the sensorium, and is perceived by the intelligent being which distinguishes between the ideas belonging to the external world and those referring to self. It is there felt as an obscure power of the individual declaring itself in the manner of an instinct, — as a power which affirms itself constantly, and derives sustenance from all ideas connected with the self or individual being, finding in them causes of restriction and extension of its sphere of action. There are no absolute proofs that these reflections of the striving power are not received and collected in a particular part of the brain of which the structure is adapted for the purpose; in other words, that there is not a region set apart for the affections: but, on the other hand, there is a total absence of facts which might render it probable that organs are set apart for the different appetites, and, at all events, only one identical appetite, one original striving for the maintenance of the integrity and extension of the power of self, exists. This one striving or *appetitus* has different objects, and the direction of its action is determined by the organic conditions of those organs which afford specific modes of intercourse with the external world.*

Mere changes in the state of the body are sufficient to increase or diminish the disposition to different passions, joy, sadness, or desire. The passions and desires of love are sometimes not excited when an adequate external cause is present on account of the organism being at the time little disposed to sympathetic action and excitement; while a trifling external cause very easily produces them if the nervous system and generative organs are in a state of organic tension. A passion or feeling,—such as confidence, candour, or friendship, which may never exist while a person is fasting,—may be experienced when the organic tension has undergone a change. Hence we see that the power or degree of the organic tension predisposing to the mental striving, de-

* See a further reference to Gall's doctrines at page 835*, or page 837 of the first edition.

termines the intensity of the idea relating to self which happens to be present to the mind, and gives to it its impulse or violence. An excessive degree of excitability of the organic conditions compensates for deficient power of the exciting cause, and *vice versâ,* so as to produce an equal result, an equal *quantum* of passion.

The emotions of the mind, on the other hand, produce organic effects in many or most parts of the organism. Even ideas devoid of any accompanying emotion, when of sufficient intensity, excite particular phenomena in other parts than the brain, namely, in the organs of sense, and in the muscles, as is evinced by the "visions" or "phantasms," and by the motions which may be excited by the idea of a motion, such as yawning (see page 932). But the effects of the emotions upon the organism are proportionally much stronger and more extensive.

Everything opposed to the striving of self to maintain its integrity produces a depressing effect upon the mental power and the corporeal actions, painful sensations and impeded movements; everything which favours that striving of the mind has, on the contrary, an exciting influence upon sensation and motion; and in both cases the processes of nutrition and secretion are modified. The organic influence is communicated to the body from the brain. It extends in all directions along the course of the nerves, and produces stronger local effects according to the different dispositions of the individuals. The effects are greatest in those organs which realise the conceived objects of the passion: thus they are strongest in the sexual organs, when the passion is that of love, and in the digestive organs, when the appetite for food is the one present. It must not, however, be hence supposed that the different passions have their seat in the different peripheral organs. These organs play no part in the passions, further than when excited during the prevalence of emotions they react on the brain and on the organic states of the body. In those passions in which the fulfilment of the desires is not attained by means of special organs, the organic effects of the passions extend very generally through the nervous system, modifying the movements, sensations, and nutritive processes, — elevating and increasing their energy in the exciting passions, and depressing them in the depressing passions. A person who is the subject of a particular local idiosyncrasy, experiences the exciting or depressing effect principally in the affected organ; for example, in the liver, in the heart, in the intestinal canal, or in the system of the spinal cord.*

The fundamental emotion of sadness has for its object the idea of something painful; the fundamental emotion of joy, from comfort up to open rejoicing, has for its object the idea of something pleasant. The painful something is in the simplest case, and generally in animals, a

* See page 816*, or page 818 of the first edition; also page 933.

painful corporeal sensation. The diminution or restriction of the free power of self arising thence is sadness. When ideas take the place of sensations, the unpleasant or painful object of the passion of sadness is the idea of a painful sensation without the reality of the sensation; and even the idea causes sadness, and in its turn excites really unpleasant and painful sensations. Every idea, however, even though having no reference to pain, if it involves a constraint of the power of self, is painful, and excites sadness, $A-a$. The constraint or subtraction of something from the feeling of self, A, by the idea $A-a$, is sadness. As long as the feeling of self is not reduced to the same level, $A-a$, the sadness continues, and is renewed each time that the idea A recurs to the mind, if the cause, $-a$, is not removed. But when the equilibrium has been restored, that which was painful to the mind has lost its sting, and hence it is that mental afflictions are cured by time. The simplest kind of pleasure, and that ordinarily felt by animals, is produced by the corporeal sensation of ease and pleasurable feelings, and by the freedom of our corporeal actions; and the mere idea of these physical states is pleasing. In general, however, we derive pleasure from all ideas which seem to extend the sphere of action of our self, and which removes an obstacle to its free play, $A+a$. This emotion or striving of the mind, accompanied by the expansion of the feeling of self from A to $A+a$, is ease and joy: it continues until the equilibrium is restored between A and $A+a$. When this latter change has taken place, the idea a has no longer any influence in exciting emotions, unless the idea A enters the mind, and is again converted into that of $A+a$.

The conception of a pleasure, of which we are not in possession, excites desire. Desire consists in two different ideas respecting the state of our self being thrown into tension as opposed to each other, while the immediate restoration of the equilibrium between them is not possible. The idea of the thing desired is a; the idea of the actual state of our self is $A-a$; and the idea of the possible state of our self is $A+a$. We strive or desire to bring these two ideas into equilibrium, but an impediment maintains the state of tension. This tension between the ideas $A-a$ and $A+a$, arising from the striving of the mind, constitutes desire, which differs from joy in that the two ideas $A-a$ and $A+a$ are not converted one into the other, but balance each other, the idea $A-a$ exciting the idea $A+a$, and on the other hand the idea $A+a$ that of $A-a$. As soon as the actual state of self is enabled to expand from $A-a$ to A and $A+a$, the state of desire becomes joy, which in this case is called satisfaction. The tension between the actual state of self, $A-a$, and the state A, is the striving to remove something which diminishes the power of self: the tension between $A-a$ and $A+a$ is the striving to obtain that which shall increase the power, or expand the feeling, of self.

The influence of the passions is apt to render our ideas respecting the relations of external things inaccurate. As soon as ideas of external things, or even truths and opinions, are conceived by us to have a relation to the integrity or power of our self, so soon, as will appear from the preceding paragraphs, are we thrown into the condition which fits us for regarding them with feelings of passion. Opinions respecting external things thus regarded acquire such an intensity as to be incapable of refutation by reasoning. In itself no idea relating to external things is ever in this sense intense or strong, but merely distinct or indistinct, and convincing in different degrees. By intensity or strength of opinions, therefore, we here mean only the power or quantity which they acquire, through the influence of passion, in the consciousness of the striving self. The greater the uneasiness which an unpleasant idea excites, the more capable does this idea become of calling up other allied ideas. The passion which the unpleasant idea produces renders it still more unpleasant or painful, while the idea itself, in its turn, increases the strength of the passion. While therefore the mind alternately regards the idea of the disturbing circumstance, and the idea of its own disturbed state, the idea of the unpleasant nature of that circumstance must increase to an inadequate degree, and thus become incapable of being neutralised by contrary reasons, or of being corrected. Hence it is often impossible to convince a person under the influence of passion of the true nature of external circumstances, except by previously quieting the state of passion, or, in other words, by freeing the mind from the restriction under which the feeling of self is labouring, or from the too great expansion which has been given to that feeling. This is effected most easily in an indirect manner; for everything which is capable of expanding the feeling of self, whatever be its nature, will quiet the passion arising from the idea of the restriction of self. When passion is calmed, the accompanying ideas lose their unnatural intensity and become subject to the simple equilibrium of contrary ideas or opposite reasons. An opinion which acquired intensity from passion may therefore be neutralised or supplanted by an opposite opinion similarly exalted. If a person is unpleasant to us, and we on that account, and without other sufficient grounds, entertain a bad opinion of him, and dislike or hate him, a pleasure afforded us by this person, if sufficiently great, will completely remove our prejudice, by causing us, with no better reason, to approve him. Here one idea rendered intense by passion, is dispelled by another of similar intensity. The jealousy of lovers affords us examples of opinions which have acquired even a ridiculous degree of intensity from being attended with passion. The passions take part in the most noble as well as in the most base efforts of men, and communicate to the ideas that intensity which is necessary in the transactions of life, for the carrying out of preconceived resolves, for absolutism, and for the revolution of existing conditions. Mere opinions concerning the manner of life, nature, or religion, which have been cherished, and become a part of men's selves, are adduced by them, when under the influence of passion, as truths. Mysticism consists in a similar one-sided direction of the ideas, and disregard of what is correct in the opposite ideas; those ideas only concerning religion being followed which are pleasing to the self of the believer, while those are avoided and hated which are unpleasing. The correctness of the ideas is here neutralised by their intensity. Fanaticism is of similar nature, but is more active in its effects.

In the foregoing pages we have elucidated the physiological nature of the passions, as far as it is at present known. With respect to their statical relations to each other, it is impossible to say anything that shall excel the masterly exposition given of them by Spinoza. I shall therefore extract those of his aphorisms which relate to this subject. It must be remarked that they merely express the law which would prevail in the mind of a man supposed to be under the entire influence of passions, and that this law will of course be modified by the human reason.

*Aphorisms of Spinoza respecting the statics of the mental emotions or passions.**

The mind seeks as far as is possible those conceptions which increase or extend the power of action of the body.

The mind, when it conceives an idea which diminishes or limits the power of action of the body, strives to recall other ideas by which the former shall be excluded. Hence it follows that the mind opposes the conception of ideas which diminish or limit the power of action of itself and of the body.

If the mind has been at any time excited by two passions or emotions simultaneously, the presence of one of these emotions will at all subsequent periods cause the other to arise in the mind.

Anything may be the accidental cause of *pleasure*, of *unpleasant feelings*, or of *desire*. If the mind has been excited simultaneously by two contrary emotions, namely, by an idea which gives pleasure, and by one which produces an unpleasant feeling, the return of one of these emotions at a future period will recall the contrary one. The first idea in this case will be the accidental cause of pleasurable or painful emotions.

Hence the mere circumstance of our having regarded a thing with pleasant or with unpleasant feelings of which it is itself not the efficient cause, will cause us to *love* or to *hate* that thing. And hence it follows also, that our merely conceiving that a thing bears a resemblance to an

* Ethik. 3ter Theil. [For an account of Spinoza's views, see Bayle's Historical and Critical Dictionary, art. "Spinoza;" and Hallam's Introduction to the Literature of Europe, vol. iv. p. 243—263.]

object which the mind is accustomed to regard with pleasant or with unpleasant feelings, will cause us to love or to hate that thing, although its point of resemblance to the object in question is not itself the cause which excites the emotions of pleasure or displeasure.

When we conceive the idea that a thing which is accustomed to fill our mind with an unpleasant emotion bears a resemblance to another thing which always excites in us as strong a feeling of pleasure, we shall love and hate that thing at the same time. This wavering in the feelings is the same thing as doubt in the intellectual operations.

The idea of anything past or future excites in the mind the same emotions, pleasant or unpleasant, as the idea of a thing which is present. For the idea, considered in itself alone, remains the same, whether it concerns the past or future.

From the preceding truths, we may deduce the nature of hope, fear, confidence, despair, joy, and sadness. *Hope* is an inconstant feeling of pleasure, arising out of the idea of a future or past thing, concerning the result of which we are in doubt. *Fear*, on the contrary, is an inconstant feeling of something painful or unpleasant in the mind, also excited by the idea of a doubtful circumstance. If the state of doubt is removed while these emotions exist in the mind, the hope becomes *confidence*, and the fear *despair;* or, in other words, constant feelings of pleasure or pain arise in the mind respecting the same thing which has been the object of hope or of fear.

Joy is the feeling of pleasure induced by an idea of a past thing, respecting the result of which we had been in doubt; and *sorrow* or *sadness* is the very opposite of joy.

If any one conceives that the thing which he loves is about to be destroyed, he will feel pain; but if, on the contrary, he conceives that its existence continues, he will experience pleasure. For whatever excludes the presence of the thing which is loved, limits or impedes the efforts of the mind to maintain the state of pleasure.

If any one conceives that what he hates is about to be destroyed, he will have pleasure. For the mind strives after those ideas which exclude the presence of things capable of diminishing the power of action of the body.

Whoever conceives that the being he loves is filled with pleasant or unpleasant feelings, will himself be filled with similar feelings,—*pity* and *sympathy*. For ideas of things which presuppose the presence of that which is loved, strengthen the mind in its endeavours to have present to it the conception of the loved thing itself; and *vice versâ*. This feeling of pleasure presupposes, however, the presence of the thing which experiences pleasure, and is an affirmation and perfection of that which is loved. Hence it further follows, that if we conceive that the thing which we love is filled with pleasure by any person, we shall ourselves be filled with love towards that person: while, on the other hand, if we have the idea that he fills it with unpleasant feelings, we shall experience the feeling of hate towards him, — *approbation* and *repugnance*.

When any one conceives that the object of his aversion is experiencing unpleasant feelings, he will feel pleasure, and will feel pain if that which he hates appears to his mind to be experiencing pleasure,— *malicious joy* and *envy*. For as far as the hated thing is filled with unpleasant emotions, it is destroyed, and we are desirous of excluding the presence of those things which exclude ourselves.

When we conceive the idea that any person fills with pleasure that which we hate, we become filled with hate towards him likewise: but if we conceive that he fills the same thing with painful feelings, we are moved with love towards him.

We strive to affirm whatever, according to our conceptions, fills ourselves, or that which we love, with pleasure; and, on the other hand, we have an impulse to deny everything which, as we conceive, fills us or that which we love with pain, — *extravagant pride, self-deception, overrating of friends and lovers.*

Inasmuch as we are *proud,* from a visionary conception of ourselves, we are able to effect everything which we can attain by the mere idea.

We endeavour to affirm everything which we conceive to give pain to that which we hate, and to deny whatever we conceive to fill the same object of our hate with pleasure,—*contempt, vilification,* and *detraction.*

The idea that a thing similar to ourselves, concerning which we as yet experience no emotion, is affected by a mental emotion, will excite in our own mind a similar emotion, — *sympathy, pity.* For this idea suggests the other idea that we may ourselves be exposed to this emotion.

The idea that a person, with reference to whom we have experienced no emotion, fills with pleasure a thing which bears resemblance to ourselves, will cause us to feel love towards him. On the contrary, the idea that a person fills such a thing with unpleasant feelings, will cause us to hate him.

We cannot hate the object of our pity on account of its causing us pain; for if we could feel hate towards it on that account, then we should have pleasure in its suffering: while pity consists in pain being felt on account of the pain suffered by our like.

We shall rather endeavour, to the utmost of our power, to free that which we pity from its suffering. For thereby we shall remove our own suffering and that which is opposed to our own existence, — *benevolence, generosity.*

We strive to bring to pass whatever we conceive to lead to pleasure, but endeavour to rid ourselves of and to destroy everything which opposes us and induces pain or unpleasant feelings.

We also strive to do all those things which we believe to be regarded with pleasure by men similar to ourselves; but, on the other hand, avoid doing what, in our conceptions, is avoided by them. For pleasure and unpleasant feelings are excited in our minds by the knowledge that others regard us with pleasure or pain,—*desire to please, affability.*

When we give praise, we affirm the fact which excites in us pleasure.

When a person has done something which he conceives will fill his like with pleasure, he himself will be filled with the feeling of pleasure combined with the idea of himself as the cause; or, in other words, he will regard himself with pleasure. If, on the contrary, he has done anything which, according to his conception, will fill his like with displeasure, he will regard himself with unpleasant feelings. For pleasure and displeasure experienced by beings similar to ourselves, cause the same emotions in our own minds,—*self-satisfaction, vanity, pride, shame, repentance.*

Whenever we conceive that another person loves, desires, or hates something which we ourselves love, desire, or hate, our feeling of love, desire, or hate, will be strengthened. But if we conceive that he dislikes what we love, then we shall experience a vacillation in the emotions of the mind. For the pleasure of another causes us pleasure, and the pain of another has a similar result for us.

Hence it follows, that every one strives to the extent of his power to make others love what he loves, and hate what he hates,—*ambition, proselytism, the desire of exciting suspicion.*

When we have the idea that any one enjoys a thing which one person only can possess, we shall endeavour to deprive him of the possession of it. For the idea that our like enjoys a thing causes us to love and desire it; but we conceive the possession of the other person to be an impediment to our pleasure,—*envy.*

When we love something like ourselves, we endeavour as far as is possible to make it love us in return. We desire that the being like ourselves which excites pleasure in us should also have pleasure excited in it. This pleasure involves the idea of self as the cause.

We shall be so much the more proud and vain, and have so much the more pleasure in the contemplation of ourselves, the greater the emotion of pleasure which we conceive to be excited by ourselves in the mind of the being whom we love.

The idea that the object of our love unites itself by an equal or stronger bond of friendship to another than to ourselves, will fill our mind with hate towards the object of our love. For the person preferred excites in us painful feelings or envy, and the cause of that feeling is the object of our love. Hence there is a vacillation in our mind between the emotions of love and that of hate and envy,—*jealousy*.

When a person remembers a thing which has formerly given him delight, he wishes to possess that thing under the same circumstances; but when he finds that one of the circumstances or conditions are wanting, he experiences painful feelings,—*longing*.

Desire which arises from pain or pleasure, and from hate and love, is so much the stronger, the stronger the emotion is from which it springs.

When any one has commenced to hate a former object of his love, to such a degree that his love is quite destroyed, his hate will be greater than it would have been had he never loved the same object. For the conversion of love into hate requires many more causes than the simple production of hatred.

When a person hates another, he will seek to do him injury, provided he do not fear the production of greater evil to himself from that course; and, on the other hand, one who loves another will endeavour to confer benefits on that other person. For to hate any one is to regard him as the cause of pain to one's self. To put an end to this pain, one's endeavours will be directed to the annihilation of the existence and destruction of the cause.

The idea that we are hated by another person without cause, excites hate in us in turn. Hate causes us pain, and the person hating us is viewed with a feeling of displeasure as the cause of that pain.

When any one conceives the idea that the person whom he loves hates him, he will be assailed by the feelings of love and hate simultaneously, as was shown in the foregoing paragraphs.

If a person conceives that another, whom he neither loved nor hated, has done him an injury out of hatred, he will immediately seek to inflict the same injury on that other person.

If a person conceives that he is loved by another person, and believes that he has afforded no cause for that love, he will love in return. For the pleasure excited by us in another excites pleasurable feelings in us. Hence the proneness to yield to false as well as true love, and to flattery.

Again, if a person conceives that he is loved by another whom he hated, he will be assailed by hate and love at the same time.

When a person has from love or hope of fame conferred a benefit on another, he will experience pain if he sees that the benefit is received with ingratitude. (Ingratitude itself is the result of a contest between more powerful present feelings and the ideas of former conditions.)

Hate is increased by reciprocal hate, and may be annulled by love.

Hate, which is entirely vanquished by love, is succeeded by love; and this feeling is then stronger than it would have been had hate not preceded it. For the power which conquers the hate is stronger, and is excited more strongly by equal causes.

When any one conceives that another person similar to himself hates a thing also similar to himself, and which he loves, he will hate that person. For the person hating the loved object desires it, and thus excites painful feelings.

When a person belonging to another station in society, or a different people, fills us with pleasure or displeasure, and when with those feelings are united the idea of the person, and that of the station and people as the causes of that pain or pleasure, we shall love or hate, not only the person who excited those feelings, but all persons of the same station or people.

The pleasure which arises from our regarding the hated thing, as annulled or filled with another evil, is not unaccompanied by some feeling or pain, inasmuch as we regard a thing similar to ourselves as destroyed.

Love or hatred towards a person is annulled when the pleasure or pain which it excites receives another cause; and it undergoes a change when the cause is distributed amongst several persons.

Love or hatred towards an object which we conceive to enjoy freedom of action, must, when excited by a similar cause, be stronger than when felt towards an object which obeys the laws of necessity. For in the latter case the cause is not confined to one, but extends to a chain of events.

Anything may accidentally be the cause of hope or of fear, as anything may accidentally be the cause of pleasure or of pain,—*good or evil forebodings, superstition.*

Different persons may be differently excited by one and the same object; and even the same person may be excited differently at different times by the same object.

An object which we have previously seen at the same time with others, and which we conceive to have no quality which is not common to several other things, excites us less than an object which we believe to have special properties. The interest felt in the latter case, when accompanied by the feeling of pleasure, constitutes *admiration, veneration, and homage:* when accompanied by a feeling of pain, it is *alarm* or *horror.*

When the mind contemplates itself and its power of action, it experiences pleasure, and this pleasure is greater in proportion to the distinctness of that conception.

The mind strives to conceive only such ideas as set its own power in action. It experiences pain when its own inability or want of power is the subject of its conception. This pain is fostered by the idea of *faults* or *blame.*

Men envy the virtue only of their equals.

Pleasure, pain, and desire, and every mental emotion compounded of these, as well as the wavering of the mind between two feelings, or the emotions due to this state, are manifested in as many different forms of love, hate, hope, fear, &c. as there are varieties of objects which excite them.

Each mental emotion in one individual differs from the same emotion in another, only so far as the natures of these individuals differ from each other. In like manner the passions of animals differ from the human passions, only so far as the nature of animals is different from that of man.

Besides the pleasure and desires which are passive, there are others which belong only to our active state. Such is the pleasure which the mind feels in the contemplation of its clear ideas, and in the conception of its own state of action.

All those emotions which have reference only to the active state of the mind, are modifications either of pleasure or of desire. *Courage* and *gallantry* are, according to Spinoza, emotions of this kind. Such is Spinoza's account of the feelings.

Of the varieties of Disposition. (*Gemüthsart.*)

The disposition is the character of the mind as respects the ideas and emotions which refer to self, and to beings allied to self; the suppressed and manifested excitements, and their reciprocal (statical) consequences; and, lastly, the contest between these actions of the mind and the reason.

A person whose mind is but little susceptible of the states of pleasure, pain, and desire, and whose body does not readily undergo the organic changes ordinarily produced by affections of the feeling of self, is said to have an unfeeling disposition, to be cold and indifferent. One who possesses the opposite qualities has a feeling disposition or nature, and his feelings are said to be fine or uncultivated, according as reason does or does not modify and soften the play of the affections.

In a more limited sense, a person is said to have an unfeeling disposition, who, though susceptible of strong pleasurable and painful feelings and desire, from ideas relating to his own individual self, is, nevertheless, little affected by the pleasure or pain of his fellow men; and who consequently has not made the self of his fellow men a part of his own self; extending, as it were, the bounds of his own existence. While whoever has done this is acknowledged to possess, in this more limited sense, a feeling disposition.

The essential foundation of a feeling nature or disposition, in both the first and second sense in which the term is used, is not the power of conceiving complex ideas and relations of ideas. For the excitability of the disposition is connected on the one hand with a particular class of ideas, which relate to self or the individual, or to like beings; and, on the other hand, with the capability of experiencing emotions or strivings of the mind, and changes in these emotions under the influence of ideas of the kind just mentioned. Hence men of small intellect may have much "feeling," and men of great intellectual faculties be "unfeeling." With respect to the feeling disposition in the second sense, namely,—the disposition which feels for others,—persons devoid of it will, if endowed with strong intellectual faculties, employ these faculties principally for their own interest; while those who possess such a disposition, whether their intellect be strong or weak, will be interested in the well-being of their fellow men; not merely after reflection, but immediately from sympathy, and will feel pleasure or pain in their happiness or suffering.

For this kind of disposition it is necessary, whatever should be the extent of the reasoning faculties, that the idea of self, and of that which is useful to it, be balanced by the idea of that which is useful to all men alike, or that the idea of self should embrace that idea also. A man whose mind has attained this state, to which education contributes much, acts justly and for the common good after reflection, or he acts in the same way from benevolence, experiencing himself pleasure or pain; in which case his conduct is due to "feeling." In children, the striving for the preservation and advantage of self is at first the principal feeling; for the idea of self is first developed, and connects itself with certain disturbances of the organism with sensations and actions. At a later period, and as the result of education, the feeling of self includes the whole family, and their common interest, and thence extends still further, to limits which vary in different cases.

Men who have the same degree of excitability have also different dispositions, according as they are prepared by organisation, more particularly for the emotions of pleasure, for those of pain, or for desire, and according as the one or the other kind of ideas meets with a stronger organic indisposition to action, or to the depression of the active state.

Animals also are of very different dispositions; they are joyous, melancholy, compassionate, envious, spiteful, affectionate, and jealous. All are capable of manifesting the different emotions or passions; but the susceptibility of changes in their organic system from different ideas varies very much in degree, and the instinctive ideas, which arise like dreams in their mind, are provisions for the more ready excitement and recurrence of certain trains of feelings.

In man the moral feeling modifies the play of the passions, and to a certain extent, causes it to depart from the laws laid down by Spinoza.

As long as we are under the influence of passion on account of ourselves or of certain other persons, the term "good" expresses merely a relative idea; that, namely, appears good, which favours the existing states of pleasure or desire, while everything is "bad" which opposes those feelings, and excites the feeling of pain and the desires consequent on it. One and the same thing may be good to-day and bad to-morrow. In respect of what is good for all men, that which appears good to us during a particular state of passion may be either good or bad. For envy and pity may spring from the same sources, as the laws already laid down respecting the statics of the passions show. A man who is at one moment full of pity or sympathy, may at the next be envious, without having greater reason for being the one or the other.* Animals are capable of feeling pity or sympathy for each other, and even to a certain extent for man. When he confers good on them, and excites the feeling of pleasure in them, they come to him with pleasure and participate his suffering. In this there is no trace of moral feeling.

The sacrifice of the good of all, or of many to the good of self, is in some measure restricted, in consequence of the affections of men and animals for their own immediate interest being counterbalanced by other passions, which have also reference to their self; namely, by the fear of punishment,—and in many by the emotions produced by superstition. Superstition, however, is nearly as prolific a source of evil, as of good deeds.

When the prevailing idea in our mind respects that which is generally useful or good for our family, for our class, for the corporation or body of men to which we belong, or for our fellow countrymen, we conceive a more general notion of "utility" or "goodness." The idea of that which is good for a limited number of persons, and for their different conditions, is, however, still far removed from the notion of what is morally good. The greater the number of persons to whom a good thing conveys a benefit, the more nearly does the idea of it approach the moral good, which implies the notion of what is useful and good to all men. This notion becomes still more perfect, when the thing regarded as good is good for all men, not merely at the present time but under all circumstances and in all times. Such is also the good which is desirable for the individual self under all circumstances; a notion from which is excluded everything which is good merely in the present condition, but not in those which may follow.

The submission of self to the divine laws ruling the universe is

* Spinoza, Ethik. 4 Buch.

reason, which recognises individual things as parts of the general whole. Reason produces the notion of the highest good, which is opposed to and restrains the idea of the relative good suited only to the temporary conditions of man; and this is conscience. The contemplation of the imperfection of our own self, which frequently is not guided by the notion of the general good, together with the striving to attain this good, and the feeling of dependence and fallibility, constitute the religious feeling, the prevalent emotion of the pious. The contentment and pleasure, which accord with reason, form the happiness of wise men, who neither despise all other pleasures nor fail to avoid painful ideas, as far as they can do so without acting contrary to the dictates of reason.*

We shall here conclude our account of the passions, with the remark, that they are capable of association, mutual neutralisation, and concatenation; just as are the simple ideas. Many so called passions are really a connected series of different states of emotion; such is the passion of jealousy. This will be readily intelligible when the foregoing exposition of the passions is compared with the account previously given of the more simple relations of conceived ideas.†

SECTION III.

Of the mutual reaction of the Mind and Organism.

CHAPTER I.

OF THE MUTUAL REACTION OF THE MIND AND ORGANISM GENERALLY CONSIDERED.

The different views which may be entertained respecting the connection between the mind and the body, have been discussed in the first chapter of the first section of the present book. We have here to consider their modes of reaction on each other. But before entering upon the particular details of this subject, we shall premise some remarks

* See Spinoza, Ethik. 5 Buch. Fichte, Anleitung zum seligen Leben. Berlin, 1806.

† For further guidance in the wide field of psychological enquiry, I must refer the reader to the different systematic treatises on the mind, and to those works which treat of logic in connection with psychology and metaphysics. Aristotle De Anima. Spinoza, Ethica. Herbart, Lehrbuch zur Psychologie; Königsberg, 2te Auflage, 1834. Stiedenroth, Psychologie; Berlin, 1824. Beneke, Lehrbuch der Psychologie; Berlin, 1833. Schubert, Geschichte der Seele; Stuttgardt, 1839. Bobrik, System der Logik; Zürich, 1838. Carus, Vorlesungen über Psychologie; Leipzic, 1831. Flemming, Beiträge zur Philosophie der Seele; Berlin, 1839.

upon the organic elements of the whole body, as well as of the brain, and upon the monads of metaphysical philosophers.

a. Of the elementary particles of organic bodies, monads of physiologists.

The elementary parts of the brain are, like all the other elementary particles of the animal body, developed from cells; and all these cells are produced from the primary cell or germ, which has the organic properties of the whole. The secondary cells from which the different tissues of the body are produced by various processes of transformation,* differ from the primary cell in respect of their productive power. The primary cell produces all the secondary cells, while the latter are able only to reproduce their like. The cells of cartilage generate only new cartilage cells; the cells of horny tissues, only cells of similar nature; and muscular fibres, only muscular fibres. Hence, we must perceive, that an entire organism, in the form of the primary cell or germ, cannot be reproduced except by the co-operation of all the different secondary cells, or by the dynamic property of the whole, maintaining its integrity and exerting its ruling power over all the different tissues. The fully developed organism, however, consists of a system of parts, all essential to constitute the whole, which are, in a measure, independent of each other, and have the power of generating their like. These particles or cells may be termed secondary monads, inasmuch as they have their origin in the primary monad of the germ, and represent, together, that primary monad in the developed or unfolded condition. The different (secondary) monads composing the organism have, by virtue of their structure and composition, different endowments, viz. those of motion, sensation, nutrition, secretion, &c.; or we may say, that different forces of nature are rendered manifest in them by virtue of their structure. The brain becomes the organ of the mind in consequence of the structure it receives, and of the reciprocal action of its elementary parts, which are cells (the grey corpuscules of the ganglia and cerebral substance), and fibres, developed from cells; just as the cells of muscular fibre and the muscular fibrils become the organs of motion. Nevertheless, it must not be imagined, that the mind, on this account, is itself compound. The increase in number of the elementary particles of the brain has not any influence on the number or mass of the ideas, but only on their lucidity, distinctness, and facility of association. And in accordance with this, we find, that the loss of portions of the cerebral substance, in injuries of the head, does not deprive the mind of certain masses of ideas, but diminishes the brightness and clearness of the conceptions generally. Different ideas, however, are communicated simultaneously to the sensorium, from the different regions of the brain, to which impressions on nerves of sense are conducted.

* See Book VIII, Section II. Chapter II.

The structure of the brain and body generally, being that which we have described—the active particles of both being identical in nature, and alike produced from cells; it is easy to understand how the monad-like particles of the brain should communicate the state excited in them by ideas, to the similar particles of the body, and *vice versâ*. But the mode of action and reaction of the elementary particles of the brain, in the production of ideas, remains a perfect mystery.

It should here be clearly understood, that by monads I do not mean atoms, but those organised perishable elementary parts, of which Schwann has shown all the tissues to be originally composed; parts, which, though subordinate to the plastic power of the whole organism, have yet different compositions and endowments, and are so far independent, as not only to reproduce their like while within the organism, but even to continue their organic action for a certain time after their separation from it, and which frequently coalesce, several together, to form compound structures of similar endowments, such as the muscular and nervous fibres. Mayer had* expressed the notion that organisms were formed of active primary particles or organic monads, long before it could be anticipated that all the tissues would be actually shown to have originally the same structure. I had also an indistinct conception of a similar idea, when, in the first part of this work, in 1833, I endeavoured to explain the regeneration of divided Polypi and Planariæ, and the formation of double monsters by division of the germ. Purkinje, likewise, had been led by his anatomical researches to conceive the existence of independent elementary particles, endowed with special properties and serving the purposes of the organism. Schwann's recent work† furnishes the material for a general theory of organic beings.

b. Monads of the Metaphysicians.

The sense in which we have used the term organic monads in the preceding page, is very different from that in which Herbart employs the word "monads" in his treatise on mind and matter. According to Herbart,‡ the mind is a simple substance (Wesen), without parts, without extension, and without any complexity in itself (Vielheit); matter, itself, consists of simple active substances or monads (atoms), destitute of extension, which exist in space, without forming a *continuum*, but which are in a state of equilibrium of reciprocal attraction and repulsion, and thereby acquire the appearance of a body possessed of extension. Matter is impenetrable only with respect to those substances which are not able to produce a change in its existing equilibrium of attraction and repulsion. Every organic body is a system of monads, which are themselves

* In his Supplemente zur Lehre vom Kreislaufe.

† Mikroskopische Untersuchungen. Berlin, 1838. 8.

‡ Lehrbuch zur Psychologie, p. 122—133.

the subjects of a system of internal states, arising from the reciprocal action and reaction of the monads on each other. The combination determined by providence, is the cause of the particular form of an organic body. In the germ, the whole system of internal states subsists in a concentrated condition, without the corresponding form. The mutual reaction of the mind and body on each other, accordingly, consists of the action of the mental monad upon the internal states of the monads of the body, and *vice versâ*. The monad which conceives the ideas, and which, like all Herbart's monads, can be regarded only as a mathematical point, requires no fixed seat in the brain, but may move through a certain space, without the least suspicion of such motion being conceived in its ideas, and without the least trace of it, capable of detection by anatomical research, being left behind. Such change of seat of the mental monad, may be regarded as a very fruitful hypothesis for the explanation of abnormal states of the mind. Herbart further remarks, that there is no reason for supposing the seat of the mind to be the same in all animals and in man. Its seat, he says, may probably lie in the spinal chord in brute animals, particularly in the lower classes. It cannot also be regarded as certain, that each animal has only one mind. The contrary, indeed, appears to be the case in worms, of which, when divided, the separated parts continue to live as independent beings; and in the nervous system of man there may be very many elements, which, in their internal constitution, are far superior to the mind of the lower animals. In separated parts of organic bodies, moreover, life is maintained for a period without the presence of mind. Bobrik* also adopts this view, and deduces from it the explanation of different organic processes. In order that unity, totality, and adaptation to the proposed end should attend the mobility of the vital forces, it is indispensable, says Bobrik, that there should be a ruling monad, able to combine into one system the aggregate of monads already prepared for organic mobility. This ruling monad is the "form." Among the different elementary parts which are gradually developing themselves, some attain such a perfection of their internal conditions, as to become the "forms" of new organisms, or seeds fit for propagation. If this view were applied to the active corpuscules or organised elementary parts of organic bodies, each of those particles, in an organic body, would be a subordinate system of active atoms of only temporary duration, whilst the active atoms or monads of Herbart composing it would be in-susceptible of destruction.

c. Of the action of the mind in the organised structures of the brain.

Herbart's hypothesis respecting the monads and the nature of matter, certainly explains the action of the mind upon matter, without the mind

* System der Logik. Zürich, 1838.

itself being supposed to be material; since, according to his view, the mental phenomena are the result of the action of one simple immaterial substance upon other simple immaterial substances or monads.

On attempting, however, to account for the conception by the mental monad of ideas of objects extended in space, in consequence of changes produced in other parts of the organism, and again, for the action of the mental monad upon numerous fibres of the organism simultaneously, we meet with inexplicable difficulties. The problem requiring solution has always been to explain how the mind, a simple substance, not composed of parts, can acquire from the affection of parts of the body having a certain relative position, the perception of objects having extension in space and particular forms. How, for example, it can obtain the perception of visible objects, occupying a certain extent in space and having a certain form, from the affection of certain points of the retina; each point of the retina being perceived as occupying a given portion in the field of vision. All perceptions by the sense of vision of objects, having extension in space, are dependent on the different points of the retina being perceived in the same relations of contiguity as those in which they really exist. We may represent such points of the retina by letters, thus:—

a. b. c. d.
e. f. g. h.
i. k. l. m.

We meet with the same difficulty in the case of the sense of touch. For we certainly owe our power of distinguishing by touch, the forms and other qualities of extension in external bodies, to our perception of the relative position of the different parts of our own body. The whole apparatus of vision is so contrived, as to convey an exact representation of the relative position, even of distant objects, to the extended surface of the retina. But if the mind is a substance, to be conceived only as a mathematical point, how can the idea of position be obtained from the simultaneous affection of certain points of the retina? It might, indeed, be imagined, that such a monad would receive impulses, as it were, from all sides, and that the idea of visual space would arise from the impulses thus given by other monads to the mental monad. But there is no indication in the brain of any provision for such a concentration of all sensual impressions upon a single point. Adopting Herbart's hypothesis, the most ready way of getting rid of the above-mentioned difficulties, would be to deny that we can perceive the relations of position in the sensations of our body. And this has really been done at different times. Steinbuch,* several years since, maintained that we owed our perceptions of the extension and relative position of objects entirely to the motions accompanying those perceptions. Thus, the retina, he said, does not

* Beiträge zur Physiologie der Sinne. Nürnberg, 1811.

perceive the relation of contiguity or position in the different points of it which are affected in vision, but, that knowl edge, concerning the objects of vision, is obtained from the action of the muscles of the eye. An illuminated point of the retina is, by the conscious contraction of one of the muscles of the eye, converted into a line of light. In order that other parts of the retina should be illuminated, different degrees of contraction of those muscles are required. According to this view, the act of vision consists not in the retina being the seat of an image, in which external objects are represented in their relative position, but in a succession of muscular contractions, which are necessary, in order to expose different parts of the retina to the same pencil of light. Each point of the retina is supposed to stand in a special relation to a particular degree of contraction of the muscles of the eye, and, hence the illumination and sensation of particular parts of the retina become, by education, but unconsciously, associated with certain degrees of conscious muscular contraction. On more narrowly analysing this view, however, we find that it takes for granted a perfect impossibility. For, unless the distinct points of the retina are by nature different from each other, in the quality of their sensation, it is impossible that they should be distinguished and recognised as distinct, in repeated impressions on them; and unless they are so distinguished, no particular degree of muscular contraction can become associated with them in the memory. And, in fact, Tourtual, who rejects the theory that we can distinguish in sensations the relative position of different points of our body, still admits, that the impressions which the mind receives from all the different points are different in quality, and supposes that it is only by this difference that they are distinguished from each other. But if we reflect, that a new-born animal gives evidence of the perception of position and form, by means of the sense of sight, in its immediately applying itself to the teats, we shall scarcely doubt the fact that, antecedently to all education, impressions of form and position or extension in space are perceived in the retina. Now, admitting the mind to have the power of distinguishing the relative position of different parts of the body, the possession of such a power by a point-like monad appears inconceivable. Even if we suppose that the monad is able to travel over all parts of the retina, and thus to collect an aggregate impression from the different changes it might undergo in its course, there would still be a difficulty in reconciling this view with the simultaneous existence of the different parts of an image,—with the power which we enjoy of perceiving in a moment all parts of an impression occupying a considerable extent. The more probable view, therefore, is, that the mind is present at the same time in all parts of the brain, without itself being composed of parts, and that it recognises the extension and qualities of form and position in the impressions on the senses, by virtue of its general presence.

This, however, must not be regarded as an explanation: for it still remains a mystery, how the closely contiguous particles of nervous substance in the organs of sense can be distinguished from each other in the mind. For if we suppose that they are conceived by the mind, as so many contiguous points exerting a repulsive force upon each other, still this is merely a figurative expression, and the conversion of impressions on organised matter into ideas remains as difficult of conception or as inconceivable as the relation of mind to organisation generally.

It is very easy to cut the knot, by saying, that organisation and the mental principle are different names for the same thing; that the apparent difference between matter and mind is the result of the different manner in which we regard them, and does not really exist. But we cannot lose sight of the fact, that the brain is an aggregate of numerous differently organised parts, and in this respect a highly complicated piece of mechanism; while the mind exists in a latent state, in the germ, independently of this mechanism, although incapable without it of manifesting itself or acting upon the body. The manner in which the mind makes use of this highly complicated and delicate piece of mechanism, is certainly inconceivable.

The problems, concerning which I have here been endeavouring to give my readers some clear conceptions, are, it is true, no subjects for physiological research, and their solution, if possible, must be expected from metaphysical philosophers; but, nevertheless, I have thought it the duty of the physiologist to analyse those questions which lie on the borders of his own science, and to compare, critically, the different results of speculative enquiries, with the view of advancing at a future period more nearly to the truth. I here again refer to the exposition of the cosmological systems given at the commencement of this section. They, together with the doctrine of monads just considered, comprehend the circle of the most general possible conceptions on this subject.

CHAPTER II.

PHENOMENA RESULTING FROM THE ACTION OF THE MIND AND BODY ON EACH OTHER.

So soon as the structure of the brain is developed, and the action of the senses commences, ideas or mental actions also arise; and, just as light may be developed in an inorganic body, by a mechanical shock and change in its physical condition, in the same way changes in the action of the mind may be produced by changes impressed on the organisation of the brain or on the matter which enters into its structure. On the other hand the operations of the mind, with which the organisation of the brain keeps, as it were, equal pace, induce changes in the structure and component matter of that organ, and of all other parts of the body which are under its influence. The ideas and thoughts are not themselves composed of parts, but they are developed in matter which has organisation and parts, and the distinctness of the conceptions is entirely dependent on the condition of this divisible matter.

Hence we may infer that, whatever changes the mind produces in the organism generally, are effected through the medium of the brain—the organ in which alone the mental force, elsewhere latent, is manifest, and from which its influence radiates, as from a centre, to all other parts of the body. Every organ, also, by virtue of its power of acting on the brain itself through the medium of its nerves and of the blood circulating through the whole organism, must have an influence upon the ideas and upon the power of mental conception. This influence may be either exciting or depressing, so that the power of the mind to conceive ideas may be either increased or impeded. The impressions communicated from different organs of the body to the brain can, of course, produce no other distinct ideas than those of sensations, and the peculiar import of these sensations. But since local changes of particular organs may produce the sensations of pleasure or suffering, or of the tendency of the organ to its specific function, and may thereby excite the ideas of the expansion and restriction of self and of desire, which are associated with those sensations, it is evident that the disposition to a state of emotion may be kept up by the state of other organs than the brain.

1. *Influence of states of the body upon the intellect and emotions.*

The excitement of certain organic states of the brain, by the bright scarlet aërated blood, is a necessary condition for the action of the mind. Hence, the abstraction of blood in large quantity produces syncope and loss of consciousness. Even the quality of the blood, however, exerts an influence on the intellectual operations. The most common instance of an influence exerted on the mental faculties by a cause of this kind, is afforded in the effects of digestion. The digestion of food introduces a quantity of imperfectly assimilated matter into the circulation. Until this new material has undergone the necessary changes, and while certain matters, altogether unfit for nutrition, are mingled with it, it is not adapted to excite those states of the brain which are necessary for the proper manifestation of mind; and as it is conveyed to that organ by the circulating blood, it produces an injurious change in it, and impedes or disturbs the mental functions. Hence, the indisposition to mental labour experienced by some persons after meals. This disturbance of the intellectual operations is still more evident, as the result of the material changes produced by the alterantia nervina (spirituous liquids and narcotics). Some "secreta" and "excreta," as bile and urea, are equally unfitted for producing the natural organic states of the brain. The former substance being absorbed into the blood, produces not only indisposition to the exercise of the intellect, and diminution of its power, but also depression of spirits, by disturbing those organic conditions of the brain which influence the emotionary feelings.

A second source of causes disturbing the action of the mind, through the medium of changes produced in the brain, is found in those states of other organs, which act on the brain through the medium of the nerves. Every part of the body, which stands in the relation of active sympathy with the central organs of the nervous system, is capable, when itself in a state of strong excitement, of exciting strongly the brain, and thereby the mind also; or, when in a state of depressed action, of diminishing the activity of their functions: hence, delirium and stupor are effects of those states in some parts of the body. The emotions of the mind are also affected in this way; long continued disturbance, or arrest of the functions of important organs, giving origin to a fretful, dejected state of feelings, which is nothing else than a state of impeded strivings of the mind. Those organs which are engaged in effecting chemical changes in the organic matters of the fluids, such as the internal viscera, act on the mind in two ways, for they depress the power of action of the central organs, not only through the medium of nervous connection, but also by changes impressed on the blood. The effect of the latter mode of action varies in degree, according to the kind of change produced in the blood by the viscera. Hence it is that the abdominal viscera are distinguished above all others, by the influence of their chronic maladies, in giving rise to a long continued depression of the strivings of the mind.*

There are organs of the body, particular states of which excite passions connected with their functions; such are the sexual organs and the stomach. These organs excite sensations of particular kinds, and ideas of things fitted to restore the integrity of self, which is felt to be in an impaired or restricted state. On the other hand the idea of that which would restore the integrity of self, or increase its power, determines currents of nervous energy towards the particular organ. For, as we have already seen, this idea of a state which can be realised by a particular organ, excites a current of nervous influence towards that organ, whether it be a muscle or a gland. In this way is the disposition to the passion of love excited by particular states of the sexual organs or of the spinal cord, the medium of nervous communication between those organs and the brain. If both the sexual organs and the spinal cord have a certain degree of tension, the mind is thrown into such a state, as causes corresponding ideas to arise. The active state of the organs

* See page 816* of the second edition, or page 818 of the first edition, where the seat of the passions is shown not to be in those viscera.

excites the idea, and the idea may produce that condition of the organs; but, unless the organs are in a state of potency, the ideas to which they are related remain cold, and do not influence the organic conditions and actions. Particular kinds of food, also, have an influence on particular states of passion by their action on the corresponding organs of the body. Lastly, the state of the whole nervous system, and the degree of its excitability, and of the facility with which impressions are propagated through it, exert an influence on the emotions. For those persons, in whom any excitement spreads very rapidly through the nerves, and still more rapidly leaves behind it a state of exhaustion, are more liable than others to all emotions in which the feeling of self undergoes a violent and sudden change and depression, such as fear, anxiety, terror, &c. But they whose nervous system is differently constituted, and is not exhausted or depressed in consequence of previous excitement, experience from sudden excitement only the emotion of courage, and manifest persevering efforts to maintain or extend the power of self. Animals display different tendencies of their organic states and functions, according as they are by nature timid or courageous. In man, these dispositions to particular emotions vary with the organic state of the body: a person, gifted with great coolness and presence of mind, may be so altered, temporarily, by a particular state of his nervous system, as to be startled like a naturally timid person, by any sudden occurrence; whilst abundant food and a glass of wine will give courage to the faint-hearted.

The operations of the mind are affected in the greatest degree by changes in the organic conditions of the brain itself, such as inflammation, malformation, and pressure. Every state of irritation of the brain causes delirium; every thing which impedes the organic actions in the brain produces syncope, stupor, or complete coma. Hence the most various structural changes in the brain, as tubercles, pus, extravasated blood and water, give rise to nearly the same symptoms. Pressure of blood, still within its vessels, also produces insensibility. And the effects of inanition are, in this respect, exactly the same as those of pressure.

Structural changes in the brain itself are much more prone to disturb the intellectual faculties than to excite or depress the passions. A depressing passion cannot be intense without the concurrence of ideas, in a certain degree of intensity, which shall keep up the passion; but when the organic actions of the brain are impeded, this intensity of ideas is impossible: hence, even in these cases, the principal effect of structural change of the brain, appears to be impairment of the intellectual faculties. The organic conditions, on which the integrity of the intellectual faculties depends, exist, without doubt, in the brain itself; but the elements which maintain the emotions or strivings of self, in all parts of the organism.

2. *Influence of ideas and emotions of the mind upon the body.*

The influence of ideas upon the body gives rise to a very great variety of phenomena, which border on the marvellous. It may be stated as a general fact, that any state of the body, which is conceived to be approaching, and which is expected with perfect confidence and certainty of its occurrence, will be very prone to ensue, as the mere result of that idea, if it do not lie without the bounds of possibility. The case mentioned by Pictet, in his observations on nitrous oxyde, may be adduced as an illustration of such phenomena. A young lady, Miss B., wished to inspire this intoxicating gas; but in order to test the power of the imagination, common atmospheric air was given to her, instead of the nitrous oxyde. She had scarcely taken two or three inspirations of it, when she fell into a state of syncope, which she had never suffered previously; she soon recovered.* The influence of the ideas, when they are combined with a state of emotion, generally extends in all directions, affecting the senses, motions, and secretions. But even simple ideas, unattended with a disturbed state of the passions, produce most marked organic effects in the body. This we shall now proceed to demonstrate.

a. Influence of the mind upon the senses. Phantasms.

Phantasms or hallucinations are perceptions of sensations in the organs of the senses, dependent on internal causes, and not excited by external objects. These phenomena have been repeatedly confounded with mere ideas, and have been regarded as ideas which are not distinguished from realities. But the very belief in their reality is owing to their being seated in the senses, and having all the truthsomeness of real sensations; moreover, this belief in their reality is not an essential character of such phenomena. It would be an error of the understanding to believe in the reality of mere ideas. But these phantasms may present themselves with all the distinctness and force of a real sensation, with colour or with sound, and yet not be mistaken for real impressions from without. The false views entertained respecting these phenomena, have arisen from the hallucinations of the insane having been principally the subject of observation: hence I avoid the use of the term hallucination. The name of visions is a more correct expression for the states now under consideration, when they affect the sense of sight. For they are really affections of that sense, and have their seat as truly in its apparatus as any visual perceptions from external impressions. Even the sensations of the sense of sight, excited from without, afford us the opportunity of observing the influence of ideas on the state of the

* The case is given in the German translation of Sir H. Davy's Researches on Nitrous Oxyde (Untersuchungen über das oxydirte Stickgas, 2. Bd. Lemgo. 1814. p. 326).

retina; since certain parts of images acquire an extreme distinctness, from being made the subject of more particular conception by the mind, or, in ordinary language, from the attention being particularly directed to them. (See page 1085.)

Without actual sensations, we are accustomed to conceive the presence of outlines, and, consequently, of forms, in the dark field which appears before the closed eyes. This seems to result from a few particles or points of the retina becoming the subject of conceptions. No illuminated and coloured image is perceived in this case. For such a result, it would be necessary that the particular points of the retina should be conceived as being, not in the state of rest, but in that of action, on which the appearance of light and colour depends. This production of colourless figures in the field of vision, by an action of the mind, is, however, sometimes so perfect, that outlines of objects on which the eyes have been long fixed, return with great distinctness. For example, the forms of structures which have been attentively examined with the microscope, suddenly present themselves to our vision, even though many hours have elapsed since they were actually seen. But not merely outlines of objects which have been presented to our sense of vision, are reproduced; new configurations also appear at times, when external impressions are excluded. This happens frequently to children of active imagination, when they are placed in the dark: faces and terrific forms seem to present themselves to them in outline, and devoid of colour and light. All these phenomena appear to result from some kind of reciprocal action, which takes place between the sensorium and the retina.

The subjective images of which we are speaking have sometimes, however, both colour and light; different particles of the retina, of the optic nerve, and of its prolongations to the brain, being conceived as existing in special states of action. This happens rarely in the state of health, but frequently in disease. These are the true phantasms which may occur to the sense of hearing and other senses, as well as to that of vision. The process by which "phantasms" are produced, is the reverse of that to which the vision of actual external objects is due. In the latter case particles of the retina thrown into an active state by external impressions, are conceived in that condition by the sensorium; in the former case, the idea in the sensorium excites the active state of corresponding particles of the retina or optic nerve. The action of the material organ of vision, which has extension in space, upon the mind, so as to produce the idea of an object having extension, form, and relation of parts, and the action of such an idea upon the organ of vision so as to produce a corresponding sensation, are both equally wonderful; and hence, the spectral phenomena or visions are not more extraordinary than the ordinary function of sight. The following are the states of the body in which the above phenomena are observed:—

a. Immediately before sleep, at the time of waking, and when half awake. Who has not observed the vivid images which present themselves to the eye before sleep; the light which sometimes appears to the closed eyes at that time; the forms sometimes brightly illuminated, which suddenly present themselves, and quickly change; or the sudden sound, as if one called loudly in our ears, which, in that state, is heard without any external cause?* A close attention to one's own condition at the time specified, is quite convincing as to the phenomena in question being real sensations, and not merely ideas. Any one who can watch the changes which take place in himself, at the time when sleep is coming on, will sometimes be able to perceive the images distinctly in the eyes. On waking, too, in a dark room, it sometimes happens that images of landscapes and similar objects still float before the eyes. Aristotle,† Spinoza,‡ and still more recently Gruithuisen, have made this observation. I have, myself, also very frequently seen these phantasms, but am now less liable to them than formerly. It has become my custom, when I perceive such images, immediately to open my eyes and direct them upon the wall or surrounding bodies. The images are then still visible, but quickly fade. They are seen whichever way the head is turned, but I have not observed that they moved with the eyes. The answers to the enquiries which I make every year, of the students attending my lectures, as to whether they have experienced anything of the kind, have convinced me, that it is a phenomenon known to comparatively few persons. For among a hundred students, two or three only, and sometimes only one, have observed it. This rarity of the phenomenon, is, however, more apparent than real. I am satisfied that many persons would perceive these spectres, if they learned to observe their sensations at the proper times. There are, however, undoubtedly many individuals to whom they never appear, and in my own case they now sometimes fail to show themselves for several months at a time, although, in my youth, they occurred frequently. Jean Paul recommended the watching of the phantasms which appear to the closed eyes, as a means of inducing sleep.

b. The facts already mentioned prove that the images seen in dreams, —not the mere ideas of things conceived in dreams,—are phenomena of the same kind as the phantasms. For the images which remain before the eyes when we awake, are identical with the objects perceived in

* A detailed account of these phenomena is given in Moritz and Pockel's Magazin der Erfahrungsseelenkunde, 5 b. 2. p. 88; by Nasse, in his Zeitschrift für Anthropologie, 1825, 3. p, 166; and in J. Müller Ueber die Phantastischen Gesichts-erscheinungen. Coblenz. 1826, p. 20.

† In his Essay on Dreams, chap. iii.

‡ Opera Posthuma, epist. 30.

our dreams.* Even the blind sometimes see in their dreams images of luminous objects.†

The phenomena hitherto described, may occur to any person in the state of health.

c. The diseases in which the occurrence of phantasms is frequent, are fever, nervous irritation of the brain, phrenitis (in which disease they remain for some time during convalescence), narcotism, insanity, and epilepsy.‡ The well known bookseller of Berlin, Nicolai, when suffering from intermittent fever, saw coloured pictures of landscapes, trees, and rocks, of half the natural size, which appeared to him even before the cold stage set in, and resembled framed paintings. If he kept his eyes closed, they underwent constant changes; some figures disappeared, while new ones showed themselves. As soon as he opened his eyes the whole vanished. Inflammation of the optic nerve is also attended with the perception of luminous phantasms. A very remarkable case was observed by Lincke,§ in which the extirpation of an eye was followed by the appearance of luminous figures before the orbit, as long as the inflammation consequent on the operation endured. In another case,¶ a female, who was stone blind, complained of having luminous images with pale colours before her eyes. These cases prove that the presence of the retina is not a necessary condition for the production of such phenomena; but on the contrary, that the deeper seated parts of the essential organ of vision are alone required. It is an old and frequent observation, that pressure, exerted on the brain, in persons who have been trepanned, causes them to see flashes of light. Esquirol knew an insane person who saw visions, and in whom, after death, be found both optic nerves in a state of atrophy from the eye to the chiasma.||

In cases of insanity, phrenitis, cerebral irritation, and narcotism, the phantasms are seen even when the eyes are open, and combine with the impressions produced on the sense of vision by real objects.

Simple cerebral irritation, in persons who are not insane, may give rise to what is called the seeing of visions. According to the tendencies of the mind, the phantasms seen under these circumstances will be of a religious, consolatory, and benignant character, or fearful forms of living or dead persons, as in the case of the so called "second sight" of northern nations. The vision may be seen with the eyes open, the

* See Goethe, Vorrede zur Farbenlehre; also the excellent remarks of Gruithuisen, in his Beiträge zur Physiognomie und Eautognosie, p. 236.

† See J. Müller, op. cit., and Herman in Ammon's Monats-schrift, 1838.

‡ For an account of phantasms seen in the state of narcotism, consult Sir H. Davy's Researches on Nitrous Oxyde. Richerz, in Muratori, über die Einbildungs-kraft. 2. th. Leipz. 1785, p. 123.

§ De fungo medullari oculi. Lips. 1834.

¶ Berliner Monats-schrift, 1800, p. 253.

|| Dict. de Scienc. Méd. Art. Hallucinations.

images from internal causes mingling themselves with those of real objects. In this case, it may happen, that the images of external objects are seen through the phantasms as through a veil. In some instances persons see the forms of other individuals; in others, their own forms. According to the degree of mental culture of the subject of these visions, are they regarded as real, or as the result of a disordered state of the sensorium. In the former case, the spectre-seer not only mistakes his own condition, but he is regarded erroneously, both by the superstitious and credulous multitude, and by the more sceptical persons, who think him a madman or visionary. When a person who is not insane sees spectres, and believes them to be real, his intellect must be imperfectly exercised.

We have instances of persons seeing spectres, and recognising their true nature, in the case related by Bonnet and in Nicolai. Bonnet* knew a gentleman gifted with perfect health of body, with candour, good judgment, and memory, in whom, from time to time, when he neither had recently awoke nor was inclined to sleep, figures of birds, carriages, and buildings appeared, independently of all external cause, and moved before his eyes. Sometimes the carpet of his room seemed all at once to change its pattern. The spectral images, here, were as distinct as real objects. This gentleman, however, judged rightly as to the nature of the phenomenon, and corrected any first erroneous impressions.

Nicolai, whose case is so frequently quoted, was accustomed to be bled twice a year, and to have leeches applied two or three times annually for the relief of hæmorrhoids. During the latter part of the year 1790 both these measures had been omitted, and it was early in 1791 that the spectral illusions first appeared to him. After a violent quarrel and agitation of mind, he suddenly perceived at a short distance in front of him, a form like that of a deceased person. Later in the same day there appeared several other walking figures, which continued to appear for some days. Nicolai could in no way regulate the appearance of these phantasms by his will; he could not even determine the appearance of one person rather than another. The figures were for the most part those of strangers. They appeared both by day and night, and presented the different colours of the flesh and dresses, though the colours were paler than in natural objects. After the lapse of four weeks, during all which time Nicolai continued to walk abroad, the phantasms began to talk. At the end of about two months leeches were applied to the anus, and on the very same day the phantasms began to fade and to move more slowly. At length they seemed to dissolve away, leaving fragments visible for a considerable time.† It is

* Analytische Versuche über die Seelenkräfte. Bremen, 1780. 2 Th. p. 59.

† Berliner Monats-schrift, 1799. Mai. It is known only to a few persons, that

very rarely that the power is possessed of producing at will, in the form of phantasms, while the eyes are closed, images of the objects conceived as ideas in our minds. The cases of Cardanus, Goethe, and a few others mentioned in my essay already referred to, are instances of this power. Goethe in his tract "Zur Morphologie und Wissenschaft," says, "when I closed my eyes and depressed my head, I could cause the image of a flower to appear in the middle of the field of vision; this flower did not for a moment retain its first form, but unfolded itself, and developed from its interior new flowers, formed of coloured or sometimes green leaves. These were not natural flowers, but of fantastic forms, although symmetrical as the rosettes of sculptors. I was unable to fix any one form, but the development of new flowers continued as long as I desired it, without any variation in the rapidity of the changes. The same thing occurred when I figured to myself a variegated disk. The coloured figures upon it underwent constant changes, which extended progressively, from the centre towards the periphery, exactly like the changes in the modern kaleidoskope."

In the year 1828, I had the opportunity of conversing with Goethe upon this subject, in which we were both much interested. He knew that I frequently saw different figures in the field of vision, when I lay quietly down to sleep, with my eyes closed, but before sleep had actually come on; and he was very desirous of learning what forms these images took in my case. I explained to him that I had no voluntary power over either the production of these images or their changes of form, and that they never presented the slightest tendency to a symmetrical and vegetative development. Goethe, on the contrary, was able to give the type for the phantasm, and then the different variations ensued in it, as it seemed, independently of the will, though with regularity and symmetry. This difference accorded well with the characters of our minds, of which the one had all the creative power of the poet, while the other was engaged in the investigation of the actual phenomena of nature.*

b. Influence of ideas upon motions.

Ideas produce motions even more readily than they produce sensations. The following are the conditions in which such phenomena occur:—

1. The resolve to execute a particular motion sets in action the corresponding cerebral nervous fibres, and the motion is effected, if it be possible, through the medium of the cerebro-spinal system of nerves. (See the account of the voluntary movements at page 934.)

Goethe, who had been offended with Nicolai, satisfied his revenge by caricaturing him as the Proctophantasmist, in the scene on the Blocksberg, in Faust.

* Compare Abercrombie's Inquiries concerning the Intellectual Powers, Edinb. 1830. On the phantasms of the sense of hearing, see my own work already referred to, p. 80, and Froriep's Notiz. B. x. p. 10.

2. The idea of a particular motion also determines a current of nervous action towards the necessary muscles, and gives rise to the motion independently of the will. In this way the movements of yawning, laughing, &c., are produced involuntarily, when another person is seen to yawn or laugh. (See page 932.)

3. Any sudden change in the ideas, though without emotion, and having reference to mere external objects, may excite involuntary motions; such as that of laughter. We have instances of a similar kind in the motions which occur when two ideas are suddenly conceived to contradict each other, or when the solution of a difficulty is conceived unexpectedly.

4. The idea of our own strength gives strength to our movements. A person who is confident of effecting anything by muscular efforts, will do it more easily than one not so confident in his own power. The idea that a change is certainly about to take place in the actions of the nervous system, may produce such a change in the nervous energy, that exertions hitherto impossible become possible. This is still more likely to be the case, if the individual is at the time in a state of mental emotion.

5. The passions or emotions themselves give rise to involuntary actions or relaxations of muscles, according as the state of passion is dependent on exciting or depressing ideas. The same passions occurring frequently induce a fixed expression of the features, and betray the characteristic temper of the mind, in the same way that each passion which occurs declares itself by its corresponding physiognomical motions. (See pages 932—934.)

c. Influence of ideas upon nutrition, growth, and secretion.

The phenomena dependent on the influence of ideas of the mind upon the organic processes of the body are very analogous to the foregoing. They may be arranged as follows:—

1. Excessive exercise of the mind diminishes the activity of the nutritive processes.

2. An idea having reference to a secretion causes a stream of nervous energy to be directed towards the secreting organ; and, if the mind is at the same time occupied by a passion or an emotion, the effect just mentioned is more marked. Thus, the saliva is secreted in greater abundance when the idea of food occurs to the mind; the secretion of milk is increased when the young are about the mother, and when the idea of them, rendered intense by emotion, occupies her mind; the conception of voluptuous ideas causes the semen to be secreted in larger quantity.

3. The idea that a structural defect will certainly be removed by a certain act increases the organic action of the part, and sometimes pro-

duces a cure. Hence, the cure of warts by what is called sympathy; *si fabula vera.*

4. The passions sometimes excite profuse secretions, such as a flow of tears, or perspiration, or diarrhœa; sometimes they repress the organic chemical processes by which the secretions are formed, so as to alter their quality. From the latter cause, the milk of a woman who is nursing becomes after a fit of passion indigestible and irritating to the child. Under certain circumstances, also, the passions cause the suppression or retention of secretions: thus the urine is watery, from the natural ingredients of that fluid not being eliminated, after a fright; and anger, grief, and other emotions give rise to jaundice, by causing the matter secreted to be re-absorbed into the capillary blood-vessels of the liver, instead of being carried out by the branches of the bile duct.

5. Predispositions to particular diseases of nutrition speedily manifest themselves by actual lesions under the influence of passions. Grief, and deep suffering, in a very short time develop phthisis, liver disease, and affections of the heart, when a predisposition to those maladies previously exists.

6. The culture of the mind by observation and varied attainments has an ennobling influence on the corporeal form, and particularly on the lineaments of the face. A comparison of the forms and features most general in the different classes of society leaves no doubt as to the truth of this remark. The form which is acquired becomes hereditary. This influence is most manifest in the most exclusive ranks of society, which seldom intermarry with other ranks, and in which the education of the children is carefully attended to. The only way in which we can conceive the form of the features to be influenced by the culture of the mind is, that all excess of nutritive matter is removed from them, and their formation more strictly confined to the type of the organism.

Of the mental phenomena in compound and divided animals, and in animals united by abnormal concretion.

a. In compound animals.

Among the lower animals there are many which really represent systems of numerous individuals, united by one common stem. Plants, likewise, are aggregates of many concurrent individuals rather than simple organisms. For the leaf-buds of a plant are individuals which have all the same structure, have the power of independent existence when separated artificially or spontaneously, and are capable of developing new systems of similar individuals. The vessels of each bud are prolonged in the vascular layers of the common stem as far as the root, and thus the stem resembles a fasciculus of distinct individual plants, which develop themselves at different points of its length.

The compound animals comprehend the compound Vorticellinæ, Polypifera, Entozoa, and Mollusca, as well as all those animals which propagate by division, at the period when their separating parts are not wholly detached. The distinct individuals of the compound animals are sometimes united by a common stem, of which they represent the branches, and from which they are developed by the formation of buds; as in the case of the compound branched polypes. Sometimes they are united in a radiate manner, which is the form of the Botrylli; whilst in other cases many are connected in one mass, or, like the Infusoria, which propagate by longitudinal division, they are united in a lateral series; or, again, like other Infusoria, and some Annelida, — which propagate by transverse division,—they are connected in a longitudinal chain. Most plants, and all the compound animals, are to be regarded as families of individuals, which either are developed singly upon the common stem, as in the majority of instances, or are compound even in their embryonic condition, as is the case with the Botrylli, according to the observation of Sars.* In some instances the different individuals composing the compound animal have certain important organs in common. Thus, in the Sertulariæ, the canal of the stem communicates with the digestive cavities of each single polype. In the Hydræ, it was observed by Trembley that the digestive cavity of the young polype at first formed part of that of the parent animal, and that the food passed from the one to the other. In the Nais, also, during the development of several new individuals by division, the intestinal canal is continued through the whole series, and the parent animal takes food for them all. In those Annelida which undergo spontaneous division, the imperfectly formed new creatures, which are merely composed of a certain number of the segments of the parent animal, at one period evidently obey the sensorium seated in the cephalic portion of the parent, and execute its desires and resolves. But, in proportion as their separation becomes more complete, and the parts which are to form the new animals become independent, and acquire new centres of nervous action by development of their cephalic portion, each of these new worms, also, becomes endowed with special will and desires, which it manifests distinctly enough even before it is quite separated, by its attempts to detach itself from the body of the parent worm.

The distinct polypes, which are united by a common stem in the compound Polypifera, are independent individuals, endowed with an independent will and nervous centre. The irritation of a single polype causes the retraction of that one only, and not of all the polypes of the stem. The stem itself has no individuality; it has no desire, and is incapable of conceiving any objects of desire. In it, however, resides the power of producing new individuals by the process of germination.

* Froriep's Notizen, 1837, No. 51.

In the persistent branched polypiferous animals the stem is not even capable of motion by the will of the individual polypes. Rapp, it is true, observed occasionally slight motions of a peculiar character in the stem of Veretillum, but these did not resemble voluntary motions. The Hydræ, while they are undergoing multiplication by germination, are compound systems of individuals, but these individuals after a time separate from each other; and the stem in them does not bear the same relation to the separate polypes as it does in the permanently compound Polypifera. The stem of the Hydra constitutes from the first the main part of the parent polype, and is subject to the cephalic portion of that individual; while, on the other hand, the young polypes manifest the influence of their will only as far as the point at which they are connected with the parent trunk, and at which their separation from it afterwards takes place.

b. Double monsters of the human species and of brutes.

Respecting the mode of formation of these double monsters, all that is essential has already been said. The following natural divisions include their various forms. The abundant examples contained in the Museum of Berlin may all be referred to one or other of the following general heads:—

I. The axis of the body in part double.

a. The upper part of the trunk double, while the lower part is single. *Axis sursum duplex.* Of this form of double monster, in which the cephalic and spinal axis are bifid at the upper part, there are all degrees, from the monster with a double muzzle or double head, to that in which the whole upper part of the body, as low as the sacrum, or still lower, is double.

b. The lower part only of the trunk or axis of the body double. *Axis deorsum duplex.* Of this form, also, there is every degree, even to that condition in which the entire trunk, and even the posterior part of the head, are double, and only the snout single.

II. *Axis duplex.* Two bodies with their axes distinct, united by identical parts with or without defect at the point of union.

a. Union without deficiency of parts; all parts of the two embryos being perfect. In this case each embryo seems to be partially cleft. For example, in the head of one $a\frac{b}{b}$, the two halves of the face, b and b, are separated from each other, the occiput, a, remaining undivided; and, in the same way, the two halves of the face, β and β, in the head $\frac{\beta}{\ }\alpha$ of the other embryo, are separated, while the occiput, α, remains single. Hence there is this confusion, $a\frac{b\beta}{b\beta}\alpha$, of the parts of the united heads; each face, $b\,\beta$, of the double head being composed of halves, which belong to two different embryos. The examination of the cranium and brain proves that this is the case.* The syncephalus, synthorax, syngaster, as well as the pygodidymus of Gurlt, when not combined with deficiency of parts, are varieties of this form of monstrosity. The syncephalus, without deficiency of parts, is the true Janus-monster. But there are cases of synthorax and syngaster, in which the condition of the thorax and abdomen is the same as that of the head in the Janus-monster.

b. Two embryos united by identical parts, with defect at the place of coalescence. Monstrosities of this kind are due to the same principle as the coalescence of corresponding organs of the two sides of the body in single monsters. The coalescence and loss of parts may be situated either at the side or at the front of the body. Such are the syncephalus aprosopus, in which the faces of both embryos are deficient, and the corresponding forms of the synthorax and syngaster. From the lateral syncephali there is a gradual transition to the monsters with partially double axis.

c. Two bodies united by dissimilar parts.

III. *Implantatio.*—Two bodies united, but only one perfectly developed, while the other remains in a rudimentary state.

a. Implantatio externa.—1. *Implantatio externa æqualis*, in which the parts of the imperfect embryo are connected with corresponding parts of the perfect one; as, for example, where the posterior parts of the body of a diminutive fœtus hang to the front of the thorax of a fully formed child; or where a third foot, parasitic hand, or supernumerary jaw is present. 2. *Implantatio externa inæqualis*, in which the perfect and imperfect fœtus are connected by dissimilar points.

b. Implantatio interna; where one fœtus contains within it a second.

IV. Parts of the body external to the axis, cleft so as to be double. It is sometimes difficult to distinguish this form of monstrosity from the preceding.†

Our knowledge respecting the mental phenomena of double monsters is very limited, the opportunity of observing them occurring very rarely, and most of these monstrous fœtuses dying soon after birth. Some few observations, however, have been instituted upon the most important forms of monstrosities. In that form in which the upper part of the axis is double, and the lower part single, it is found that the two heads do not each possess voluntary influence over the entire lower half of the body, as might have been expected; but that the right head moves only the right half of the body and the right lower

* Compare J. Geoffroy St. Hilaire, Hist. des Anomalies, tom. iii. p. 110.

† On the anatomy of the double monsters, consult Barkow, Monstra animalium duplicia per anatomen indagata. Lips. 1828.

extremity, while the left head moves the left half of the trunk and left lower extremity. These results have been obtained by observations instituted in the case of Rita Christina.* Irritation of the right foot also was felt only by the right head, and irritation of the left foot only by the left head. It was only when the middle line of the body was touched that it was felt by both heads. This form of monstrosity, therefore, would appear to result rather from the fusion or coalescence of two embryos, with loss or destruction of the intermediate parts, than from the partial division of one germ. In Rita and Christina the intestinal canal was double as low as the ileum, but thence downwards it was single. The desire of evacuating the bowels was almost always felt simultaneously by both. There can, consequently, be no doubt that the single part of the intestinal canal was produced by the coalescence of two intestinal tubes, of both of which a part of the walls was lost.†

With respect to the monsters in which the brain and cranial cavity are single, while the muzzle or the trunk is double, I have myself had the opportunity of making a single observation upon the laws of their sensations and volition. It was in the case of a calf, of which the body and occiput were single but the anterior part of the head and the muzzle double, there being three eyes, of which the middle one resulted from the fusion of the internal eyes of two faces. It is now many years since I saw this calf alive; I was able to observe it only for a short period, and know nothing of its anatomy. As the creature was not my property, I was interested only in ascertaining how it was affected by sensations. I touched, therefore, one of the mouths with a stick and was surprised to see the tongues of both mouths protruded simultaneously and in exactly the same manner. I cannot exactly recollect whether both tongues diverged when protruded, or whether they both moved towards the same side; but I am rather inclined to think that the former was the case. It is much to be desired that the opportunities of observing such cases should not be neglected. The simultaneous manifestation of one will in both the double parts of such monsters would accord better with the idea of their being produced by partial division of the germ, than with that of their being due to the coalescence of two germs.

The cases of *implantatio* are most frequently met with. The parts of the imperfectly developed embryo, when destitute of head, are generally void of sensibility, the perfect individual being conscious of no sensation from impressions made upon them. Such was the case in the body examined during life by Burdach,‡ in which four well-formed

* Serres, Recherches d'Anatomie Transcendante et Pathologique. Paris, 1832.
† Compare J. Geoff. St. Hilaire, iii. p. 189.
‡ Med. Zeitung des Vereins für Heilkunde in Preussen, ii. 209.

extremities hung from the superior abdominal region. This monster is preserved in the Anatomical Museum of Berlin. The appended extremities receive no nerves from the larger trunk, but are nourished by its mammary arteries.* Cases of this kind, however, have been observed, in which irritation of the rudimentary remains of the second embryo was felt by the fully developed individual.† And this appears in no way impossible, when we consider that the new noses formed by the rhino-plastic operation are at first insensible, but gradually acquire feeling. Hitherto, it has never been observed, that both heads of a double-headed monster have exerted voluntary influence over the entire single trunk. The possibility of this occurring, however, at least in the lower animals, cannot be absolutely denied. It is, indeed, much to be desired, that some accurate observations should be instituted upon the double-headed Hydræ with single trunk, which, as Trembley has shown, may with great ease be artificially produced, by dividing longitudinally the cephalic end of a polype. In the branched Vorticella, Carchesium polypinum of Ehrenberg, which propagates by spontaneous longitudinal division, the separate individuals thus produced are seated upon one stem endowed with muscular contractility. In this animal, therefore, the subjection of one common trunk or stem to two centres of volition may, perhaps, exist.

c. *Influence of the mind of the mother upon the fœtus.*

The connection subsisting between the mother and the fœtus resembles that between the parent polype and the gemmæ or buds developed upon it, which have each an individual vitality, and gradually acquire an isolated condition and independent centres of action. The will of the parent trunk has no influence over the motions of the developed germ, and we have no more reason to expect such an influence in the case of the human subject and mammalia. In the Nais, which multiplies itself by spontaneous division, the part which subsequently becomes a new individual moves under the directing influence of the brain of the original worm; but this is a different case: it is not the development of a new organism from an unorganised germ, but the mere isolation of a part from another organism, to the will of which it has been subject.

The influence of the mind of the mother upon the nutritive processes of the fœtus must also be considered in this place.

The general question which should first be determined is, whether the influence of the mind is so extended that determinate ideas of physical and tangible phenomena are able to cause their own realisation by corresponding plastic changes in any part of the organism.

* For a description of several similar cases, see J. Geoff. St. Hilaire. Op. cit.
† Ibid. p. 227. 231.

That the mind has such an influence over the sensations and motions is beyond a doubt. But the question is, whether the idea of a special form with a particular colour can cause the organism to realise this form and colour by a change in a part of the skin of the body. This question is involved in that respecting the influence of the imagination of the mother upon the organisation of the fœtus; but in the latter case we are required to admit that the mind can exert an influence even external to the organism to which it belongs.

The cure of small organic lesions, such as warts, through the medium of the imagination, cannot be adduced in support of the affirmative of the above question; for in such cures the mental idea does not produce a definite form, but merely excites an increase of the natural nutritive process. The natural organic action being increased is inimical to the existence of a morbid growth, such as a wart; and, hence, the latter wastes. But the imagination of the mother is supposed to produce some positive results,—a modified structure, even in form corresponding with the efficient idea. That such an influence exists is improbable, from the mere circumstance that it is supposed to extend from one organism to another; while the connection of mother and child is nothing more than the closest possible juxta-position of two organisms in themselves perfectly distinct, which exert an attraction on each other by their contiguous surfaces, and one of which receives its nutriment and warmth from the other. But there are many other reasons which tend to refute this old and popular superstition. Nearly all the monstrosities born in Prussia are brought under my observation; and, nevertheless, I can assert, that a new form scarcely ever presents itself, but, on the contrary, that the great mass are constituted of certain kinds of monstrosities constantly repeated, which belong to the great categories of arrests of development, divided or cleft parts, defects, coalescence of lateral organs with deficiency of the intervening parts, &c. In the accounts given of these monsters, however, it is frequently stated that the mind of the mother when pregnant was strongly affected by some object, and the way in which this happened is described, although the monstrosity presents not the slightest resemblance to the object in question. Moreover, when we consider that every woman during her pregnancy must certainly be frightened several times, and that very many have once at least, if not oftener, a presentiment of evil from such frights without any result following, we certainly must perceive that, when a monster happens to be born, circumstances will not be wanting to afford an explanation of its occurrence conformably with the popular belief.

The only way, therefore, in which the mind of the mother can reasonably be supposed to affect the fœtus, is by a sudden emotion in the former producing an equally sudden change in the organic actions subsisting between her and the fœtus, so as to bring about an arrest of development in the latter, or to fix its forms at certain transitory stages of metamorphosis; without the idea in the mother's mind having any direct influence upon that part of the fœtus in which these arrests occur. Most monsters are abnormally formed in several distinct parts, and frequently we find arrests of development in very different and distant parts of the same fœtus.

If we are correct in denying that ideas conceived in the mind of one organised being, can be realised in the structure of another individual; then it will be scarcely probable that one person can influence the ideas of another in any other way than by speech or signs. Even though it should be admitted, that organic beings may exert unknown or what are called "magnetic" influences on each other, and, perhaps, without contact, through the medium of the nerves; still the communication of ideas or particular states of the mind from one person to another, as in the pretended phenomena of animal magnetism, &c., would remain as improbable as it is inconceivable.

CHAPTER III.

OF THE TEMPERAMENTS.

The temperaments are peculiar permanent conditions or modes of mutual reaction of the mind and organism. They are chiefly dependent on the relation which subsists between the "strivings" or emotions of the mind, and the excitable structure of the body. Men differ in their capability of conceiving merely simple or general ideas; in their faculty of abstraction, reasoning, memory, imagination, and power of combining ideas: such differences, however, do not constitute the temperaments, but rather the varieties of talents. The temperaments at present recognised, have been distinguished from the earliest times, and no better division of them could perhaps be offered. The views on which the older writers based their division of these temperaments, were, however, as incorrect as their notions respecting the primary elements of the human body. Galen's distinction of the sanguine, phlegmatic, choleric, and melancholic temperaments was founded on the hypothesis of the Greek philosophers, concerning the four elements of nature,—air, water, fire, and earth, and the corresponding qualities of heat, cold, dryness, and moisture. It was supposed that there were four corresponding primary components of the human body, namely, blood, phlegm, bile, and black bile; and the preponderance of one or other of these components in different persons was imagined to produce the different temperaments.

It would very little aid the elucidation of this subject to relate all the various divisions of the temperaments that have been proposed. We might certainly expect to find the temperaments connected with the great functions of the body, and with the systems of organs subservient to those functions; for example, to find different temperaments produced by the preponderance of the vegetative (nutritive), motor, or sensitive systems. In this case we should have a vegetative, a motor, and a sensitive temperament. But the mental peculiarities of the temperaments are not dependent on the excessive development of these systems of organs. Great muscular power is far from producing a choleric individual; and the phlegmatic temperament occurs both in those whose vegetative or nutritive functions are well, and in those in whom they are ill performed. All well nourished and stout persons are not phlegmatic, and many who are very thin have that temperament in a marked degree. Choleric persons, also, may be well nourished or thin, of a muscular or of a delicate build; and the same may be said of the sanguine. All the attempts to characterise the temperaments by a particular structure of body are defective. We ought, in fact, to distinguish from the temperaments particular physiological constitutions of the body, which are really dependent on the relative development of the different systems of organs, such as the muscular, vegetative, and sensitive constitutions; though these may be combined with peculiar temperaments.

Much confusion has arisen relative to this subject, from a proper distinction not having been drawn between the pathological constitutions of the body and the temperaments of the mind. It has been imagined that persons of the phlegmatic temperament are bloated, pale, and leucoplegmatic; a state which would indicate a relative excess of the liquor sanguinis in comparison with the red particles of the blood. Hence a predisposition to diseases of the fluids. Scrofula and chlorosis were supposed to attend this temperament. The sanguine temperament has been confounded with the phthisical constitution or consumptive habit, and has been regarded as predisposing to fever, pulmonary disease, and active hæmorrhages. Choleric persons, again, are supposed to be liable to hepatic disease. All such notions arise from the error of not distinguishing the leuco-phlegmatic, phthisical, hepatic, and nervous constitutions, and other abnormal predispositions of the body, from the temperaments of the mind. There are many choleric persons, who, when labouring under emotion, suffer in any other organ sooner than the liver; who, for example, become affected with indigestion, palpitation of the heart, or nervous tremors and twitchings. The morbid bilious constitution of the body must exist in persons who have a yellowish tint of the skin, and suffer disorder of the liver, not merely when they are affected with grief and anger, but when they are subject to any mental emotion.

According to my view, the temperaments are entirely dependent on the different degrees in which different individuals are disposed to the strivings and emotions arising from the depression or excitement of the feeling of self; in other words, on the different degrees of disposition to the states of desire, pleasure, and pain, and on the extent to which these states of the mind are promoted by the composition and states of the organs of the body. We have already stated it to be probable, that the strivings or emotions of the mind are due to that fundamental property of organic beings, which causes them to seek the integrity of self, and which, without even exciting distinct sensations, yet influences the conception of ideas and enters into combination with them.

When the organisation of an individual is such, that his mental strivings or emotions are neither intense nor enduring, he is of the *phlegmatic* or unexcitable temperament, in which the ideas of things, and the combinations of these ideas, remain more or less completely mere ideas, uncombined with any strong feelings of the restriction or expansion of self,—unmodified by pleasure, pain, or desire. The phlegmatic temperament to which we here allude, is by no means a pathological condition. In persons of this temperament ideas are conceived with as much rapidity as in others, and there may be the same power of mind as in other temperaments. When the intellectual faculties are good, this temperament will render a person capable of more difficult acts, and successful in a more extraordinary degree, than would be possible were his impulses rendered stronger by a more passionate temperament. Such a person, whose mental strivings, or emotions, are not violent, remains cool and undisturbed, and is not drawn away from his determined course to the performance of acts which he would repent on the morrow;—he is more sure and trustworthy than persons of an opposite temperament, and his success more to be depended on: in times of danger and at moments of importance, when good judgment, calculation, and reflection are needed rather than very quick action, his powers are all at his command. Great energy of action, which is dependent on the susceptibility of the strivings of self, is not to be looked for in a truly phlegmatic subject, such as I have described; but in place of it, all the good effects of delay and cautious calculating endurance. Circumstances which would excite the choleric and sanguine to hasty passionate acts, and would cause them painful and bitter feelings, are regarded by the phlegmatic without emotion, exciting merely his meditation; so that he neither complains nor takes part in them, but pronounces dispassionate reflections upon mankind and their conditions. He does not feel his misfortunes strongly, bears them with patience, and is also not affected in any great degree by the sufferings of others. He contracts few friendships, but when he has formed them does not break them, and may be a perfectly trustworthy and useful man in society. Where rapid action is required the phlegmatic person is less successful, and others leave him behind; but when no haste is necessary, and delay is admissible, he quietly attains his end, while others have committed error upon error, and have been diverted from their course by their passions. The phlegmatic person knows his proper sphere, and does not trespass on that of others or come into collision with them. From this conduct, as well as from an orderly and steady course of action, in which he keeps his object in view, and avoids self-deception, he derives a contented tone of mind, free alike from turbulent enjoyments and deep suffering.

That kind of phlegmatic disposition which is characterised by sluggishness, apathy, want of sympathy, irresolution, tediousness, difficult comprehension, and slow mental progress, and which prefers pain not acutely felt to labour and exertion, is an abnormal or pathological condition. The more excitable or unrestrained temperaments are the choleric, sanguine, and melancholic. The passions are the manifestations of the emotions or strivings of the mind, and of the restraint or exaltation of these strivings, attended with feelings of pain or pleasure, and produced by ideas of particular objects. The striving of the mind may be so strong, and the attendant organic actions so inexhaustible, as to overcome all impediments; or the pleasurable or painful emotion may be intense, while the sensibility is excessive, and the reaction by continued strivings of the mind and organic action relatively feeble. In the first case the temperament is the choleric; in the second, it is either the sanguine or the melancholic, both of which are dependent on the same essential quality of mind, and more nearly allied to each other than to the other temperaments.

The choleric person exhibits a power of action remarkable both for intensity and endurance, under the influence of passions or desires which have reference to himself or others. His emotions are highly excited whenever he experiences any opposition or check to the strivings of his mind, whether these strivings tend to the extension of the power of self, or merely to the maintenance of its integrity; and his ambition, his jealousy, his revenge, and his love of rule, know no bounds as long as he is under the influence of passion. He reflects little, but acts unhesitatingly, either because he alone is right, or more especially because it is his will so to act; and he is not readily convinced of his errors, but persists unalterably in the course to which his passion prompts him until he ruins both himself and others.

In the sanguine temperament the main tendency of the mind is to the feeling of pleasure; while there is great excitability but little durability of the states of emotion when excited. An individual of this temperament is much the subject of pleasurable feelings, and seeks that which will excite them; he readily sympathises, and forms many friendships, but as readily relinquishes them; frequently changes his inclinations, and is little to be depended on; he is easily enraged, but as soon relents; promises readily and much, and is sincere at the time, but neglects his promises if they are not immediately performed; conceives many projects, but never executes them; is charitable towards the faults of others, and expects the same indulgence for his own errors; lastly, he is easily appeased, is open-hearted, amiable, good-tempered, social, and uncalculating.

The feeling of pain is the fundamental tendency of the mind in the melancholic temperament. The melancholic person is as easily excited as the sanguine, but in him painful sentiments are of longer duration and more frequent than pleasurable feelings; the sufferings of others excite his deep sympathy; he fears, repents, mistrusts, and has misgivings on every occasion, and pays especial attention to everything which favours this tone of mind. He is prone to fancy himself offended and injured, or neglected; impediments which he meets with render him dejected, timid, and doubting; and he loses the power either of acting or of judging. His desires are full of sadness, and of the feeling of having suffered a loss: his grief is immoderate and inconsolable.

These delineations of the principal features distinguishing the temperaments might easily be extended; but to enter into any further details would be exceeding the bounds of our proper field of inquiry.

CHAPTER IV.

OF SLEEP.

The excitement of the organic processes in the brain which attends an active state of the mind, gradually renders that organ incapable of maintaining the mental action, and thus induces sleep, which is to the brain what bodily fatigue is to other parts of the nervous system. The cessation or remission of mental activity during sleep, in its turn, however, affords an opportunity for the restoration of integrity to the organic conditions of the cerebrum, by which they regain their excitability. The brain, whose action is essential to the manifestation of mind, obeys, in fact, the general law which prevails over all organic phenomena,—that the phenomena of life being particular states induced in the organic structures, are attended with changes in the constituent matter of those structures. Hence, the longer the action of the mind is continued, the more incapable does the brain become of supporting that action, and the more imperfectly are the mental processes performed, until at length sensations cease to be perceived, notwithstanding the impressions of external stimuli continue. This is entirely analogous to what frequently occurs during the waking state in the case of individual sensations. A coloured spot regarded stedfastly for a long time becomes at length invisible, and nothing more than a general impression on the retina, without defined details, is perceived. In persons of feeble nervous system long direction of the sight to one object causes the whole field of vision to become dark. Not merely the action of the mind, but the long-continued exertion of other functions of animal life, such as the senses or muscular actions, induces the same exhaustion of the organic states of the brain, and thereby want of sleep and sleep itself; for these different systems of the body participate in the change which the organic condition of any one of them may undergo. Lastly, impairment of the normal organic state of the brain by the circulation through it of blood charged with imperfectly assimilated nutriment, as after full meals in which spirituous drinks have been taken, also induces sleep. The narcotic medicaments act still more strongly by the change they produce in the organic composition of the sensorium. Even the increased pressure of the blood upon the brain, produced by the horizontal posture, may become the cause of sleep. In many persons, for instance in myself, sleep is brought on at will by the assumption of the recumbent position, while the thoughts are kept in an unexcited state.

The duration of the periodical state of sleep, and the time at which it occurs, are dependent partly on external and partly on internal causes. Sleep generally occurs at night-time, while the waking state is coincident with day, on account of the senses, and consequently the brain, being subject to many causes of excitement during the day, but to few or none at night. The causes which determine the duration of sleep and waking are seated, however, in the organism itself. The day may become the time of sleep instead of night; and if a person keeps himself in a state of activity every night, he will sleep as long by day as he would otherwise have slept by night. It is, moreover, the nature of many animals, for example of the so-called nocturnal animals, to be in action during the night, and to rest by day.

The periodical recurrence of sleep and the waking state is, therefore, essentially connected with something in the nature of animals, and is not dependent on the simple alternation of day and night. But the periods of sleeping and waking, in accordance with a pre-established harmony of nature, have been made to agree with those of the earth's revolutions.

In this respect the short periods of twenty-four hours, during which the alternation of sleeping and waking occurs, correspond to the longer periods of alternate rest and activity which animals present in the rut, in their migrations, in the changing of their feathers (moulting) and hair, and in hybernation and the summer-sleep. For, although hybernating animals fall into the torpid state on account of their inability to maintain undiminished their state of vital activity and power of developing heat without the aid of external warmth, yet, even in them, as the experiments of

Czermack and Berthold have shown, there is an internal cause resident in the organism itself, which renders periodic rest necessary for the restoration of their excitability. The rellmouse, Myoxus glis, frequently is torpid in the summer; and the dormouse, Myoxus avellanarius, hybernates in the winter, whether it is in the open air or kept in a heated chamber; the only difference being that the sleep is more profound in a cold atmosphere, and comes on earlier than in the heated room. In the open air the animals become torpid as early as October; while in the warm room they wake every day for a certain time until about the middle of December, when the sleep becomes more and more continued, and deeper, so that it is not again interrupted, or only very rarely, before the middle of March. The cause of hybernation, therefore, according to Berthold, is not external cold alone, nor the want of food, but a general deficiency of vital energy, analogous to that displayed in the moulting of birds and similar phenomena, and connected with the changes of the seasons.*

The daily sleep of plants, and their winter sleep, present in this respect exactly similar phenomena, and prove that neither the internal tendency to periodical phenomena, nor the dependence on external stimuli, is peculiar to organic beings supplied with nerves and a central source of action.†

The waking of plants is manifested by the expansion of their leaves, and the turning of their upper surface towards the light. The sleep of plants, first noticed by Cordus, and afterwards observed by Linnæus to be a general phenomenon, consists in the leaves assuming the erect position, and folding themselves together. During the day, also, plants inhale carbonic acid, and exhale oxygen, while at night they absorb oxygen from the atmosphere. The movements attending the sleep of plants are most evident in the youngest leaves of the stem, and in the petals of the flowers, and least manifest in the older leaves. The sleep of young animals, also, is most profound. There are plants, as well as animals, which sleep through the day and are awake by night; the stimuli afforded by day being in both cases less adapted than the conditions of night to maintain the activity of the organism. In most plants, as in animals, sleep is the result of the state produced by the continued stimulus of light, and of the absence of this stimulus during the night-time. For, according to the experiments of Decandolle, the period of the sleep of plants may be reversed by producing artificial night and artificial day. But still there is a cause both of the sleep and waking seated more deeply in the organism itself. From the observations of

* See Muller's Archiv. 1835, p. 150; 1837, p. 63.

† See the instructive paper on the sleep of plants, by E. Meyer, in the Vorträge aus dem Gebiete der Naturwissenschaften und der Œconomie, herausgegeben von C. von Baer. Königsberg, 1834, p. 127.

Duhamel, Ritter, and Decandolle, we learn that the leaves of plants kept in constant darkness, open and close their leaves at regular intervals.

In general characters, therefore, the sleep of animals and that of plants resemble each other. There are, however, points of great dissimilarity. The position which the leaves assume during the sleep of plants is the same which they have when young, and as yet unfolded. But this position in sleep is not the result of relaxation; for it does not easily admit of being changed, so that the leaves break off in the attempt. Moreover, in the sensitive plants, the position which the leaves have during sleep is the same that they take when irritated. A stimulus applied to a sensitive plant at one spot, in such a manner as to give no mechanical shock to the whole plant,—for instance, the stimulus of heat applied by means of a convex lens, — is propagated gradually to other parts, the leaves closing in succession, according as they lie at a less or greater distance from the irritated point. It appears from the researches of Lindley and Dutrochet, confirmed by Meyer, that two forces are in action in the intumescence at the base of the leaf-stalk, (see page 867, fig. 55,) one of which tends to raise the leaf, the other to depress it. If the external, or lower side of the intumescence is divided, the leaf is depressed towards that side, as if by turgescence of the opposite side of the intumescence, and division of the internal or superior side produces the opposite result. The elevation and folding of the leaves, which occurs in the absence of light, may be regarded as the effect of the want of the stimulus of light upon the upper surface of the leaves; for in that case, the corresponding part of the intumescence, wanting its proper stimulus, might be supposed to become passive; whilst the inferior half of the intumescence being, perhaps, less dependent on the influence of light, might remain in an active state, and by turgescence elevate the leaf. The same movements, however, are produced by mechanical and chemical stimuli; they cause the leaf to assume the same position as when the upper half of the intumescence is divided. A mechanical shock, therefore, acts exactly as an arrest of action, or like the exclusion of the appropriate stimulus; and it would seem that this disturbance or arrest of action exerts a great influence on one side of the intumescence, and none on the other. We can give no other explanation of the action of stimuli upon the sensitive plants, which would be applicable also to the causes inducing their state of sleep. According to this view, however, the movements of these plants lose all their analogy with the contractions of animal tissues. But the inferior half of the intumescence, the cellular tissue of which remains in a state of turgescence during sleep, may, on the other hand, be compared to that part of the animal organism which continues to perform its functions during the corresponding state in animals.

The sleep of animals is a phenomenon dependent on a change in the animal part of the organism alone. All the functions of organic life — namely, the processes ministering to nutrition, with all the involuntary movements attending them,—pursue their ordinary course. Even the involuntary movements of the animal system of muscles, such as those of respiration, and many other movements of the same kind, as we shall presently show, do not partake of the repose of sleep. The organic system has its periods of remission and rest, but these are not coincident with the sleep of animal life, and are very different for different organs. The heart has its period of rest after each beat; the intestines and uterus have theirs, also, at different times; and the change and new formation of the hairs and feathers show us that the nutritive processes, also, have alternate periods of rest and action. Even the growth of a single tooth, spine, or feather, presents to us a cycle of states, in which the formative process has different degrees of activity. For, during the formation of the shaft of the latter organs, or the fang of the tooth, the nutritive action can be by no means the same as at the time when the crown of the tooth, the point of the spine, or the barb of the feather, is formed. In animals whose hair is knotted, like the vibrissæ of the seal, the nutritive process, on which their growth depends, must consist of a regular succession of alternate remissions and exaltations, since these structures grow only at their root.

All the phenomena of organic life, and, indeed, all the phenomena presented by the animal body, with the exception of the true animal functions which are under the influence of the mind, obey, like the development of the germ, a law of absolute necessity; although, like it, they conform to a well-adapted plan; and the nutrition and maintenance even of the organs of animal life are not dependent on the operations of the mind or intellect. We may, therefore, regard sleep and the waking state, as the result of a species of antagonism between the organic and the animal life; in which the animal functions, governed by the mind, from time to time become free to act, while at other times they are repressed by the organic force acting in obedience to a law of creative nature. It is true that even in the waking state the organs of animal life are under the dominion of the organic force; but the different properties of the muscles and cerebro-spinal nerves, which are the result of organisation, are engaged in actions very different from those of the organising process. In sleep, on the contrary, when these animal functions entirely, or for the most part, cease, the organic processes are almost the only ones which continue; and, during that state, even the organs of animal life are rendered capable of renewed action by the operations of the organising force, which proceed without the consciousness of the animal, though accordant with a well-contrived plan and with reason.

In consequence of all parts of the organism participating to a certain extent in the states of excitement which affect primarily only one part, the waking of the system of animal life, and its consequent increased excitement, must be gradually imparted to those organs which are under the influence of the organic nervous system; and any functions which these organs may perform, in addition to the mere process of organisation, will be in some measure affected. Hence it is that the heart's action becomes rather more frequent at the time of waking than it was during sleep. The radiation or extension of excitement from the animal system to the organic ceases during sleep, and so far the organic part of the body has at that time a remission of action, though in a less degree than the animal system. If the waking state of the animal system is maintained much longer than natural, this extension of excitement from it to the organic system not merely becomes more manifest, (for instance, in the acceleration of the heart's action,) but the great exhaustion of the organised material by continued action is imperfectly balanced by the organising process. Hence the signs of defective nutrition, which soon show themselves when watching is long protracted.

Having considered thus far the nature of sleep generally, we will now study more minutely its phenomena. On the commencement of sleep the senses cease to perceive external impressions, and the play of ideas, and the emotions, are entirely or in greater part silenced. The will ceases to rule the muscles; the eyelids, which experience the sensation of fatigue, are no longer under command; the head droops, and this state of inaction soon extends over the whole animal system of organs.

When sleep is perfect there is generally a complete absence of voluntary motion; while the involuntary movements of the organic muscles, and those movements of certain animal muscles which are only in part under the influence of the will, such as the respiratory movements, continue; the movements last mentioned merely ceasing to be influenced by volition. The movements of the heart, and the respiratory movements, are somewhat less frequent than in the waking state. The action of some animal muscles is increased during sleep, they being apparently released from some counteracting force which opposed them in the waking state. Such is the case with some of the muscles of the eyes, as well as with the muscles of the extremities in birds which sleep standing on one or both legs. During sleep the eyes have a peculiar position. At that time, as well as in a state of mere sleepiness, both eyes are turned inwards and upwards. This movement is still more strongly displayed in disorders of the nervous system; for example, in epilepsy and catalepsy. This position of the eye during sleep also gives it a very different expression from that which it has in death. The iris is contracted in a person asleep, and the pupil consequently narrowed; but on his awakening the pupil always dilates, becoming first, indeed, very wide, and then undulating, until it acquires the mean size which it has in the waking state. (See page 685, 1st edit. and page 736, 2nd edit.) A greater amount of external warmth is required for the body during sleep than at other times; and immediately after the awakening from sleep there is frequently great sensibility to cold.

When, during sleep, the conception of ideas by the mind does not entirely cease, dreams arise. These are for the most part composed of simple ideas and emotions; but general notions sometimes come into play, and movements affected by the animal muscles may be combined with the ideas as in the waking state. This condition of the mind is "dreaming," as long as the sensorium is disturbed by something which gives to the operations of the mind a character opposed to that of the ordinary conceptions and thoughts of the same person. The ideas conceived in dreams so far resemble those of the waking state, that they may refer to any period of the past life; just as in our ordinary condition we may look back to all periods of our life, and think at one moment of yesterday, and the next of times years past. If the ideas which occupy the mind during the waking state have a certain degree of persistence, the same ideas will recur in dreams during sleep. The dreams of some persons, on the other hand, refer chiefly to times long past. Many blind people, after they have been some time deprived of sight, cease to dream of visible objects, but their dreams accord with their present mode of intercourse with the external world. Other individuals who have lost their sight, continue through their whole life to dream of visible objects. The important circumstance, therefore, regulating these dreams of visible objects by blind persons, is not the time which has elapsed since the sight was lost; for Huber, who had been blind since his eighteenth year, when in his sixty-sixth still dreamed of objects which appeared distinctly visible to him, though these dreams referred to the time at which he was possessed of vision. The facts which we learn from such cases are, that the internal parts of the apparatus of vision are alone essential to the production of phantasms, and that ideas recur, which were originally conceived previously to the loss of sight.*

In the simplest form of dream the action of the mind is confined to the mere conception of simple ideas, to the exclusion of general notions;—an inferior kind of intellectual action, which characterises the mind of brute animals, and also, for the most part, the human mind in the state of intoxication, on account of the disturbance of the organic conditions of the brain in that state. These dreams are accompanied by phantasms (see page 1394). The senses which are thus excited by internal causes may also be called into action by external causes of adequate intensity; but these external impressions, on account of the weakness of the reasoning faculty during sleep, suggest incorrect ideas. A person asleep feels himself in an uneasy position, and believes that he is bound and held down by force. His arms are folded one over the other, and he

* See Froriep's Notizen. 838, p. 118.

thinks they are held so by another person. In such cases, the images of persons performing the actions thus conceived in the dream are also produced. Again, the sensation of the urinary bladder being full may be perceived during sleep; but the dreamer, believing that he is awake and out of bed, is led by this sensation actually to evacuate the urine. The increased excitement, of which the sexual organs are from time to time the subject, gives rise to the conception of corresponding images even in dreams. The lamp burning during sleep and the extinguishing of it also exert an influence upon the images conceived in dreams. The cessation of a noise to which the sleeper is accustomed, such as the sound of a mill, excites ideas in the mind in the same way as a sudden noise occurring after previous silence. The serenade and its cessation are both perceived during sleep; but incorrect ideas and phantasms are connected with these sensations, which become interwoven in the web of our dreams.* The predominant emotions of the mind, also, influence the character of the dreams. When the mind is under the sway of depressing passions, the dreams will have a terrible or mournful character.

Sometimes we reason more or less correctly in dreams. We reflect on problems, and rejoice in their solution. But on awaking from such dreams, the seeming reasoning is frequently found to have been no reasoning at all, and the solution of the problem, over which we had rejoiced, to be mere nonsense. Sometimes we dream that another person proposes an enigma; that we cannot solve it, and that others are equally incapable of doing so; but that the person who proposed it, himself gives the explanation. We are astonished at the solution which we had so long laboured in vain to find. If we do not immediately awake, and afterwards reflect on this proposition of an enigma in our dream, and on its apparent solution, we think it wonderful; but if we awake immediately after the dream, and are able to compare the answer with the question, we find that it was mere nonsense. I have, at least, several times observed this in my own case. In dreams in which we seem to hold a conversation with other persons, the remarkable circumstance is, that the arguments and counter-arguments which rise in the mind, are connected with the ideas of the corresponding persons, just as notions are associated with certain signs. It occasionally happens in such dreams that questions are asked and no answer given, because we are ourselves unable to answer them.† Sometimes possible combinations of circumstances are presented to our minds in dreams, with the character of forebodings, and with all the distinctness of reality; and as anything which is possible may become actual, these circumstances may really occur without there being anything wonderful in the matter. For instance, if we are much interested in a person, and regard him with some

* Various other examples are adduced by Prevost, from the observation of his own dreams. Biblioth. Universelle, 1834. Mars. Froriep's Notizen. pp. 888, 889.

† Compare Prevost's Remarks. loc. cit.

kind of emotion, know him intimately though not perfectly, and, though we think him honest and sincere, have, nevertheless, conceived it to be remotely possible that he is the reverse; this person may, in our dreams attended with phantasms, appear in situations which show him to be dishonest and insincere: and if it should soon afterwards be proved that such really is the case, the dream appears wonderful, although it is nothing more than a play of ideas excited by a leading thought, which is cherished with the passions of fear and love. Sometimes the sick perceive in their dreams countenances of beneficent persons who advise them to adopt this or that proceeding; and the measures thus suggested occasionally prove successful. Physicians, however, who frequently meet with such prophetic dreams, have remarked, that they in many instances prescribe for themselves measures which are manifestly injurious, and which, therefore, are not carried into effect.

The indistinctness of the conceptions in dreams is generally so great that we are not aware that we dream. The phantasms which are perceived really exist in our organs of sense. They afford, therefore, in themselves as strong proof of the actual existence of the objects they represent, as do our perceptions of real external objects in the waking state; for we know the latter only by the affections of our senses which they produce. When, therefore, the mind has lost the faculty of analysing the impressions on our senses, there is no reason why the things which they seem to represent should be supposed unreal. Even in the waking state phantasms are regarded as real objects when they occur to persons of feeble intellect. On the other hand, when the dreaming approaches more nearly to the waking state, we sometimes are conscious that we merely dream, and still allow the dream to proceed while we retain this consciousness of its true nature.

It very frequently happens, that in our dream we seem to be incapable of executing certain movements which we desire to perform. For example, we desire to escape from a danger, but cannot move; here the dream corresponds to a real state of the sensorium, which is in sleep unable to determine the nervous actions necessary for voluntary motion. Some persons, however, have in dreams a certain command of voluntary motion; and, while they sleep and dream, talk confusedly, or, sometimes, even coherently. The same exertion of voluntary power, also, is required by persons sleeping in difficult postures: for instance, by postilions sleeping, as often happens, on their horses; also by birds, which sleep standing, sometimes only on one leg. In fact, it is necessary to constitute sleep and dreams that a very large portion of the ideas which can be called into action in the waking state should be passive; but those ideas which are active may, unless the sleep be very deep, call the organs of motion into activity. The near connection of the different pathological states of sleep with each other is here rendered manifest. The speaking of distinct coherent words during sleep, the rising from bed, and the performance of different acts in that state, are all phenomena of exactly the same kind. The somnambulist is scarcely to be separated from the *somnostatist*,—the bird standing while it sleeps.

The simplest degree of somnambulism is observed in children of excitable nervous system, who, while they yet sleep, become restless, call out, cry, and are quieted and comforted by persons speaking to them, whom they understand, and even recognise when their eyes are open; although, notwithstanding they are thus capable of voluntary movements and susceptible of ideas from external impressions on their senses, they do not for a long time awake from the dream which has alarmed them. In this case the mind is in a certain degree awake, but there are not at first present ideas of sufficient distinctness to restore the mass of ideas, disturbed by the dream, to a state of equilibrium. This state is similar to that of a person just awaking from sleep, with whom we may converse, although he gives confused answers, and confounds what is going on around him with the images and ideas which belonged to his dream.

In more extreme degrees of somnambulism, the dreamer rises and performs all the acts of life under the guidance of those ideas which are in an active state, and of the sensitive impressions connected with those ideas. He performs acts determined by his dream, and when they are attended with danger he is unconscious of it; he crosses, for example, narrow planks, as a child would do, that is not aware of danger and therefore does not tremble. It is not really very difficult to walk over an inclined plane, if we do not know that it is greatly elevated above the ground; and we should be able to walk over many roofs if they were placed upon the ground. The somnambulist associates only ideas which bear some relation to those already in action. No other ideas exist for him. He sees and hears; but is disturbed by nothing which is foreign to the train of ideas which constitute his dream, unless he be actually awoke.

Sleep ceases as soon as the susceptibility of the brain for those organic states, which are necessary for the play of ideas and reasoning, is perfectly restored. The condition of the various parts of the body is then again distinctly perceived. But sensations of sufficient intensity produced by external objects, or even strongly excited ideas in dreams, will arise from sleep which is not normally at an end. Strong emotions felt in dreams, such as fear and other passions, very frequently put such an abrupt end to sleep. The emotions here excite actions of the body, as in the waking state, and a stronger and increasing excitement is thus diffused through the system of the sleeper, which at length frees the brain from its fettered state.

As soon as we awaken, we analyse the first impressions on our senses, think where we are, whether in this or that chamber, and consequently whether in this or that town; we try next to recollect what time of day it may be, and correct the errors which we may in the first instance fall into with regard to this question. Sometimes the play of the ideas during sleep is so limited, and so completely unconnected with the ordinary ideas respecting the individual existence of the sleeper, that on awaking he has to collect the ideas having reference to his individuality in order to know who he is.

Sleep, in a greater or less degree, as Aristotle correctly remarked, falls to the share of all animals.* Some brute animals even dream; the dog, for example, barks in his sleep. In some, the periods of sleep are less distinct and regular; and this is particularly the case in the cold-blooded animals. They, however, appear to be subject to states analogous to sleep. Frogs, which croak a part of the night during summer, generally become quiet after midnight, especially when the pairing season is passed. Insects and spiders are frequently found in a lethargic or torpid state; and it is probable that all animals in which no regular periods of sleep and waking have hitherto been observed, have an equivalent for sleep in the state of inactivity and rest which they from time to time present.

To return to man. — Persons in whom the organic functions predominate, who are stout and full-blooded, sleep longer and require more sleep; and the contrary is the case with thin persons. Individuals of excitable, but at the same time energetic constitutions, and who are with difficulty fatigued, require less; those of an excitable, but more readily exhausted habit of body, require more sleep. In youth sleep is longer, and is more indispensably requisite, than in old age. This difference seems to depend on the greater predominance of the nutritive organic functions in youth. Hence the great length of time passed in sleep by the new-born infant. This disposition to sleep is constant in the child as long as the organising action finds material in new nutritive matter supplied by food; and the child awakes when it requires nourishment. In the adult, also, abundant food induces sleepiness, partly by giving increased activity to the organic functions, and thereby disturbing the reaction of the animal functions, and partly by the pressure which the crude and imperfectly assimilated nutriment newly introduced into the blood exerts upon the brain. As causes favouring sleep, we must reckon also the impressions made on the sensorium by general stimulants of the skin, as friction of the surface, baths, &c., and the effects produced on the sensorium from within by sedative and narcotic medicines.

* De Somno et Vigiliâ.

BOOK THE SEVENTH.

Of Generation.

SECTION I.

Of homogeneous or non-sexual generation.

CHAPTER I.

OF THE MULTIPLICATION OF ORGANIC BEINGS IN THE PROCESS OF GROWTH.

a. In Plants.

On a superficial comparison of the fully developed state of plants with their earliest condition, it is manifest that during their growth the organs which compose them undergo a multiplication, and that parts, which in the very young plant exist singly or in small number, are in the full-grown plant exceedingly numerous. The stem has sent out branches; and these branches have again given off side branches, to which they bear the same relation of central axes that the original stem bears to them. The leaves, also, which were at first very few, have undergone a manifold increase. A more attentive examination, however, soon shows that in this process something more than a mere multiplication of the organs of a single individual has taken place; and that, in fact, the full-grown plant consists of a system of individuals,* of a multiple of the vegetable organism which constitutes the plant in its earliest condition. This is demonstrated by the properties which parts of this compound system separated from the rest display. A branch of such a plant, separated from the stem and set in the ground, presents all the characters of the parent organism, and continues to live, nourishing itself and increasing. Even a subordinate portion, or twig, cut from this branch, manifests exactly the same properties. A portion cut from the end of the axis of very many plants, provided it contain stalk and leaves, will vegetate, and serve to continue the species. Now, the part separated from the parent stock in these instances, and still continuing to grow, most closely resembles the young plant in the condition in which it appears when first developed from the seed; and since each of the similar parts which together constitute a tree may be regarded as a young plant, endowed with the power of vegetating so as to form a large tree, so the fully developed tree itself must be viewed as a system of

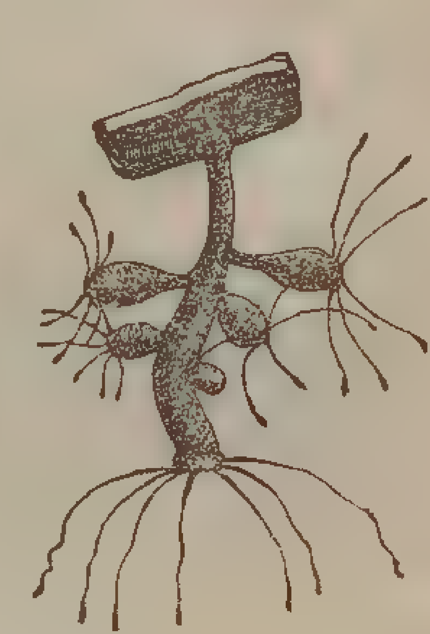
* Darwin, Phytonomia.

individual vegetable organisms associated together, and exerting a reciprocal influence on each other during their life, but yet separable as independent beings. The stem of a plant is the common fasciculus in which all the separate individuals are bound together. Hence it is that the thickness of the stem diminishes from below upwards in proportion to the number of branches given off; and by minute anatomical investigation it is revealed, that not merely the pith or medulla of the stem is continuous with that of the branches through the medium of the medullary rays, but also that the vessels entering into the composition of all the young twigs are prolonged downwards through the stem towards the roots. Every new development of leaf-buds throughout the tree is attended with the formation of a new stratum of vessels, corresponding to these leaf-buds, in the stem, while the older layers undergo the process of lignification. But although the prolongation of the vessels of each young sprout, through the stem to the root, is essential for the nutrition of the individual sprouts, and for their common life, yet it is not a necessary element in their individuality; for, when a twig is cut from a tree, it is separated from the greater part of its downward prolongations, and nevertheless constitutes a young plant, capable of developing itself to a compound vegetable system like that of which it formed part. The vessels of which we are speaking, as being prolonged from the individual twigs or sprouts to the roots, have their origin in the leaves; and the leaves, therefore, must be the parts in which the property of individuality more peculiarly resides. It is true most leaves will not develop themselves to perfect plants; but the principle is sufficiently established by the fact, that the leaves of many plants placed in the ground may be made to vegetate. This is the case, for example, with the leaves of the lemon, orange, Ficus elastica, and other plants; leaf-buds are developed at the margin of these leaves in the same way as they are ordinarily formed on the stems of the plants. The leaf, therefore, must be regarded as an individual organism, containing in "essence" or "potentially" all that is comprehended in our notion of the species of plant to which it belongs, and capable of propagation by the development of branches. Almost all the organs of plants, indeed, are leaves; even the different parts of the flower are shown by the theory of the metamorphosis of parts to be leaves modified in form and function. On the other hand, however, the stem itself, when stripped of all its leaves and branches, cannot be looked upon as an aggregate of mere imperfect fragments of individuals. In this truncated condition the stem is still a multiple of the germ. For leaf-buds may be developed and sprout even from a stem thus truncated. All these facts, therefore, confirm the truth of the proposition, that the fully developed plant is a multiple of individual plants,—a compound system of individual organisms, the essential parts of which are certainly contained in the leaves, though they exist also in the stem when stripped of its leaves.

b. Animals.

The power of multiplying the vital force resident in the germ is not peculiar to plants. Animals, and it would seem all animals without exception, possess the same property. There are many instances in the animal kingdom in which the multiplication of individuals in the process of growth is quite as distinct as in vegetables; but in other cases it can be proved to take place only by induction from a series of facts. The young polype developed from the ovum or gemmule of a compound polypiferous animal is at first a single individual, actuated by a single independent will. But in proportion as this young creature appropriates to itself new matter and grows, it becomes transformed into a multiple system of individuals, like that presented by a full-grown plant, and is then evidently regulated in its movements by many distinct centres of volition. A common stem unites all the component simple animals, and in the Sertularia the cavity of this stem communicates with the cavity of each polype, while out of its wall new polypes sprout. Those compound polypes which consist of a mere aggregate of independent simple animals, united into one mass, are not referred to in the foregoing description.

Fig. 144.*



One of the simple fresh-water polypes, or Hydræ, also, may, as we have learned from Trembley's observations, be transformed in the process of growth into a system of individuals analogous to a plant, with the exception that in the case of the compound Hydra the elementary parts of the young polypes are not continued in an isolated manner through the trunk of the parent individual, and that the digestive sacs of all form part of one common cavity. Each of the individual polypes composing the compound Hydra [Fig. 144] is actuated by an independent will; may be separated from the rest; and is, in form at least, a perfectly simple animal.

Thus far we have considered only those organisms which in their compound state, attained by growth, consist of a system of individuals not merely "potentially," but "actually;" the separate members of the compound system having each its proper structure and independent will.

We now proceed a step further, and find animals which in form appear perfectly simple, and have only one directing will, but nevertheless are systems of parts endued with individual life, and capable of propagating

* [Figure of a polype multiplying in the process of growth, after Trembley, Mémoires pour l'histoires des polypes, pl. viii. fig. 7.]

the form and organisation of the species. In these animals the component parts or segments undergo multiplication during the process of growth, and a certain number of them becoming separated, whether spontaneously or artificially, preserve the faculty of individual life. The parts thus separated were for a time subject to the will of the parent animal, and in that respect were mere members of its body; but, when about to separate themselves from the rest of the system, they acquire a more intimate relation to each other, become actuated by a distinct will, and have, as it were, their own proper centre of action, even while they form part of the body of the parent worm. At length they become detached, and display free voluntary motion. The young individual thus produced consists at first of few constituent parts or members; grows, however, by the appropriation of new matter, and forms another compound system capable of dividing spontaneously or of being divided into several portions, "potentially" endowed with individual life. For a time this multiple individual is subject to the influence of a single will, and is only so far a multiple animal as the parts which compose it have the capability of becoming independent individuals, which as yet they are not "de facto." Subsequently, the individual parts, though still connected, are actual independent beings. Many Annelida and Entozoa may, indeed, be divided artificially into several distinct individuals, and are, therefore, not really simple animals, but systems of parts, each of which, however small its size, contains all that is essential to the idea of an independent organism, and has the power of producing an organism of the same species. The young Nais proboscidea is composed of fourteen segments only. During its growth an increase of these segments takes place at the caudal extremity, and, after a time, a part of the new segments begins to be separated by a constriction from the rest of the worm. Long before division takes place, however, new segments are formed by the parent animal at the constricted part; these new segments in their turn begin to be cut off from the body of the old worm, while others are produced above them. In this way we have sometimes presented to our observation a parent worm with three young ones, still forming part of one system which has itself been developed from a separated part of a former system.* (See fig. 145.)

When a Nais has in the process of growth thus multiplied its organism, the portions capable of separating from the parent animal, and of becoming separate individuals, already have the form of a young Nais; there being a repetition in the multiple animal of certain segments which the young and simple animal possesses only in small number. But an animal may in form present none of the characters of a multiple of individuals, and yet be constituted of a number of parts capable of becoming inde-

* O. Fr. Müeller, Naturgeschichte einiger Wurmarten des Süssen und Salzigen Wassers. Copenhagen, 1800. See also Gruithuisen, Nov. Act. Nat. cur. xi.

Fig. 145.*

pendent beings. To this category belongs the Hydra, at the time when it is a simple polype animated by one will and destitute of sprouts. In this state, indeed, the polype is not a multiple of independent individuals, but it is really a multiple of all that is necessary for the development of a polype; for separated portions of its body rapidly grow and acquire the form of perfect animals, arms being protruded, and a digestive cavity developed within them. The experiments of Trembley, indeed, have shown it to be a matter of indifference whether the Hydra be divided longitudinally or into transverse ring-shaped segments, or whether portions are merely cut out of their side; the separated fragments being in all cases transformed into perfect polypes.† It would appear, therefore, that aliquot portions of the body of a polype, the limits of which are undefined, contain, like the leaves of plants, all that is essential to an individual of the species, and when no longer subject to the system of several such parts, united in the form of a simple animal, manifest the formative property resident in them, and become perfect polypes. In this respect the Planariæ resemble the polypes. It is true they never undergo multiplication during their growth, so as to form a system of independent beings, each endued with a distinct will, but always remain with respect to their volition simple animals. They may, however, as Dugès has shown, be divided into eight or ten separate segments, each of which will manifest independent life; and in summer, within the space of four days, will assume the form of a perfect individual of the species.‡

* [Figure of the Nais proboscidea. 1. Body of the parent worm; 2, 3, and 4, three young worms in different stages of development; 5, part at which new segments are being formed. After O. Fr. Müller, Von Würmern des süssen und salzigen Wassers. Tab. i.]

† Trembley's Mémoires pour servir a l'histoire d'un genre de polypes d'eau douce. Leide 1744.

‡ Froriep's Notizen. No. 501.

It must not be supposed that the Hydræ and Planariæ, more than other animals, are deficient in organisation,—in the possession of organs and tissues. The structure of the Planariæ is already known with tolerable accuracy, and although, notwithstanding the advances made in the anatomy of the Hydræ, there is still much to be desired with respect to them, yet we cannot doubt that they are as perfectly organised as other polypes. In polypes, generally, the different structures are known to be most definitely marked; their movements are affected by muscles as in other animals; the arrangement of these muscles as well as of the intestinal canal is known; and in the Actiniæ, and even in the compound polypiferous animals, the generative organs have been exactly described. Since, therefore, separated fragments of a Planaria or of a Hydra, and of the latter animal very small fragments, contain within themselves the power of forming an entire animal, it is evident that this formative power must reside in a mass of different structures, as muscular fibres, nervous fibres, &c., which in the body of the parent animal were subservient to special functions of its system and were subject to the influence of its will. It follows from this fact, that an aggregate of animal tissues of different physiological properties may be animated with a force quite distinct from the specific endowments of the respective tissues. The properties of the tissues included in the separated portion of a Hydra are, for example, contractility of the muscular fibres, the influence which the nervous fibres exert upon the muscular fibres, and so on. These properties are dependent on the structure of the individual tissues and on the state of the organic matter in them. The formative power, on the contrary, which actuates the whole mass, is identical with that force by which the parent polype was developed.

The cause which compels a particular portion of a Hydra or Planaria to the performance of a subordinate function, is the mutual reaction of its component organic matter with that of the entire organism, which is endowed with a centre of nervous action, or a brain. In this condition the primitive formative force of each part remains latent, and its organisation is subservient to the central influence of the organised polype. As soon, however, as the portion of organised matter of a Hydra or Planaria ceases to be in contact with the rest of the organism which has a centre of action, it becomes withdrawn from the influence of that centre; and then the tendency to individual organisation is manifested. In the process which ensues, the different tissues already formed within the separated mass probably lose their distinctive characters, and become all transformed into formative matter (" cytoblastema"), and germinal or formative cells; the elementary parts of the tissues of the new animal being subsequently produced by the transformation of those cells. For it is thus that the different tissues of the embryo are developed.

The same, or very nearly the same law, prevails in plants. As long as the leaf, organised as a special organ of the plant, is connected with the branch, its faculty of reproducing an entire individual of the same species is kept in a latent condition, in consequence of the mutual reaction of the leaf, as an organ of the plant, with the entire branch or plant itself. For, though not possessed, like the polype, of a central source of action, diffusing an influence through the whole organism, yet every plant is maintained as an united system by the co-ordinate mutual reaction of all its constituent parts. If this mutual reaction is arrested by the dissolution of continuity between the leaf and the stem, the organisation which the former received for a special purpose in the general economy becomes useless, and the latent power of reproduction manifests itself by the formation of a bud, or the germ of a perfect plant.

If this view is correct, a separated part of a plant, such as the leaf of an orange or lemon-tree, which, placed in the ground, would put forth buds, ought, when grafted on the parent plant, to become attached and remain a mere leaf. I am not aware that any experiments of this kind have been performed, and intend the remark only as hypothetical. The supposition is, however, in some measure justified, since similar experiments on the polype have succeeded. Trembley divided a polype (Hydra) transversely, then brought the two halves together again, and kept them carefully in contact. Before the close of the same day they had united, and on the next day the union was so perfect that a small worm, taken as food by the anterior portion, passed also into the inferior half. At first the line of union was marked by a constriction; but at the end of a fortnight this had quite disappeared, and on the tenth day after the operation this polype put forth sprouts or buds. Trembley succeeded, likewise, in causing the anterior and the posterior half of two different polypes to unite, and the polype thus produced likewise budded, and produced young polypes both above and below the line of union.* It is a very important circumstance in this experiment that the lower half, after being cut off, again united as a simple portion of the entire polype, the anterior half of which contained the centre of nervous influence; that it remained as such during the long period through which the observation was continued, and did not develop itself to an independent individual, as it unquestionably would have done, had it, instead of uniting with the anterior half of the polype, been permitted to remain unconnected, and not in contact with it.

A further circumstance of importance is the difference of plastic power which Trembley found to distinguish portions taken from different parts of the polype. Very small segments cut in the most various directions from the body or cephalic portion of a hydra, became converted into new polypes; each assumed the proper form, soon acquired a

* Trembley, op. cit. pp. 292, 293.

central influence over other parts of the body, and independent voluntary motion; whereas the arms, when separated from the body, manifested no reproductive power. In animals higher in the scale, namely, Insecta, Arachnida, Crustacea, and Salamandrina, entire organs, such as the extremities, the eyes, or the lower jaw, are reproduced when lost, and this is sufficient to prove that the organisms of these animals are not mere aggregates of their constituent parts, but still retain within themselves the power of restoring the perfection of the whole when entire organs are lost. In these animals, however, the separated parts or organs never are developed into entire new individuals, but for the most part resemble in that respect the arms of the hydra.

It must also be considered, that since in the higher animals all the elementary tissues are developed from cells, and since, during the process of growth the number of the elementary parts of the tissues is increased by the addition of new cells, a full-grown animal of the highest organisation is also a multiple of the original sum of constituent parts or elements. In a full grown Nais these multiples of the original sum of constituent parts are arranged in a consecutive series, and may be expressed thus: $a\,b\,c+a\,b\,c+a\,b\,c+a\,b\,c$. In other animals in which the sums of the different constituent elements cannot be isolated, not being arranged distinctly in a consecutive series, the young animal may be expressed by $a\,b\,c$, and the-full grown creature by $a\,a\,a\;b\,b\,b\;c\,c\,c$, or by $a^n\,b^n\,c^n$. The multiple of the cells composing the liver, for example, may be represented by a^n; that of the cells of the nervous system by b^n; and that of the cells of the muscular system by c^n. These aggregates cannot in the higher animals become new individuals. But even here the full-grown organism may be regarded as virtually a multiple of the germ, since in the process of growth it has become capable of the formation of germs. It is true, the concurrence of two sexes is in this case necessary for the development of the new germs. But both these sexes may reside in one individual, as in all hermaphrodite animals, where fecundation is effected either mutually by two individuals, or, by each singly, as in the Tæniæ. A solitary individual organism, which in the perfect state produces fruit, or, in other words, scatters germs capable of becoming by development new individuals, must contain within itself the power of multiplication; and in this point of view every full-grown individual even of the higher animals, is, with regard to the power of individual vitality, to be regarded as virtually a multiple of the primitive vital force and more particularly of the germ.

The question here presents itself: how small a portion of an organic body may contain the force necessary for the reproduction of the species? In the higher animals which propagate only by sexual generation, this force resides only in the germs of the ova, which are large cells containing the "germinal vesicle," and its nucleus, or the "germinal spot" of Wagner; while all other parts of their body, however large or small, are destitute of the reproductive power. In those plants and animals which propagate their species by buds or sprouts, the germ consists of a mass of cells which may be produced at almost any part of the body of the parent. In some of the lower animals the same reproductive power is possessed by every aggregate of organic elementary parts, that is of such elementary parts as were originally developed from similar cells, but which subsequently have acquired the form and properties of muscular and nervous fibres, and of fibres of cellular tissue, &c. In the lowest organic beings the power of producing new individuals is not merely manifested by separate portions of most parts of the body, but in some cases subdivision, even into the ultimate particles of the organism, does not destroy this power: isolated elementary particles are adequate to the propagation of the species. In plants, generally, all the tissues are produced from cells; but there are plants in which any single cell, separated from the rest of the organism, suffices for the reproduction of the entire plant, if nutritive matter be supplied. We have examples of this in the filiform fungi, such as the fungus of mould and the vegetable, which, according to the observations of Cagniard Latour and Schwann, forms the active part of yeast, and the growth of which in large quantity gives rise to the fermentation of saccharine liquors. This fungus of yeast consists of cells arranged in simple or branched threads; and it grows by some of the cells developing upon their free surface a small prominence which becomes a young cell. This young cell soon attains the perfect size, but has scarcely reached its full development before it, in its turn, begins to put forth a bud, which is the germ of the next cell. (See fig. 149, p. 1436.) Single cells of this kind also separate themselves from the threads of which they formed part, and still in the isolated state form new cells by the process of budding, and thus propagate their species. All this process takes place so rapidly, that its different steps may be watched by means of the microscope.* The same phenomena are presented by all the simple fungi. The dust-like powder of the fungus so destructive to silkworms, the muscardine, is composed of cells endowed with the power of reproducing plants of the same species; hence we may easily conceive that a single grain or cell of this powder, introduced into a brood of silk-worms, may cause their entire destruction.†

CHAPTER II.

OF THE MULTIPLICATIONS OF INDIVIDUALS BY THE DIVISION OF PERFECTLY DEVELOPED ORGANISMS.—FISSIPAROUS GENERATION.

SINCE organic beings in the fully developed condition are virtually multiples of the germ which produced them, they are capable of multi-

* Poggendorf's Annalen, xli. p. 184. † See Audouin, Annal. des Scienc. Nat. 1837.

plication by mere division, without the formation of new germs. This fissiparous generation is observed in animals quite incapable of the development of buds or "gemmæ." It may be the result either of the artifical interruption of contact and organic reaction between the different parts of a body, or of spontaneous division. In either case the separation may be complete, or only incomplete. When it is incomplete, the organic being appears as a compound or multiple system, the independent individuals of which are still connected by a common stem.

1. *Artificial fissiparous generation.*

The increase of organic beings by spontaneous division, which occurs for the most part only in the animal kingdom, is a less easy process than the multiplication by artificial division. Artificial division produces absolute interruption of continuity between parts which have already undergone perfect organisation, and at the same time are equally endowed with vital force; and it thereby causes the force resident in each part to assume an active state, so as to produce a new organism. Polypes, therefore, may be divided in any direction, and the separated portions will develop new individuals. While, on the contrary, spontaneous division always takes place in certain determinate directions, in which it is productive of the least disturbance of the internal organisation.

Multiplication of all plants, and of many of the lower animals, may be effected by artificial division. Branches, twigs, or sprouts, separated from a tree, are organisms which continue to live and maintain the species, when they are either planted in the ground or engrafted upon another plant. These cannot, however, be properly adduced as examples of true multiplication by division, effected independently of previously formed buds; for cuttings of plants are generally provided with fully-formed leaf-buds. It is true a portion of a stem, deprived of its branches, and presenting on its surface no appearance of buds, will grow when planted. De Candolle, indeed, states that grafting will succeed when portions of bark, apparently containing no buds, are employed. Meyen, however, remarks,* with respect to this experiment, that adventitious buds formed in the medulla of the stock might force their way through the engrafted bark; and adds, that even a willow twig, stripped of its bark and used as a rose-stock, put forth new sprouts after the lapse of several weeks, probably in consequence of the development of adventitious buds in the medulla or pith. Moreover, the growth of separated leaves, when placed in the ground, cannot in all cases be regarded as proving the possibility of multiplication by division without the formation of buds. When leaves of Bryophyllum calcinium, for example, are planted, they grow by the evolution of the buds which already exist in the axillæ of the marginal dentations. Even the cases in which leaves of perennial

* Pflanzen-physiologie, b. iii. p. 84.

plants, destitute of buds and quite incapable of developing them while attached to the parent stem, strike root in the ground and send up stem and leaves, are not conclusive; for, here the whole leaf is not transformed into the growing plant as the fragment of a hydra is transformed into a new polype, but develops a bud by its own vital power. This leaf, therefore, since it has the power of forming a bud, has itself individual life, and is already a simple plant. Leaves which thus grow when placed in the ground, are described by Meyen as sending out first the the root and then the bud. The multiplication of lichens by artificial division is to be explained in the same manner.

Multiplication by artificial division in animals is most likely to be successful when the organism consists of a succession of parts of similar structure, the number of which increases during growth. Annelida and Entozoa, for example, have this conformation, and transverse sections divide them into segments, each of which still contains similar though shortened portions of the nervous system, bloodvessels and intestinal canal. But this condition, although it facilitates the artificial fissiparous generation, is, as has been already mentioned, not absolutely indispensable. For in the multiplication of Hydræ and Planariæ by artificial division, the body of the animal may be cut in any direction, and each of the resulting fragments, though certainly not containing the essential parts of the organism, merely shortened, has the power of reproducing the individual. The property of producing a new organism of the same species is, therefore, possessed by any mass of elementary particles of the animal's body. Experiments have shown that there are three modes in which artificial division may be successfully performed.

1. *Transverse division.* It is principally when the organism has a linear and parallel development, consequently in plants and worms (Annulata or Annelida and Entozoa), that multiplication of the individual may be effected in this manner. But if the same worms, in which this mode of division succeeds, are divided longitudinally, the lateral halves do not live and develop new individuals. The transverse division succeeds very easily, as O. Fr. Müller showed in the naides. Hence Ehrenberg separates these worms, under the name of Somatotoma, from the Annulata. In other genera of the Annelida, though the separated parts of the animal after transverse division live for a long period, no reproduction seems to take place. The posterior third of a Nereis was kept by O. Fr. Müller alive, and possessed of voluntary motion, for three months; but it underwent no further development. Bonnet, however, states, that having cut a common earthworm in two, he obtained two perfect individuals. When, in Müller's experiments, a Nais proboscidea had been divided transversely, the posterior half acquired in from three to four days a new head and proboscis. The division and decapitation of the parent worm seemed, also, to have no perceptible

influence on the spontaneous development of a young animal from the posterior part of the headless portion; and sometimes the head of this new creature, formed by spontaneous division, was developed as quickly as the head of the decapitated parent worm. During the warm season the hinder portion of a Hydra which has been cut into several portions acquires a new head and arms, in the course of twenty-four hours; and in two days it takes food. The process of reproduction occupies fifteen or twenty days in cold weather. Small segments of a Hydra have the same property.

2. *Longitudinal division.*—When Hydræ are divided longitudinally, the cut edges quickly apply themselves one to another so as again to form a tube; and, within so short a space of time as an hour, the external figure of the polype was seen by Trembley to be entirely restored, with the exception of the arms, which also were reproduced in a few days. A polype thus divided took food three hours after the operation. Bands cut longitudinally from a Hydra likewise quickly reproduce entire polypes. The artificial division of the trunks of vegetables in the longitudinal direction comes under the same head.

3. *Division in all directions indifferently.*—It is principally in the inferior plants, for example the lichens, and in the Hydra amongst animals, that the fragments resulting from the division of the individual in the most various directions have the reproductive power. Trembley having laid open Hydræ from one extremity to the other, cut them into several portions in the most various directions, and found that each portion became a perfect polype. If the portions into which the Hydra is divided are of such form that their borders cannot unite to form a tube,—if, for example, they be very narrow bands,—the digestive canal of the new polype is formed by the development of a cavity in the substance of the separated fragment. Imperfect division of a polype produces a Hydra with two or more heads, or a fasciculus of polypes united by their substance, though endowed with independent centres of organic and animal life. By partially dividing a polype in the longitudinal direction, from the head towards the tail, Trembley produced polypes with from two to seven heads. By laying open a polype longitudinally, and then cutting it in different directions, but so as not entirely to separate any portion, he produced a compound animal with several heads and several tails; each of the portions into which the polype was imperfectly divided being converted into the head or the tail of a new being, which still remained connected with the rest of the divided body.

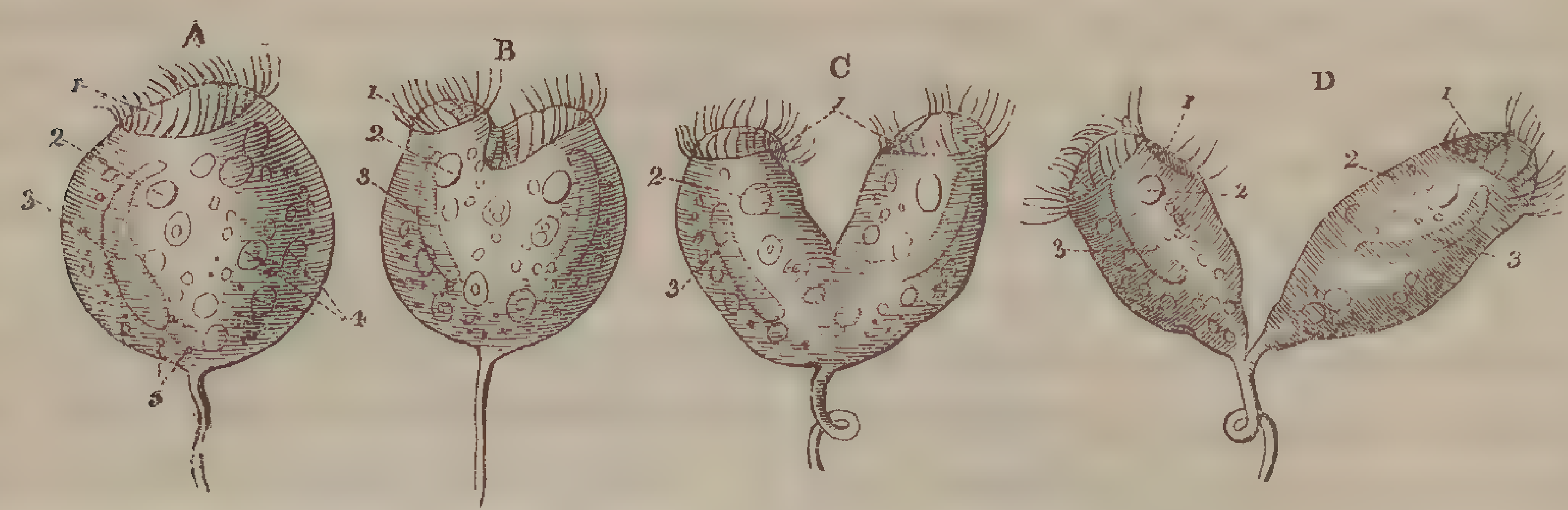
2. *Natural or spontaneous fissiparous generation.*

Spontaneous division takes place, for the most part, either transversely or longitudinally, or in both directions at the same time. It is only in animals that this mode of generation occurs to any extent, and hence it has been employed, together with other characters, by Ehrenberg as a means of determining in doubtful cases whether simple organic beings belonged to the animal or to the vegetable kingdom. Fissiparous generation is a very common mode of multiplication amongst the infusoria, though they also propagate by ova. Sometimes the gemmiparous mode of generation also is observed in the same genera. The higher animals never multiply by spontaneous division; and even the Rotatoria present no instance of it, though it occurs again in the Annelida. The complexity of the process must be greater in proportion as the organisation of the animal is more complex, and as there is less repetition of similar organs in its different parts. The non-symmetrical arrangement of organs on the two sides of the body does not, however, absolutely preclude the possibility of multiplication by spontaneous division, for animals which have a convoluted intestinal canal, as in the Vorticellinæ, propagate in this manner. In these cases there is [no ?] reason to think the division owing to the masked development of a bud, for the perfectly organised animal is seen to become divided in the longitudinal or transverse direction by a gradually increasing constriction. The cause of the spontaneous division is the striving of the organism, rendered virtually a multiple by the process of growth, to concentrate the sway of the organic force upon smaller masses. In proportion as the size of the system, as yet under the rule of one centre, increases, in the same degree do the organic particles which compose it seem to lose their attraction for this common centre, and gain a mutual attraction for each other in smaller groups, which then form independent centres. The plants which present the phenomenon of fissiparous generation are the Palmellæ, in which it has been observed by Morren.

The observations of Ehrenberg* show that the mode of generation by spontaneous division prevails much more extensively amongst the Infusoria than in other organic beings. The monads propagate their species by transverse and longitudinal division; and even those which are furnished with a shell are not exempt from this mode of multiplication. The Volvocinæ undergo division in the interior of their envelope, which afterwards bursts; the young animals resulting from the division being then set free, to undergo in their turn the same process. The Baccillariæ divide spontaneously in the longitudinal direction, and, their division being imperfect, form for a time compound, chain-like bodies. Some, as the Gomphonema, are, after their longitudinal division, able to detach themselves entirely from the stem by which they at first remain connected. The Vorticellæ divide in the longitudinal direction, and

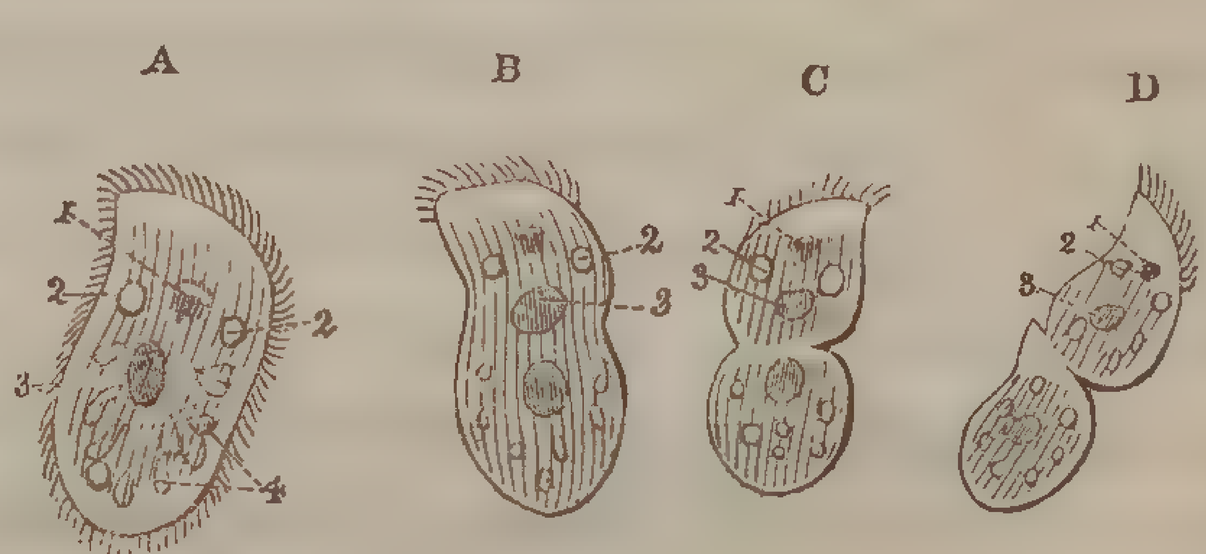
* Die Infusions-thierchen, als Volkommene Organismen. Leipz. 1838.

Fig. 146.*



then set themselves free from their common stem (see fig. 146). The families of Enchelia, Trachelina, Colpoda, and Oxytrichina also multiply by longitudinal and transverse division (see fig. 147).

Fig. 147.†



The results of the observations of O. Fr. Müller and Gruithuisen, upon the generation of the Naides by spontaneous division, have been already related. After a constriction has shown itself, marking the point of separation between the body of the parent worm and its posterior part, which is to be developed into a new individual, but long before the separation is effected, a head and proboscis is formed upon the latter at its anterior extremity, and the part immediately in front of this begins in its turn to be separated from the parent worm; so that sometimes a nais is seen with three young individuals still connected with it (see fig. 145, p. 1425). Fissiparous generation is also observed among the Planariæ.

The spontaneous division of animals is generally complete, but sometimes it is incomplete. Monads, which undergo imperfect division in the longitudinal and transverse directions, alternately form bodies like clusters of berries. Successive divisions in the longitudinal direction give rise to series of individuals united by their lateral borders. Repeated imperfect division in the transverse direction produces linear series of individuals. Of the latter nature Ehrenberg regards the Vibriones, which often are observed to consist of two or three, or very

* [Vorticella microstoma multiplying by spontaneous longitudinal division. The figures A, B, C, D, show successive stages of the process. 1, mouth; 3, sexual gland; 2, contractile sac; 5, ova; 4, gastric sacs. After Ehrenberg, Infusionsthierchen, taf. xxv.]

† [A polygastric animalcule, Chilodon uncinatus, multiplying by spontaneous transverse division. The figures A, B, C, D, show successive stages of the process. 1, mouth, surrounded by a fasciculus of bristles or teeth; 2, contractile sac; 3, sexual gland; 4, stomachs. After Ehrenberg, Infusions-thierchen, taf. xxxvi.]

many articulated portions, remarkable for their quivering motion. The ramified Vorticellinæ,—Carchesium and Epistylis of Ehrenberg,—are produced by imperfect dichotomous division, the resulting halves remaining attached to each other by the stem prolonged from their posterior extremity. This mode of division is observed, though only in few cases, among the polypifera; it occurs, according to Ehrenberg, in the Caryophyllæi, and gives rise to their dichotomous, tufted, and pedicillate forms, two polypes being produced from one, four from two, eight from four, sixteen from eight, and so on.

The occurrence of spontaneous division in the vegetable kingdom is still subject of dispute. Ehrenberg * declares that no plant with which he is acquainted, no part of a plant, nor even a cell of any plant, undergoes multiplication by spontaneous division. The only modes of increase in plants, according to his view, are elongation and the formation of buds; the cases of apparent division depending merely on the separations of buds or gemmules. Meyen,† on the contrary, maintains the frequent occurrence of this mode of increase in the case both of entire plants and of the cells of plants. Meyen founds his opinion partly upon the genus Closterium, which Ehrenberg, on the other hand, refers with several other organic beings difficult of examination, but all multiplying by spontaneous division, to the animal kingdom. The other instances adduced by Meyen seem to me to be examples of the formation of spora by division, and of the separation of individual cells. There are, however, vegetables of such simple structure that they consist of a mere filiform tube; and here spores are formed by the mere constriction, and, in fact, division of this tube; the spores being the "simpla" of a virtual "multiplum." There are other structures in which the cells produced as buds from the parent cell, and forming a connected chain, constitute the "multiplum" of the plant, which then separates into its "simpla" by true division. Meyen adduces observations on Palmellæ, Oscillatoriæ, Nostochinæ, and filiform Fungi. The spherical coloured mass which constitutes an individual of the genus Palmella, is always included in a coating of mucous matter within which, as the parent cell, the spontaneous division of the coloured mass takes place. After its division is effected, each portion of the mass comes to be invested by its proper mucous coat, and at the same time the external common vesicle of mucous matter is absorbed, though sometimes before its absorption it expands considerably, so that the new individuals, with their fully-formed proper investments of mucus, can be seen free in its interior. The green mass in the simple tube of the true oscillatoriæ was seen by Meyen to be at first undivided, but to become subse-

* Bericht über die zur Bekauntmachung gecigneten Venhandlungen der K. Pr. Academie der Wissenschaften, 1836. p. 34.

† Neues System der Pflauzenphysiologie, b. iii. p. 440.

quently split into several masses. Sometimes the green matter became divided into a greater or less number of long segments, and then the tube separated into portions corresponding to these segments. Here the spontaneous division appears to me to consist in division of the spor-moss. The bead-like threads which in the genus Nostoc lie in a gelatinous mass (the phycomater) increase in length, according to Meyen, by the spontaneous division of their component vesicles or cells. When the old Nostoc perishes, those cells escape from the gelatiniform mass, each having the power within itself of enlarging and becoming a new Nostoc. The spores of the Nostoc consist of a greenish and somewhat hardened gelatiniform substance, and are filled with a mucous colourless fluid; during the formation of the new plant, the coloured wall of the spore swells and becomes the gelatinous mass of the Nostoc, while in the contained fluid there appear opacities which produce the first vesicles. These vesicles subsequently undergo repeated spontaneous division, and thus become the bead-like spore-threads. The moss and liverwort tribes also, according to Meyen, do not form their seeds within parent cells, but produce them by division, and the individual seeds are first separated by constriction from the larger parent-seed. Meyen regards the increase of the cells of some articulated confervæ, for example, Conferva glomerata, by the protrusion of a part of their walls, and the subsequent separation of the protruded part by a constriction, as an example of the same process. In the lower fungi, as the Penicillium glaucum, also, the development of the sporules is effected, according to Meyen, by the division of the thread-like tube (see fig. 148). In the fungus of yeast, Saccharomyces, which consists of a string of cells, each new cell is formed as a bud from the extremity or side of an old cell (see fig. 149). The component cells of the fungus readily separate from each other, and, when isolated, bud again, and produce new systems of cells. Each cell of the plant is here a spore, or is an individual, which undergoes multiplication by the process of budding, while the newly formed individuals readily separate themselves

Fig. 148.*

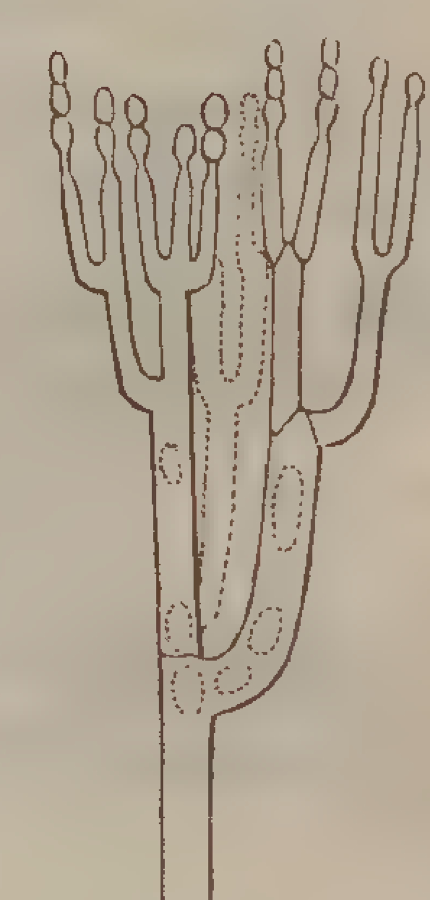
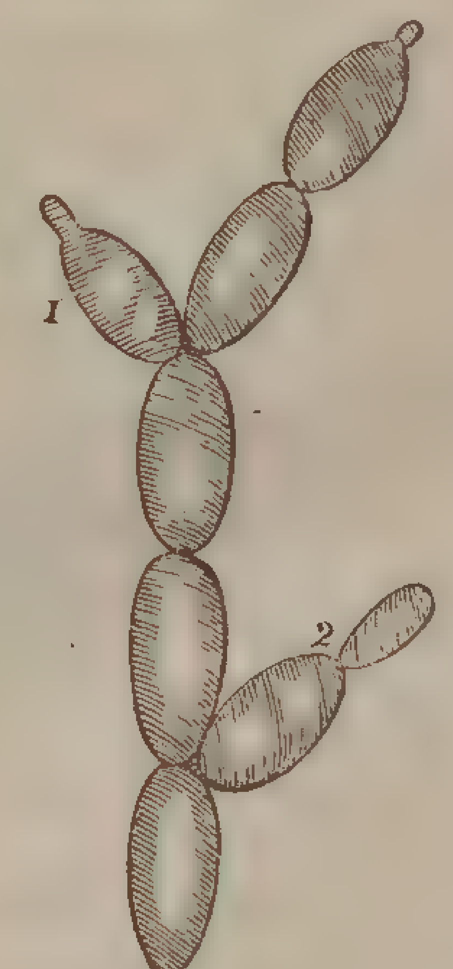


Fig. 149.†



* [Figure of Penicillium glaucum, showing the development of spores by division of the tubular cells. After Meyen, Pflauzenphysiologie, tab. x. fig. 20.]

† [Figure of the fungus of yeast, Saccharomyces cerevisiæ. 1, a cell, developing a bud from its extremity; 2, a bud becoming separated from the parent cell. After Meyen, op. cit. tab. x. fig. 22.]

from the systems of which they first form part. The spontaneous division of the fungus of yeast consists, therefore, in the separation from each other of individuals originally produced by the process of budding,—the gemmiparous process. It is very analogous to the separation of the young polypes which bud from the body of the fully-developed parent polype; in other words, to the resolution of a compound system of perfect polypes, produced by the development of buds, into separate independent individuals.

CHAPTER III.

OF THE PROPAGATION OF THE SPECIES BY BUDS.

THE formation of buds is essentially due to the following process:—A portion of the substance of an organised being, which is superflous for its individual life, separates itself in an undeveloped state of organisation from the organism of that being, so far as to assume a special individuality of life, without, however, losing its organic connection. From the germ thus produced the special organisation of the species is subsequently developed in the form of a new individual, which may either retain its organic connection with the parent trunk or become detached. This production by one living individual of the germ of a new living individual, presupposes that the parent trunk already contained within itself the organic force for several beings, and was, in fact, a virtual "multiplum." The process of the formation of buds, though a variety of imperfect spontaneous division, differs from the true fissiparous mode of generation. For, in the latter process, the perfectly developed organism divides into two, or more, perfectly organised segments. Here, therefore, the entire production of a special structure in the separated parts is not required, since the special organisation already exists, and only needs such changes as will restore to integrity the parts involved by the line of division; while, in the process of the formation of buds, the new individual represented by the bud is not perfectly organised, but is merely endowed with the power of developing a perfect organism. The bud of a plant is, therefore, to use the words of C. Fr. Wolff, the "simple plant," and the bud put forth by an animal, the "simple animal." A bud originally consists merely of the primary elements of all organisation, namely, cells, and contains even these in proportionally small number. The buds of plants are masses of ordinary vegetable cells. The vessels of the parent plant have not the least share in the formation of the original bud, and have no connection with it until a later period. The bud appears in fact originally to be a mere prolongation of the cellular tissue of the pith, as Duhamel, Treviranus, Meyen, and others state. It is not separated from the pith of the mother plant by any septum; merely cells of smaller size being interposed between them.* Usually the buds of plants are developed upon the parent stock, but sometimes they fall off and are developed separately, as in the cases of some monocotyledonous and dicotyledonous plants and the Hepaticæ.

The ovum is distinguished from the bud not only by the circumstance of sexual influence being necessary for its development, but also by its inability to undergo further evolution while forming part of the parent organism, and by its being insulated from the parent plant by distinct membranes. The spores, developed independently of sexual intercourse by many of the more simple plants, cannot be regarded as germs of ova.

The causes which determine the development of buds in the parent plant are partly internal and partly external. The more simple organisms form a substance which has the power of developing new individuals with the proper organisation of the species. When this substance does not receive a special structure adapted for the performance of some function of the existing individual, and therefore is not subjected to the proper vital force of this individual, it exerts its power of independent organisation, and forms a new individual. The limits of this individual are determined by the larger or smaller size of the mass of elementary parts (cells), which thus become connected by a special mutual reaction, while they are excluded from an equally intimate reaction with the parent organism, and are also separated mechanically in some way or other, by heterogeneous substance, from other masses of substance capable of forming buds. Wherever, therefore, in an organic body substance is formed which the organism does not require for the constitution of special structures, and does not retain under its central influence, there buds are formed. The formation of this substance seems explicable by the same supposition as that which was proposed to account for spontaneous multiplication by division; namely, that the organism being a virtual "multiplum," and increasing by growth, strives to concentrate its organising force upon smaller masses.

Another cause determining the formation of buds in plants is an intermission of the activity of the vital force of the individual in the production of special structures from the organic matter, or an intermission in the general nutritive function. In many plants the formation of buds takes place only at the periods when the exterior growth ceases for a time, and when the leaves have fallen off. Hence it is, also, that plants may be most successfully transplanted when they are destitute of leaves. On the contrary, the more the juices of a plant are expended in the multiplica-

* See Treviranus, Physiologie der Gewächse, b. ii. p. 630.

tion of the elementary tissues and organs, the less capability is there for producing compound "multipla," which are composed neither of *a*, nor of *b*, nor of *c* alone, but have the properties of *a*, *b*, *c*, &c. united.

Any circumstance which arrests the general growth of the organism at any point, or only interrupts the continuity of the cellular tissue, may determine the formation of buds in plants. Hence buds are produced at the margin of fleshy leaves when they have been subjected to moderate pressure, and also in wounds of the bark.*

1. *Of the formation of "buds" or "gemmæ" in plants.*

a. Buds of the inferior or non-vascular plants.—The buds of the plants of low organisation consist partly of aggregates of cells, partly of single cells. In the moss and liverwort tribes they are of the former kind. Those of the articulated Confervæ and filiform Fungi, on the contrary, are single cells, which are either portions cut off by gradual constriction from the parent cell or tube (gemmation by spontaneous division), or are produced by the protrusion of the wall of the parent cell, and the subsequent separation of the protruded portion as a distinct cell, by the process of constriction. Buds of this kind are formed in the way first-mentioned in the filiform Fungi, such as the Penicilium glaucum (in fig. 148, p. 1436); in the latter mode in the articulated Confervæ, such as Conferva glomerata, and in the fungus of yeast (see fig. 149, p. 1436). There is no essential difference in the two processes.

b. Buds of the more highly organised vascular plants. — Axillary and Terminal buds. — The buds (leaf-buds) of the higher plants are either formed in the axes of leaves, or at the extremity of the stalk or stem. The leaf-like structures which sometimes appear as scales enveloping the apex of the axis of the bud or the embryonic nucleus of the future axis, may be absent, in which case the nucleus of the bud is naked. This body is formed of cells which, by spontaneous development, become the new sprout. The cellular pith of the stem of the plant is continuous with the cellular nucleus of the axillary and terminal buds. The development of the special organisation of the plants from the cells of the existing buds is always attended with the formation of new buds for the next period of vegetation.† In the production of the special structure of the species, therefore, something in addition is always generated, which does not form a component element of the present organism, but contains the organic force for future vegetation.

In phanerogamic herbs the buds are sometimes naked, sometimes covered with scales. The simplest buds are in these plants mere masses of cells. In the Lemna the bud issues from the cleft of the paren-

* Treviranus, Op. cit. pp. 625, 626.

† See Meyen, Pflanzen-physiologie, b. iii. pp. 5. 7.

chyma in the form of a small leaf which subsequently becomes a new plant; but even before its escape from the cleft it possesses a root folded up within it.*

The buds of trees, on the contrary, are composed of enveloping scales and included parts. The structure of such buds is described by Treviranus † as follows: — The bud itself appears between its coverings (tegmenta) as an elongated or roundish cellular body, the groundwork of the future leaves. At the point where a bud is to be formed the pith or medulla of the stalk undergoes enlargement, and dilates the surrounding woody mass. The pith, which was hitherto colourless, develops now a dark green cone of small-celled tissue, surrounded by a sheath which, in a transverse section, appears as a delicate line. This sheath of the cone is formed of the innermost layer of wood, and the liber, which meet at the margin of the woody mass. The sheath thus formed is not closed at the inner extremity of the cone, where the bud rests upon, and where it consequently communicates directly with, the pith of the stem. The colourless inner bark of the twig or branch is continued over the outer side of this sheath, and forms the scales of the bud, while the external green bark ceases at the base of the outermost scales. As soon as the transformation of the bud into a branch commences, spiral vessels are developed. Inferiorly these vessels apply themselves to the woody mass of the stem, while in the opposite direction they follow in their development the extension of the bud. Lastly, they form the commencement of a new layer of wood, which belongs in common to the new twig, and to the axis from which it springs. In the twig this new layer of wood has the first place next to the pith; in the larger branch it has the second place. Flower-buds are distinguished from leaf-buds by the circumstance that they can produce no further generation of buds except by sexual fecundation. When fecundated they resemble the deciduous leaf-buds. In rare cases, however, an unimpregnated flower-bud becomes developed into a branch. Thus, according to Meyen, the nucleus of the unimpregnated ovum of Poa (a genus of the grass-tribe) grows and becomes a new individual; the development of which, however, remains imperfect. (These are the so-called viviparous plants.)

Adventitious leaf-buds.—Buds which are neither axillary nor terminal, but which make their appearance through the bark of the old stems and branches of trees, are thus named. They are connected with the medullary rays, and through their medium with the cellular pith, which reaches the surface at all points of the stem and branches, and thereby renders possible the formation of adventitious buds at all points. Adventitious buds are sometimes developed in extraordinary number on the stems of trees which are no longer able to vegetate by the axillary

* Treviranus, Physiologie, der Gewächse, b. ii. p. 631.
† Op. cit. b. ii. p. 632; b. i. p. 258.

and terminal buds, in consequence of both the axillæ of leaves and the terminal axes having been cut away.

Buds on leaves.—There are many plants also, in which buds are developed either normally or under the influence of particular circumstances on their leaves. The best known instance of this is afforded by Bryophyllum calycinum, where the buds are seated in the notches of the margin of the leaves, forming there conical knots. These buds sometimes undergo further development while still upon the plant; but they do so more readily after the leaves have fallen off. Leaf-buds of this kind are met with in many ferns, and among the higher organised plants in Malaxis paludosa, Cardamine pratensis, and the genus Lemna.

Tubers.—These are subterraneous stems with unusual development of the cellular pith and cortical portion, between which the vessels are placed. Buds develop themselves in this tuberous portion of the stem just as they do in the aërial stem. Since the original stem in annual tuberous plants dies every year, the portion of the stem in which the tubers are developed seems destined for the continuance of the species. The subterraneous stems, on which the tubers are destined to be formed, are developed while the plants are quite young, as offsets, which have the same structure as the aërial stem. When the tubers begin to be formed these shoots enlarge at one or more places in consequence, partly, of the increase of the medullary substance, and, partly, of thickening of the cortical portion. The spiral vessels consequently lie between two inordinately developed cellular masses, the cells of which contain granules of starch. At first the tubers are but small, so that the spiral vessels are not much separated from each other; but with the increase of the tuber they become more spread asunder. A tuber may form at any part of a subterraneous stem. The axis or nucleus of the bud is here, as elsewhere, a prolongation of the medulla; it is, namely, a conical body produced from the surface of the medullary mass, and accompanied by spiral vessels, which makes its way through the cortical portion of the tuber, and appears at the surface seated in a depression. The buds for the succeeding periods of vegetation are visible even in young tubers of the size of a pea.*

Bulbs.—Bulbs, according to Treviranus, are buds, the scales of which have become fleshy or succulent. They are developed at the side of the base of the stem, and remain for a time connected with it by cellular tissue and vessels; in consequence of the desiccation of this bond of connection, however, they at length become free. Bulbs may form on the aërial as well as on the subterraneous stem. Bulbilli of the aërial stem occur in the genera Lilium, Allium, Saxifraga, Dentaria, and many

* Meyen, op. cit. b. iii. p. 26—31.

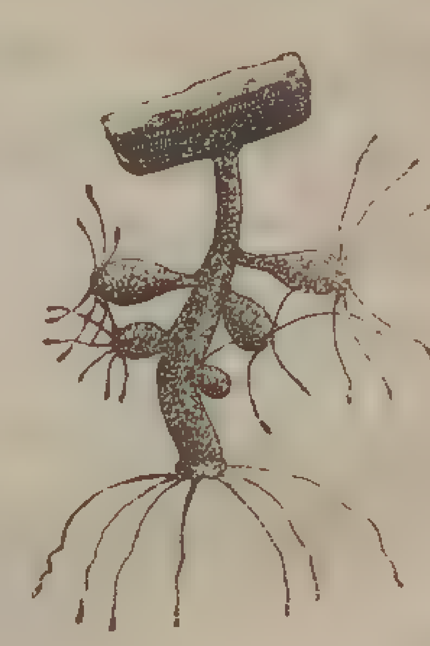
others, where they are developed in the axillæ of the leaves or of the floral envelopes. When the axis or nucleus of these bulbs begins to be developed into the new plant, it derives nutriment from the fleshy leaves.

2. *Of the gemmiparous generation of animals.*

In the animal kingdom, the propagation by the formation of gemmæ or buds is met with to the greatest extent in the class Polypifera, and less frequently in the Infusoria; for example, in the Vorticellinæ. Sars observed its occurrence in Cytais and other of the Acalephæ. Of the Entozoa the order Cystica alone presents examples of this mode of propagation. In Cœnurus, the vesicles which bear the numerous heads are at the same time germ-stocks, upon which the new individuals are developed as buds. In Echinococcus, the parent animals take the form of vesicles, on the inner or outer surface of which new individuals are developed, and to which they are for a time connected by a thin filament; but, subsequently, the young ones become free.* Hence the old Echinococci have the form of vesicles containing other vesicles, and have been incorrectly called acephalocysts.

The more intimate steps of the process by which buds are developed in animals have not been observed, nor has any satisfactory microscopic examination of the structure of an animal gemma ever been made. The facts, however, with which we are acquainted relative to the development of the animal tissues, place it beyond doubt, that the buds developed by animals, like those of plants, are at first mere masses of cells, and that these cells not merely increase in number but undergo a special arrangement and transformation so as to produce the different tissues of the body. In the Hydra the gemmæ appear first as small roundish prominences upon the surface of the cylindrical body of the animal, at any point of which, except the arms, they may form. These gemmæ soon acquire the proper form of the polype (see fig. 150); but at first, as Trembley has shown, the cavity of the young polype is continuous with that of the parent hydra.

Fig. 150.†



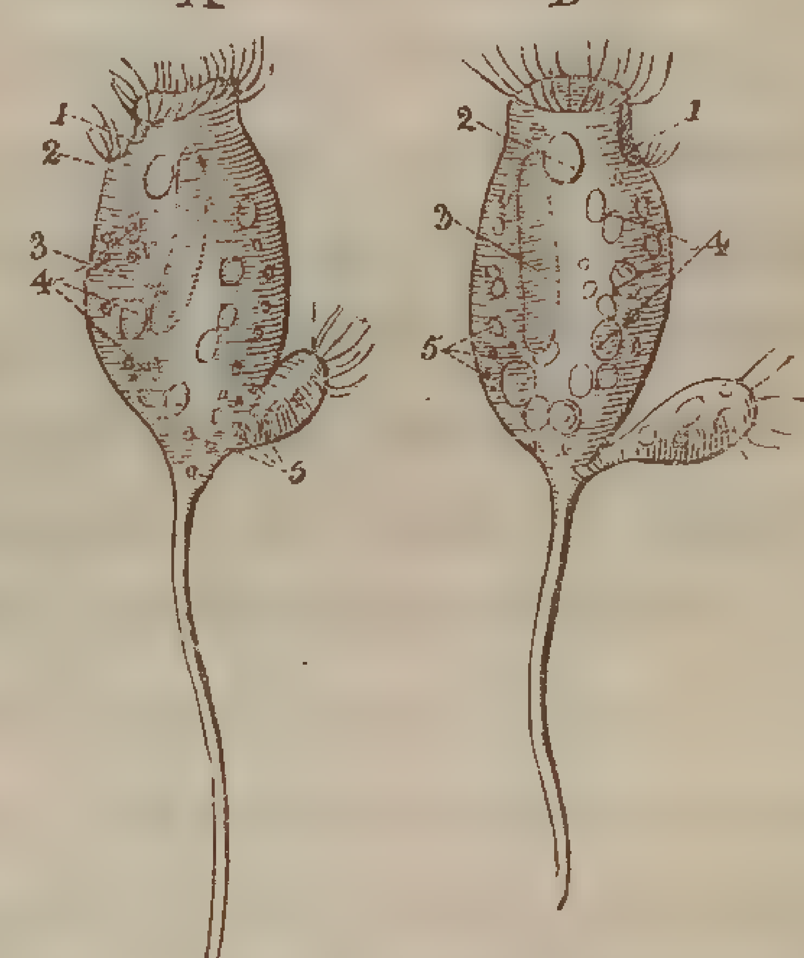
In the Sertulariæ the gemma is at first an obtuse projection from the stem, closed at its extremity, but containing a cavity which communi-

* See J. Müller, in Müller's Archiv. 1836. Jahresb. CVII. Von Siebold in Burdach's Physiologie, b. ii. 2to. Auflage.

† [Figure of a hydra, from which several young ones are being developed; at first in the form of round buds. The parent polype has just taken a worm, and a part of the food has passed into the cavity of each of the young ones. Trembley, Mem. pour l'Hist. des Polypes. Planche, viii. fig. 7.]

cates with the canal of the stem. Subsequently the organisation of the polype takes place, and then the extremity of the gemma opens and the arms of the polype are put forth.* The formation of gemmæ is very frequent amongst the Polypifera, but less so amongst the Infusoria. Spallanzani and Ehrenberg have observed it in the Vorticellinæ, (see fig. 151.) Perhaps the naides should be regarded as multiplying by the formation of buds. For since the young individuals are formed from the hinder part of the parent animal (see fig. 145, p. 1425), and since at this part new segments are constantly being formed, it is possible that the young organisms which separate from the parent body are merely gemmæ which have undergone development, and consequently that the apparent spontaneous division of the parent body is really a throwing off of terminal buds developed upon the parent stem.

Fig. 151.†



The compound polypiferous animals increase by the production of gemmæ, which do not separate from the parent stock, and thus give rise to a constantly extending mass, which includes successive generations of united individuals. In many animals,—as the Ascidiæ, Xeninæ, Sertularinæ, and Alcyonellæ, the gemmæ are formed upon stoles or running stems.‡ We have seen that in plants, after the terminal and lateral branches are cut away, the stem will produce buds. A similar fact is observed with respect to the polypifera: sometimes, when all the individual polypes have perished, the formation of buds upon the stem will continue.

CHAPTER IV.

OF THE SEPARATION OF THE BUDS OR GEMMÆ, OR OF THE DIVISION BETWEEN THE STEM AND BUD.

Buds may separate spontaneously or be detached artificially, so as to become perfectly independent individuals, either in their simple state or when they have already by development acquired the organisation

* Lister, in Philos. Transact. 1834, Pt. ii. [Also Farre, Philos. Transact. 1837.]

† [Vorticella microstoma multiplying by gemmation. A and B show successive stages in the development and separation of the young animal. 1, mouth; 2, contractile sac; 3, sexual gland; 4, stomach; 5, ova. After Ehrenberg, Infusionsthierchen, t. xxv.]

‡ See Ehrenberg, in Bericht über die Verhandl. der Akad. der Wissensch. Zu Berlin, 1836.

proper to the species. All these varieties of the phenomenon may occur in animals as well as in plants.

a. Artificial separation of gemmæ which have undergone development.—Gemmæ of the Hydra which have acquired the proper form of the polype live when separated artificially from the parent animal. This mere separation of two perfect individuals must be distinguished from the artificial division of a single animal.

In plants, this separation of a fully-developed bud, or of a sprout, is very often performed, either for the purpose of planting it in the ground or of grafting it upon another stock. This, however, is not such a perfect example of the separation of individuals developed from buds, as are some cases observed in the animal kingdom; for the cuttings and scions of plants are usually not mere twigs calculated to vegetate by the extension of already existing parts, but sprouts which contain other buds ready to undergo development.

b. Artificial separation of buds which are still in the embryonic condition.—Of this an example is afforded us in the propagation of potatoes. For separate buds or eyes cut out of the old tuber, with a portion of cellular tissue surrounding them, vegetate when set in the ground.

Buds of plants separated while in this simple state will also grow when engrafted together with a portion of bark and wood upon other plants. No experiments of the same kind have been performed upon animals.

c. Spontaneous separation of buds which have undergone development.—The bud of a Hydra which has acquired the perfect organisation of a polype, and has long evinced by its movements its individuality and independence of action, at length separates itself spontaneously from the parent stock, the division being effected by gradual constriction at the point of their connection.

In the compound polypiferous animals the buds which have become developed into perfect individuals, remain, as in plants, connected with the perennial parent stock, which their successive generations aid in extending.

d. Spontaneous separation of simple embryonic buds.—The spontaneous separation of simple buds or gemmæ from the parent stock is very frequent in plants. The separation of the bud-like spores of the filiform fungi and mosses, of several of the liverwort tribe, and also of some ferns, are examples of its occurrence.

The formation of tubers and bulbs upon a parent stock, which may either perish annually or be persistent, also ends in their separation, together with the mass of nutriment with which they have been furnished by the subterraneous stem of the parent plant; and the aërial bulbs or "bulbilli" of the genera Dentaria, Saxifraga, &c. are likewise deciduous.

In animals, such deciduous buds or gemmæ seem to be rare. The existence in animals of a non-sexual mode of generation by means of spores, was formerly admitted in many cases, but the more accurate examination of the generative organs in those animals has rendered it probable that in many such cases the reproductive power of the apparent spores depends on sexual fecundation. It has hitherto been found impossible to establish an absolute line of distinction between the two kinds of germs even in plants, namely, in the Cryptogamia. Germs which are produced without sexual influence are essentially of the nature of buds or "gemmæ," whether they consist of single cells or of many.

Deciduous buds resemble very closely in their nature the germs of ova, that is germs rendered capable of development by sexual influence. In both the perfect organisation of the plant or animal is wanting, and both are composed simply of one or more cells, which are endowed with the power of producing the entire organisation of the species. But, while in deciduous buds, spores, &c. the process of development requires no other conditions than the ordinary external vital stimuli, or general conditions of life, the germs of ova, on the contrary, are incapable of further development until they have been exposed to a "complementary" agency. Both the germ of the ovum and the semen possess the power of affecting the determinate organisation of the species, for the new individuals present peculiarities both of the male and of the female parent, but neither can exert its power until by reciprocal action with the other the deficiency in its endowment has been supplied. Buds and the bud-like spora are subject to no such condition. The fissiparous and gemmiparous modes of propagation differ from sexual generation, also, in the greater certainty with which they preserve the peculiarities of the individual. Hence, the method of planting cuttings, or that of grafting, is always perferred when it is desired to have all the properties of the parent stock in the new individual. The sexual mode of generation affords much more scope for variations, and can be trusted only for the propagation of the species, but with no certainty for the reproduction of the peculiarities of the individual.

The germs of ova, however, not unfrequently acquire the nature of buds or spora. Many observations have rendered it an established fact, that butterflies, kept perfectly isolated from the male insect, have laid eggs, from which young have been developed. Still better known is the fact pointed out by Bonnet, that the Aphis, though kept apart from the male insect, from the very time of its escape from the egg, nevertheless produces living young. In some rare instances, also, for example, in the genus Poa, as has been mentioned already, a new individual is developed from the unimpregnated flowers of plants, as from a bud. In these cases, therefore, the germ of the female acquires insensibly the nature of a bud; the defect in its reproductive power, which renders the semen of the male necessary, being removed.

CHAPTER V.

THEORY OF NON-SEXUAL GENERATION.

THE production of new organic beings from individuals already existing, may *à priori* be conceived to take place by either of the two following processes:—It may be the result of the entirely new formation of germs by the parent organism; or it may be effected by the mere unfolding or setting free of germs contained within the parent from the commencement of its existence. The latter view is the one adopted in the theory of "evolution," which has numbered amongst its supporters physiologists of the highest reputation, as Bonnet, Haller, and even Cuvier. According to this theory, the first created embryos of each species must contain within themselves, as it were, in miniature, all the individuals of that species which shall ever exist, and must contain them so arranged, that each generation should include not only the next, but, encased within it, all succeeding generations. Hence this theory has also received the appellation of the "emboitement" theory. The encased germs have at one time been supposed to exist in the ova, at another time in the spermatic animalcules.

Opposed to this theory is that of "Epigenesis," according to which, existing organisms do not contain the germs of future individuals, encased within them *ab initio;* but each new germ is an entirely new production of the parent organism. Casper Friedich Wolff was the celebrated and successful advocate of this view, which has been received by the best of modern naturalists. The "evolution" theory in its first crude form was completely refuted by Wolff* and Blumenbach.† For the germ certainly does not contain the miniature of the organic being in its perfect form, nor can such an opinion be any longer maintained. The germ of the embryo of vertebrata, in the earliest period of its development, presents not the slightest resemblance to its subsequent form. The various organs in the process of their development do not undergo a mere increase of size from a miniature condition, but we see them actually formed before our eyes. All the tissues of the body are formed from cells, and all the organs are composed of those tissues. In order, therefore, that the "evolution" theory should be tenable in the present state of science, it would be necessary to give it a more subtle form. There are two states in which the same organism exists at different periods, namely, that of the germ, in which it possesses the power of producing the proper organisation of the species, but has not yet assumed that organisation; and, again, the state in which its organisation is perfected, and in which it in part returns to its original state, and produces germs.

* Theorie der Generation, Halle. † Ueber den Bildungs-trieb, Göttingen 1791.

Now, supporters of the evolution theory at the present day could only maintain, that the organisms of future generations are encased in the form of germs,— that the perfectly formed organism contains the next generation in the condition of germs or embryos, and these, again, the succeeding generations as other germs. Encased generations of individuals of this kind do exist; for example, in the polypes and naids; and even the human female, when pregnant, encloses one generation in the developed state, the fœtus, and in the ovaries of this fœtus the germs of a third generation, as ovula with their germinal vesicles. The eye, aided by the microscope, can detect no further encasement than that of the ova, germinal vesicles, and germinal spots; but still it might be maintained, that, though not discoverable by human vision and instruments, such further encasement may exist; and arguments of this kind are unanswerable. The problem may, however, be investigated in a simpler form than that in which it presents itself to us in sexual generation. We may leave out of consideration the mysteries of the latter process, and compare the theory of evolution with the facts of non-sexual generation. We have seen that an organic body may undergo multiplication by division, by the formation of buds, and even by the process of growth. We have stated, moreover, that the cells, which are the ultimate elements of organic bodies, multiply themselves partly by the formation of new cells in their interior or on their exterior, and partly by undergoing division, and by the separation of protruded diverticula. Lastly, there are organisms where each cell is a germ or embryo which produces the new germs of the species, by the protrusion of parts of its walls, and the subsequent separation of the protruded portions in the form of new cells.

These facts afford the most decided refutation of the evolution theory. A perfectly developed organism, which was shortly before governed by a single will, is divided, and immediately two wills are manifested. Such, at least, is undeniably the case when some worms are divided artificially; each half of the former individual moves itself independently. Again, in the spontaneous division of a perfectly developed organism two independent individuals are produced from one, in a manner which renders it certain that the multiplication is not due to the evolution of pre-existing encased germs. The evolution theory is also inapplicable to explain the gemmiparous mode of increase of the lowest plants, (as the articulated Confervæ and the fungus of yeast,) where a multiplum is produced by the division of a single cell, or where a cell protrudes a sacculus at one part of its walls, which at first is part of the old cell, but becoming separated from it by gradual constriction of its neck forms a new germ (see page 1436).

Since, therefore, the germs of organic bodies do not contain within them the seed of the next and all succeeding generations, and since they acquire the power of forming multipla in the process of growth and by the assimilation of surrounding matter; no other alternative seems to be left for us than to admit that the multiplication of all organisms takes place by division. The essential vital principle of organic beings either has the property of undergoing division *ad infinitum*, with losing its specific plastic power, or it is rendered capable of this division for the endowment of several organisms by the appropriation of foreign matter and the forces resident in that matter. In the latter case we must admit, either that the seed for all living beings exists in a latent state in the material world, and is extracted from it by productive individuals, or that the material world is animated by a force which, Proteus-like, can assume many forms, but which, having combined with matter so as to constitute a specific organism, is compelled by the form which it has assumed to certain specific actions.

An important step in the elucidation of the process of generation has recently been made in the discovery of the vital endowments of those elementary particles which the observations of Schwann, now well known and fully confirmed, have shown to compose both animals and plants in the embryonic state. All parts of plants and animals are developed from cells. The germ of animals, and of many plants, is a simple cell, and the essential part of the gemma or bud, is either an aggregate of cells, or a single cell. The embryo of plants and animals, also, when in the process of development, is composed of a number of cells similar to the first, or germ cell. In the lower plants,—for example, in the filiform Fungi,—any one of the component cells separated spontaneously or artificially from the aggregate of cells which form the plant, is adequate to the production of many similar cells. From these facts we may deduce two conclusions, which have been already noticed by Schwann,* and of which one or the other must be true, to the exclusion of any third view.

I. Since all tissues and organised parts are produced from cells similar to those which singly or in certain number compose the germ; since all cells within the growing organism by their influence on the surrounding nutrient matter can determine the formation of new cells either in their interior (as in the case of the cells of cartilage, and of the chorda dorsalis) or on their exterior (as in the case of the cells of epithelium); and since in the lowest plants each cell separated from the organism can become a new organism, and in some simple animals, as the Hydra, a fragment separated from their body has power to develop an entire new individual; since, lastly, the elementary tissues composing such a fragment of a polype, whatever their form and nature, whether muscular fibres or nervous fibres, are all modifications of cells, it is concluded not merely that an organic being may be constituted by a single

* Mikroskopische Untersuchungen, p. 220.

cell; but that every perfectly developed organism is a mass of cells, or of parts developed from cells, each of which has the power of developing an entire new organism.* This view is evidently correct with regard to certain organic beings, such as the filiform Fungi, and, to a certain extent, even in the case of the Hydra; but it is not proved to be applicable to all organic beings. Let us, however, for a moment suppose its universal tenability, and inquire to what further inferences it would lead.

If every component cell of an entire organism, and even the product of cells possess the power of reproducing the entire individual, by the formation of new cells, by their aggregation in definite forms, and by their transformation according to the necessities of special functions; on what does it depend that these cells not merely remain aggregated together, but for the most part unite only in the form proper to the species? Is it that the attainment of one common result by a number of cells, each of which contributes to that result, depends on the mutual reaction of all the component cells, just as the different individuals in a state combine to obtain an object common to all, or as all the bees of a swarm contribute to its general economy? or are there certain dominant cells or monads to which the rest are subordinate, so long as they form part of the entire organism, as seems to be the case in the Hydra, portions of which when detached are capable of individual life, although while they form part of the entire polype they are subordinate to its form and will? But, how is it that certain component cells of organised bodies, though similar to other cells and to the original germ-cell, nevertheless produce only cells of the same kind as themselves, and are totally incapable of acting as the germs of entire organisms? Why, for example, do the cells of the horny tissues cause the formation of new cells of the same kind in the nutrient matter in contact with them, and the cells of cartilage produce new cells within their cavity, and yet never become embryos or buds? and why do certain parts of the body of the Hydra, as the arms, when cut off, fail to grow into new polypes? The explanation of this latter difficulty may be that these cells, though endowed with the force which should reproduce the entire organism, yet in consequence of the special metamorphosis of their substance into horny or other matter have suffered such an impairment of their vital activity, that they not only fail to reproduce a new individual of the species when separated from the organism, but even while forming part of it lose the vital power of the germ, and fall off as particles of dead matter. These are questions and suppositions which naturally present themselves to our mind in the consideration of the foregoing facts, but they must not be regarded as necessary conclusions.

* Schwann, op. cit. p. 227.

In this first theory, however, too great importance seems to be ascribed to the cells. The difficulties met with in applying it to the higher animals are so great, that its universality becomes highly improbable, though its correctness in the case of the lower organic beings is incontestable.

II. The second view which may be adopted is, that the power of reproducing the entire organism is not possessed by all the cells formed during the process of growth, and by the elementary parts of the tissues produced by their transformation; but, on the contrary, that this power at first resides in only one or a few cells which constitute the germ, and that, although it does undergo an increase during the process of growth, yet there arise at the same time many other cells, such as the cells of the horny, cartilaginous, and muscular tissues, which are endowed with the power of determining only the formation of new cells of their own kind. All the various cells of the organism, thus partial in their endowments and differing even chemically from each other, constitute together in the developed state what existed only in an undeveloped condition, or "potentially," in the germ-cell, or in the reproductive cells of the bud or gemma. Growth, therefore, partly consists in the conversion of the "potential" or undeveloped organism of a single cell, into a developed organism with many cells, specially endowed and distinguished both by structure and chemical qualities. Since, however, these cells, endowed with special subordinate functions, in their turn give rise to the formation, each after its kind, of new cells in the matter of the growing organism, and thus multiply themselves, the fully developed organism contains a multiple of its simplest elements. The body of the adult contains a multiple of the cartilage cells of the embryo, a multiple of its muscular fibres, &c.

The fully formed organism must not, however, be regarded as merely a fully developed individual; it is much more than this. It has still the essential force of the "potential" or undeveloped organism,—the power of multiplication by buds and generation; and this power is not the mere result of the mutual reaction of the special elementary particles of the developed organism, but is a force which still pervades the whole organism. This may be readily proved; for, independently of the fact that the head of a Hydra separated from its body will reproduce the body, we know that a man or a woman who has lost both legs still retains the power necessary for the generation of a perfect offspring, and would doubtless preserve that power if deprived of many other parts. Moreover, the mode of generation by the division, whether artificial or spontaneous, of a fully developed organism, shows us that there is a grade in the scale of organisation where the power of maintaining individual life and the structure of the species does not depend on the mutual reaction of all the various component particles or cells, but persists even when the sum of those particles is subdivided.

Further, it must be remarked, that from the earliest period of the growth of all organic beings, not merely the cells which constitute them as a developed organism are formed and multiplied, but cells or aggregates of cells are also produced, which represent "potential" individual organisms, or which, in other words, possess the power of themselves generating all the other cells which have special structures and functions in a developed organised body. During the growth of all organic beings, therefore, a double multiplication takes place,—namely, first a multiplication of the particles constituting the existing form; and, secondly, a multiplication of this form (that of the species) in an undeveloped state,—that is, in the state either of the germinating bud or spore, or of the germ, which requires fecundation before it can undergo development. The substance capable of development without impregnation, in its simplest condition a single cell, may in some cases be formed at all or most parts of an organic body; thus buds may be produced at almost any part of a Hydra or a plant. In other cases, the germinal substance is formed in a special organ,—namely, in the ovary, in the form of the germinal vesicles of the ova, just as the semen is formed in the testes. We have already observed, at an early part of this section, that all growth consists in the formation of a virtual "multiplum." We now perceive that this multiplication takes place in two ways,—namely, in the multiplication of the cells constituting as it were the mechanism of the individual organism, and in the formation of potential undeveloped multipla of this organism in the form of primary or germ-cells. Both these modes of multiplication are in progress from the earliest period of development; for, during the growth of the young sprout of a plant the germs of new buds are generated in it, and the ovaries of the child contain the germs for a new generation.

SECTION II.

Of Sexual Generation.

CHAPTER I.

OF THE SEXES.

In sexual generation the germs, though endowed with the power of propagating the distinctive properties of the genus and species, and even of the individual, are incapable of undergoing their destined organisation until they are acted on by another substance allied to them, though distinct in its nature from them, — namely, the semen. The semen itself also propagates the peculiarities of the genus, species, and individual, but only by means of its influence upon the ovum, which is the immediate seat of all the changes attendant upon the production of a new individual.

The semen and ova are sometimes generated in different individuals, in which case fecundation is effected by the concurrence of the two sexes, or by the contact of the semen of the one sex with the isolated ova of the other, brought together artificially out of the body. Sometimes both semen and ova are formed in different organs of the same individual, which is the case in all hermaphrodite plants and animals. Dualism of the sex, therefore, does not necessarily involve dualism of the individuals; on the contrary, sexual generation, as well as multiplication by buds and division, may be effected in a single individual.

Animals having only the female sex were formerly supposed to exist; and, indeed, all the lower animals, for example, the polypes, Acalephæ, and Echinodermata, were referred to that category; ova being perceived in all the individuals of these orders of animals; while the male organs, which are recognised less easily by the presence of spermatic animalcules, were not discovered. Since, however, double sexual organs are now known to exist in the Echinodermata, and since male organs have been demonstrated in the polypes, Medusæ, Radiata, and Infusoria,* the notion that any animals are of the female sex alone is quite inadmissible. Besides, an ovum, capable of undergoing development without impregnation by male semen, would not be an ovum but a deciduous bud or gemmule; and an animal producing such germs could not be regarded as of the female sex. There are many animals which form buds, but these buds are not deciduous; they undergo development on the parent stock. Some animals, as Cœnurus and Echinococcus, propagate by buds alone; others, on the contrary, as the polypes, both by buds and ova. In the Hydra, the ova as well as the buds appear on the surface of the cylindrical body in consequence of the ovaries having that situation; but the ova are distinguished from the buds by their hard horny shell.

In plants the male and female organs of generation are sometimes united in the same flowers; sometimes developed in different flowers on the same stem (monœcious plants); and sometimes, lastly, wholly separated, different individuals of the species bearing either only male or only female organs (diœcious plants). The last mentioned arrangement of the sexes is the most rare in plants, while in animals it is very

* [The parts supposed by Ehrenberg to be the sexual organs of the Infusoria are shown in figs. 146, and 147, page 1434.]

frequent, and in Insecta, Arachnida, Crustacea, and Vertebrata is universal. In plants of which the sexes are separate, it often happens that amongst the flowers of the prevailing sex a few of the other sex will show themselves, as is exemplified in Mercurialis annua, Spinacia oleracea, &c. In hermaphrodite animals fecundation is effected either by the concurrence of two or more individuals, or by each individual independently.

a. In the former case two individuals either fecundate each other simultaneously, the male organ of each impregnating the female organ of the other, which is the mode of impregnation in many Mollusca and worms (Annelida and Entozoa); or only one individual is impregnated in each act of copulation, the sexual organs being so placed that mutual impregnation is impossible; a condition, which Henle has observed to exist in the genus Helluo. In this animal fecundation is effected by the concurrence of two individuals; but while one introduces its penis into the other it does not itself receive the penis of the latter. In such cases, however, reciprocal impregnation is sometimes effected by the union of several individuals in a series, so that *a* is impregnated by *b*, *b* by *c*, *c* by *d*, and *d* by *e*. This mode of impregnation occurs in the Lymnæi, which are found swimming in the water thus united in a series. The last link of such a series of course is not fecundated, while the first does not fecundate.

b. In those hermaphrodite animals where fecundation takes place in each independently, it is generally effected by the semen finding its way to the ova within the body of the animal, as in the Radiata, according to Ehrenberg, and in the Distomata, according to Siebold. But in some cases the two kinds of sexual organs are repeated several or many times in the articulated body of the animal, and then two parts of the same animal may be bent towards each other and act respectively as male and female. It is not rare to find two tapeworms united and impregnating each other reciprocally. Once, however, a tapeworm has been observed impregnating itself; this observation was made in 1824 by a young naturalist, Fred. Schultze, whose early death was a loss to science. I was present when the fact was shown by Schultze to Rudolphi.*

The Articulata and Vertebrata present no instance of normal hermaphrodism. But in the other divisions of the animal kingdom nature has been so inconstant in respect of the sexes, that hermaphrodite orders, and orders with separate sexes, occur in the same class, and even families of both kinds in the same order.

The Infusoria, Radiata, Echinodermata, and Annelida appear, from

* See Rudolphi, in Abhandl. der Acad. der Wissensch. zu Berlin, aus der Jahre 1825, p. 45.

the results of anatomical investigations, to be generally hermaphrodite.* In many of the Infusoria Ehrenberg has discovered the male and female organs. The Polypi are likewise for the most part hermaphrodite. Amongst the Campanulariæ, however, there are, according to the observations of Ehrenberg and Lowen, distinct male and female individuals. Many polypes of the stock were observed by them to have all the organisation necessary for individual life, whilst in others the arms and internal organs essential to individual life were atrophied, and these appeared to be converted into ovaries. These metamorphosed polypes had, indeed, been previously described as ovaries by Cavolini and others.† Nordmann has published similar observations respecting his Tendra zostericola, in which the male and female cells are situated close to each other. The testes of the male polype consist of eight vermiform organs placed near the tentacles. The ova of the female cells are fecundated by the spermatic animalcules of the male polypes.‡ In other Polypi, as the Actiniæ, both ovaries and testes are known. R. Wagner § has discovered seminal animalcules in convoluted tubes of the Actiniæ. Similar tubes have been seen by Edwards || in compound Polypifera; but it is not known whether they contain seminal animalcules.¶ Amongst the Acalephæ the Medusæ, at least, appear from the recent researches of Siebold to possess separate sexes. The males of the Medusa aurita are smaller than the females,— have not the small sacs in the tentacles, and never contain ova. In the testes of the male Medusa Siebold has detected spermatozoa.**

The class Entozoa includes genera devoid of sexes,—hermaphrodites and genera with the sexes in distinct individuals. The Cœnurus and Echinococcus among the Tænioidea cystica (the Cystica of Rudolphi) seem to propagate wholly by the development of the buds. The Tænioidea cestoidea (the Cestoidea of Rudolphi) are hermaphrodite, and afford instances both of self-impregnation and of reciprocal impregnation. In the animals of this order the generative organs and their external openings are repeated in all the fully developed segments, and the fecundated ovaries are sometimes excluded from the

* [The existence of separate sexes in the Echinodermata has been observed by Valentin (in the Holothuria), Wagner (also in the Holothuria), Rathke (in the Asterias), and by Peters (in the Echinus). See Valentin in Froriep's Notizen, bd. xii. No. 7. Rathke, Froriep's Not. b. xxi. No. 269. Peters, Müller's Archiv. 1840, p. 143.]

† See Lowen, in Wiegmann's Archiv. iii. p. 249.

‡ Ann. des Sc. Nat. xi. p. 185.

§ Wiegmann's Archiv. i. No. 5, 213.

|| Ann. des Sc. Nat. 1835, December.

¶ [See also Wagner's observations on the separate sexes of the polype, Veretillum, Froriep's Notiz. xii. No. 7. Dr. A. Farre observed a number of animalcules, like Cercariæ, in the visceral cavity of Sertulariæ. Phil. Trans. 1837, Pt. ii.]

** See Müller's Archiv. 1837, p. 438.

segments containing them, and sometimes separated together with those segments. The ova, therefore, do not escape by the same orifices through the medium of which they were fecundated. The orifices of the sexual organs are, according to Mehlis,* very differently placed in the different genera of the Cestoidea. Thus, in the Bothriocephali, the two orifices are situated one in front of the other in the middle of the abdominal surface of each segment. In the genus Tænia they are found at the bottom of a cup-shaped depression at the margin of the segments: and, in the genus Triænophorus, the orifice of the male organ is at the margin, that of the female organ in the middle of the segment. The fluke-worms, Trematoda, are almost without exception hermaphrodite. Some of them have been regarded as devoid of sex; but, probably, without reason, since the phenomena of the generation of such worms would rather accord with a diœcious disposition of sexes. Animals of this doubtful nature are the Cercariæ generated in the body of snails, in tubes which are free, and generally, though not always, present independent movements, but which have been called ovistocks or germ-stocks. These moving tubes, the yellow worms of Bojanus, to which great attention has been directed by the observations of Nitzsch, Bojanus, Von Baer,† and Von Siebold,‡ are evidently organised, and in some cases can be seen to have a cœcal digestive cavity. They vary in form according to the species of Cercariæ which they contain. The Cercariæ lie in different stages of development between the outer tube and the intestinal cœcum, and move freely. After their escape from the tubes, they throw off their tail and envelope themselves in a new covering, so as to assume the state of a chrysalis; but what further change they undergo is not known. The observation of Siebold, that the parent tubes sometimes contain, together with the Cercariæ, young tubes of the same form as themselves, suggests the suspicion that both the tubes and the Cercariæ belong to the same species of animal; that the tubes are the fructiferous individuals, and the Cercariæ either males or individuals of no sex. We have instances in other animals,—for example in Lernææ,—of the female departing very considerably from the form of the species; and we have already mentioned that among the Polypi entire individuals are sometimes converted into ovistocks. The ramified and fixed germinal tubes containing Distomata, which Carus § has described, are, however, quite enigmatical; and it is equally difficult to explain the fact observed by Von Siebold,|| that the embryos of Monostomum mutabile contain a parasite of the form of the yellow worms of Bojanus,

* Isis, 1831, p. 69. † Nov. Act. Nat. Cur. t. xiii. pt. 2.

‡ Burdach's Physiologie, bd. ii. 2te Auflage.

§ Nov. Act. Nat. Cur. t. xvii. pt. i. || Wiegmann's Archiv. i. p. 45.

which entirely fills their cavity. Is this the result of metamorphosis occurring during embryonic life?

Other entozoa, namely, all the Nematoidea of Rudolphi, as the Ascaris, Strongylus, Oxyuris, Spiroptera, Trichocephalus, and Filaria, have the sexes on distinct individuals.

Some worms also which do not belong to the class Entozoa, as, for example, the genus Gordeus, have the sexes distinct, and in that respect resemble the nematoid Entozoa. The Planariæ, on the contrary, are hermaphrodite, as are likewise all the Annelida.

Of the Mollusca, one entire order, the Cephalopoda, have the sexes distinct, while the Gasteropoda and Acephala have both hermaphrodite genera, and genera with distinct male and female individuals. The majority of the genera of Gasteropoda are hermaphrodite, the Pectinibranchiata, however, as the Tritonium, Murex, Paludina, &c. have the sexes distinct.*

The existence of the two sexes in the order Conchifera was known to Leuwenhock, who recognised the ova and spermatozoa in distinct individuals; and this discovery, which was long neglected, has been recently confirmed in the most conclusive manner by Von Siebold. The ovaries or testes lie at each side of the foot, where this organ exists, and resemble each other very closely in external characters; but are distinguished by microscopic examination; the ovaries of the female being found to contain merely ova with their essential parts, the germinal vesicle and germinal spot, and the testes of the male only spermatic animalcules. According to Siebold's researches,† the genera Anodonta, Unio, Mytilus, Tichogonia, Tellina, Cardium, and Mya, and according to my own observation Pholades also, have the sexes thus distinct. Some conchifera, however, have the sexes united; for Wagner found both ova and spermatozoa in all the individuals of the genus Cyclas.‡

Insecta, Arachnida, Crustacea, and all Vertebrata have the sexes distinct; and the erroneous assertion that hermaphrodite genera, or genera having only the female sex, exist amongst them, has arisen from the superficial observation of the general similarity of form which the sexual organs sometimes present, for example, in many fishes; or from the comparative rarity of the individuals of one sex, for example of the males in the genus Apus.

In these classes, when the sexes are distinct, the individuals may be either male, female, or of no sex, though, more correctly speaking, the individuals of the latter kind are unfruitful females, or at least females

* The Patella and Chiton also have been observed by R. Wagner (Froriep's Not. xii. p. 7) to have distinct sexes. See also Edwards and Peters (L'institut. 1840, No. 334), on the existence of distinct sexes in the genera Carinaria and Firola.

† Müller's Archiv. 1837, p. 381.

‡ See also Edwards on the hermaphrodism of the Pecten. L'institut. 1840, p. 336.

arrested in their development, since they contain imperfect ovaries. Individuals of this third kind occur in several genera of insects, as Bombus, Apis, and Formica. Those of the bee kind are called working-bees. The unfruitful ants are destitute of wings, and are directed by their instinct to protect and nourish the larvæ. The imperfect females or working-bees of the genus Bombus are not indeed incapable of pairing; at least, some of those which come out of the larva state in the spring do, according to Huber, pair with the males of the same generation; but they produce only males. These latter males alone are destined to fecundate the proper or perfect females, the brood of which forms a new colony. Amongst the true bees, Apis mellifica, the working bees are smaller than the perfect females, though they resemble them in many respects. The working bees are barren; but they are rendered fruitful if, while in the larva state, and very soon after their escape from the egg, they receive a particular kind of food, namely, that destined for the nourishment of the queen-bee; and if they are at the same time placed in a larger cell they acquire all the properties of the queen-bee. If, however, after having received the food proper for the queen-bee, they are placed in a small cell, they produce only males, and are distinguished from the perfect female by their smaller size. The working-bees, therefore, are females, the ovaries of which, in consequence of the nature of their food during the larva state, have remained undeveloped, and which, at the same time that they have suffered this imperfect evolution, have received special instincts. A swarm of bees consists of about fifteen or twenty thousand working-bees, six or eight hundred males, and a single perfect female.*

Instances of the arrest of development of the male or female sex without any approach to mixture of the characters of the two sexes, or to a true confusion of the sexes, occur also as an abnormal condition in the higher animals and the human species; and these cases must be distinguished from those of abnormal mixture of the sexual characteristics or hermaphroditism. The subjects of hypospadia, in whom testes are present, and still more the eunuch, are imperfect males.

The individuals of the two sexes in each species of animal are generally distinguished by peculiarities of form, and often also by peculiar colours, or even by difference of size. Sometimes the female is larger, occasionally even to an extraordinary degree larger than the male, as is the case for example in the genus Lernæa, where the tiny male remains through its entire existence fixed over the orifice of the sexual organs of the female.† In other instances, as in many birds, the male excels

* See Latreille in Cuvier's Règne Animal, t. v. p. 361. On the ovaries of the working-bees, consult Ratzeburg, Nov. Act. Nat. Cur. t. xvi. pt. II.

† See Nordmann, Microgr. Beiträge.

the female both in his size, strength, and beauty of his markings.* The most important differences, however, between the two sexes are those evinced in their instincts, which are more constant than the differences of form. The female is entrusted with the protection of the offspring, and for this purpose dreamlike incentives to action, or instincts, arise in her sensorium. As soon as the egg is laid and seen, the female bird feels an instinctive attachment to it, and never leaves it except for short periods. The females of mammalia have the same maternal instinct after the birth of the offspring. The young animal seems to form part of its mother, who protects and defends it in all dangers. The entire or principal care of the young belongs for the most part to the female; and the case of the male Alytes obstetricians, which bears the ova upon its feet, is a rare exception.

The male of the human species is of larger proportions, stronger build, and more marked outline than the female; has respiratory and vocal organs of larger dimensions; is less easily affected by external impressions; and is in every respect not only physically but also morally of greater strength. He yields less easily to pleasant and unpleasant or painful feelings, is more energetic and constant in his efforts and desires, and more courageous; but he is also more selfish, and more ambitious of honour and fame. He excels the woman in capacity for all intellectual labours and in fruitfulness of mind; and is more cautious, systematic, and reserved in his intercourse with his fellow-men, more difficult to turn, and more haughty; but at the same time more upright and magnanimous. The field of his activity lies in the intercourse and contest of human faculties,—in the relations of society.

The woman, more delicately formed, is weaker both in body and in the faculties of the mind than the man; she is more excitable and sensitive, more timid and pliant, more superstitious, more vain, more excited by feelings of pleasure and disgust, and less so by desires. She is gifted with finer feelings of propriety and adaptation, and with a lively imagination; but is without the creative power and the clearness of intellect of the man; while, on the other hand, the reproductive power of her body is greater. Friendship towards her own sex is rare in woman, but her love for her husband and children is proportionately strong; so that her whole mind may be occupied by those feelings. Moreover, woman is distinguished by her modesty, meekness, patience, and amiability; by her readiness to sacrifice her own good and herself for the sake of others; by her tenderness, sympathising disposition, and piety. The field of her activity is her home and family.†

* For an account of the varieties presented by the animal kingdom in this respect, consult Rudolphi's Beiträge zur Anthropologie. A complete history of the phenomena of the sexes will be found in Burdach's Physiologie, bd. i.

† Compare Rudolphi, Physiologie, bd. i. p. 259.

We have already seen how the male and female reproductive substances, the semen and ovum, differ from the bud or gemma. The former, like the bud, have the faculty of reproducing the form of the parent organism; the semen, namely, gives the individual peculiarities of the male, and the ovum those of the female. Unlike the germ of buds or gemmæ, however, both the ovum and the semen are imperfect, inasmuch as neither can manifest the reproductive power until it is united with the other. In hermaphrodite animals the two imperfect substances which are thus complementary of each other are formed in the same organism; in animals with distinct sexes they are formed in different individuals, and these individuals of different sexes, though perfect in all the characteristics of the species, yet are in respect of the reproductive power both imperfect, and therefore seek each other, as it were for the purpose of supplying the deficiency. This fact is represented figuratively in the "Banquet" of Plato by the fable of the two halves of a human body.

CHAPTER II.

OF THE SEXUAL ORGANS.

The sexual organs consist, in both sexes, of a formative organ, the testis or the ovary, and of an efferent organ, the oviduct, or the vas deferens. In the female efferent organ, the ovum in its passage from the ovary generally becomes invested by some new secretions, which are either destined to serve as nutriment, or to form a shell. In many animals one part of the oviduct also forms the receptacle for the ovum during its development, and is called the uterus. A uterus in this sense exists in the viviparous genera of Fishes, Amphibia, and Mammalia, as well as in Man. The secretion of the testes also in its course to the exterior of the body becomes, in many cases, mixed with other secretions, which are poured out by accessory secreting organs connected with the male efferent organ. In those animals in which the two sexes are distinct, but in which impregnation is effected internally, there are superadded at the orifice of the efferent apparatus the organs of sexual connection. The essential sexual organs, however, which are universally present, are the formative organ and the efferent apparatus. The sexual organs of both sexes present two perfectly distinct types, which are characterised by the relation which the formative and efferent organs bear to each other. In one type the efferent organ has the place of a true efferent duct, its walls being continuous with those of the cavities of the formative organ; in the other, the two essential parts of the sexual organs are wholly unconnected, and the ovum, or semen, first makes its way through the parietes of the formative organ into the abdominal cavity, and escapes thence by a special canal. The product of the formative organ may in this case either fall free into the abdominal cavity before making its way out by the efferent canal, or it may be at once received from the ovary or testis into the open end of the tube which is in the neighbourhood.

The male sexual organs of all Invertebrata, and of by far the greater number of the Vertebrata, are formed after the first type,—that in which the efferent part is continuous with the formative part of the apparatus. Such is their form in Man, Mammalia, Birds, Reptiles, Amphibia, and most Fishes. The female sexual organs are less frequently formed after this type. They are, it is true, formed in this manner in most Invertebrata; but the contrary is the case in Vertebrata, with the exception of the osseous fishes, in the greater number of which the ova are formed in the walls of a hollow tube,—the prolongation of the oviduct; so that the ova escape at once into the interior of the efferent duct, and never pass at all into the abdominal cavity.

It is seldom that the male sexual organs are formed in accordance with the second type, in which the efferent duct opens directly out of the abdominal cavity, and has no communication with the testis. They have never this form in Invertebrata, and among the Vertebrata, only in some few fishes,—namely, in the Cyclostomata, (the Petromyzon, Ammocætes, and Myxinoidæ,) and in eels. Rathke has discovered the existence of the structure of the male organs just described in nearly all those fishes. The testes of the male Petromyzon is a cellular organ attached to the vertebral column. In the month of May the abdominal cavity is full of fluid semen, which, under pressure, escapes in a full stream from a papilla situated close to the anus. The canal through which the secretion here escapes from the abdominal cavity is extremely short, and is not elongated into a tube within the abdomen. The escape of the semen is effected in exactly the same manner in the myxinoid fishes and in eels.*

The female sexual organs of Invertebrata are very rarely formed after the second type; the only instances of their having that structure, with which I am acquainted, occur in the Echinorhynchus, where, according to Von Siebold, a separate efferent tube, or oviduct, opens by a funnel-shaped extremity into the abdominal cavity, while the ova escape into the abdominal cavity before they are received into this tube to be conveyed by it out of the body; and in the Sepia, in which, also, Krohn† has observed the ovary and oviduct to be separate. In vertebrate animals, on the contrary, this type is the prevailing one: the only exception to it being met with in osseous fishes. The simplest form of the female efferent organ, when it is distinct from the ovary, is found in

* Set Rathke's Beiträge zur Geschichte der Thierwelt, p. ii. and Müller's Archiv. 1836, p. 178.

† Müller's Archiv. 1839, p. 353.

the Cylostomata, in eels, the Cobitis tænia, and in the Salmonidæ; in which fishes it is a simple opening leading from the abdominal cavity to the exterior. In the female Petromyzon, the abdominal cavity is in the month of May full of ova, which flow out of the opening just referred to, when the belly of the fish is compressed. In the sturgeon,—Acipenser sturio,—similar openings exist, and the ova may escape from the abdomen through them, or through funnel-shaped tubes which communicate with the ureters in both sexes. In Acipenser huso, and others of the sturgeon family, the external abdominal openings do not exist, and the funnel-shaped tubes communicating with the ureters are the only means of escape for the ova. In the sharks and rays, reptiles, Amphibia, birds, and Mammalia, the short efferent canal of the Cyclostomata is extended into a long tube,—the oviduct. The end of this tube, which opens into the abdominal cavity, sometimes lies close to the ovary, as in man, Mammalia, and birds; and in the seals, otters, martens, and ferrets its dilated extremity appears, from the observations of Albers, E. H. Weber, and Treviranus,* to envelope the ovary in the manner of a capsule; whilst in other cases, the ovary and the infundibulum of the oviduct are at a considerable distance from each other, as in the sharks and rays and Amphibia. In the shark family, the two oviducts meeting above the liver form there a common infundibulum, while the ovaries lie on the outer side of the liver, or beneath it. In the rays and Amphibia the two oviducts remain distinct; but even in the latter class they extend to the most anterior part of the abdominal cavity, far beyond the ovaries.

Many animals have but one ovary, and many, indeed, only one oviduct. In the myxinoid fishes the ovary is single, and is situated to the right side of the mesentery, suspended by a special fold of peritonæum. Scyllium carcharias, and Mustelus, among the shark family, have a single ovary, which in them lies in the middle line. In many osseous fishes, also, Rathke found both the ovary and the testis single. In most birds, the Raptores excepted, only the left ovary and oviduct are developed, the right existing in the embryo, but becoming atrophied.† The reverse of this condition is presented to us in the multiple ovaries of some animals. The Tænioidea cestoidea, which do not propagate by the formation of gemmæ, like the cystoid worms, but are distinguished by their jointed structure, and by the repetition of the male and female sexual organs in each of the fully-formed segments, afford a remarkable example of the multiplication of the sexual organs without multiplication of the individual. The gemmiparous cystoid worms are compounds of many individuals united on a single stock. In many cestoid worms, also, separate

* See Tiedemann's Zeitschrift, i. p. 180.

† See Wagner's account of the Predacious Birds, with double ovary and oviduct, in the Abhandl. der K. Baiersch. Acad. ii. 1837.

segments fully formed become detached with thousands of ova contained within them. A similar example of equally great multiplication of the ovaries is presented to us in the Comatulæ and Crinoideæ among the Radiata, in which each pinnula of the arms contains an ovary, so that one Comatula has a thousand or more ovaries.* Here, again, only the generative organs are multiplied, the animal remains a simple individual; and we are reminded of the multiplication of the sexual organs in plants.

The oviducts either open separately into a cloaca, as in fishes, reptiles, and Amphibia; or previously coalesce to form a single median tube. The uterus either is single, as in apes, or has two cornua, or is perfectly double. The true double uterus exists in the sharks and rays, and in several Mammalia,— namely, in the greater number of the Rodentia, the Ornithorynchus, &c. In Ruminantia, Pachydermata, Solidungula, Carnivora, and Cetacea, the uterus has a single body and external orifice, but has two horns. The uterus of the Marsupiata is peculiar in its structure. The middle part, or body of the organ, terminates inferiorly in a *cul de sac*, without having any communication with the vagina, but gives off two cornua superiorly, and two other cornua laterally, which pass downwards, and open into the vagina.

In many cases where impregnation is effected within the female sexual apparatus, special organs of intromission are provided. They do not, however, seem absolutely necessary for that purpose; for there are many animals in which impregnation is internal, and in which it is effected merely by the cloaca of the male, or the papilla of the seminal ducts being applied to the cloaca of the female, as for example in the viviparous Amphibia and many birds.

The males of fishes, and all the Amphibia, and also of the singing and predacious birds, are destitute of penis. In many other birds, on the contrary, in reptiles and in Mammalia, this organ is present. The penis, the organ through the medium of which the pleasure of the act of coition is excited in the male, and by which the semen is conveyed into the interior of the female sexual organs, is not formed after the same type in all classes of animals. There are two perfectly distinct forms of the penis, which are not modifications of the same type, but which are sometimes associated together.

1. The first form is that presented by the organ of intromission in the Crocodilida and Chelonia, in the ostrich (Struthio camelus), and in Mammalia. Here the penis consists either of two solid fibrous bodies, as in Chelonia and Crocodilida, or of two bodies, fibrous only on the surface, and internally cellular, and capable of erection, as in Mammalia. These bodies are united in the middle line, and are fixed at the abdominal aspect of the external sexual region. At their inferior or posterior surface there is in crocodiles, tortoises, and turtles, the ostrich,

* See J. Müller, in Müller's Archiv. 1837. Jahresb. p. xcvii.

and the young fœtus of mammalia, a groove invested with mucous membrane and cavernous tissue. This groove, which is the cavity of the corpus cavernosum urethræ not yet closed, remains permanently in that condition in the Crocodilida, Chelonia, and the ostrich, but in Mammalia and man becomes closed, so as to form a tube of which the glans penis is the continuation. In many monkeys, bats, and rodent and carnivorous animals, the anterior portion of the penis and glans (which is often very much elongated) contains a portion of bone destined to support the canal. In the wading birds the rudiment of a penis often exists in the form of a lip or tongue, with a groove at its posterior surface which looks towards the cloaca. The ostrich has besides the two fibrous bodies of the penis a third elastic body, which retracts the penis when it is not in the state of erection, causing it to become spirally bent. This third body is cavernous or cellular internally, and hence is enabled also to extend the penis.

Of the three cavernous erectile bodies which exist in Mammalia, one only is found in the Crocodilida, Chelonia, and ostrich,—namely, that of the urethra, which is cleft.

2. The second form of the penis occurs distinctly only in serpents and lizards. The organ of intromission here lies not at the abdominal but at the dorsal or caudal boundary of the external sexual region. It consists of a hollow cæcal tube, the walls of which contain erectile tissue. The open end of this tube is directed forwards, towards the cloaca, and on its inner surface there is a groove. In serpents and lizards there are two such organs. During the act of copulation they are everted, as we may evert the finger of a glove, and then the groove comes to be placed on their exterior, and serves to conduct the semen from the cloaca. In the viper kind, Crotalus and Python, each of the tubular organs we have described is bifurcate at its cæcal extremity, so that when everted, the penis appears forked. In serpents and lizards the penis is retracted and inverted again after erection by muscles which are attached to the cæcal end of the tube.

3. In ducks, geese, and the rhea, cassowary, and emeu, the first and second forms of the penis occur in combination with each other. Here there is a solid portion attached to the anterior or abdominal wall of the cloaca, formed of a fibrous structure, and having a groove on one surface, and another tubular portion of the same structure as the penis of serpents and lizards, and like it capable of eversion. The latter part is here, however, not double, and, except during the venereal orgasm, lies convoluted, like a piece of intestine, near the cloaca. The open end of this tube is situated at the extremity of the solid portion of the penis, and in the act of coition it becomes everted and protruded, so as to give the penis double the length which the solid portion alone possesses. The groove on the interior of the tube becomes placed on

its exterior when it is erected, and then forms a continuation of the groove of the fibrous portion of the penis. After the act of coition is completed, the tubular part of the penis is retracted, and again inverted by an elastic band.*

The females of the duck and goose kind, and of the rhea, cassowary, and emeu, have a clitoris formed on the same type as the male organ, though of much smaller dimensions.

The clitoris of Mammalia has the same structure as the penis of the male in the embryo condition: both are formed on the same principle. The clitoris of the female embryo (which is then proportionally large), and the penis of the male, at first resemble each other exactly in external form. In both the corpus spongiosum s. cavernosum urethræ is cleft, so as to form an open canal. Both, also, have musculi ischio-cavernosi (erectore spenis s. clitoridis) and constrictores pudendi. But when the perinæum closes in the male, the latter muscles form the acceleratores urinæ. The clitoris, on the other hand, becomes shorter, and the lips of its groove are converted into the nymphæ. As long as the perinæum remains open, the place of labia externa is supplied in the male fœtus by the folds which afterwards form the scrotum, but which are as yet empty, the testes being in the abdominal cavity. In many of the Mammalia, as the Cetacea, Ornithorhynchus, elephant, and Hyrax, the testes never leave the abdomen; but in most mammals, and in the human subject, they descend before the termination of fœtal life, lodged in a fold of peritonæum, into the scrotum; and subsequently the diverticulum of the peritonæum, which descends with them, becomes cut off from the abdominal cavity. In several animals, again, as the rat family, the hamster, and others, the communication between the cavity of the abdomen and that of the scrotum remains open, and the testes may, by the action of muscles, be brought to be at one time within the abdominal cavity, and at another time external to it.

In the genus Stenops, among the monkeys, the urethra traverses the clitoris, although the vagina has its usual position more posteriorly.

CHAPTER III.

OF THE UNIMPREGNATED OVUM.

Our knowledge concerning the unimpregnated ovum has been brought to its present state by the labours of modern anatomists, particularly by the exertions of Purkinje, Von Baer, R. Wagner, Coste, and Valentin. So successful has been their study of this subject, that in it, as in all the

* See J. Müller, in the Abhandl. der Acad. der Wissench. zu Berlin. 1836.

most perfect parts of science, the numerous individual facts can now be referred to simple laws.*

In many invertebrate animals the ova are developed in the interior of cæcal tubes, in which they are not surrounded on all sides by organised tissues, so as to be separated from each other; but in many other of the Invertebrata, and in all the Vertebrata, they are formed within the cells of the ovary. These cells are invested singly by numerous blood-vessels, and are united together by a fibrous substance of a greater or less degree of firmness, called the *stroma*. When the ova lie in insulated cavities of the ovary, the wall of these cavities, formed of the condensed stroma, is called the capsule or *theca*. The following essential parts may be distinguished in the ova of invertebrate animals, fishes, Amphibia, reptiles, and birds,—even in those of the smallest size.

1. The capsule of the ovum, *ovicapsule*, which is in some cases, as in many Invertebrata, insulated from the proper tissue of the ovary, and may even escape with the ovum; but which in other instances, as in the oviparous Vertebrata, coalesces with the theca of the ovary, forming there what is termed the *calyx* (see figs. 152 [4], and 154 [1]). On the side directed from the ovary the calyx is often thin but thicker on the side next to the ovum, to which it is connected merely by a pedicle (figs. 152 and 154). The thin side of the calyx in the ovary of the bird often presents a white band of an arched form, and distinguished from the rest of the calyx by the absence of blood-vessels (fig. 152 [3]). This band, the *stigma*, indicates the situation at which the dehiscence of the calyx will subsequently take place to

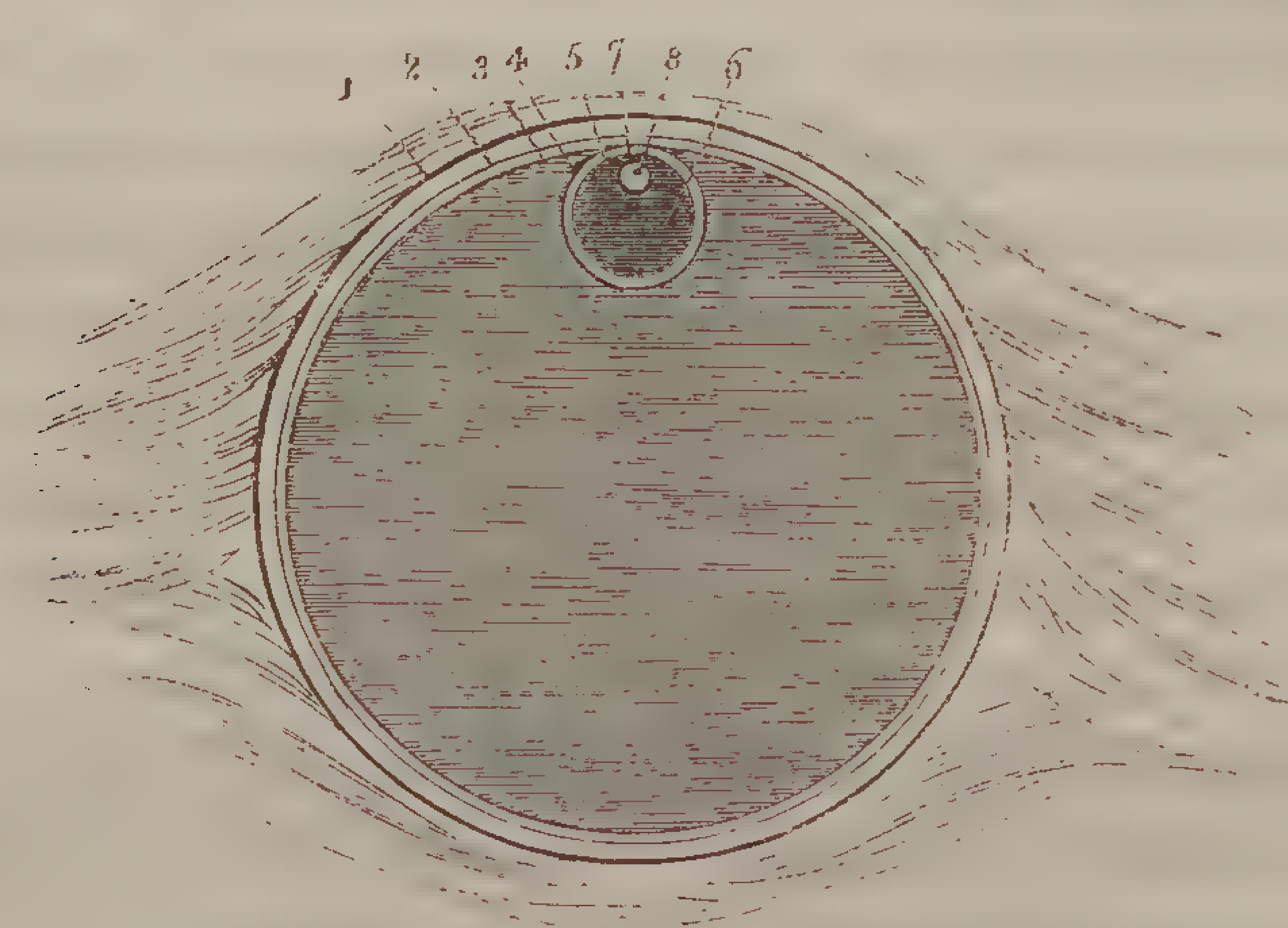
Fig. 152.†

* The following are the most important works on this subject:—Purkinje, Symbolæ ad ovi avium historiam ante incubationem, Lips. 1830; and Encyclop. Wörterbuch der medic. Wissensch. Art. Ei. Von Baer, De ovi mammalium et hominis genesi, Lips. 1827. Coste, Recherches sur la génération des Mammifères, Paris 1834. Bernhardt (et Valentin), Symbolæ ad ovi mammalium historiam ante imprægnationem, Vratislav, 1834. Valentin, Entwickelungs-geschichte, Berlin 1835. R. Wagner, Müller's Archiv. 1835, p. 373; Prodromus historiæ generationis hominis atque mammalium, Lips. 1836; Abhandl. der K. Baiersch. Acad. 1837, p. 2; and Lehrbuch der Physiologie, Icones Physiologicæ, Leipz. 1839. Krause in Müller's Archiv. 1837, p. 26. Carus, ibid. 1837, p. 442. Jones, London Med. Gazette, 1838, p. 680. Schwann, Mikroskop. Untersuch. Barry, Philos. Transact. 1838 [and 1839]; and Edinburg Philos. Journal, 1839. The best figures of the ova of Invertebrata given by the older writers are those of Poli, Goeze, Della Chiaje, and O. Fr. Müller. The ova of fishes had been best shown by Cavolini, Erzeugung der Fische und Krebse, tab. i. fig. 4; and Sonnini, Hist. Nat. des Poissons, t. ii. tab. iii. fig. 4. The structure of the ova is correctly indicated, though it was not understood by these writers.

† [Figure of the ovary of a common hen, after Carus. 1, imperfectly developed

allow the escape of the ovum. Schwann has observed a circumstance which is worthy of remark, as aiding in identifying the capsule of the ovum of different classes,—namely, that a stratum of epithelium cells exists on the inner surface of the ovicapsule in fishes, and also on the inner surface of the *Graafian vesicles* or capsules of the ova of Mammalia. Both Jones and Barry, with justice, regard the ovicapsules of oviparous animals as identical with the Graafian follicles of Mammalia (fig. 153 [2 3]).

Fig. 153.*



2. Within the ovicapsule lies the *yolk*, surrounded by the *vitelline membrane* (fig. 153 [6 5], and 154 [5 4]). This membrane is at first in close contact with the capsule, but subsequently becomes separated from it in many animals by a tolerably large interval. The granules of the yolk are found by Schwann to be cells containing a finely granular matter and oil globules.

3. In the substance of the yolk is imbedded the *vesicle of Purkinje*, or vesicula germinativa (fig. 153 [7]). This vesicle is of greatest relative size in the smallest ova, and is in them surrounded closely by the yolk, nearly in the centre of which it lies. During the development of the ovum, the germinal vesicle increases in size much less rapidly than the yolk, and comes to be placed near to its surface. Ovula and germinal vesicles can frequently be detected in the ovaries of the fully developed embryo.

4. The germinal vesicle contains a transparent fluid, and in addition to this, the *germinal spot*, macula germinativa, or nucleus germinativus of R. Wagner (fig. 153 [8]). This germinal spot consists of one or

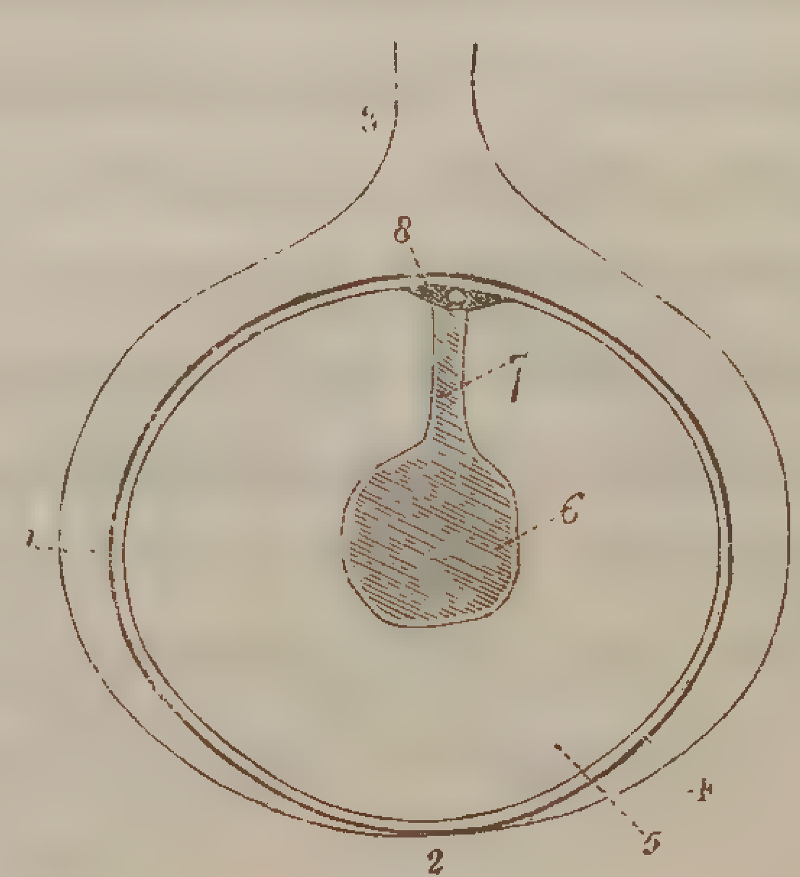
ova; 2, an ovum nearly fully developed in its calyx; , the stigma, or line of dehiscence; 4, a calyx from which the ovum has escaped.]

* [Diagram of an ovicapsule, or Graafian vesicle of a mammal, containing the ovum. 1, Stroma or tissue of the ovary; 2 and 3, external and internal tunics of the Graafian vesicle; 4, cavity of the vesicle; 5, thick tunic of the ovum or yolk sac; 6, the yolk; 7, the germinal vesicle; 8, the germinal spot.]

more somewhat opaque corpuscles, and is possibly the analogue of the nucleus of formative cells. It is simple in the germinal vesicle of the human subject, of Mammalia, birds, reptiles, and many Invertebrata, and is recognisable even in the ova which are least advanced in development. In Amphibia, the osseous fishes, and several invertebrate animals, the germinal spot is multiple. As the ova advance in development granular matter is deposited on the inner surface of the germinal vesicle, and renders the germinal spot or spots indistinct, and sometimes even invisible. In some of the Invertebrata the germinal spot itself seemed to Wagner to have a special investing membrane.

In the larger and fully formed ova of the oviparous Vertebrata, the germinal vesicle is found lying at the surface of the yolk, imbedded in a disk-shaped layer of granular substance, the *germ-disk*, or discus proligerus of Baer (see fig. 154 [8]). The vesicle is prominent above the surface of this disk, which is continued from side to side beneath it. The middle of the yolk is occupied by a kind of cavity filled with a more transparent mass, and from this cavity a canal, filled with a similar substance, extends towards that point of the surface at which the germinal vesicle is situated (fig. 154). The substance filling this cavity and canal of the yolk is found, by Schwann, to consist of cells, distinguished from the ordinary cells of the yolk by their smaller diameter, and by their containing a nucleus. The part of the yolk in which this canal and the germinal vesicle, or the germinal disk are placed, is lighter than the other parts, and, consequently, in ova which have acquired the albumen and shell in their passage through the oviduct, the yolk always places itself so that the germ lies uppermost, whatever the position of the entire egg may be.

Fig. 154*



It results from the observations of Purkinje and Baer, that the germinal vesicle disappears at the time when the ovum leaves the ovary, and before impregnation has taken place. Baer found no germinal vesicles in the ova of frogs which had reached the oviduct: the vesicle appears to dissolve away and to mingle its substance with the granular mass of the germinal disk. In the hen's egg the germinal disk measures about one line in diameter; it is seen immediately under

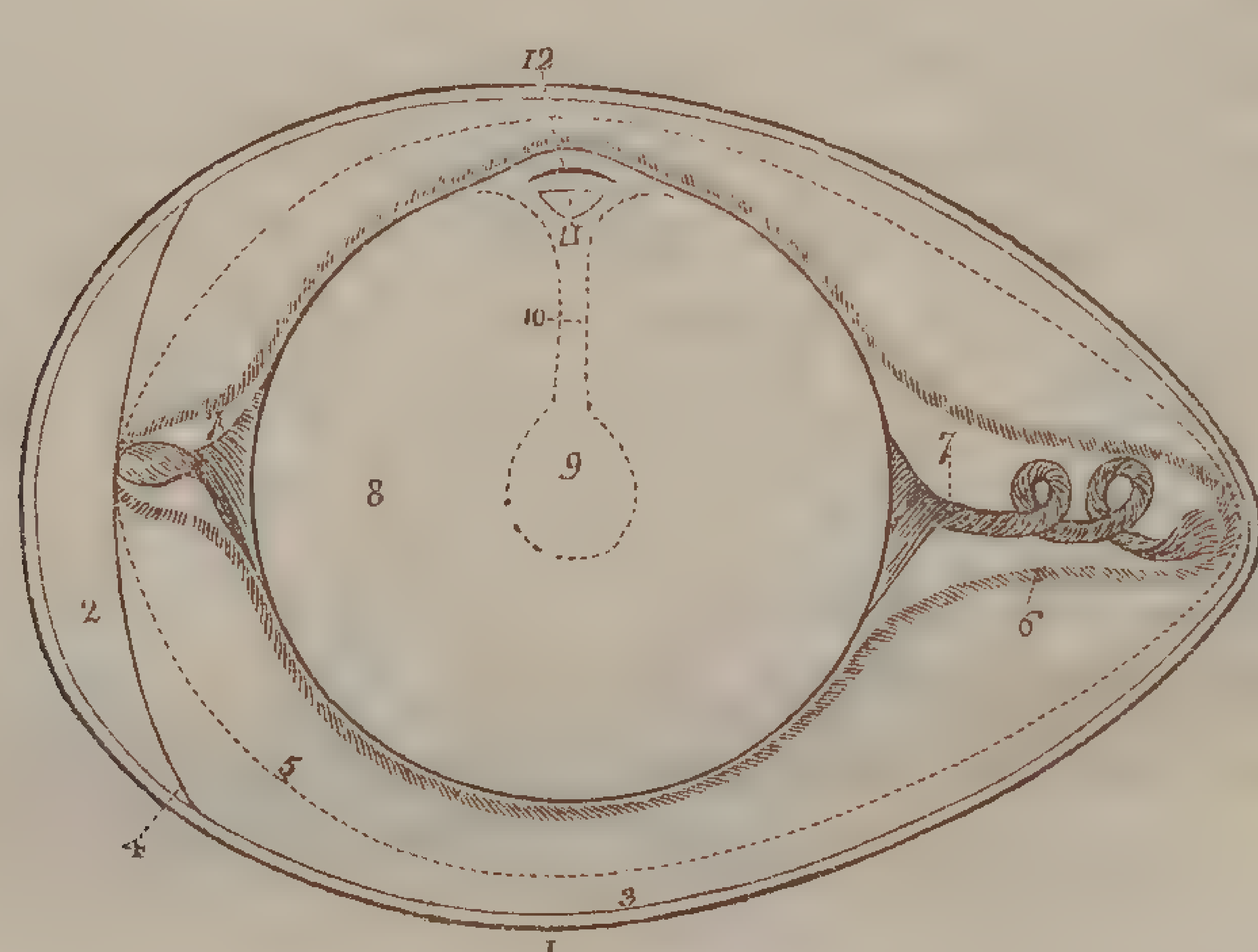
* [Diagram of a calyx from the ovary of a bird, containing a fully-developed ovum cut perpendicularly, after Von Baer. 1, The calyx; 2, situation of the stigma where the calyx is attenuated; 3, the pedicle of the calyx; 4, the yolk sac; 5, the yolk; 6, the yolk cavity; 7, the canal; 8, the germinal disk, or discus proligerus, with the germinal vesicle.]

the vitelline membrane in all eggs which have left, or are about to leave the ovary, whether they are impregnated or not: in it the first rudiments of the embryo are formed. Beneath the germinal disk in the hen's egg there is a granular mass called the *cumulus proligerus*, nucleus cicatriculæ, or nucleus of the germinal disk. This mass consists, according to Schwann, of cells similar to those of the transparent centre of the yolk, while the germinal disk itself is composed of cells filled with coarse granular matter.*

The ova of oviparous Vertebrata, when they leave the ovary, consist merely of the yolk with the vitelline membrane, and the other parts contained within these. The albumen and shell are added in the oviduct.

The separation of the ova from the ovary may take place independently of impregnation: such is the case, for example, in frogs and in birds. The ova of frogs, indeed, always leave the ovary and are received into the oviduct long before their impregnation, which is not effected until they have wholly escaped from the body of the female. After the separation of an ovum its calyx remains; but it gradually wastes and becomes confounded with the mass of the ovary. In the oviduct of many oviparous animals the ovum receives an investment of albumen, which is secreted by the tube. In birds, the more dense internal layer of this albumen, which adheres to the yolk, is continued in the form of two spirally twisted bands towards the extremities of the egg; these are the chalazæ, which are produced by the revolving motion of the egg in its descent through the oviduct (see fig. 155). The shell

Fig. 155.†



* [Dr. Martin Barry's account of the changes which the germinal vesicle undergoes at the time of impregnation, and of the other immediate consequences of the action of the semen on the ovum, differs in many important respects from that given in the text. It will be found in the 5th Chapter of the present Section.]

† [Diagram of a bird's egg after impregnation, supposed to be cut perpendicularly, after Von Baer's figure, as modified by Wagner. 1, Shell; 2, folliculus aeris; 3, membrana testæ, which divides into two layers at 4; 5, boundary of the more dense middle

also is due to the secreting action of the oviduct. The oviducts of sharks and rays are furnished with two large glands for the formation of the horny shell of their ova. The shell of the bird's egg consists of the membrane of the shell, and of the carbonate of lime deposited thereon. The lining membrane of the shell is itself composed of two laminæ, which separate from each other at the large end of the egg, in proportion as the fluids of the egg evaporate, and thus form the folliculus aeris (fig. 155 [2]), which is found in that situation in all eggs which are not perfectly fresh.*

The ova of mammalia and the human subject find the nutriment necessary for the development of the embryo in the uterus. Hence the extremely small quantity of yolk with which they leave the ovary, and their minute size; their diameter, in their most perfect condition, being scarcely so much as one-tenth of a line. In their relation to the ovary, also, they differ in many particulars from the ova of oviparous animals. Owing to their extreme minuteness, the ovula of man and mammiferous animals for a long time escaped observation. Prevost and Dumas had remarked, that the ova found in the oviducts of animals, shortly after impregnation had taken place, were much smaller than the follicles of Graaf; and in two instances they actually saw the ovulum within the Graafian follicle, but they did not pursue the subject any farther. The merit of discovering the ovulum of mammiferous animals and man really belongs to Von Baer.

The vesicles or follicles of Graaf, or the ovicapsules which contain the ovula of mammals and the human subject, are connected together by a very firm stroma, which, with them, constitutes the ovary. They are but slightly prominent above the surface of the ovary in most Mammalia, but in the Ornithorhynchus are raised on pedicles as in birds. Each capsule is formed of two membranes, the more internal of which is like the ovicapsule of oviparous animals, lined with epithelium (membrana granulosa of Baer). The ovulum occupies only a very small part of the cavity of the Graafian vesicle or capsule, the remainder being filled with an albuminous fluid in which microscopic granules float. (See fig. 156, and fig. 153, page 1466.) In immature capsules the ovulum is proportionally larger and lies more nearly in the centre; while in those which are fully formed it is placed close to the inner wall of the capsule,

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portion of the albumen; 6, boundary of the most dense albumen; 7, the chalazæ; 8, the yolk; 9, the yolk-cavity; 10, the canal or duct leading to the cicatricula; 11, cumulus proligerus; 12, the germ.]

* [According to Mr. Town (Guy's Hospital Reports, vol. iv. p. 390), there is a second delicate membrane within the well-known membrana testæ. The two layers of the latter are adherent throughout; and the folliculus aeris is formed by the newly-described membrane alone separating from it and passing directly across at the large end of the egg.]

imbedded in a granular zone (fig. 156 7). In both conditions, however, according to Barry, the ovulum is attached to the parietes of the follicle by peculiar granular bands or *retinacula* (fig. 157). In order to examine an ovulum, one of the Graafian vesicles, it matters not whether it be of small size or arrived at maturity, should be pricked and the contained fluid received upon a piece of glass. The ovulum then being found in the midst of the fluid, by means of a simple lens, should be placed under the compound microscope. Owing to its globular form, however, its structure cannot be seen until it is subjected to gentle pressure under a second thin lamina of glass, or by means of a compressorium.

Fig. 156.*

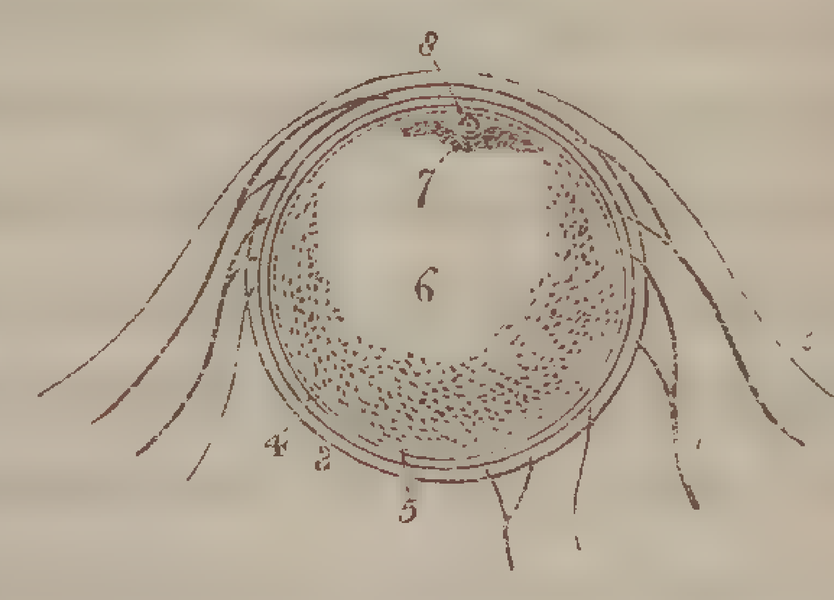


Fig. 157.†

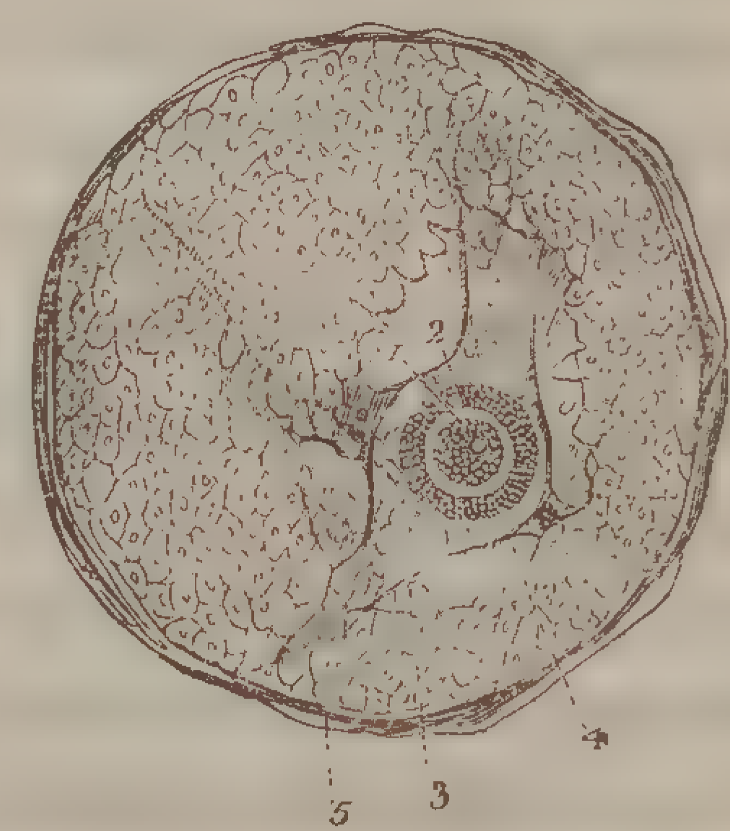
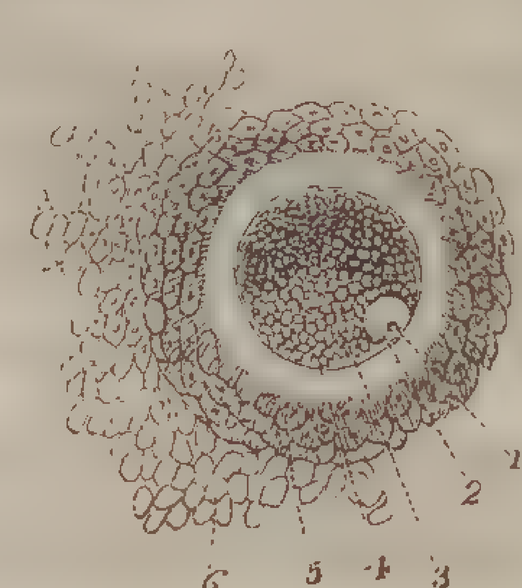


Fig. 158.‡



The external investment of the ovulum is a thick membrane, which, under the microscope appears as a bright ring (fig. 158 3), bounded externally and internally by a dark outline. This membrane is called by Valentin and Bernhardt, *zona pellucida;* by R. Wagner, chorion. The anatomists who have occupied themselves most with the examination of this part of the ovulum, are divided in their opinions respecting its nature. According to Krause, it is composed of an albuminous mass, enclosed in a delicate membrane; while Wagner and Bischoff regard it as a simple tunic, because it tears with a uniform margin. Schwann admits that such is the character of its edge when torn, but nevertheless inclines, as does Dr. Barry§ also, to Krause's opinion.

* [Graafian vesicle of a mammal, after Von Baer. 1, Stroma of the ovary with blood vessels. 2, Peritoneum. 3, External coat; and 4, internal coat, of the Graafian vesicle. 5, Membrana granulosa (of Baer). 6, Fluid of the Graafian vesicle. 7, Granular zone or disk, containing the ovum (8), and regarded by Barry as identical with the " retinacula" shown in fig 157.]

† [Ovum of the rabbit in the Graafian vesicle, after Barry. 1, The ovum, with its thick tunic or zona pellucida. 2, the tunica granulosa (of Barry). 3, the retinacula. 4, cavity of the vesicle of Graaf, seen through an opening in the membrana granulosa of Baer, which lines the vesicle. 5, coats of the Graafian vesicle.]

‡ [Ovum of the Hog, after Barry. 1, Germinal spot. 2, Germinal vesicle. 3, Yolk. 4, The broad zona pellucida or tunic of the yolk sac. 5, The tunica granulosa of Barry, formed of a dense layer of granules similar to those contained in the fluid of the Graafian vesicle, and also to those which compose the membrana granulosa of Baer, and the " retinacula" of Barry. 6, Adherent granules.]

§ [According to Dr. Barry, the zona pellucida is a solid transparent membrane. He

Within this transparent investment lies the yolk, which consists of granules or cells and fat globules. This substance forms a globular mass which is usually in close contact with the inner surface of the investment above described. But sometimes in ova, which have attained the most perfect maturity, an interval can be seen between the yolk and its outer tunic, and this interval is rendered greater by the imbibition of water; so that it would seem probable that the mass of yolk is invested with a special membrane-like layer of granules.

For a long period after the existence of the germinal vesicle in the ova of oviparous animals was generally known, it remained undiscovered in the ova of mammiferous animals and man; and it then appeared doubtful, whether the ovula of the latter animals should not be regarded as analogous to the germinal vesicle of the oviparous classes. The germinal vesicle of the ovulum of Mammalia was first discovered by Coste, in 1834, but we owe the most accurate information respecting it to the researches of Valentin and Bernhardt. The vesicle is of largest relative size in the least advanced ovula. Its diameter is about $\frac{1}{60}$ of a line. The germinal vesicle can be seen while yet within the ovulum, if the latter be flattened by cautious pressure; and sometimes the ovulum may by the same means be ruptured, so as to allow the germinal vesicle to escape uninjured. Within the germinal vesicle, and close to its surface, is the germinal spot of Wagner, the diameter of which is no more than $\frac{1}{200}$ or $\frac{1}{300}$ of a line. The germinal spot is somewhat opaque, the rest of the contents of the vesicle transparent.

The discus proligerus does not exist in the ovulum of Mammalia, at least not with its characteristic form. But R. Wagner imagines that its place is here supplied by the continuous layer of granules which surrounds the entire yolk.

According to Carus, all the essential parts of the ovulum can be detected in the ovary of the mature embryo of the human subject, or of mammiferous animals.

CHAPTER IV.

OF THE SEMEN.*

Great as are the advances which our knowledge of the ovum and female germ has made during the last few years, they do not surpass those

states, however, that internal to this there is a much thinner membrane (the true membrana vitelli), which exists while the ovum is contained in the ovary but disappears by liquefaction in the Fallopian tube, at the same time that the chorion begins to be formed. See Dr. Barry's Researches on Embryology, 2nd series, p. 322, 333, and 339.]

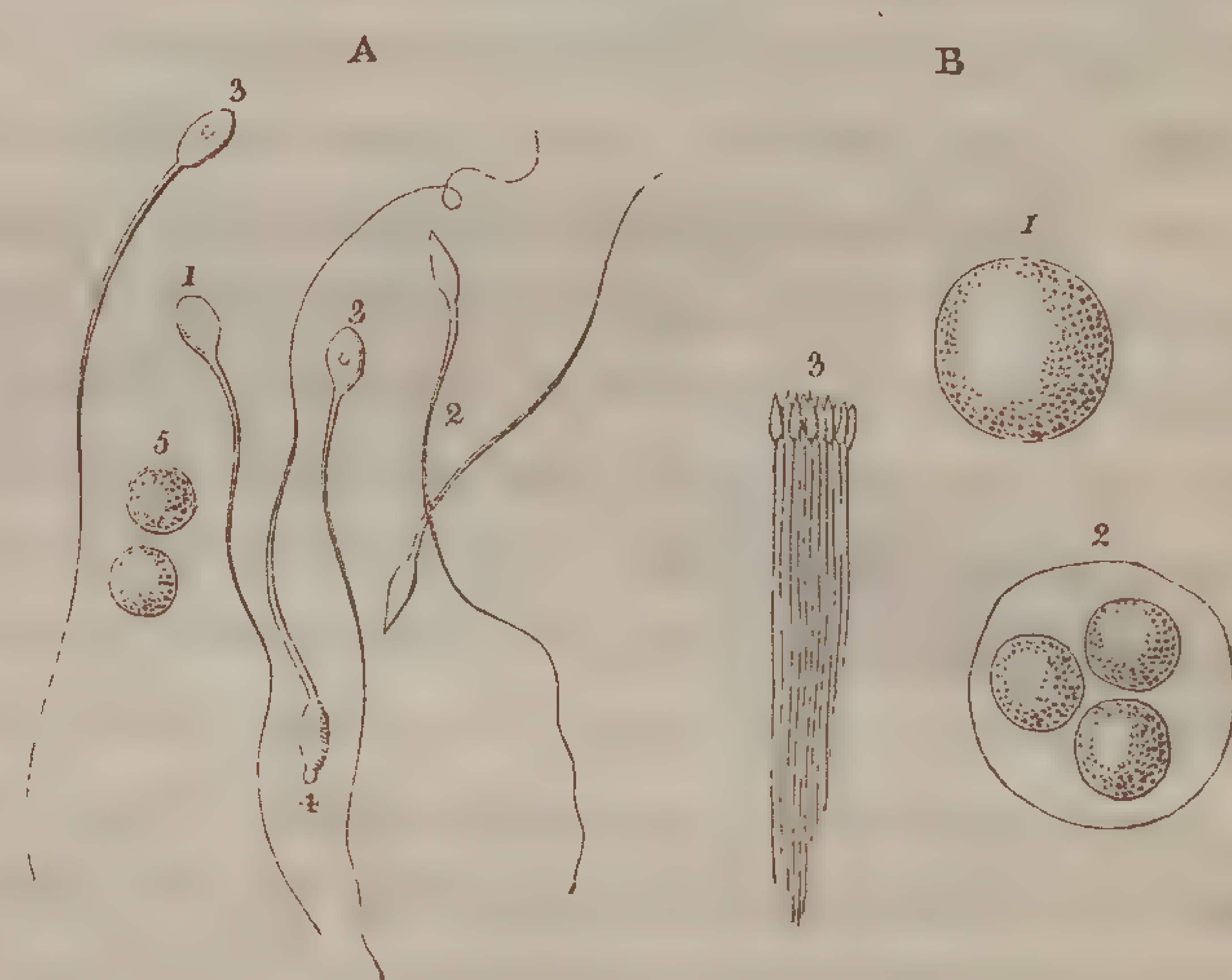
* *Bibliography.* [Leeuwenhoek, Anatomia seu interioria rerum. Lugd. Bat. 1687. Arcana naturæ. Delphis, 1695. Epistolæ physiologicæ. Delphis, 1719. Gleichen, über die Samen und Infusions-thierchen. Nürnberg, 1778. Prevost et Dumas, Ann. des.

by which our acquaintance with the fecundating fluid of the male has arrived at its present state of perfection. The semen has been made the subject of minute investigation by many anatomists, but with most success by Wagner and Von Siebold.

The ova or germs of the female are formed at a very early period, even in the embryo; but the semen and its essential elements are generally not present until the time of sexual maturity.

The semen of animals is a thick white or yellowish white fluid, having a peculiar penetrating smell. It becomes more transparent when exposed to the air, and is coagulated by alcohol; but its chemical properties are, with reference to the theory of generation, less important than its vital endowments.* It is composed of three distinct elements, a fluid, granules, and animalcules—the *spermatozoa.* These animalcules are found both in the vas deferens and in the vesiculæ seminales. The fluid of the semen cannot be obtained separate from its other components, and consequently its peculiar properties cannot be ascertained. The granules of the semen (see fig. 159 and 161) are described by Wagner as round bodies finely granulated on their surface, and measuring from $\frac{1}{300}$ to $\frac{1}{400}$ of a line in diameter; they must not be confounded with

Fig. 159.†



Sc. Nat. T. i. ii. Czermack, Beiträge zur Lehre von den Spermatozoen. Wien. 1833. Treviranus in Tiedemann's Zeitschrift für Physiol. V. pt. 2. Von Siebold in Müller's Archiv. 1836, p. 232, 1837, p. 381. R. Wagner in Abhandl. der K. Baiersch. Acad. 2. 1837, and Müller's Archiv. 1836, p. 225. Valentin, Repertor 1836, p. 277. Dujardin, Ann. des. Sc. Nat. t. viii. 291. 297. Donné, L'institut 1837. 206. Ehrenberg, Die Infusions-thierchen, p. 464. Valentin, Nov. Act. nat. cur. t. xix. Hallmann, Müller's Archiv. 1840. p. 467.]

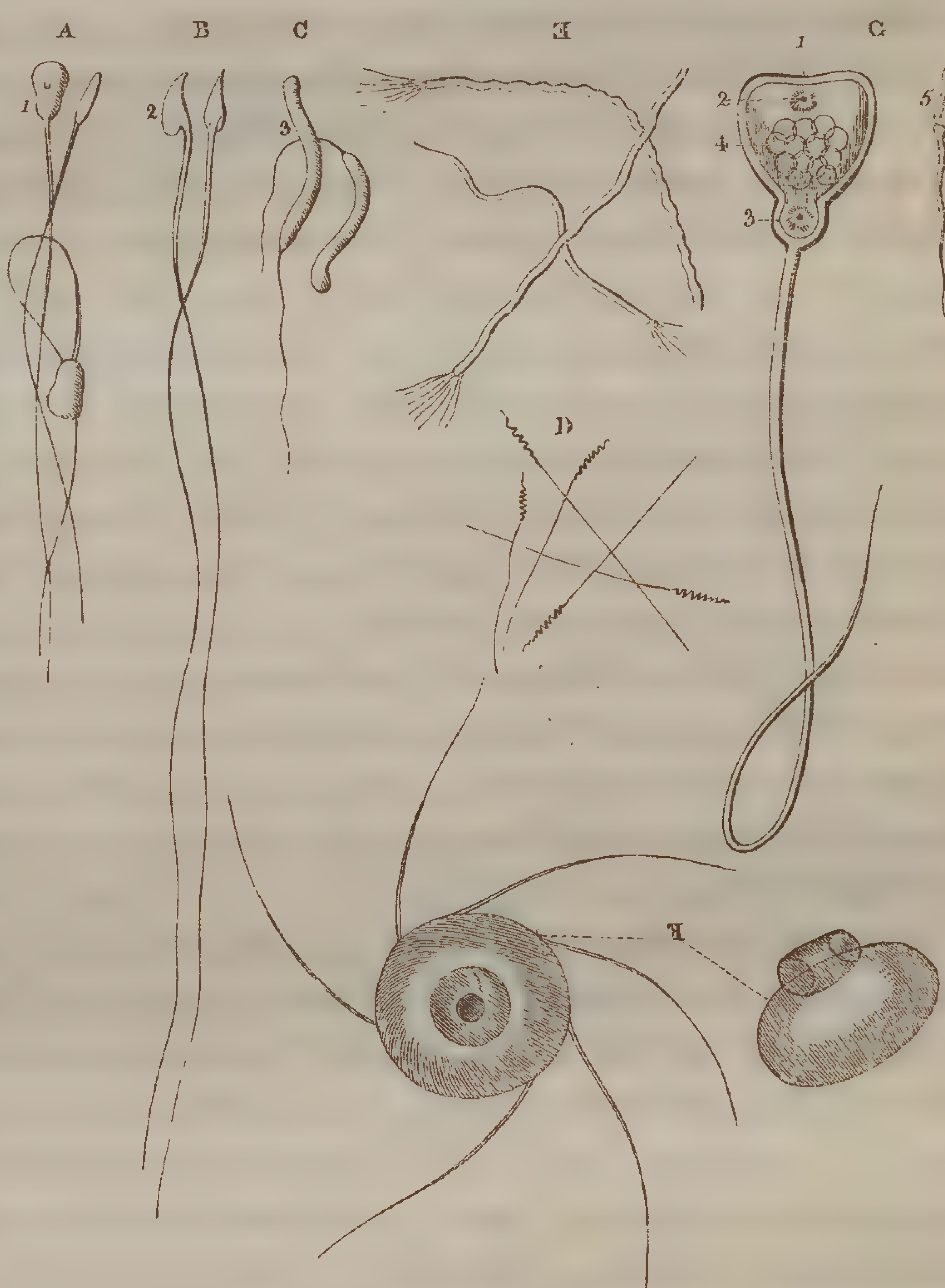
* See Berzelius, Thierchemie.

† [Spermatozoa of the human subject and their development. A, from the semen of the vas deferens. Spermatozoa fully developed; 1, with the surface depressed and smooth; 2, more acute and narrow; 3, with a circular spot in the middle of their flat surface, regarded by some observers as a sucker; 4, with a nodular process at their anterior extremity, not unlike a proboscis. B, from the semen of the testis. 1, large round corpuscules; 2, cells containing three granular roundish bodies, from which fasciculi of spermatozoa are developed (see page 1476); 3, fasciculus of spermatozoa, showing the mode in which they are grouped together in the testis. After Wagner.]

the particles of epithelium which are sometimes mixed with the semen. The spermatozoa which were discovered by a student at Leyden, named Harn, and first described by Leeuwenhock, have different forms not only in different classes of animals, but also in different families, genera, and species. Their most remarkable varieties in the vertebrata have been investigated and described by Wagner; in the invertebrata, by Von Siebold. They are as follow:—

A few principle types may be distinguished: 1, animalcules, with an elliptical body and long caudal filament, like those of the human subject (fig. 159), and most mammalia; 2, animalcules with pear-shaped bodies and caudal filament (fig. 160, A), which is their form in many other mammalia; 3, animalcules with cylindrical body and caudal filament (fig. 160, C), a form met with in several birds, reptiles, amphibia, and fishes; 4, animalcules with a spirally twisted body and a caudal filament (fig. 160, D and 161), such as exist in the singing birds, sharks, and paludinæ; 5, animalcules with the whole body filamentous or hair-like, as in many mollusca, insecta, and annelida.

Fig. 160.*



* [Various forms of Spermatozoa. A, spermatozoa from the dog; B, from the common mouse; and C, from the green woodpecker; after Wagner. D, spermatozoa from the Paludina vivipara; E, second form of spermatic animalcules from the same animal; F, bodies contained in the semen of Astacus fluviatilis; after Siebold. G, spermatozoon of the bear, after Valentin: 1, anterior margin excavated; 2 and 3, two very dark circular spots regarded by Valentin as the mouth and anus; 4, a number of delicate circles, supposed by Valentin to be the outlines of gastric vesicles, of an hepatic organ, or of the convolutions of an intestinal canal. 5, the same animalcule, less highly magnified and viewed laterally.]

The spermatozoa of the human subject measures, according to Wagner, from $\frac{1}{50}$ to $\frac{1}{40}$ of a line in length; their oval flattened body from $\frac{1}{800}$ to $\frac{1}{600}$ of a line. The tail is at its commencement so thick that its two borders can be distinguished; but towards its free extremity it becomes of extreme tenuity. The spermatozoa of most Mammalia are of the same form as those of the human subject, but are generally larger, especially in the smallest animals, for example, in those of the mouse kind; their length in the rat, being, according to Wagner, $\frac{1}{12}$th of a line. In monkeys they have great similarity to those of the human semen. In the dog, rabbit, and roebuck, the animalcules have a pear-shaped body. Their form is peculiar in the mouse kind, the extremity of their body being bent upwards and backwards like the point of a bellied bistouri or scalpel (fig. 160, B). In several Rodentia, as the squirrel, the body of the animalcule has its margin bent or rolled up. In birds, Wagner observed two forms of spermatozoa. The singing birds have spermatozoa with the anterior portion pointed and spirally twisted; the gallinaceous, predaceous, climbing and wading birds have animalcules with a narrow, straight, cylindrical body and short tail. The spermatozoa of the lizards, serpents, and frog, have a globular body and a delicate caudal filament; but those of the Salamandrina are differently shaped; in the Salamanda maculata, namely, the body tapers anteriorly to great tenuity but ends with a knot. In the Tritons or water Salamanders the body of the animalcule is still less distinguished from the tail. The appearance of ciliary motion which has been observed on their tail, has been shown by Von Siebold to be due to the motions of the extreme portion of the caudal filament, which is bent back and wound in a spiral manner around the more anterior portion. The spermatozoa of the osseous fishes have a globular body; those of the cyclostomatous fishes a cylindrical one.

The spirally twisted form of the body of the seminal animalcules is rare amongst the Invertebrata. Siebold observed it in the Paludinæ. It is also seldom that the animalcules of the Invertebrata have an anterior much thicker portion or body, though this occurs distinctly in the bivalve Conchifera, and in a less marked degree in some Gasteropoda. Most commonly the spermatozoa of invertebrate animals are filiform.

The filiform spermatozoa of Insecta, Gasteropoda, and Distomata, are affected in a peculiar manner by water. Von Siebold observed that as soon as water was brought into contact with them they became twisted on themselves so as to form single or double loops.

With the organisation of the spermatozoa we are at present quite unacquainted, and it has hitherto appeared doubtful whether they have an animal organisation. Henle and Schwann perceived a spot in the body of the human spermatic animalcule, which called to mind the sucker of the Cercariæ; but this might have been a part, bearing the same relation to the body of the animalcule as the nucleus does to the cell. In many spermatozoa there is sometimes a small knot in the middle of the tail or towards its end; I observed this knot in the spermatozoa of Petromyzon marinus, but in most of the animalcules it was absent. Similar knots in the course of the caudal filament have been observed by Meyen in the spermatozoa of plants; for example, in those of Charæ.*

The movements of the spermatozoa resemble in their characters the voluntary motions of animals. They consist in lashing, undulating, and vibrating motions of the tail. Those with the spirally-twisted body have a corresponding spiral twisting motion.† In order to see their motions well, it is necessary to dilute the semen with serum of blood. In many instances these motions of the spermatozoa continue during many hours after the death of the animal from which they are taken, and the mode of its death has no influence upon them. Wagner observed the motions of the animalcules to cease soonest in the semen of birds; sometimes they did not continue more than fifteen or twenty minutes after the death of the bird to which they belonged. In the semen of Mammalia the animalcules in many cases continued to move for twenty-four hours, and in that of Amphibia and fishes still longer. High and low temperatures cause the motions to cease; Wagner, however, saw them continue in the spermatozoa of frogs and fishes when the temperature was below 32° F. The spermatozoa will live, according to Donné, in blood, milk, or mucus. Their death, when mixed with saliva or urine, which Donné observed, must have arisen from other accidental circumstances; for Lampferhof observed them to continue their motions for a long period in saliva, and Wagner makes the same statement with respect to urine. In very acid mucus of the vagina, or very alkaline mucus from the uterus, they very quickly die, according to Donné's observation. Strychnine is stated by Wagner to kill them instantaneously; while, as we know from the researches of Purkinje and Valentin, the movements of the cilia of mucous membranes, and other surfaces, are not affected by narcotics.

The mode of development of the spermatozoa has been discovered by Wagner. During the winter the fluid of the testes of passerine birds contain merely small granules. In the spring there are granules of various forms, and, mingled with them, spermatozoa united in fasciculi. These fasciculi of spermatozoa are at first enclosed

* [The spermatozoa which present the most evident signs of organisation are those of the Bear, described by Valentin (Nov. Act. Nat. Cur. t. xix). They appeared to him to have a mouth, an anus, and stomachs or a convoluted intestine. See fig. 160, G, at page 1473, and the explanation of that figure.]

† See Wagner's Physiologie, p. 15.

in very delicate vesicles or cells, in which they lie, all with their spirally-twisted anterior portions or bodies together at one end of the fasciculus, and with their caudal extremities at the other end. These animalcules

Fig. 161.*

in the testis present no motion, but in the vas deferens the individual animalcules are free and in motion. The semen of the testis contains, besides small granular globules, large vesicles, including one or two granular globules, and similar larger vesicular bodies, enclosing several such granulated globules. These vesicles have a close relation to the development of the spermatozoa; for Wagner observed that a finely granulated matter was at length deposited between the globules which they contain; that these globules then disappeared; and that a linear arrangement of granules began to be visible, which at length assumed distinctly the form of the fasciculi of spermatozoa above described. The process of development of the spermatic animalcules is the same, according to Wagner's observation, in frogs and Mammalia (see fig. 159). In birds the spermatozoa are produced anew each year, and disappear in the autumn. In Mammalia their formation commences at an early age; in rabbits their development is completed, according to Wagner, at the third month after birth; in cats and dogs it is effected much later,

* [Development of the spermatozoa of Certhia familiaris (the common Creeper); after Wagner. 1, Granules of the semen, granula seminis, obtained from the testicle when very much reduced in size during the winter; 2 to 10, different bodies found in the semen, taken from the testicle when very turgid during the summer; 2, 3, granula seminis, of which many are probably merely cells of epithelium; 4, 5, 6, cysts, or vesicles containing one or several round granular globules; 7, a similar cyst, in which are seen, besides two globules, a mass of granules, and in this mass a fasciculus of spermatozoa in the process of development; 8, a similar cyst, become oval in form, while the spermatozoa have enlarged and are curled up within it,—the cyst still contains granular matter; 9, 10, cysts and fasciculi of spermatozoa still further developed; in 10, the fasciculus is ready to divide into separate animalcules.]

and in the human subject it does not take place until the period of puberty. These important observations have been confirmed by Von Siebold,* and Valentin,† [and by Dr. Hallmann,‡ who has observed the development of the spermatozoa in the cells of the testis of the ray.]

It is remarkable that in some animals (the number of which, however, is very small) no animalcules have hitherto been discovered in the spermatic fluid, even at the pairing season. The genus Astacus among the Crustacea presents this anomaly. In the river crab (Astacus fluviatilis) Henle and Siebold found, in place of the spermatozoa, peculiar motionless bodies, resembling large vesicles, with a smaller more opaque portion projecting from one side, and with long hair-like filaments attached at different points of their surface (see fig. 160, F). Valentin has observed similar bodies in the seminal fluid of the lobster.

It is yet a question which cannot be answered with certainty, whether the spermatozoa are independent parasitic animals, or merely animated particles of the organism in which they exist. Ehrenberg is inclined to regard the spermatozoa as distinct animals, and places them with the Cercaria in the class of the true Entozoa. Treviranus, on the contrary, adopts the opposite view, and compares the spermatozoa to the grains of pollen. The absence of spermatozoa in the semen of some animals, and the existence of perfectly organised animals in the seminal reservoirs of the Sepia,§ are circumstances favourable to the former opinion: while, on the other hand, the absence of structure, such as other individual animal organisms possess, in the body of the spermatozoa; their presence in nearly all animals, and reappearance in almost the same form in the male generative organs of some plants; the fact of their being developed in a uniform manner from cells, and not from other spermatozoa; and the analogy which may be perceived to subsist between them and other organic cells, particularly the cells bearing cilia;

* Müller's Archiv. 1839, p. 436. † Repertorium, 1837, p. 143.

‡ Müller's Archiv. 1840, p. 467.

§ See the account of these bodies given by Carus in the Nov. Act. Nat. Cur. t. xix. p. 1; also Philippi in Müller's Archiv. 1839. [Carus imagined that these bodies were distinct animals, and described their large intestine, small intestine, stomach, proventriculus, and œsophagus. It has, however, been clearly shown by Von Siebold (Beiträge zur Naturgeschichte der Wirbellosen Thiere, Dantzig 1839), that Carus was in error, and that the original description given by Needham was, as far as it went, perfectly correct. They are really capsules containing the semen of the Cephalopod. The spongy mass, believed by the English microscopist to contain the semen, is, according to Siebold, composed almost entirely of spermatozoa, which have an oblong body, and long thread-like tail. Needham's observations were made on the Loligo; Siebold's on the Cyclops. Their views have been confirmed by Peters (Müller's Archiv. 1840, p. 98), and by Mr. Owen in his Lectures at the Royal College of Surgeons, 1840. (See Lancet, May 14, 1840).]

are all circumstances opposed to that opinion. The spermatozoa resemble the cells bearing cilia, in their motions continuing after they are separated from the parent organism; and their caudal filaments may be compared to the cilia, while the nucleus of their body finds its analogue in the nucleus of the ciliated cells. In the character of their movements, however, the spermatozoa do not at all resemble the cilia, but present much more resemblance to animals moving voluntarily.

The most weighty argument against the special and individual animality of the spermatozoa is their close connection with the fecundating property of the semen. Not only are they absent from the semen of many animals, and particularly of birds, except at the pairing time, but their development is imperfect in hybrid animals, which are generally incapable of reproducing their kind, or at most pair with individuals of one of the unmixed species, and produce forms which then return to the original fixed type. Hebenstreit, Bonnet, and Gleichen, all failed to detect spermatozoa in the semen of the male mule. More recently Prevost, and Dumas,* and R. Wagner, have examined the seminal fluid of hybrid birds, and have found the spermatozoa either absent or imperfectly developed. This fact of the spermatozoa being imperfectly developed in such animals is most important. In hybrids of the goldfinch and canary, the testes sometimes remain very small, but sometimes attain somewhat more than half the volume of those of birds of the parent species. In the latter case, the fluid of the testes is imperfect as respects the spermatozoa and their germinal cells. In it Wagner found a few vesicles containing opaque molecules, and filaments enlarged at one extremity; but these filaments were never united in regular bundles, were not in normal number, and lay without regular arrangement, interspersed amidst the molecules. Such imperfectly developed spermatozoa remain of smaller size than those of the species which have produced the hybrid animal; their larger extremity is irregular in figure, is sometimes wedge-shaped, generally elongated, or curved at the point, but never twisted into the characteristic spiral form. In female hybrids Wagner† found numerous yolks with their germinal vesicles in the ovaries, but these ova never showed themselves advancing towards maturity.

Spermatozoa are sometimes met with in the male sexual organs of plants, but much more rarely than in animals. It being very difficult to distinguish the motion which the contents of the pollen grains of the higher orders of plants present from the molecular motion of Brown, we shall notice merely the spermatozoa of the Cryptogamic plants. Some phenomena referrible to spermatozoa of plants were observed by

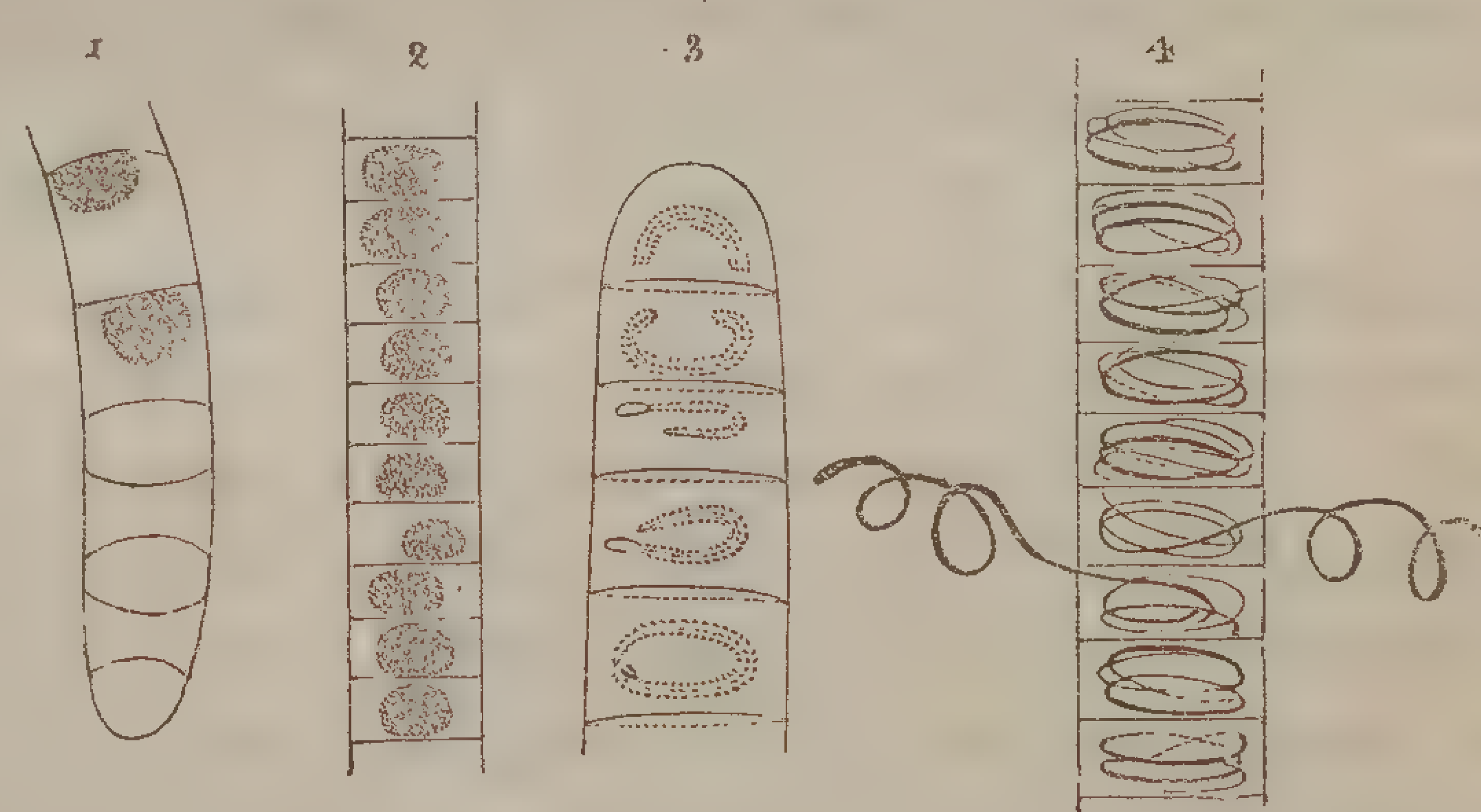
* Annal. des Sc. Nat. i. p. 183.

† Physiologie, pp. 25, 26.

Schmiedel and Fr. Nees Von Esenbeck. Unger first examined more closely the spermatozoa of the Sphagna, and it is to him and Meyen that we owe the most detailed information on the subject. The contents of the anthers of Sphagna consist of cells, each of which contains a filament with a somewhat elongated ellipsoid head rolled up in a spiral form. These thread-like animalcules move while still within the cells, escape from them, and then continue their motions. Meyen describes them as he observed them in the genera Hypnum, Mnium, Phascum, Polytrichum, and Sphagnum.* The spermatozoa in the cells of the anthers of the Hepaticæ, for example, of Marchantia and Jungermaneria, present, according to the observations of Meyen, similar appearances.

The spermatozoa of the Chara † are developed in articulated filaments found in the anthers, and connected with them. In each of the series of cells which form the articulated pollen thread, a globular cell of a mucous substance is developed (1, 2), and in the interior of each of these cells a single spermatic animalcule. At first the animalcules are shapeless (3); in cells further advanced in development they can be seen to be spirally convoluted, but are still motionless; and in others still nearer to maturity they present an active rotatory motion (4). If these animalcules are watched under the microscope they can be observed to break through the wall of the cell in which they were contained, and to issue with their larger end forwards. Professor Meyen has had the kindness to show me all the steps of this process with the aid of the microscope. These animalcules of the Chara are of very great length, so that, except in the convoluted state, they could not be contained in

Fig. 162. ‡



* Compare Unger, Nov. Act. Nat. Cur. t. xviii. pt. 2. p. 785.

† They were first well described by Varley. The most complete account of the spermatozoa of plants will be found in Meyen's Pflanzen-physiologie, p. 218. Tab. xii. fig. 17—28.

‡ [Filaments of the anthers of Chara vulgaris with spermatozoa in different stages of development, after Meyen. 1, a filament, in which only two of the mucous cellules are yet formed; 2, a filament, in which a cellule has been developed in each compartment; and in the filament 3, the formation of the spermatozoa in their mucous cellules is commencing; and in the last filament, 4, their development is complete, and two are escaping from the compartments which contained them.]

their cells. When they have escaped into the surrounding water they move with their thin threadlike extremity foremost. In their form they resemble the intestinal worm Tricocephalus, being thicker at one end and tapering gradually into an extremely long filament. The thicker part is spirally twisted, while the threadlike part assumes in its energetic motions various positions. These spermatozoa live many hours after their escape from the cells of the pollen threads.

CHAPTER V.

OF PUBERTY, SEXUAL INTERCOURSE, AND FECUNDATION.

I. *Puberty.*

THE period of puberty, the commencement of that part of life which is distinguished by the capability of propagating the species, does not occur exactly simultaneously in the two sexes; and still greater variety in this respect is caused by differences of nation and climate. Puberty declares itself in the female sex of our climate about the 13th, 14th, or 15th year, and is indicated by the occurrence of menstruation. In the male sex puberty commences about the 14th, 15th, or 16th year, and is attended with the secretion of semen, and with the occurrence of discharges of that fluid. In hot climates the body undergoes the changes of puberty earlier than in cold climates. It is stated that in the hot regions of Africa they take place in the female sex as early as the 8th year, and during the 9th year in Persia. Young jewesses are also said to menstruate earlier than other females in our own country. The capability of reproduction generally ceases in the female sex, together with the function of menstruation, between the 45th and 50th years. The duration of the reproductive power in man cannot be so exactly defined; in general, it continues longer than in woman, and not unfrequently very old men manifest a remarkable degree of virile power.

The changes in the system which characterise the period of puberty are partly local, affecting the generative organs, and partly of a general nature. The local changes consist in the growth of hair on the pubes in both sexes; in the menstruation of the female; in the copious formation of semen, and occurrence of erection in the male; and in the enlargement of the breasts in the female sex. The general changes of the system affect principally the respiratory and vocal apparatus, the entire form of the body and the physiognomy, the character of the mind, and the feelings relating to the sexes. The respiratory organs acquire an increase of volume at the age of puberty, especially in the male sex; and the vocal apparatus undergoes those changes of dimensions and acoustic properties which have been described at another part of this work (see page 1031). The whole body attains its most perfect form; while the features receive their stamp of individuality, and present signs of serving to express the passions, though they are not yet so strongly marked as in many adults. Sexual ideas arise instinctively and obscurely in the mind, and set in action the creative power of the imagination; but, at the same time, by their influence on the whole mind, call into play the noblest mental faculties, so as to elevate and adorn the feeling of love.

Menstruation is the periodical discharge from the female generative organs of a bloody fluid poured out by the inner surface of the uterus. The first discharge is usually preceded and accompanied by some symptoms of general disturbance of the system, namely, by abdominal congestion, pain in the loins, and a sense of fatigue in the lower limbs. Its periodical return is also attended in most women by abnormal symptoms, which are different in different individuals. The menstrual periods occur usually at intervals of a solar month; their duration being from three to six days. In some women the intervals are as short as three weeks, or even less; while in others they are longer than a month. Aristotle* made the extraordinary statement that menstruation rarely occurs every month, but in most women only every three months.

The menstrual discharge differs from ordinary blood in no other respect than that of containing only a very small quantity of fibrine, or none at all.† The blood corpuscules exist in it in their natural state.

Menstruation does not occur in pregnant women, nor in most cases in those who are suckling. But in rare instances it continues even during pregnancy.

Menstruation, in the strict sense, is peculiar to the human female. A kind of menstrual discharge was occasionally noticed by Rengger in the female of Cebus Azarræ; but this did not occur at regular periods. It was small in quantity, continued two or three days, and returned after intervals of three, six, or even ten weeks. This sign of maturity did not show itself until the end of the second year.‡ Geoffroy St. Hilaire, and Fr. Cuvier,§ have observed many facts of a similar kind among the monkey tribe. They noticed discharge of blood with enlargement of the sexual organs in Cercopithecus, Macacus, and Cynocephalus; but they maintain that these appearances were coincident with the monthly heat. During the periodical sexual heat in other

* Hist. Anim. 7. 2.

† Lavagna, Meckel's Archiv. 1818, bd. iv. p. 151.

‡ Rengger, Naturgeschichte der Säugethiere von Paraguay. Basel. 1830, p. 49.

§ See their work, Hist. Nat. des Mammifères. See also Ehrenberg, Abhandl. der Acad. zu Berlin. 1833, pp. 351—358, on the occurrence of menstruation in the monkey tribe; and Numan, Froriep's Notizen, p. 150, on menstruation in animals generally.

animals also, as the horse and dog, there is sometimes a discharge of blood. But the menstruation of the human female is a phenomenon of a totally different nature, and has no connection with sexual excitement.

We are quite ignorant of the cause of menstruation and its periodical return. The notion of the ancients that it cleansed the body from noxious matters is evidently erroneous. The opinion, also, that its office is to relieve the uterus of the blood which during pregnancy would nourish the embryo, is unsatisfactory, since the small quantity of blood lost in menstruation does not correspond with the amount of nutriment which the fœtus derives from the mother. More probability attaches to the view that the human female is preserved from too great sexual excitement by the menstrual flux. But it is still more probable that menstruation is the result of a periodical regeneration,—a kind of moulting of the female generative organs, attended perhaps with the formation of a new epithelium. The periodicity of the phenomenon is not connected with the changes of the moon, but with some condition of the organism itself; like other periodical actions or functions, it has an internal cause. The variations of the light afforded by the moon bear no constant relation to the periods of menstruation; on the contrary, different females are menstruating on every day of the month. The intervals of menstruation also, even when most regular, are not lunar but solar months; and they are very different in different women, in consequence of the various states of their system, and quite independently of external causes.

In the male sex the tendency to periodicity is manifested only in the turgescence of the genitals, and greater excitability and potency of the spinal cord and nerves engaged in the generative function; a state which is terminated, as it were by a crisis, in the act of coïtus, or in the involuntary emission of semen. Women are much less, or perhaps not at all, subject to such periodical sexual excitement. The periodical heat occurs in the most marked degree in animals. In many of them it happens during the spring, as in most birds, reptiles, and Amphibia, in many fishes, and also in many mammals, as the rodents, moles, and horses. In other animals, as several fishes, birds, Amphibia, and Mammalia, the summer is the season of sexual heat; while in others again, as many ruminants, it occurs in the autumn; and in others, as dogs, cats, and other carnivorous animals, in the winter.* In tame animals the periodical sexual excitement is manifested with much less intensity than in the same animals in their wild state; and in many, as the elephant, sexual union never takes place while they are in confinement.

All the phenomena connected with the sexes which animals present, are dependent on the formative generative organs, the ovaries and testes,

* See the more detailed account in Burdach's Physiologie, bd. i. p. 381.

and on the influence which they exert on the rest of the organism. Not merely does castration during youth for the most part prevent the development of the sexual feelings and emotions; but even when performed at adult age that operation destroys nearly entirely the sexual excitability. Sir A. Cooper* had the opportunity of knowing during twenty-nine years a man both of whose testes had been extirpated. The operation was performed in 1801. "For nearly the first twelve months, he stated, that he had emissions in coïtu, or that he had sensations of emission. That then he had erections and coïtus at distant intervals, but without the sensation of emission. After two years he had erections very rarely and very imperfectly, and they generally immediately ceased under an attempt at coïtus. Ten years after the operation, he said he had, during the past year, been once connected." In 1829 he stated, "that for four years he had seldom any erection, and then that it was imperfect. That he had for many years only a few times attempted coïtus, but unsuccessfully; that he had once or twice dreams of desire and a sensation of emission, but without the slightest appearance of it."

II. *The act of sexual union.*

The act of sexual union, as regards the male sex, consists of erection and the ejaculation of semen. Erection is the result of the arrest of blood in the corpora cavernosa of the penis, effected most probably, as Krause † shows, by the action of the musculi erectores penis, which compress the deep veins of the organ as they issue from the corpora cavernosa, though they can exert no influence on the vena dorsalis. In the horse the veins of the corpora cavernosa give off such numerous communicating branches in different directions, that it is more difficult to explain there the act of erection.‡ The part played by the arteriæ helicinæ in this act is not known; they cannot, however, be its sole cause, since in several animals, as the elephant, they do not exist, and even in the horse have quite a rudimentary form. It is in these animals that the muscle-like bands, passing between the veins of the corpora cavernosa, which were first observed by Hunter, are most highly developed. The remote source of the power of erection is the spinal cord; and hence the loss of this power in cases of Neuralgia dorsalis or Tabes dorsalis.

The emission or ejaculation of the semen is a reflex action excited by irritation of the sensitive nerves of the penis. The act of ejaculation

* On the structure and diseases of the testis, pp. 53, 54.

† Müller's Archiv. 1837.

‡ On the cause of erection in the horse, consult Guenther, Untersuchungen und Erfahrungen im Gebiete der Anatomie, Physiologie und Thier-arzneikunde. Hannover, 1837.

is itself the result of two movements; namely, of the persistent contraction of the organic muscular fibres of the vesiculæ seminals, and of the repeated periodical contraction of the animal muscular fibres of the ejaculator seminis and other perinæal muscles. Sudden irritation and injury of the medulla spinalis gives rise to emission of semen, which is then not necessarily attended by erection. Discharge of semen is an ordinary phenomenon in decapitated criminals. That the vesiculæ seminales are really receptacles of semen is beyond a doubt, since spermatic animalcules have been discovered in their contents in the human subject after death. They are, therefore, not mere secreting organs as Hunter supposed.* Hunter, however, proved by a series of observations, that when one testicle is extirpated, the vesicula seminalis of that side does not undergo diminution in size; and his view respecting the office of the vesiculæ was correct, so far as regards their secreting a mucous fluid. In the act of coition, however, the semen comes directly from the vesiculæ seminales, and not from the testes. It is, moreover, mixed in the urethra with the secretion of Cowper's glands, and with that of the prostatic gland, of the nature of which we are quite ignorant.

In both sexes the act of coition is attended with pleasurable sensations, but their respective share in the act itself is very different. In the female there is no expenditure of nervous power in the production of erection, no energetic rhythmic muscular contractions when the venereal excitement has reached its height, and no emission of semen; but merely an increased secretion of mucus from the mucous follicles of the vagina, excited by the impressions on the sensitive nerves of the female sexual organs, and serving to lubricate the passage. The man feels exhausted after the act; the woman does not. It appears, therefore, that the nervous excitement and actions of the male during the act of coition, attain, in a short period, a great degree of intensity, and are as rapidly depressed, while there is no evidence that such is the case in the woman. The clitoris, which is known to be the part most susceptible of the pleasurable sensations in the female, is not, like the penis of the male, rendered by friction the seat of intense sensation and nervous excitement during coition, and hence its excitability is found not to be wholly exhausted after the act is completed. We are, therefore, justified in concluding that the sensitive excitement of the woman is neither so rapidly rendered intense, nor so rapidly depressed, as that of the man; and this conclusion accords with the fact, that women bear frequent sexual intercourse better than men, and are much less frequently affected with Tabes dorsalis, in consequence of sexual excess. The clitoris, though agreeing with the penis in its mode of development, yet differs from it essentially in its functions, since it is generally in-

* Hunter's works [Palmer's edition], vol. iv. p. 20.

capable of true erection. In the genus of monkeys, Ateles, the clitoris is normally of extraordinary length, and this circumstance has given foundation to the accounts related of the structure and habits of some female monkeys. The clitoris of the females of the genus Ateles has very large corpora cavernosa, in which, however, I have found merely fat; while the sensitive nerves of the penis, the nervi dorsales, were very large.* This large size of the clitoris is peculiar to the genus Ateles; in other genera of monkeys the organ presents nothing unusual.

III. *Separation of the ova from the ovary, and their reception into the Fallopian tubes.*

In oviparous animals the separation of ova from the ovarium may take place either independently of impregnation by the male, or as the result of that act. In the Amphibia, the ova of which are impregnated out of the body of the female, for example, in frogs, the ova have separated from the ovary, and have accumulated in the oviduct long before the time of fructification. The ova of the female frog having accumulated in the oviduct, and distended it to a considerable size, are expelled from it by the action of its walls during the excitement of copulation, and are immediately impregnated by the male, who sits on the back of the female firmly embracing her.

In fishes, also, the ova seem to separate from the ovaries before fecundation. For in the majority of fishes there is no sexual union. The male and female, under the venereal excitement, accompany each other through the water, and the ova being deposited by the female are fecundated by the semen which the male emits. There are some fishes, however, as the Blennius viviparus and other viviparous fishes, in which internal impregnation is effected, either by the semen emitted by the male finding its way with the water into the internal generative organs of the female, or by an actual act of copulation as in the sharks and rays.

Birds, also, which begin to lay their eggs after copulation and impregnation, continue to lay them when they are kept quite separate from the male bird; and here, also, the ova evidently separate from the ovary independently of impregnation. The same is the case with some insects, as, for example, butterflies; for they also deposit mature ova when they have been kept isolated from the male from the time of their entrance into the chrysalis state.

In Mammalia, on the contrary, the separation of the ova from the ovary seems to be dependent on the act of impregnation. It has, it

* See Fugger, De Singulari Clitoridis in Simiis Generis Ateles Magnitudine et Conformatione. Berol. 1835.

is true, been stated, that cicatrices of the ovaries, resulting from the escape of ova, have been seen in the bodies of virgins;* but that is certainly not an ordinary occurrence. Usually, it is only after a successful union of the sexes, that one or more Graafian vesicles are found turgid. At a somewhat later period, after coition has taken place, the turgid and vascular vesicle of De Graaf bursts, and the ovulum is received into the Fallopian tube. These results of a fruitful union of the sexes, the change in the condition of the ovary, the dehiscence of the Graafian follicle and escape of the ovulum, are now known to be consequences of the direct action of the semen on the ovary itself, and not of its action merely on the external generative organs. For Professor Bischoff and Dr. Barry have made the important discovery, that the semen of male mammiferous animals which have been induced to copulate, is really conducted through the entire length of the Fallopian tube to the ovary.

The mode in which the ova, unimpregnated or impregnated, are transferred from the ovary to the Fallopian tube or oviduct is far from being accurately known.

In Mammalia and birds the proximity of the ovary to the infundibulum of the Fallopian tube must, to a certain extent, facilitate the entrance of the ovum into the latter; but even here there is a phenomenon, as yet unexplained, in the Fallopian tube applying its infundibulum, or fimbriæ, at the time of impregnation, not merely to the ovary, but exactly to that part of it at which there is an ovicapsule on the point of bursting. This erectile turgescence of the Fallopian tube, and its close application to the ovary, have been many times observed in mammiferous animals,—namely, by De Graaf, Kuhlemann, Haighton, Cruikshank, Von Baer, and Wagner. The phenomenon continues during the first few days after coition has taken place. Von Baer observed it in pigs and sheep as late as the fourth week, while Wagner found that it ceased in pigs about the eighth or tenth day.

It is still more difficult to explain the passage of the ova into the Fallopian tube in those animals in which the infundibulum of the tube lies at a considerable distance from the ovary, as is the case in the Amphibia, and sharks and rays. In the Amphibia the infundibular extremity of the tube lies at the most superior or anterior part of the abdominal cavity, far above the ovary, and in the sharks and rays the disposition of the parts is apparently still more unfavourable to the transit of the ova into the Fallopian tubes; for in them these tubes terminate by a common orifice in the middle line, above the liver and just beneath the diaphragm or septum, which separates the cardiac cavity from the abdomen, while the ovaries lie at the sides of the

* Home, Philos. Transact.

liver, or beneath it in the middle line close to the vertebral column. It is very probable, that in these cases the motion of cilia on the surfaces between the ovaries and Fallopian trumpets effects the transit of the ova. The observation of Mayer, that the peritonæum of frogs presents the ciliary motion, is in favour of this view. Valentin informs me in a letter, that he has detected ciliary motion on the surface of the peritonæum, between the liver and ovary; and also on the peritoneal covering of the kidneys and ovaries in sharks. I learn also from C. Vogt, that the whole internal surface of the abdominal cavity presents the ciliary motion in the female salmon, a fish which has no oviduct, the ova falling into the cavity of the abdomen, and escaping from it by the simple openings already described (page 1461). The ciliary motion which exists on the inner surface of the Fallopian tubes and of its fimbriate appendages in Mammalia, must in them also have great influence in aiding the entrance of the ovum into the tube. Henle has discovered the existence of ciliate epithelium even on the outer surface of the fimbriæ in the human subject.*

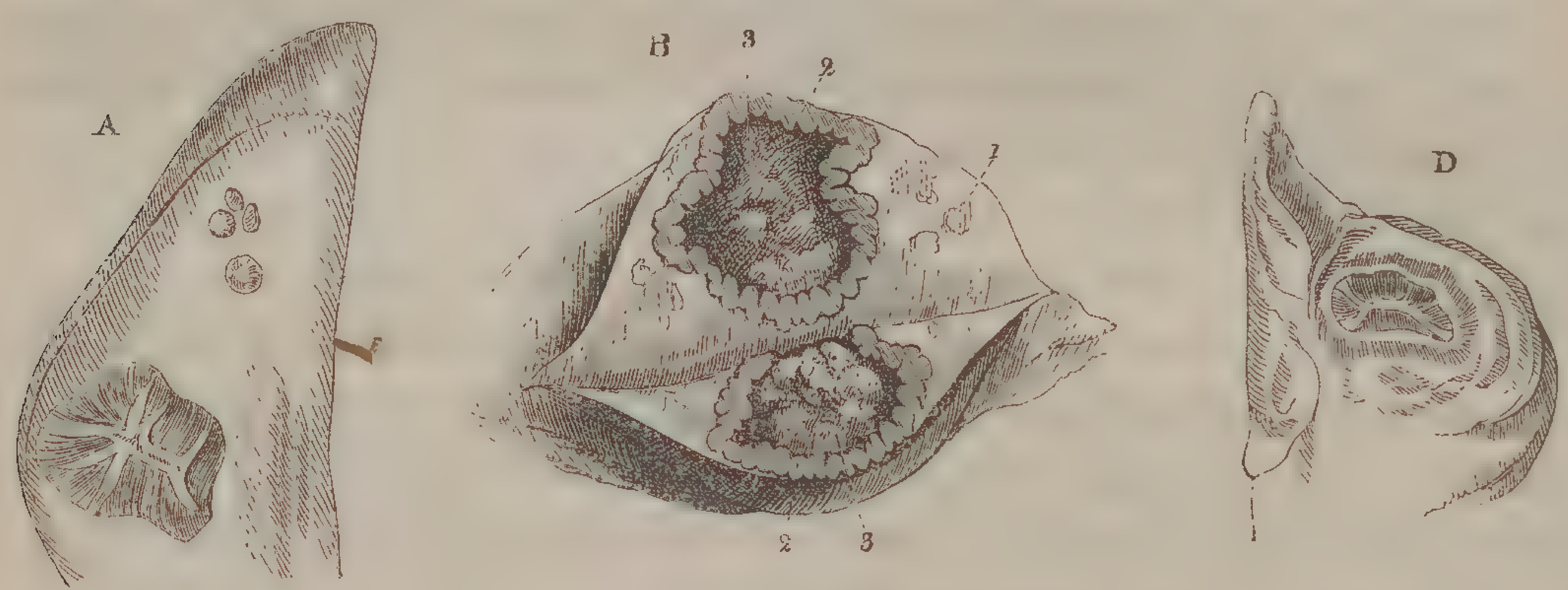
The changes which precede the expulsion of the ovum from its capsule, and which the capsule afterwards undergoes, are the following:— Both in oviparous animals and in Mammalia the posterior part of the capsule swells before the escape of the ovum; but in Mammalia this tumefaction is much greater than in other animals, and the swollen capsule appears very vascular. Even before the ovulum has left its cavity, the capsule becomes in a great part filled with a brownish yellow substance. In consequence of this change the contents of the capsule are protruded against its outer wall, which has become thinner, and now projects with the ovulum beneath it in a hemispherical form above the surface of the ovary and thickened follicle. An aperture, the stigma, is then formed at the most prominent point. Immediately after the escape of the ovulum the cavity of the follicle, or Graafian vesicle, appears very small; in a short time it becomes quite filled with a granular mass, and a kind of wart is developed in the situation of the former opening. This wart afterwards disappears, and then the altered follicle remains with the form of the round corpus luteum. In oviparous animals the calyx gradually diminishes in size after the escape of the ovum, and is retracted into the mass of the ovary and absorbed.

According to Dr. Barry,† the corpus luteum of mammiferous animals is developed in the vascular covering of the ovisac, or external tunic of the Graafian vesicle. Dr. R. Lee,‡ on the contrary, supposes that it is

* Müller's Archiv. 1838, p. 114.
† Phil. Trans. 1839. Pt. ii. p. 317.
‡ Med. Chir. Trans. vol. xxii. p. 329.

formed externally to both coats of the vesicle. [Dr. Montgomery* and Dr. Paterson,† again, state as the result of their observations, that the substance of the corpus luteum is deposited between the two coats of the follicle. The forms represented by this body at different periods after impregnation are shown in fig. 163.] The true corpus luteum

Fig. 163.‡



appears never to be produced except as the result of conception. False corpora lutea, on the contrary, are frequently met with. They generally, according to Dr. Montgomery, appear to be formed by an extravasation within the Graafian vesicle. A thickened state of the coats of the vesicle, which ensues in advanced age, sometimes simulates a corpus luteum. False cicatrices of a vesicle have an irregular form, and want the small round opening which is the result of conception. In the ovaria of women who had died during menstruation, Dr. Lee saw other appearances which might have been mistaken for corpora lutea. The Fallopian tubes were red and turgid; the peritoneal coat of one ovary was perforated by a small circular opening, around which the surface of the ovary was elevated, and of a bright red colour, and the opening sometimes communicated with a cavity; but the distinctive characters of the corpus luteum were wanting.

IV. *Fecundation.*

The semen might be supposed to effect fecundation in different ways. Its immediate action might be on the organism of the female, the

* On the Signs of Pregnancy, p. 216.

† Edinb. Med. and Surg. Journal, Nos. 142 and 145.

‡ [Corpora lutea of different periods. B. Corpus luteum of about the sixth week after impregnation, showing its plicated form at that period. 1. Substance of the ovary. 2. Substance of the corpus luteum. 3. A greyish coagulum in its cavity; after Dr. Patterson. A. Corpus luteum, two days after delivery. D. In the twelfth week after delivery; after Dr. Montgomery.]

fecundation of the ovum being a secondary and indirect result of this action; or it might be exerted directly upon the ovum itself. In the former case, the semen could be conceived to act as a stimulant of the female genitals, producing a state of excitement of which fecundation is the effect; or it might be absorbed into the blood of the female, which would explain not only the changes that take place in the ovary, but also the more general results of fecundation. There have, indeed, been writers who, resting on these theories, have imagined the possibility of fecundation being effected in other than the ordinary way, by means of semen infused into the blood. Observations, however, have shown that the fecundation, following union of the sexes, results from the direct action of the semen upon the ovum. This is proved partly by the experiments of Haighton,* in which ligature of one Fallopian tube before copulation prevented the impregnation of the ovary of that side, while fecundation always took place in the ovary of the opposite side on which the Fallopian tube was left free; and partly by the cases in which, either artificially or naturally, impregnation is effected quite independently of the female organs of generation. The ova of frogs are naturally impregnated independently of the genital organs of the female, the semen of the male being shed upon them after their expulsion. The experiment of the artificial impregnation of the ova taken from the body of female frogs, by means of semen from the testicle or vesicula seminalis of the male frog, has been well known since the time of Spallanzani. In this experiment fecundation takes place if the ova and semen are brought into immediate contact, but is prevented by the interposition of a thin but impermeable medium, such as taffeta. The experiment succeeds in the case of these cold-blooded animals, even when the male and female individuals from which the semen and ova are taken have been dead several hours. Rusconi† has recently performed similar experiments on artificial impregnation with the ova of fishes, and with the same results.

It is equally certain that fecundation does not depend on any influence of the entire male organism, but on the semen alone. This, indeed, was proved long since by experiments of Spallanzani and Rossi, who found that semen of a dog, introduced by means of a syringe into the generative organs of a bitch, effected impregnation. There can, therefore, be no doubt that the essential cause of fecundation, wherever it takes place, is not any influence of the male organism upon the female, but the action of the semen itself upon the female germ.

Two views have been taken of the mode of action of the semen on the ovum. Some physiologists have believed it to be immediate, while others have supposed it to take place through the intervention of a

* Phil. Trans. 1797. † Müller's Archiv. 1836, p. 278.

peculiar emanation, the aura seminalis. The falsity of the latter opinion is sufficiently proved by Spallanzani's observations, already referred to, which show the necessity of absolute contact of the semen with the ova of frogs, for producing fecundation. Where the ova were suspended above the semen, and very close to its surface, no fecundation took place; while semen, diluted in the proportion of three grains to eighteen ounces of water, was efficient for impregnating by contact. Spallanzani found a drop of this fluid adequate to impregnate ova.*

But it is not merely in Amphibia and fishes that the contact of the semen with the ova is thus necessary for fecundation; the fact of the semen being conveyed in Mammalia from the uterus along the Fallopian tubes, even to the ovary, proves that the same condition obtains in all animals. The semen passes into the uterus either soon after or during the act of copulation. Leeuwenhoek, on several occasions, detected spermatozoa in the uterus of mammiferous animals, which had recently had sexual union. Prevost and Dumas† discovered them in the uterus twenty-four hours after the act of copulation, and on the third and fourth days in the Fallopian tubes. Bischoff's observations‡ are still more conclusive. In a bitch which had had coition with a dog nineteen hours before, and again half an hour before it was killed and examined, he found spermatic animalcules upon and between the fimbriæ of the tubes. In a second instance, in which the examination was instituted forty-eight hours after coition had taken place, he detected the seminal animalcules not merely in the uterus and Fallopian tubes, but also on the ovary itself. In Mammalia, therefore, as well as in other animals, it is an ascertained fact, that the semen and ovum are brought into immediate contact.§

The situation in which the impregnation of the ovum takes place is very different in different animals. We have already seen that the ovum may be separated from the ovary before as well as subsequent to impregnation. Hence it follows that impregnation may take place in three situations.

* See Spallanzani, Expériences pour servir à l'Histoire de la Génération. Genève, 1786.

† Annal. des Sc. Nat. tom. iii. p. 119.

‡ Wagner's Physiologie, p. 49.

§ [Dr. Barry's observations were made on the rabbit. In seventeen out of nineteen instances he was unable to discover spermatozoa in the fluid collected from the surface of the ovary. On one occasion he found a single spermatozoon, which was dead, while the ova had escaped. On a second occasion he found, twenty-four hours post coïtum, several spermatozoa on the ovary. Some of these animalcules were alive and active, though not in locomotion; others were dead. There was no enlargement of the Graafian vesicles, nor a high degree of vascularity of any of the parts. Phil. Trans. 1839, pt. ii. p. 315.]

a. *Impregnation external to the body of the female.*—It has already been mentioned, that this is the mode of impregnation in most Amphibia and fishes.

b. *Impregnation of the ovum while still in the ovary.*—This is the place of impregnation, at all events, in man and mammiferous animals. In all cases of extra-uterine pregnancy, in which the ovum is developed in the ovary itself, or escaping into the abdominal cavity is developed there, it cannot be doubted that the ovum was in those instances impregnated in the ovary; but the fact of Bischoff and Barry having traced the spermatozoa as far as the ovary, proves that impregnation is always effected in that situation in Mammalia. The mode in which the semen is conducted so far through the female generative organs, is no longer a problem requiring solution; for the discovery of the ciliary motion affords a solution of it. The rapidity with which matters are made to move over surfaces furnished with vibrating cilia, may be readily shown in the frog by Dr. Sharpey's experiment. The lower jaw being cut away, powdered charcoal is strewn upon the palate, when it is perceived to move visibly and pretty rapidly in the direction of the fauces, and has frequently in a few minutes quite disappeared. The only point here which requires solution, respects the mode of introduction of the seminal animalcules into the uterus. This part of the process cannot be effected by the movement of cilia, for the mucous membrane of the human vagina presents no ciliary motion. Henle could detect no ciliary epithelium lower than the middle of the neck of the uterus. Still, notwithstanding the great narrowness of the orifice of the uterus in young females, we can conceive that the semen may be mechanically forced through it during the act of coition by the movements of the penis. It is difficult, however, to explain the occurrence of fecundation when the hymen is still perfect, or when the penis is very short or affected with congenital hypospadia. How fecundation is attained in these cases, which are rare, is quite a mystery.* I must, however, remark, that it is only in the first of them,—that of the persistent hymen,—that the possibility of fecundation appears to me to be absolutely certain. In other cases, all the conditions for absolute proof cannot possibly be fulfilled; for, that the impregnation of a female was effected by a hypospadiac and not by another man, must always be a mere matter of faith..

c. *Impregnation of the ovum in its passage from the ovary to the exterior of the body.* — Since the ova of birds separate from the ovary quite independently of fecundation, there is no difficulty in understanding that they may become fecundated not merely by the semen being

* See the remarks on cases of this kind in Burdach's Physiology, bd. i. 528.

conveyed along the walls of the oviduct to the ovary, but also by meeting the semen in their passage through the oviduct, as long as their yolk-sac is not surrounded by a layer of albumen and by the shell. In the case of the tritons, or water salamanders, no actual sexual connection takes place, but the male merely lashes the female with its tail, according to the observations of Spallanzani and Rusconi, while it emits the semen into the water; and here it is possible the semen may penetrate with the water into the generative organs of the female, which afterwards expels the ova and fixes them upon leaves. With respect to the viviparous species of oviparous animals, as the oviviparous sharks and rays, the Blennius vivaparus, the Salamandra maculata, the viper, &c. (where the ovum, enveloped in a soft membrane, in place of a hard shell, is developed within the uterus or oviduct, though devoid of a placenta or other connection with the parent organism), it is uncertain whether fecundation takes places in the ovary itself or in the oviduct.

One of the most interesting varieties in the process of fecundation is presented by insects. Connected with the vagina of the female insect is a sack or capsule, which receives the semen during the act of coition, and in which seminal animalcules can be detected for a long period after that act. In consequence of this provision the ova can be successively subjected to the fecundating influence as they are expelled. No certain proof exists that such is always the process, and that the semen does not pass from this sac up the oviducts, and impregnate the ova successively in the ovary; and in insects, such as the Phasma, the ova of which, while yet in the ovarian tubuli, have a very firm shell, it would be very difficult for fecundation to take place, while the ova are being expelled. In many insects, however, the fact of the fertilisation of the ova in their transit through the excretory passages cannot be doubted. Thus, according to Von Siebold, in the Melophagus ovinus, the ovaries open into a receptacle which, in its turn, communicates with the uterus. In the act of copulation the receptacle, or spermotheca, becomes filled with semen; and, since the ova in their transit to the uterus pass through this receptaculum seminis, it is easy to understand how an insect, after one act of copulation, can produce a succession of living young.*

Of the intimate changes on which fecundation depends, we are yet wholly ignorant; and up to the present time it was the less possible for us to become acquainted with them, since we were uncertain even as to the situation in which the process took place. The principal question

* This subject has been very fully investigated by Siebold. Müller's Archiv. 1837, p. 381.

which it is desirable to decide with regard to the nature of the fecundating process respects the part which the spermatozoa play therein. Do they serve merely to increase the sphere of action of the fertilising matter, as insects, carrying abroad the pollen, aid in the fecundation of plants, or do they themselves contain the essential fertilising principle? The observation of R. Wagner, that the spermatozoa suffer a change of form in hybrid animals (see page 1478), is in favour of the latter view. The spermatic animalcules, however, certainly bear no intimate relation to the germinal vesicle; for in the ova of oviparous animals the germinal vesicle disappears at the time of their discharge from the ovary when they are yet unimpregnated. Equally certain is it that the spermatozoa do not become the future embryos. For the germinal disk appears perfectly unchanged after fecundation, and the development of the embryo by the growth of the germinal disk to form the germinal membrane, and the subsequent changes of organisation, can be accurately traced.* Vegetable physiology has gone a step further than animal physiology in the elucidation of the act of fecundation; hence, it is important for us to examine this process as it occurs in the vegetable kingdom.

The parts of plants which have hitherto been regarded as the male sexual organs, are the anthers. The pollen grains contained within the anthers enclose a semi-fluid matter, the fovilla, composed in great part of minute globules, the nature of whose motions is yet a subject of disputation.†

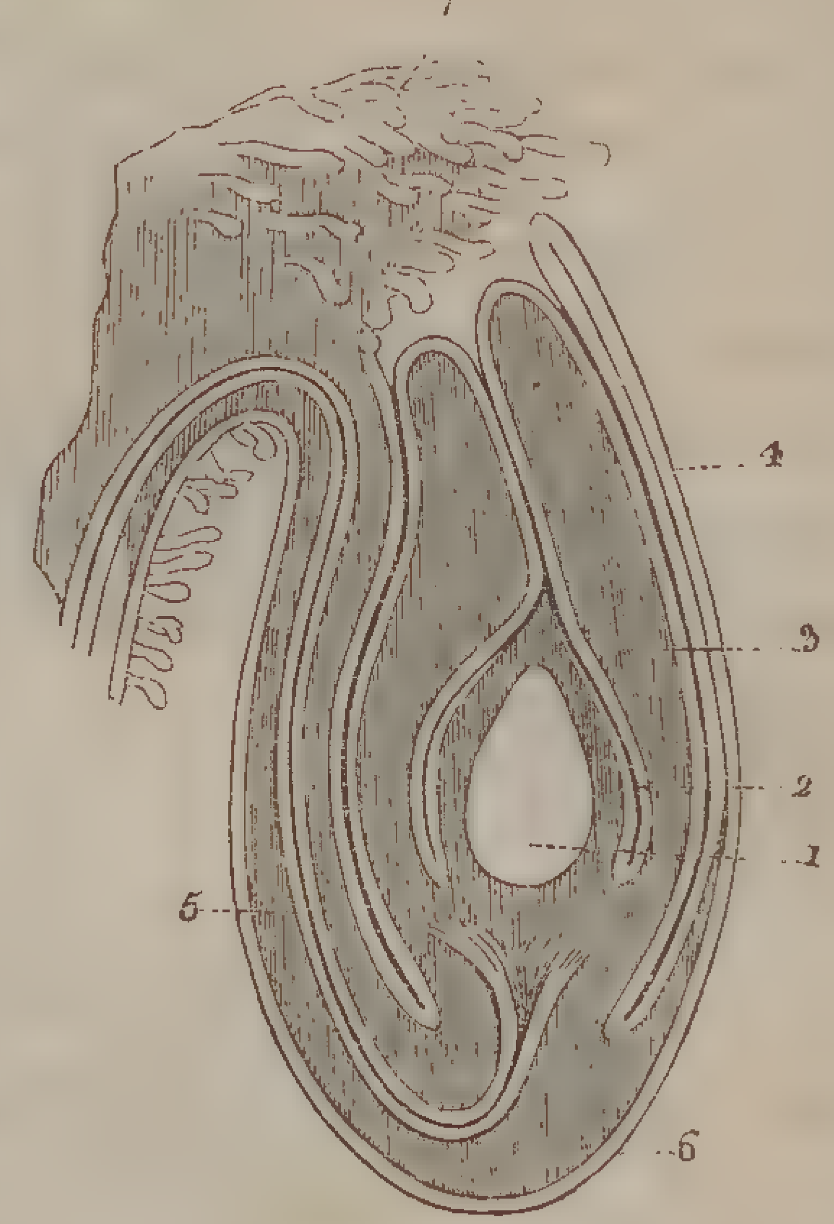
The pistil is usually regarded as the female part of the flower; its upper part is called the stigma; and its lower part is the ovarium, or germen, in which the ovula are formed long before impregnation. The stigma and ovarium are united by the style. The style is formed internally of cellular tissue, which either occupies the whole thickness of the style as low as the ovarium, or more commonly includes a central cavity, which extends from the stigma to the ovarium, where it divides into as many branches as there are ova. The ovulum has generally two coats, or integuments, the primine and secundine, which enclose the cellular nucleus or perisperm. (See fig. 164.) Both coats of the ovulum are connected with the ovarium through the medium of the funiculus which transmits the vessels that terminate in the primine and secundine. Both these coats also present at another point an opening, the micropyle or foramen, which leads to the internal portion of the ovulum, or the nucleus. In many plants the nucleus projects through the foramen in the form of a conical prominence. In the interior of the nucleus is a cavity, the sac of the embryo, which is formed by a single cell, and is of great

* [See the account of Dr. Barry's observations on the process of fecundation in Mammalia at the end of the present chapter.]

† See Meyen, op. cit.

importance in the process of fecundation. (See fig. 165.)

Fig. 164.*

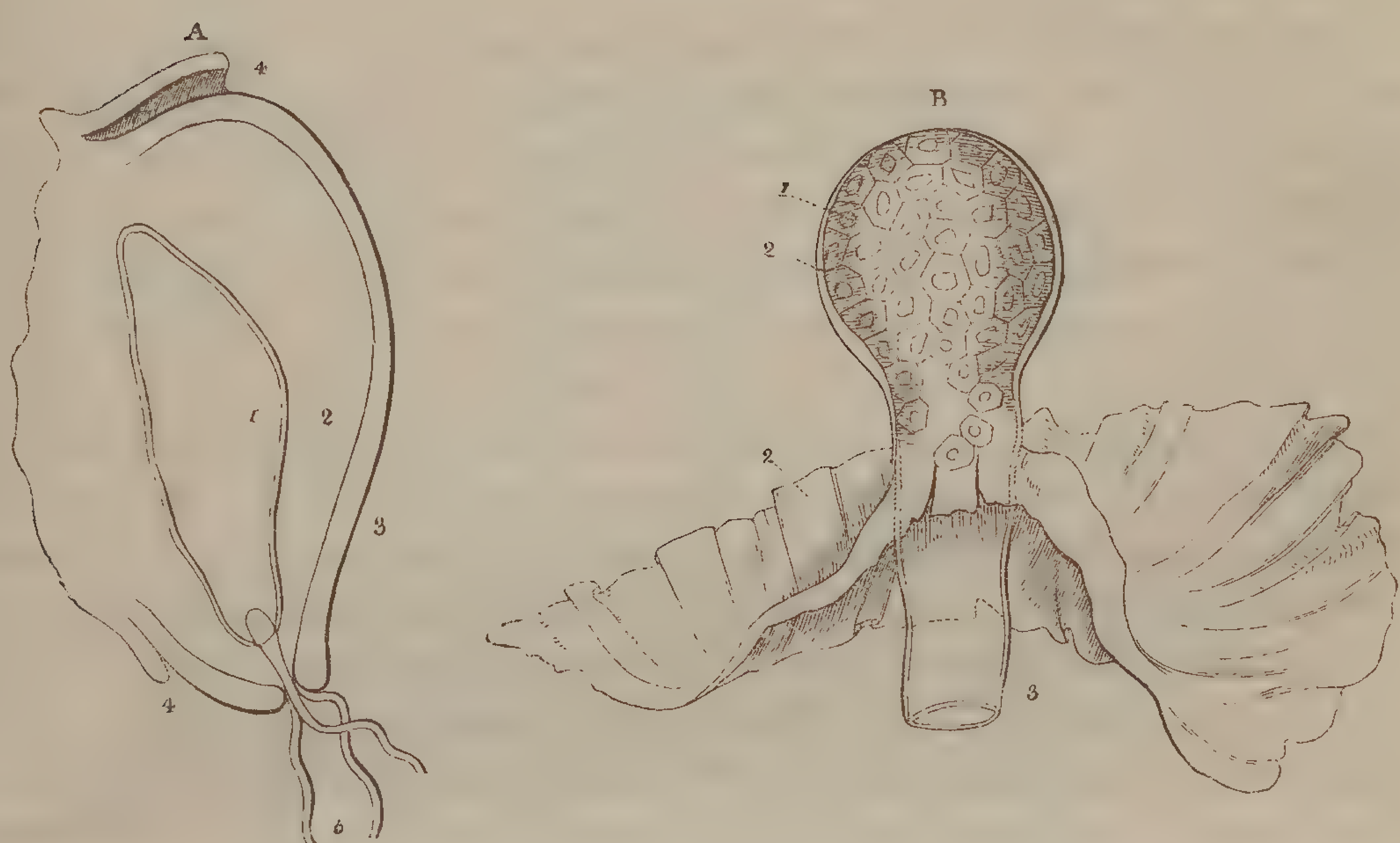


At the period of fecundation the anthers of hermaphrodite flowers approach the stigma, and shed their pollen upon it. In plants of which the sexes are distinct the pollen is conveyed to the female ovaria, often from a considerable distance, either by the wind or by insects. The intimate steps of the process of fecundation have been brought to light by modern researches. Amici observed that the pollen grains, when received upon the stigma, emitted tubes. Brogniart traced these elongating tubes into the tissue of the stigma. They are productions of the inner coat of the pollen grain, and increase in length by true vegetative growth, and by the appropriation of nutritive matters which they derive from the stigma. More recently the pollen tubes have been found to extend through the canal of the style, or its cellular tissue to the ovulum, and have been ascertained to enter the foramen or micropyle. The nature of the act of fecundation has thus, by the observations of Robert Brown, Horkel, Schleiden, and Meyen, been fully established in the case of many plants. These observations, however, have led to differences of opinion respecting the sexes of plants. Mirbel regarded the act of fecundation as the engrafting of a male cell upon a female cell. According to Schleiden's observations,† on the contrary, the pollen tube itself becomes the future embryo. He describes the extremity of the pollen tube as entering the foramen of the ovulum, as pushing the embryosac before it, and as becoming imbedded in it. (See fig. 165, A.) The part thus included in the ovulum, according to Schleiden, becomes separated by a constriction, and detached from the rest of the pollen tube; forms the rudiment of the future embryo, and is the nidus for the development of new cells. (See fig. 165, B.) According to this description, which is based on numerous observations, the doctrine of the sexes of plants must be entirely reformed, and the parts hitherto regarded as the female sexual organs must be viewed merely as a kind of uterus, in which the embryo is nourished. Other writers, and especially Treviranus and Meyen, support the old theory of the sexuality of plants.

* [Ovulum of Linum pallescens. After Schleiden, Nov. Act. Nat. Cur. t. xix. 1. embryosac; 2. nucleus; 3. secundine; 4. primine; 5. raphe; 6. cuticle; 7. placenta.]

† Wiegman's Archiv. 1837, t. i. p. 291. Nov. Act. Nat. Cur. t. xix. p. 1.

Fig. 165.*



According to Meyen the pollen merely introduces into the cavity of the nucleus a small quantity of fecundating substance, which unites with the organisable mass of mucus or gum contained in the embryosac. The part of the pollen tube which has coalesced with the cavity of the nucleus, or with the embryosac, being nourished by the organic mucus of that cavity, or of the embryosac, assumes the form of a sac or vesicle, in the interior of which cells are developed. But the pollen tube itself is at the same time detached. The vesicle which is formed in the cavity of the embryosac after the pollen tube has entered it, or which, in other words, is formed after the union of the pollen tube and embryosac, is called by Meyen the germinal vesicle. The embryo is produced by the vegetation of this vesicle, or by the formation of cells in its interior.

In considering the nature of the process of fecundation in plants, observation and theory must be entirely separated. The question to be decided therefore, is, whether the extremity of the pollen tube does penetrate the nucleus of the ovulum, pushing the embryosac before it, and then being separated from the rest of the tube, actually becomes the embryo itself? or, whether, as Meyen maintains, the part called by him the germinal vesicle, is a new structure produced by the union of

* [Fig. 165. A. Ovulum of Secale cereale, at period of fecundation, divided longitudinally; 1. embryosac; 2. nucleus; 3. secundine; 4. primine divided; 5. pollen tubes, one of which has entered the nucleus, and forms the commencement of the embryo in the embryosac. Fig. 165. B. Apex of the embryosac of Phormium tenax, inverted by the end of the pollen tube, which is already filled with delicate nucleated cells, constituting the embryo. 1. the end of the pollen tube in the inverted portion of 2, the embryosac. 3, the pollen tube. After Schleiden. Nov. Act. t. xix.]

the fecundating contents of the pollen tube and the mucous matter of the embryosac.*

The development of intermediate forms in hybrid generation proves that both the male and female plant contribute equally to determine the organisation of the new individual; but does not decide the question in favour of either of the two above-mentioned views respecting the nature of the fecundating process and the sexes of plants. For even if, as Schleiden supposes, the embryo is merely a portion of the pollen tube inserted into the nucleus of the ovulum; if this portion of the pollen tube, therefore, is *in form* the embryo; still it may be greatly influenced and modified in its endowments by forces resident in the fluids of the nucleus; and if such be really the process, it will merely prove fecundation to consist in a part of the pollen tube being rendered capable of vegetation in the peculiar form of the species by being subjected to the action of the nucleus. The pollen tube is capable of vegetative growth, independently of this influence, and begins to manifest that power before reaching the nucleus; but it is not capable of developing the entire organisation of the species. In animals the part which, by fecundation, is made capable of vegetation, namely, the germ, is derived from one of the sexes, and the unimpregnated germ does not perceptibly differ in form from the germ which is impregnated.

It remains for future observations to determine whether the pollen grain, or the part hitherto called the ovulum of plants, corresponds to the germ produced by the female animal.

[Dr. Barry† has made some remarkable observations relative to the changes which take place in the ovum immediately after impregnation, — observations which seem to bring us much nearer to a perfect acquaintance with that process. In immature ova, according to

* [Meyen has recently published some further remarks on the acts of impregnation in plants (Noch einige Worte über den Befruchtungs-akt und die Polyembryonie, von F. J. F. Meyen, Berlin, 1840). He still denies the correctness of Schleiden's observations. The essential part of the process of impregnation consists, he says (p. 11), of the complete coalescence of the end of the pollen tube with the wall of the embryosac, which he compares to the conjugation of conferva (see fig. 167, p. 1505). The germinal vesicle is formed from the substance of the united membranes, namely, from the extremity of the pollen tube and the apex of the embryosac also. There is at first a free communication at the point of coalescence between the cavities of the pollen tube and embryosac. The substances contained in them, therefore, become mixed. During the development of the germinal vesicle these substances afford nutriment to it, and when its cavity has become separated by septa from the pollen tube and the embryosac, they form within the vesicle the primary mass from which the embryo is developed. Valentin (Repertor, 1840, p. 61) objects to the application here made of the term germinal vesicle; since, according to analogy with the generative process in animals, the germinal vesicle should be a part which exists before impregnation.]

† Researches in Embryology, second series, Philos. Transact. 1839, pt. ii. pp. 312 to 316.

Dr. Barry, the germinal vesicle is situated at the centre of the yolk; but subsequently it passes to the surface. The ovum itself lies at first in the centre of the Graafian vesicle; but previously to impregnation is conveyed to that part of its surface which is nearest to the exterior of the ovary, and is held there by the "retinacula," described at page 1470. The germinal spot is at the same period placed at the surface of the germinal vesicle. Such is the condition of the mature ovum, *ante coitum;* that is to say, its essential parts lie as near as possible to the surface of the ovum and Graafian vesicle. *Post coitum,* but before the discharge of the ovum from the ovary, the germinal spot passes to the centre of the germinal vesicle, and the germinal vesicle to the centre of the yolk. The nature of these changes in the condition of the ovum, taking place after coitus, and the fact of spermatic animalcules having been traced to the ovary itself, render it exceedingly probable that these changes are produced by the contact of the seminal fluid. In further, and more minute researches,* directed to discover the state of the ovum at the moment of fecundation, as well as immediately before and after that event, Dr. Barry has made the following important observations:—He finds that the germinal vesicle is really the essential portion of the ovum, and that it is the seat of the most important changes which immediately follow impregnation. "It is known that the germinal spot presents, in some instances, a dark point in its centre. The author finds that such a point is invariably present at a certain period; that it enlarges, and is then found to contain a cavity filled with fluid, which is exceedingly pellucid. The outer portion of the spot resolves itself into cells; and the foundations of other cells come into view in its interior, arranged in layers around the central cavity; the outer layers being pushed forth by the continual origin of new cells in the interior. (See fig. 166, A. B. C.) The latter commence as dark globules in the pellucid fluid of the central cavity." "The germinal vesicle, enlarged and flattened, becomes filled with the objects arising from the changes in its spot, (See fig. 166, C;) and the interior of each of the objects filling it, into which the eye can penetrate, presents a repetition of the process above described. The central portion of the altered spot, with its pellucid cavity, remains at that part of the germinal vesicle which is directed towards the surface of the ovum, and towards the surface of the ovary. *At the corresponding part, the thick transparent membrane of the ovum, in some instances, appears to have become attenuated, in others also cleft.* (Fig. 166, D.) Subsequently the central portion of the altered spot passes to the centre of the germinal vesicle; the germinal vesicle, regaining its spherical form, returns to the centre of

* [Researches in Embryology, third series, read at the Royal Society, May 7, 1840; see London and Edinb. Phil. Mag. June, 1840, and Phil. Transact. 1840, pt. ii. p. 529.]

Fig. 166.

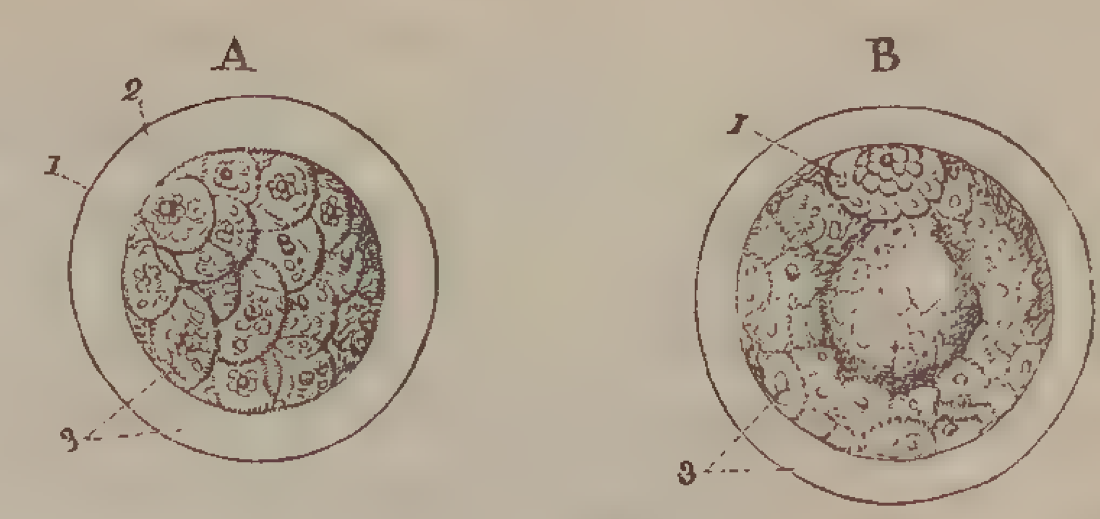


Fig. 166.

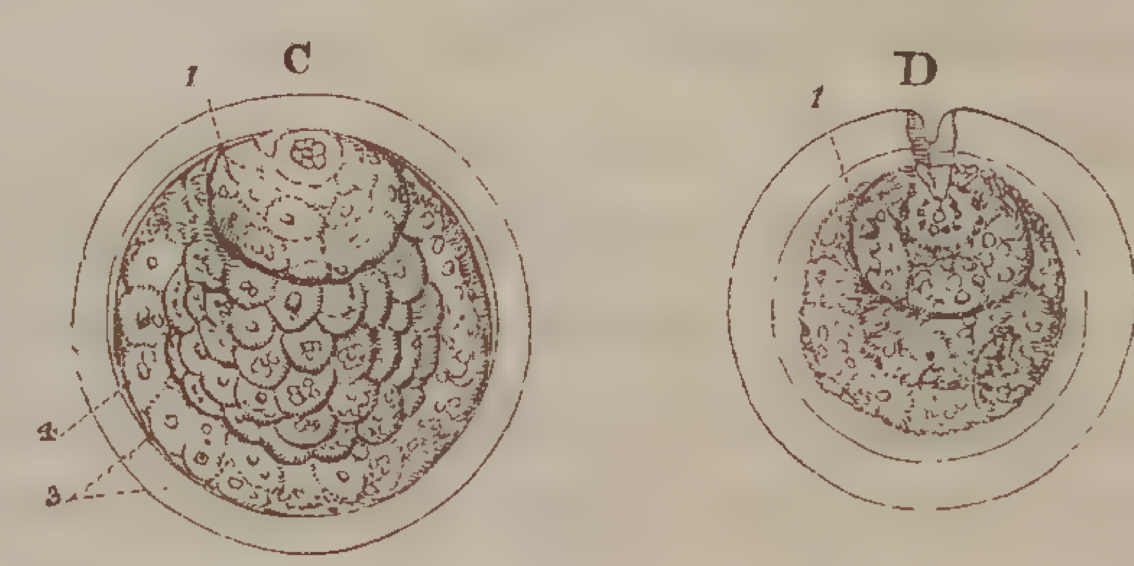
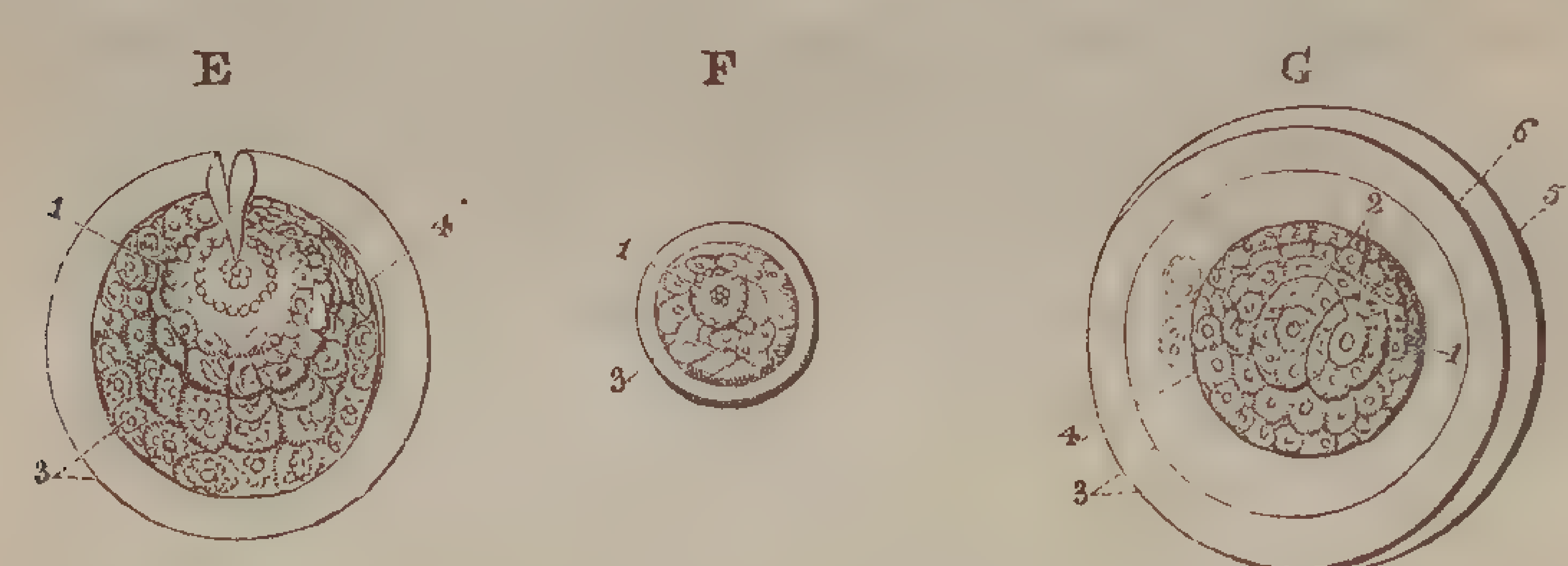


Fig. 166.



the ovum, and a fissure in the thick transparent membrane is no longer seen. (Fig. 166, E. F.) From these successive changes it may be inferred that fecundation has taken place; and this by the introduction of some substance into the germinal vesicle from the exterior of the ovary. It may also be inferred, that the central portion of the altered germinal spot is the point of fecundation. In further proof that such really is the case, there arise at this part two cells, which constitute the foundation of the new being. These two cells enlarge, and imbibe the fluid of those around them, which are, at first, pushed further out by the two central cells, and subsequently disappear by liquefaction. The contents of the germinal vesicle thus enter into the formation of the two cells. (Fig. 166, G.) The membrane of the germinal vesicle then disappears by liquefaction." The further changes which the two cells here referred to undergo, preparatory to the formation of the embryo, will be detailed at a subsequent page. It remains here only to state that the observations above related were made on the ovum of the rabbit; but that Dr. Barry has found the corresponding parts in the ovum of birds, batrachia, and osseous fishes, to be the seat of the same changes. He believes the whole substance of the cicatricula in the laid egg of the bird to have its origin within the germinal vesicle, and not to be merely the discus vitellinus, or proligerus of the unfecundated ovum in an altered state.]

* [Fig. 166 represents the changes which, according to Dr. Barry, take place in the ovum of the Rabbit at the time of impregnation and immediately subsequent to it. A. is an ovarian ovum taken from an animal killed seven hours post coitum. The Graafian

CHAPTER VI.

THE THEORY OF SEXUAL GENERATION.

*a. Casper Fried. Wolff's theory of the fecundation of plants and animals.**

THE fundamental notion on which Wolff bases his theory of conception is, that in fructification the vegetation of plants attains its end, and that as soon as flowers are developed at the extremity of the axis of a plant, that part becomes incapable of prolonging the axis by the formation of leaf buds. He then shows that the organs of fructification are merely modified leaves. The calyx of the sunflower, he says, is composed of a number of leaves smaller than the ordinary leaves of the plant, closely aggregated together. The petals, again, are merely leaves, as is evident in the grasses. The corolla of grasses is not distinguished from the calyx (or paleæ), and differs from the ordinary large leaves of the grass in no other respect than the calyx differs from them. The colour of flowers is not essential and often is gradually developed. The flower of Statice has many calyces, of which the most inferior is pale and devoid of colour, the next succeeding more and

vesicle exhibited no appearance of preparation for discharging its ovum; 1. the germinal vesicle is spherical; 2. the germinal spot exhibits incipient cells at its margin. The layer of substance immediately within the thick transparent membrane, or zona pellucida, 3, is composed of regular elliptical flattened cells. B. is an ovarian ovum, more nearly prepared for fecundation. The germinal vesicle, 1, is enlarged and flattened, and is filled with the cells developed from the germinal spot. The flattened cells on the inner surface of the zona pellucida, 3, are indistinct from partial liquefaction. C. an ovum from a Graafian vesicle which was large and vascular. The germinal vesicle, 1, is larger, and the cells within have increased in number. Between the outer layer of cells of the yolk and the zona pellucida, 3, a distinct membrane is seen. This was described by Dr. Barry, in the second series of his remarks, as the proper membrana vitelli; but he now states that it has no permanent existence, but is formed as each layer of cells approaches the zona pellucida, and disappears when those cells undergo liquefaction. D. In this ovum the pellucid centre of the altered germinal spot lies immediately under an orifice or cleft in the thick transparent membrane. An object resembling a Spermatozoa was observed by Dr. Barry in this orifice. 1. indicates the outline of the germinal vesicle. E. Here the cleft in the thick transparent membrane, 3, is still visible; but the germinal vesicle, 1, filled with cells, is returning to the centre of the ovum. The membrane, 4, separating the yolk cells from the thick zona pellucida, is again formed. F. shows the germinal vesicle, 1, nearly in the centre of the ovarian ovum and the germinal spot or point of fecundation in the centre of the vesicle. G. is an ovum from the Fallopian tube. The germinal vesicle, 1, of which the outline can be scarcely distinguished, contains two cells, 2, much larger than the rest; the cells of the yolk mass are surrounded by a proper membrane, 4, between which and the zona pellucida, 3, is a fluid. Two minute cells have escaped liquefaction in this fluid. The incipient chorion, 5, is beginning to imbibe fluid, 6, and to rise from the zona pellucida.]

* Theorie der Generation. Halle, 1764, p. 222.

more inclined to red, and the most superior, like the flower itself, of the deepest red, although its figure is not different from that of the other calyces. The seed-vessels are evidently modified leaves, for, when they are ripe and dehisce, each valve appears as a true leaf. The same is the case with the seeds. As soon as they are put into the ground, their lateral halves, or cotyledons, become transformed into leaves.

Wolff next demonstrates that the modification which leaves undergo in the formation of the flowers is dependent on an arrest of the vegetative process. The leaves which constitute the calyx of the sunflower, are, he observes, scarcely one eighth part so broad as the ordinary leaves of the plant, and are much shorter. The leaves forming the calyx (or bracts) and flower of the grasses are scarcely one-fifth part so long as the perfect leaves. He adds, that the proper leaves of a plant gradually become imperfect as they are nearer to the organs of fructification, and remarks that this is so much the case in the sunflower and many other plants, that it is impossible to say where the ordinary leaves cease and those of the calyx begin. It may be added, that the internodia of the stem are shorter and shorter in proportion as they are nearer to the flowers, and that in the position of the sepals composing the calyx of many plants, the spiral arrangement of the leaves of the stem can still be distinctly traced. The vegetative action, therefore, says Wolff, evidently becomes more imperfect and weaker towards the point of fructification; and it must, at length, entirely cease. This perfect arrest of vegetation takes place in the seeds. The want of nutritive juices is the cause of the arrest of vegetation, as is shown by the withering and fall of the fruit. If a plant which is known to put forth leaves a certain number of times, for instance, six times, before developing the organs of fructification, is set in a very poor soil, not only will its leaves generally become very small and imperfect, but it will scarcely have put forth leaves three times before fructification will take place. If this same plant is placed, not in poor, but in a very moist and rich soil, its leaves will become larger and more perfectly formed, and instead of developing leaves six times, it will put them forth nine times before it shows the organs of fructification. Moreover, if, while the fructification of a plant is thus delayed by the richness of the soil, it is transplanted to a poor soil, flowers will immediately appear. Lastly, if a plant which has already developed the calyx and rudiments of the corolla and anthers in poor soil, is quickly transplanted to rich soil, the anthers can be seen to become transformed into petals in consequence of the excess of nutriment.

In the next place, Wolff remarks that the first parts of the young plant, developed by the power of the male semen, do not differ from the ordinary leaves of the parent plant. The young plumula, is, like the leaf bud of the parent plant, composed of young leaves. Both, therefore, require for their development the same agency or cause, which was in operation in the old plant when it produced its ordinary leaves. The male semen, or the pollen, must be this cause of vegetation, which was previously deficient; or, in other words, it must be nutriment in its highest perfection. The afflux of the ordinary nutriment of the plant to the extremity of its axis by the ordinary passages, ceases; but the male semen, or pollen, is a kind of nutriment, which, instead of being conveyed through the ordinary channels, is supplied from without to the parts of the plant destined to undergo vegetation.

Wolff explains the phenomenon of conception in animals in the same way. The ovary is the part of the animal organism in which the vegetative action is arrested, and hence it may be compared to the imperfectly developed terminal bud of plants.

b. Critical examination of Wolff's theory.

In Wolff's theory of conception there is much that is perfectly correct, but its main conclusion is erroneous, and involves a false view of the nature of semen. It is quite true that fructification is the result of abortive vegetation; but this abortive development is of an extraordinary kind, and cannot be removed by the most perfect nutriment. A deciduous leaf-bud is also abortive in its vegetation, and was so, even before its separation from the parent plant; there are leaf-buds, as we have seen, which consist merely of a single cell, and which, therefore, are quite as simple as the germ formed in fructification; and, nevertheless, these leaf-buds in their internal condition and endowments are totally different from the germs of the organs of fructification. All that the deciduous bud requires for its perfect development is, that new nutriment should be supplied to it from without, either by the soil or by another vegetating organism, on which it is engrafted. The semen of the male, on the contrary, far from merely yielding nutriment, however perfect, to the unimpregnated germ, really contains within itself, just as the germ of the female does, the power of determining the whole form of the species, whether plant or animal. This fact is evident in ordinary generation, as well as in the production of hybrids. The offspring in ordinary generation, possesses, not merely the properties of the mother, but those of the father also in an equally marked degree. This is matter of constant observation, in the generation both of man and of animals. The race, form of body, propensities, passions and talents of the father, as well as of the mother, are manifested in the progeny; and since these peculiarities are communicated to the germ by the semen, they must be contained in it, just as those of the female parent are contained in the germ. The same evidence is afforded by the intermediate forms resulting from the intermixture of different species. The mule partakes of the characters of both the horse and the ass; and the hybyridising of plants as frequently gives rise to intermediate forms distinct from either parent plant, and not to be regarded as merely aborted individuals of either species. Hence, if the semen be denominated nutriment, it must be regarded as a kind of nutriment in which, no less than in the germ, are involved the specific form of the animal or vegetable, and all its individual peculiarities.

In the same way we may refute the theory of those physiologists, who regard the semen not as nutriment, but, on the contrary, as an agent which arrests the vegetation of the germ and the growth of the axis of the plant. For this arrest of vegetation occurs in plants where there are merely female flowers, and where no influence of the fecundating principle could be exerted. Moreover, since this fecundating principle has the power of determining the form of the male individual, it can be neither a mere stimulus nor an agent which simply arrests vegetation.

c. Of the nature of the ovum and semen, and of the process of conception.

The unimpregnated vegetable germ and the leaf-bud agree in both possessing "potentially" the specific form of the plant. They differ, however, from each other, in the flower-bud which contains the unimpregnated germ being unable, of itself, to put forth new buds; while the leaf-bud not only can develop itself to a new individual, but may become the stock from which an infinite number of new individuals are developed. The unimpregnated germ, therefore, though involving "in potentiâ" the form of the species, yet is, in consequence of a peculiar impediment to its organising action, unable to develop this form "in actu"; but the leaf-bud is free from such impediment. The organising action of a leaf-bud is certainly impeded when the nutriment necessary for vegetation is not supplied to it, as may happen to a deciduous leaf-bud. But the impediment to the organisation of the unimpregnated germ is much more intimately connected with its own constitution; for the germ does not undergo development even when it is supplied with the necessary nutriment. What, then, is the nature of this cause which prevents the organising action of the germ from being exerted? Since it is not merely want of nutriment, it most probably consists in the germ having defects in its constitution from which the leaf-bud is free, and which render the development of the germ in the pre-ordained form impossible. The semen or fecundating matter contains that which gives integrity to the germ. The semen, also, is capable of determining the specific and individual form of the new animal or plant, but it likewise is the subject of a defect which renders it incapable of actually developing that form, until it has united with the female germ. The defects, however,

The condition which allows for impregnation [illegible]
[illegible]

of the ovum, or germ, and of the semen, are not identical in their nature, since each contains that in which the other is deficient. The ovum and semen are not similar halves of one whole. The ovum, at least that of animals, contains the part destined to germinate, and is, in fact, the primary cell, or contains the primary cells, which form the basis of the new organism, and maintain, unbroken, the chain of organisation. The semen, on the contrary, does not itself germinate, but is a fluid excitor of germination, endowed, at the same time, with the power of determining the form not only of the species but of the individual organism which produced it.

It may here be well to glance at the mode of vegetation of cells within developed organisms. The cells of vegetables have the power of transforming the nutriment brought into contact with them into a fluid productive matter, within which new cells are developed. The formation of the new cells in this plastic matter, the "cytoblastema" of Schleiden, is determined by the influence of a pre-existing cell, and is effected by a definite process; nuclei being first formed around which the young cells are developed. Schwann's researches have shown that the cells of the animal organism grow in the same way. The germ, therefore, which is really a cell, may be regarded as a primary cell endowed with the power of producing the specific form of the plant, but defective in the respect of being incapable of producing the "cytoblastema." The semen or fecundating matter, on the contrary, though capable of determining the power of the new organic being, contains no primary cells, but resembles, more nearly, a "cytoblastema," endowed with the property of producing a definite form, but incapable of vegetating except under the influence of a primary cell already formed. We may imagine, that when the primary cell of the germ, and the "cytoblastema" of the semen are brought together, the vegetation of the primary cell will commence; while, in consequence of both the primary cell of the germ and the plastic matter of the semen exerting an influence on the products of this vegetation, the new individual must present a mixture of the forms which the germ and semen had respectively a tendency to give, and will resemble both the male and the female parent.

Conception is not the only instance in which two organisms, both of which have the power of assuming a definite form, exert a reciprocal influence on each other, nor does it, indeed, afford the only example of the complete union of two substances endowed potentially with specific forms, so as to produce one individual. In order to perceive more clearly the peculiar nature of the process, it will be useful to consider for a moment that kind of organic union, in which two distinct forms do not become fused into an intermediate one. The extreme cases which present themselves in the union of two organisms are found, on the one hand, in the engrafting of a leaf-bud upon a different stock, and, on the other hand, in the mingling of the forms of the parents, which takes place in sexual generation. Another phenomenon similar to the latter of these two extremes, is the coalescence of two buds or gemmæ, such as takes place in the process of conjugation.

1. *Engrafting of buds.* The majority of facts tend to prove, that cuttings or buds grafted upon a new stock undergo no modification from the influence of the stock on which they grow, nor themselves produce any modification of its vegetation. The evergreen oak engrafted upon the common oak, the leaves of which fall in the winter, keeps its leaves during that season. The laurel engrafted upon a wild cherry-tree, remains in leaf through the winter, while the cherry-stock becomes stripped of its leaves in the autumn.* Poor sorts of pears engrafted on pear trees of a good kind, yield poor fruit, and vice versâ. In the cases where the white jasmin, on which yellow jasmin had been engrafted, is said to have borne yellow flowers on those branches which issued from the trunk below the situation of the graft, the flowers thus apparently modified did not, according to Meyen, belong to the stock, but to the graftling which had developed adventitious buds from layers of its wood sent down between the bark and wood of the stock. It appears, therefore, that the changes which graftlings undergo, are, for the most part, limited to the improvement of the fruit, and to those modifications which may also be produced by the change of soil and of the nutriment thence derived. Grafting, either of cuttings or of leaf-buds, is, indeed, a means of preserving pure and unchanged the forms of species and even of varieties, which it is much less easy to do by sexual propagation, since, in the latter process, the form is determined equally by two different influences. The slight influence exerted on each other by two organisms which have coalesced is evinced in animals as well as in plants; it is a well-known fact, that double monsters, when they live sufficiently long, as in the case of Rita and Christina, may manifest different dispositions of mind and temper.

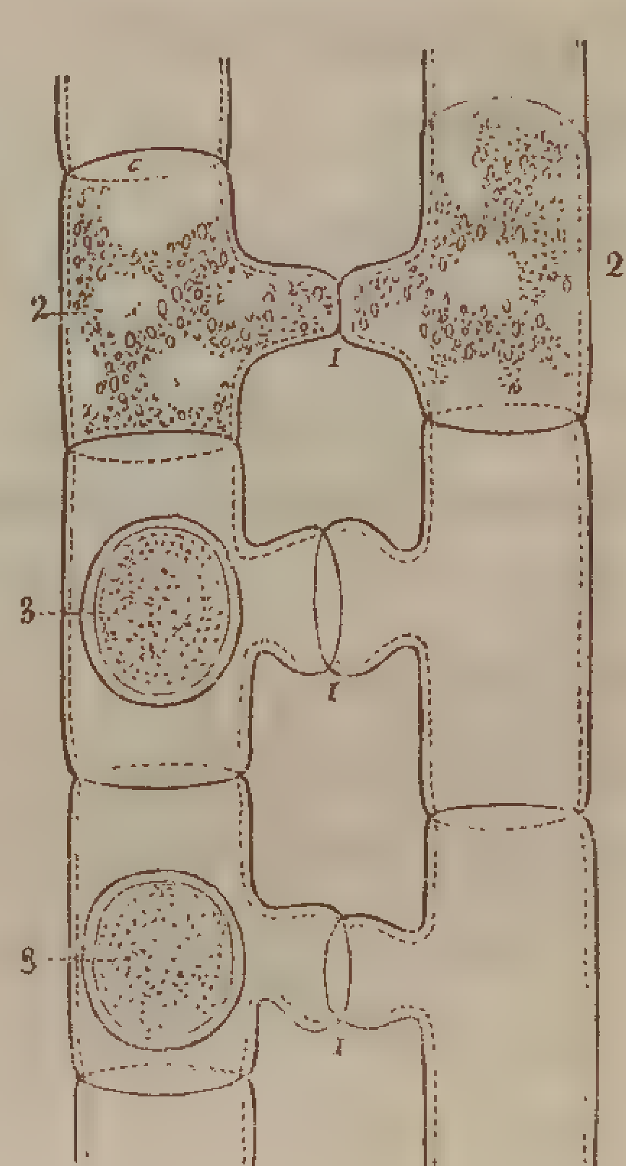
2. *Conjugation or coalescence of two buds.* Although perfectly developed and organised individuals which are organically united, cannot modify each other's form and endowments, yet it might be conceived that two buds or gemmæ, would not merely exert a modifying influence on each other, but would even become fused into one organism. This idea is suggested by the experiments which have been instituted on the Hydra. Each fragment of a Hydra, isolated from the body of the animal, may be regarded as a bud. The posterior or lower part of a polype separated from the rest of the animal is developed into an entire new individual, but if this posterior part when thus separated is again applied to the

* Meyen, Pflanzen-physiologie, t. iii. p. 92.

anterior portion, and their cut surfaces be kept in apposition, union takes place, and the part which had been isolated from it becomes again subject to the centre of individual life resident in the anterior part of the animal.

This experiment, related by Trembley, leads us to imagine further, that even two portions of a Hydra, neither of which as yet contains a ruling centre of individual animal life, but which, nevertheless, are capable of becoming new individuals, might, if they were brought into sufficiently close contact, coalesce, and form a single bud from which a single individual would be developed. Amongst the various experiments instituted by Trembley, this also occurs. In no instance, however, did it succeed; the two fragments did not unite, and there was, consequently, no fusion of two portions of organic substance, comparable to that which takes place in sexual generation. The two fragments of the polype were capable of assuming the properties of buds, but as yet they had not undergone this change. In some of the lowest organic bodies, however, there are instances of the actual fusion of two buds into one.

Fig. 167.†



The process of conjugation was first observed by O. Fr. Müller in the Confervæ; it is presented by the Confervæ conjugatæ, and especially by the genera Conjugata and Spirogyra. Ehrenberg* observed the phenomenon in a fungus (Syzygites); and it was witnessed by the same physiologist and by Morren in the Closteria. At the time when conjugation is about to take place, bud-like processes or excrescences appear on the segments of the Confervæ; the processes belonging to contiguous filaments unite, and their walls becoming absorbed, the conjugate segments communicate freely with each other. (See fig. 167 at 1.) The mucous mass (2) contained in the segments or cells, moulds itself into the form of a ball and passes from one cell into the other where the masses of the two cells unite and form a spherical body, the spore (3). In each of the conjugate filaments some cells are the recipients, while others yield their contents to the opposite cell of the contiguous filament. Vaucher observed, that in some cases, the contents of the two conjugate Con-

* Verhandl. der Gesellschaft naturforsch. Freunde zu Berlin, B. i. 1829.

† [Conferva bipunctata (Stellulina cruciata, Link) in the act of conjugation. 1, The bud-like processes of the cells uniting; those of the two lower cells of the filaments have coalesced, and their cavities communicate freely. 2, Contents of the cells before conjugation is completed. 3, The spores resulting from the process. After Meyen, Pflanzen-physiologie, t. iii. taf. x. fig. xi.]

fervæ united in the intermediate tube.* The two masses which unite to form the globular spore in the conjugation of Confervæ must be regarded as of the nature of buds and not as two different substances analogous to germ and semen, for, in the first place, their external characters are identical, and secondly, spores, or rather buds, exactly similar to those produced by conjugation, are likewise found in segments of Confervæ, quite independently of conjugation, for example, in the Spirogyra, according to Meyen.

3. *Coalescence or fusion of the germ and semen in sexual generation.* Conjugation is apparently a simple fusion of two perfectly similar gemmæ or buds. This is evidently a higher form of generation than propagation by the formation of simple buds. For the bud resulting from the process of conjugation, must participate in the individual peculiarities of two individuals, while the simple bud has the endowments of one only. This seems to be the principal purpose of the sexual mode of generation, namely, the production of an offspring with the endowments of the whole family and species, and not merely with those of a single individual. Sexual generation differs, however, from conjugation, in the circumstances of the productive matter of the one sex being the necessary complement of that of the other sex; of the one being always the recipient and the other always the additament, and of the one having already an organised form, while the other is still fluid with merely a tendency to become organised.

* For an account of the conjugation of the Closteria, consult Morren, Ann. des Sc. Nat. t. v. 1836, p. 257; and Ehrenberg, die. Infusions-thierchen. Tab. v. vi.

BOOK THE EIGHTH.

Of Development.

SECTION I.

Of the development of the ovum and embryo.

THE development of the embryo of vertebrate animals is presented to us in its most simple form in fishes and the Amphibia. Hence it is most convenient to study the process in these classes before proceeding to consider its details in the higher Vertebrata. The ovum of fishes and Amphibia has neither the amnion nor the allantois,—parts which are common to the ova of birds, reptiles, and Mammalia. Aristotle first discovered that fishes, though furnished with the yolk sac in their embryonic condition, have not the allantois. "The ova of fishes," he says, "have not the umbilical duct which passes to the chorion under the shell in birds, although they have the umbilical duct which leads to the yolk.* All the phenomena of development in these lower Vertebrata consist therefore of the changes which the germinal membrane, the embryo produced from it, and the yolk sac undergo. The formation of the embryo and yolk sac conforms in all the Vertebrata to one common type. This type suffers modifications in the different classes; and like the whole process of development, it is comparatively simplified in fishes, and still more so in Amphibia. In the latter class the entire germinal membrane, and the part analogous to the yolk sac of other animals, is expended in the formation of the embryo, while even in many fishes a yolk sac exists distinct from the part which forms the embryo.†

* Πρῶτον μεν γὰρ οὐκ ἔχουσι τὸν ἕτερον ὀμφαλον τον επὶ το χόριον τείνοντα ὁ ἐστιν ὑπο τὸ περιέχον ὄστρακον.—Aristotle, De generatione animalium, iii. 3.

† The principal works which treat of development generally in all the classes of animals, are those of Dutrochet, Récherches sur les enveloppes du fœtus, in Mém de la Société Méd. d'Emulation, t. viii. and his. Mém. p. s. à l'hist. anat. et physiol. des végétaux et des Animaux. Paris, 1837, t. ii. p. 200; Burdach, Physiologie, Bd. ii. 2te Aufl. mit Beiträgen von E. Von Baer, Rathke, Meyer, Von Siebold und Valentin. Leipzic, 1837; Von Baer, Entwickelungsgeschichte der Thiere, i. Königsb. 1828, ii. 1837; Valentin, Entwickelunggeschichte, Berlin, 1835; and R. Wagner, Physiologie, i. Leipz. 1839.

CHAPTER I.

DEVELOPMENT OF FISHES AND AMPHIBIA.

1. *Changes which take place in the yolk, previously to the formation of the embryo.*

In all animals some changes in the entire mass of the yolk seem to precede even the first modelling of the embryo. The extent of these changes, however, is very different in the different classes. They are least considerable in birds, and most so in Amphibia, fishes, and many invertebrate animals; in which they produce the phenomenon of the regular division and subdivision of the whole yolk.

The phenomenon of the division and subdivision of the yolk was first discovered in the ova of frogs, by Prevost and Dumas.* Further valuable observations on the subject have since been made by Rusconi,† Baumgaertner,‡ and Von Baer.§

The surface of the yolk of the frog's ovum presents a well-known difference of colour in its two halves; the one half being black, owing to the presence of a thin layer of black matter at that part, and the other being of a lighter colour. In the middle of the dark area there is a point where the black stratum is interrupted, and from this point a canal leads to a cavity somewhat deeper seated in the mass of yolk. A line passing from this middle point of the dark surface of the yolk to the middle of the lighter coloured surface, is called by Von Baer the axis of the ovum. Furrows extending over the surface of the yolk from the one point to the other are called meridian-furrows; those which run in a plane perpendicular to the axis are equatorial furrows or parallel furrows, according to their distance from the middle points of the two areæ.

The following is Von Baer's description of the process of division and subdivision, or furrowing of the yolk. At the end of the fifth hour after the expulsion of the ovum from the female frog, the first meridian-furrow is formed; beginning at the middle of the dark surface. (Fig. 168, A. I.) This is not a mere superficial furrow, but is a cleft extending through the whole mass of yolk, so as to divide it into two contiguous ellipsoid masses. Before this complete division of the yolk into two hemispheres has taken place, and about six or seven hours after impregnation, the second meridian furrow appears. This crosses the

* Ann. de sc. Nat. t. ii. 110.

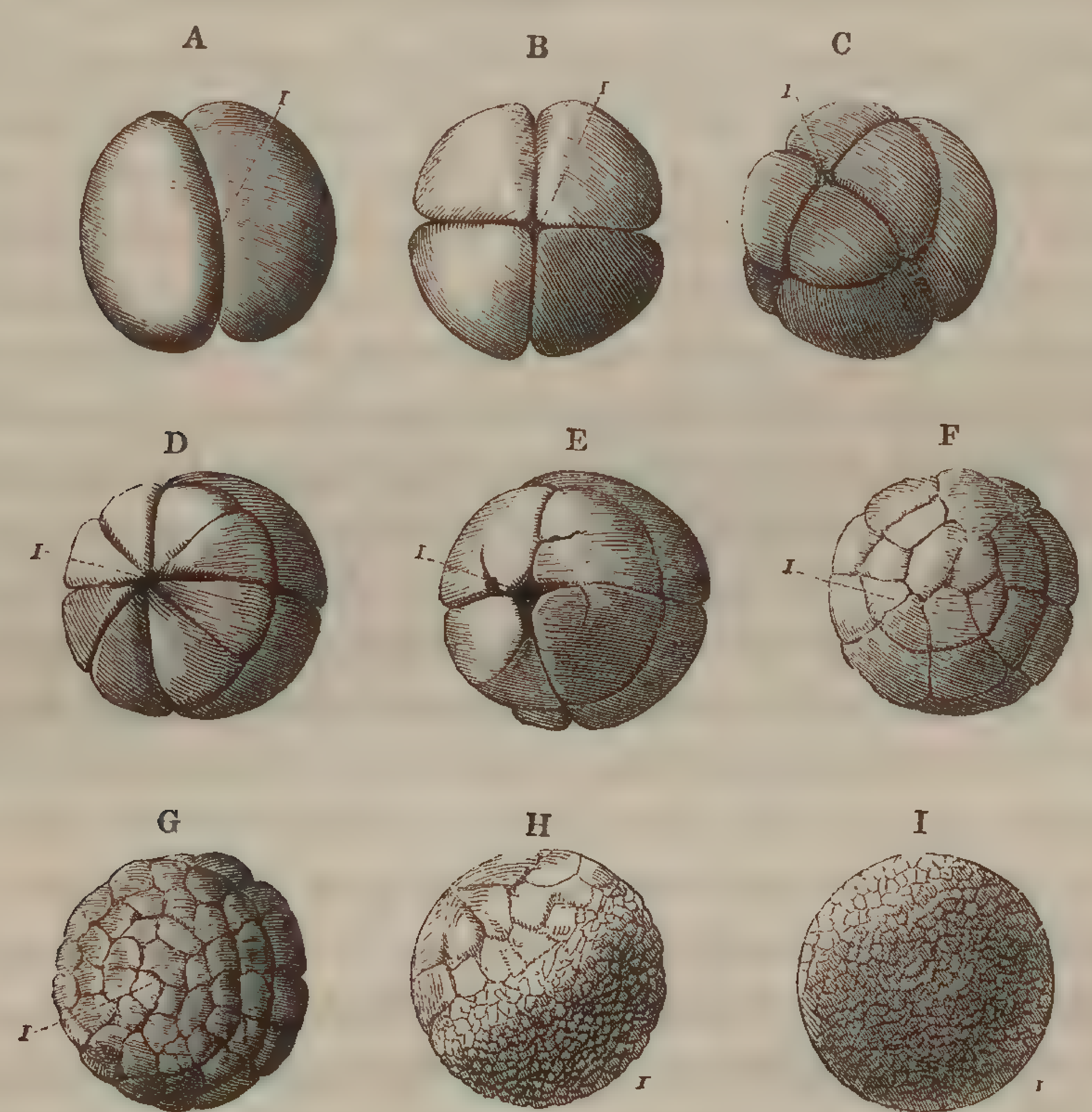
† Développement de la grenouille commune. Milan, 1826.

‡ Ueber Nerven und Blut. Freiburg, 1830.

§ Müller's Archiv. 1834, 481.

first at right angles. (Fig. 168, B.) An ovum in this state, which has been frozen, consequently splits into four segments of a sphere. The equatorial furrow soon makes its appearance. (Fig. 168, C.) Then new

Fig. 168.*



meridian furrows, and in a short time parallel furrows show themselves, until the yolk acquires the form of a blackberry or raspberry. (Fig. 168, D—G.) Lastly, the surface of the yolk becomes again perfectly smooth. (Fig. 168, H. I.) This cycle of changes may be passed through in the course of twenty-four hours. Soon afterwards the formation of the embryo commences. The lighter-coloured portion of the surface, according to Von Baer, becomes smaller and smaller, in comparison with the darker portion, and at the same time acquires an elongated form. It then becomes marked off at one end from the darker surface by a black line. This black arched line forms at length a slight depression, and the posterior extremity of the embryo is thus defined. Its anterior boundary is not so soon visible, perhaps on account of its lying entirely within the dark portion of the surface of the yolk.†

* [Fig. 168. The yolk of the frog's ovum undergoing the process of division and subdivision. The cypher I in all the figures indicates the centre of the dark surface of the ovum. After Von Baer. Müller's Archiv. 1834.]

† [Some microscopic observations by M. Bergmann of Gottingen on the structure of the smaller masses into which the yolk of the batrachian Amphibia becomes subdivided are contained in the first number of Müller's Archiv. for 1841. He finds that each of these masses is surrounded by a distinct membrane, and contains in its centre a solid transparent corpuscule.]

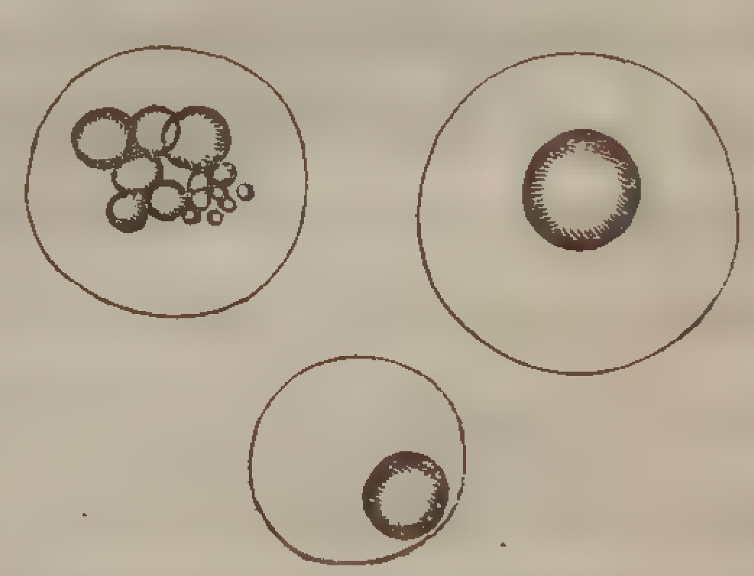
The division and subdivision of the yolk in the ova of fishes have been described by Rusconi.* Having impregnated some ova of the tench artificially, he observed that they soon afterwards lost their spherical form, and became pear-shaped, owing to the formation of a kind of intumescence at one part of the surface of the ovum. The small granules previously dispersed through the yolk now became collected at the base of this intumescence. Half an hour after the occurrence of this first change, two furrows intersecting each other at right angles appeared at the prominent part of the yolk. A quarter of an hour later two other furrows were observed at each side of the first, so that the prominent part of the yolk, which previously was divided into four lobes, now appeared to be formed of eight lobes. After the lapse of another quarter of an hour each of these eight lobes was seen to be subdivided into four smaller lobes, by the formation of six fresh furrows intersecting each other at right angles. At the end of another half hour several new furrows appeared, which crossed those which already existed, and subdivided the lobes of the prominent part of the yolk still further, rendering them so small and numerous that it was now scarcely possible to count them. The process continued until the surface of this portion of the yolk regained the smoothness which it had before the first furrow appeared.†

This process of subdivision of the yolk observed by Von Baer and Rusconi in frogs, salamanders, and the family of Cyprini among fishes, has been discovered to occur in many invertebrate animals also; for example, in the Crustacea by Rathke; in the nematoid Entozoa by Siebold, and in the Mollusca by Sars.

2. *Vegetative process which the cells of the yolk present during the development of the ovum.*

The yolk was discovered by Schwann to consist of cells. These cells have different characters in different parts of the yolk. In the bird's egg, the cells of the yolk cavity and of the canal leading from it to the cicatricula, are nucleated. (Fig. 169.)

Fig. 169.‡



The cells composing the yolk differ also in form in different animals. In fishes and the Amphibia they are most commonly spherical. In sharks (Scyllium, Acanthias, Squatina,) and in the Myxinoid fishes they are, according to my observation, elliptical. In the rays (Raja), their form is for

* Bibl. Ital. I. xxix. and Müller's Arch. 1836, p. 278.

† Rusconi, loc. cit. Müller's Archiv. 1836, p. 281.

‡ [Fig. 169. Cells from the yolk cavity of the hen's egg, after Schwann.]

the most part flat and quadrangular, with rounded edges and corners. The sharks and rays may therefore be distinguished even by the form of the yolk-cells of their ova. [In the Mammalia, according to Dr. Barry, they are oval flattened disks. See page 1514.]

The yolk has the most essential share in the development of the embryo. In some cases it is the portion of the yolk called the germinal membrane, which more especially contributes to the production of the new animal; in other cases, as in the frog, the entire mass of the yolk has this function. Rusconi was perfectly correct when he remarked that the embryo of the frog was formed from the whole yolk. The discoveries of Schleiden and Schwann respecting the growth of cells throw an unexpected light upon this subject.

Schwann has shown that the ovum of animals is a cell; that the membrane of the yolk sac represents the cell membrane, or wall of the cell; the germinal vesicle, the nucleus; and the yolk, the contents of the cell. He has further shown that the cells of the yolk are produced, in a manner conformable with the law regulating the development of all cells, within their parent cell, the ovum; and that the substance of the embryo itself is at first composed of cells. Schwann has likewise remarked that the yolk must be regarded not as mere nutritive matter, but in the light of a body having life; since the cells composing it take an essential part in the formation of the embryo. These cells effect a chemical change in their contents during the process of development, in consequence of which the yolk loses its coagulable property. Schwann, therefore, compares the yolk in respect of the share which it has in nutrition to the albumen of the embryo of plants. The proper albumen or white of the bird's egg entirely disappears during incubation, being absorbed as nutriment for the chick.

The further changes which the cells of the yolk undergo have been observed by Bischoff, Barry, and Reichert. Professor Bischoff and Dr. Barry recognised the development of cells within the yolk of the ovulum of Mammalia. Reichert has discovered that the formation of young cells within the previously existing cells composing the entire mass of the yolk is a process which continues during the whole period of development in frogs, where the entire yolk is employed in the building up of the embryo. In birds, according to the same observer, this process does not take place; the formation of young cells being there limited to that part of the yolk which more immediately contributes to the formation of the embryo.

In the ovum of the plagiostomatous fishes the cells of the yolk present transverse and oblique lines, resembling lines of division and subdivision, and frequently also constrictions corresponding to these lines. In the Squalus squatina the majority of the cells of the yolk have a line running in the longitudinal direction around each cell, and several transverse lines. In some cells oblique lines are seen, and in others which are irregular in form, these lines are also irregular, so as to divide the cells into several unequal segments. These yolk-cells of the ova of sharks and rays are contained in another cell, their matrix, which in the progress of development becomes filled with a fine granular matter. The appearance of the division and subdivision of the yolk-cells seems to be due to the circumstance of several cells lying in contact with each other. In some sharks the yolk-cells have a peculiar character. In the Scymni, for example, the granules of the yolk are large cells completely filled with numerous smaller cells which have been developed within them. In serpents and crocodiles, on the contrary, the remainder of the yolk which is attached to the fœtus contains many large cells filled with younger cells; and in the crocodile some of these cells contain a succession of cells encased one within the other.

The following observations of Reichert on the yolk of the impregnated ovum of the frog were communicated to the author in manuscript.

"The yolk of the mature egg of the frog after fecundation consists of two different kinds of corpuscules, which are readily distinguished by their size. Those of the smaller kind occupy that part of the yolk in which the embryo first appears, and constitute the germinal layer or cumulus germinativus, which corresponds to the germ with the nucleus of the cicatricula in the hen's egg. (See page 1468.) The remainder of the yolk is entirely composed of the other kind of corpuscules, which are three or four times as large as the foregoing. These corpuscules composing the mass of the yolk, in which they are pressed very closely together, are visible with the naked eye, but may be distinguished very clearly with the aid of a lens. With a magnifying power of four hundred and fifty diameters they are seen to have a nearly circular outline, somewhat inclining to the oval. They appear nearly uniformly opaque and dark, and as if formed of numerous small globules, though at the periphery these globules are so closely pressed together that they project scarcely at all beyond the outline of the large corpuscules. If one of the corpuscules of the yolk is broken by pressure, the globules composing it are set free, and then appear nearly transparent, without shadows, but with very strong outlines, resembling in their entire aspect small flat globules. They are not, however, easily destroyed by pressure, and do not run one into the other. Their size is nearly uniform; a few only being remarkable for their size, and in these a slightly granular aspect can be perceived. Besides these globules, a number of much smaller granules of bright appearance, and endowed with a molecular motion, are set at liberty by the bursting of one of the yolk-corpuscules. This description applies particularly to those corpuscules which lie in the centre of the yolk. Such as are situated nearer to the periphery, though they have the same general structure, yet are distinguished by having

Fig. 170.*

from two to four darker spots in their interior. (Fig. 170, A.) On crushing one of these corpuscules, there escape, in addition to the globules and granules already mentioned, several larger globules of a yellowish colour and granular aspect, sometimes surrounded by a lucid mass. These yellow globules were evidently the cause of the spotted appearance of the corpuscules. The nearer the part from which we take the corpuscules for observation is to the cumulus germinativus, the more distinct are the dark spots just described. The corpuscules at length appear nearly entirely composed of them, and thus there is a gradual transition to the smaller corpuscules of the cumulus germinativus, which seem to be the dark globules of the larger corpuscules in a free state. With the exception of the difference of size, these smaller corpuscules (fig. 170, C) exactly resemble the larger ones of the centre of the yolk. They are in greater part formed of the same small oil-like globules, but out of each of them a larger yellowish granular globule may be expressed (fig. 170, B), and the granules which present the molecular motion are much smaller, and appear quite dark. Several facts prove that these corpuscules are cells. As is so frequently the case when organic nucleuted cells are quite filled with granular substance, the existence of a membranous wall and of a nucleus cannot be detected by the eye; but still it cannot fail to be remarked that the corpuscules, though lying in close contact with each other, retain their distinct form, and that the contour of each corpuscule is nearly even, although it is apparently composed of a mass of globules. Moreover, the yellowish granular globules which may be expressed from many of these corpuscules correspond exactly to the nuclei of cells; the granules, endowed with molecular motion when forced from a corpuscule, escape gradually as through a cleft, and the larger corpuscules resolve themselves into the smaller

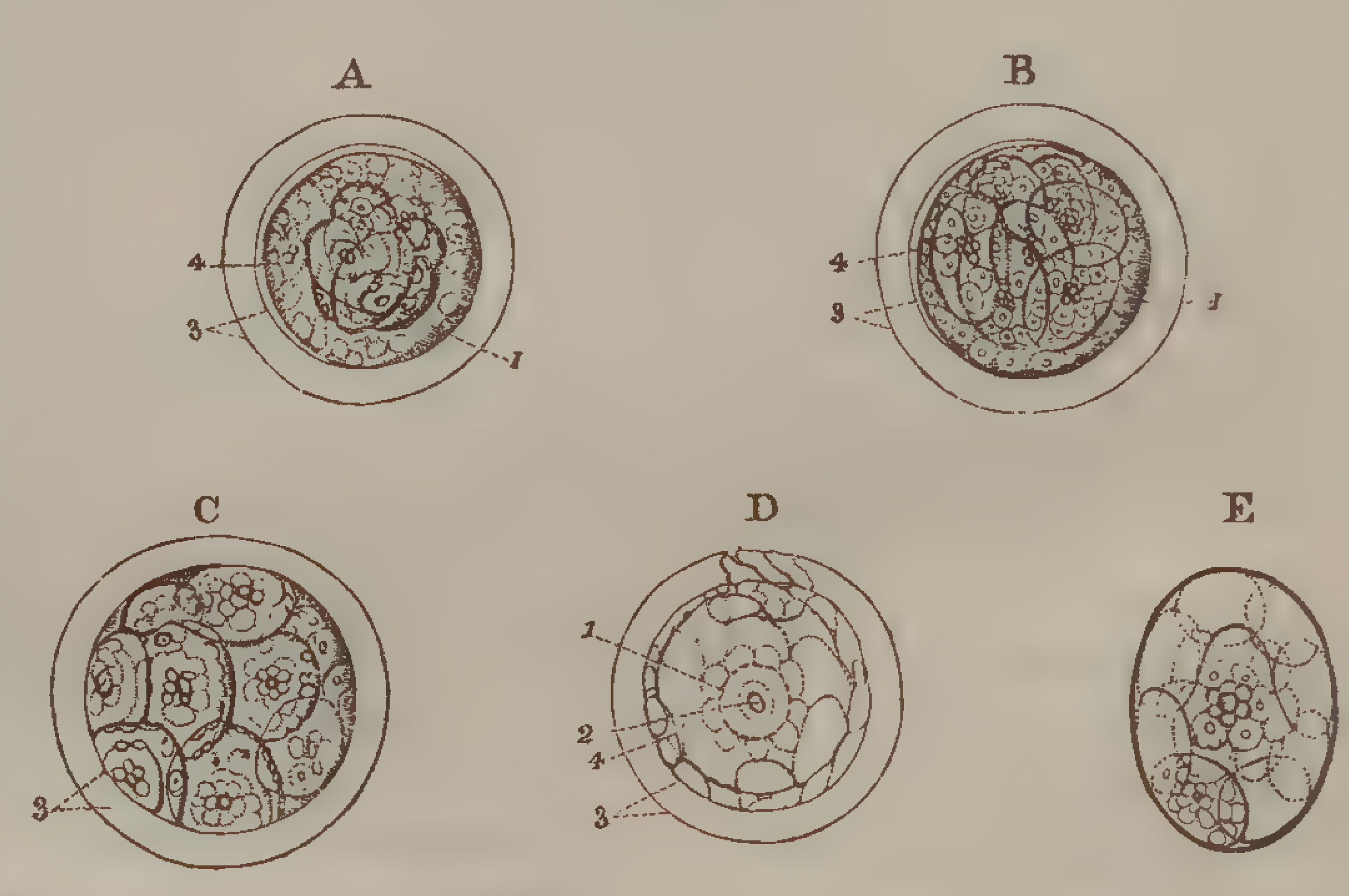
* [Fig. 170, cells from the fecundated ovum of the Frog, after Reichert. A, a cell from centre of the yolk. 1, the globular contents; 2, one of the larger globules, which is a young cell; 3, the membrane of the parent cell; B, one of the young cells set free by the bursting of a large cell. The membranous wall of this young cell is destroyed, and its nucleus, 4, is visible. C, cells from the most superficial layer of the cumulus germinativus; 1, a cell in which both nucleus and cell membrane are visible; 2, a cell in which the membrane is distinct, but the nucleus concealed by granular matter; 3, a cell in which these granular contents are nearly entirely absorbed, and a nucleus with nucleoli brought to view; 4, nuclei; 5, an intercellular space; 6, a cell in which neither the enveloping membrane nor the nucleus can be distinguished.]

ones, just as parent cells produce smaller cells within their cavity. All doubt, however, as to these corpuscules being really cells is removed by the changes which the smaller ones, composing the "cumulus germinativus," are observed to undergo during the development of the embryo. The globular contents of the corpuscules are then seen to become in part absorbed, and the nucleus (which could previously be forced out of the corpuscule by pressure), as well as the membranous wall, becomes visible. (Fig. 170, c.)

It appears, then, that the yolk of the frog's ovum consists of cells, whose nucleus and membranous wall are rendered invisible by their granular contents. Those cells which lie in the centre of the yolk are of large size, and contain no nucleus. In respect of the production of young cells, these are the least advanced. But nuclei afterwards appear in them; young cells become developed, and are recognised in those which are near to the periphery of the yolk, and most distinctly near the cumulus germinativus, as dark spots within the parent cells. The membranous wall of the parent cell now entirely disappears, and the young cells accumulate as the smaller yolk-cells in the cumulus germinativus, —a provision for the incipient development of the embryo. This process is continued as long as any yolk remains. Wherever any structures of the embryo are being formed, the smaller of the yolk-cells already developed by this process are applied to that purpose; while the place of the cells thus consumed is supplied by new ones from the centre of the yolk."

[The process described by Dr. Barry to take place in the yolk of the mammal's ovum, preparatory to and immediately after impregnation, is very remarkable. There appears to be a constant development of cells in the centre of the yolk. Each layer of these cells, while they enlarge and assume a flattened elliptic form, is pushed outwards by a new set developed internal to them. After impregnation, when the germinal vesicle has passed to the centre of the ovum, the develop-

Fig. 171.*



* [Fig. 171 represents the structure of the yolk of the ovum of the rabbit, and the changes which take place in it immediately after impregnation. In A, B, and C, 1, indicates the layer of discoid elliptic cells developed around the germinal vesicle in the centre of the yolk; 3, the thick transparent membrane of the ovum, or the zona pellucida; and 4, the more internal non-persistent membrane surrounding the most external

ment of cells here described takes place in successive layers around that body. Each layer, on reaching the exterior of the yolk mass, is often seen to be circumscribed by a proper membrane, and at length undergoes liquefaction, the layer within it then supplying its place. (See fig. 171, A, B, C.) Fig. 171, D, is a scheme illustrative of this process. Each of the flattened elliptic cells also contain minute cells arranged concentrically around a pecullid point, and the contained cells again present a similar structure. (See fig. 171, E.) The same process, in fact, which has just been described as occurring in the yolk as a whole, seems to take place in all the cells met with in the ovum.]

3. *General plan of the development of fishes and the Amphibia.*

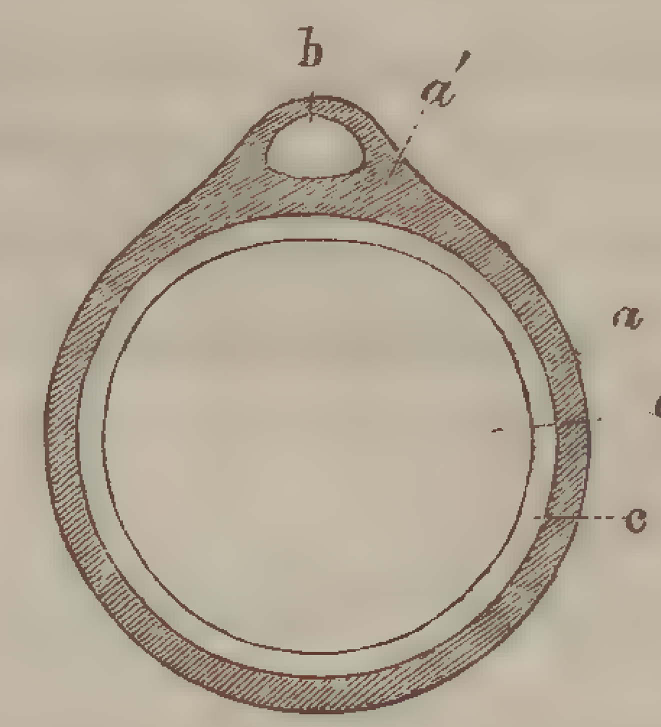
The germ first presents itself in the form of a thin stratum of yolk of definite extent—the "germinal membrane." Gradually this membrane extends itself over the whole surface of the yolk, so as to assume the form of a vesicle including the mass of yolk. In the ova of the Blennius viviparus the germinal membrane does not entirely surround the yolk until the embryo has been long formed (Rathke); while in the Cyprini it completely envelops the whole mass before any indication of the embryo can be discovered (Von Baer). The parts which form the axis of the embryo first show themselves. A groove-like depression appears at this part of the germ. Two ridges, the "laminæ dorsales," arise, one on each side of the groove. These ridges meet and unite in the middle line, and there constitute, according to the observation of previous embryotomists, the primary form of the vertebral column; while Reichert asserts that the "laminæ dorsales" are really parts of the nervous centres themselves. Along the middle line of the germ the "chorda dorsalis" is formed, a delicate continuous cord, which is afterwards surrounded by the lateral rudiments of the vertebræ, which make their appearance on each side.

The germinal membrane itself, according to the observations of Rathke and Von Baer, separates into two layers or laminæ, an internal and an external. The former—the mucous, or more correctly the organic, lamina—serves for the formation of the organic system of organs; whilst in the external, serous, or animal lamina, the organs of the animal system of the body, (as the bones, muscles, and skin,) are developed. The heart appears between the internal and the external lamina of the germinal membrane in the form of a simple canal.

layer of yolk-cells. D, is an outline drawing of an ovum, more clearly illustrating the process. The cypher, 1, here indicates the germinal vesicle, and 2, the germinal spot. E, is a section showing the structure of one of the compound discoid cells by which in some states the germinal vesicle is surrounded. After Dr. Barry, Philos. Transact. 1840, Pt. ii. p. 535.]

Figure 172 represents a perpendicular section through the embryo, germinal membrane, and yolk. *a*, is the external, "serous, or animal layer," of the germinal membrane; *a′*, one of the laminæ dorsales, or dorsal ridges; *b*, the vertebral canal; *c*, the internal or organic layer of the germinal membrane; and *d*, the yolk. We perceive that the animal part of the embryo here represents the section of a double tube, the organic part only the section of a single tube, and that the latter is contained within the lower tube of the animal layer. In the invertebrate classes, likewise, the body of the embryo is produced from a germinal membrane with an animal and an organic layer; but in the undeveloped state the two layers are simple vesicles which lie concentrically one within the other, and of which the abdominal part is in the articulata first formed, and the dorsal portion last. The section of the animal layer does not, as here, present the appearance of a double tube.

Fig. 172.



Those parts of the animal layer of the germinal membrane which form the upper tube or vertebral canal, the vertebral column and its muscles, have been named the "laminæ dorsales;" whilst those which form the inferior larger tube, and contain the organic system of parts, have been called the "laminæ abdominales" or "visceral plates."* The visceral plates are continuous along the sides of the trunk; but at the head they, at a very early period, assume the form of bands or arches descending from the cerebral capsule, and uniting at their lower extremity. There being several of these arches, a series of clefts occur between them on each side of the neck. The oral cavity subsequently lies between the most anterior of the arches and the cerebral capsule. These arches and clefts which are observed in the embryos of all vertebrate animals, are the "branchial arches and clefts" of Rathke, and the "visceral arches" and "visceral clefts" of Reichert.

The principal modifications of the process of development met with in the classes of Fishes and Amphibia are the following:—

* A different application of these terms, however, has recently been introduced by Rathke, (Müller's Archiv. 1839, p. 361; and Entwickelungs-geschichte der Natter. p. 61.) To the very thin membranous part of the abdominal walls in the embryo of all the vertebrate classes, he gives the name "Membrana reuniens inferior," and to the corresponding part in the dorsal region the name of "Membrana reuniens superior;" whilst he reserves the terms "laminæ abdominales," and "laminæ dorsales," for the thicker parts of the parietes of the abdominal and dorsal regions of the embryo, which, advancing from each side, at length meet above and below in the middle line. When these thicker laminæ have thus united and enclosed the cavities to which they belong, the "membranæ reunientes" have lost their office.

I. The Amphibia occupy the lowest place, since in them the whole germinal membrane enters into the formation of the embryo. When the structures of the axis of the embryo have gradually become developed, the cephalic and the caudal portion project above the level of the rest of the germinal membrane, and the sac which the latter forms depends from the abdominal surface of the embryo. The external layer of this sac is continuous with the central axis of the embryo, and with the inferior part of the head and caudal extremity. From it are produced the parietes of the trunk, which are part of the animal system, and are connected with the structures of the axis. The internal layer of the sac has the form of a globular vesicle, and is not immediately connected with the vertebral column and other parts of the axis. This internal vesicle which contains the yolk is the first state of the intestinal cavity. It subsequently assumes the tubular form, and develops the appendages of the canal, separating at the same time into the different coats of the intestines. Invested externally by the animal layer of the germinal membrane, or the parietes of the trunk, this internal sac gradually assumes more and more the elongated form. Openings appear at the anterior and posterior extremity of the sac, thus elongated, at the points where it comes into relation with the animal system. These openings are the mouth and anus. The embryo of the Amphibia, therefore, passes gradually from the state, represented in figure 173, to that shown in figure 174. Here A and *a* represent re-

Fig. 173.

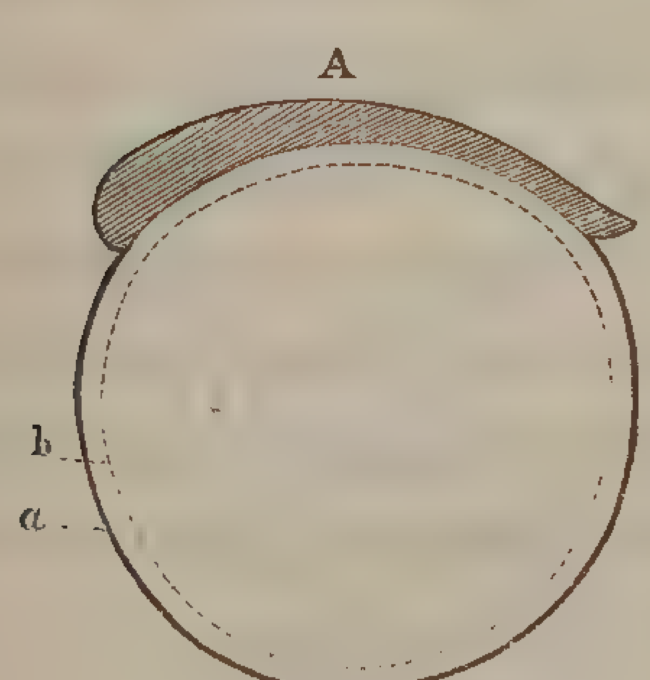
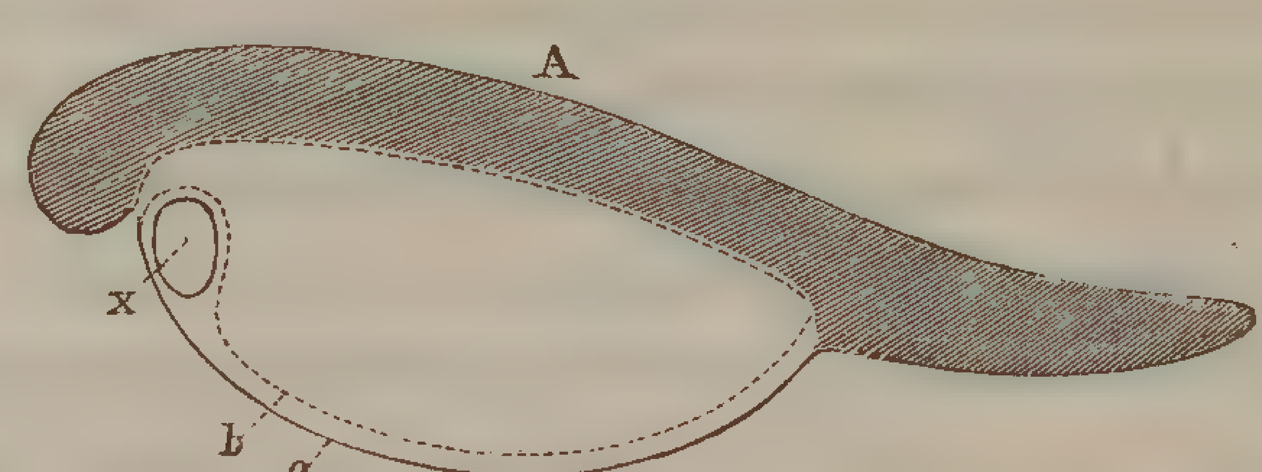


Fig. 174.



spectively the animal part of the embryo, and the animal layer of the germinal membrane; A, the structures of the axis being continuous with the parietes of the trunk or abdominal plates, *a*; *b*, indicates the abdominal part of the embryo, viz. the alimentary cavity or canal; x is the heart.

This seems to be the general plan of development of some of the Amphibia, but not of all. In the Bufo obstetricans, according to my observation,* the abdominal sac consists of an animal portion, and of an organic portion, and the intestinal canal is distinctly developed from the internal organic layer, and has already a convoluted form before the

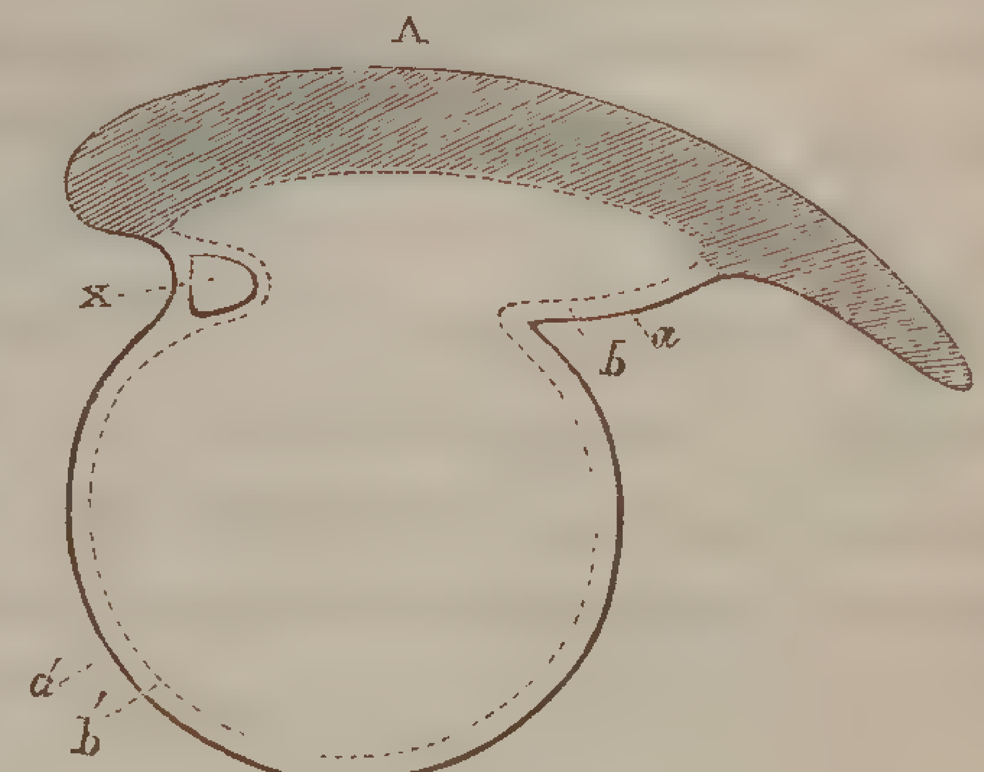
* See the figures in my work on the structure of glands (De Glandularum Penitiori Structurâ. Taf. x. fig. 6—9).

embryo leaves the ovum. (This batrachian has also a complete branchial circulation before its escape from the egg.) In the frog, however, the foregoing scheme of development is by no means applicable. In the ovum of the frog there is no germinal membrane with two distinct layers; but all the structures of the embryo are formed in succession from the yolk. According to Reichert, even when the embryo of the frog has left the ovum, the intestine is still not marked off from the mass of the yolk. The organic system of the body is here not formed until long after the complete development of the animal system.

II. Next in simplicity to the process of development of the Amphibia, we must place that presented by certain fishes. In these the external layer of the germinal membrane becomes entirely converted into the parietes of the trunk, but only part of the internal layer goes to form the intestinal canal; while the other portion is separated by a constriction, and forms a vitellary sac appended to the intestine. The constricted part forms a canal of communication between the cavity of the intestine and that of the sac containing the yolk. This yolk-bag, however, does not hang to the exterior of the body, but is included, together with the intestinal canal, within the parietes of the body, formed from the external layer of the germinal membrane. This "internal yolk-sac" is met with, according to Von Baer's observations, in the Cyprini, and, according to Rathke, in the perch and salmon likewise. In the Cyprinus family, the internal yolk-sac still exists when the young fish escapes from the egg, but has already much diminished in size; and it afterwards gradually disappears entirely. The duct of communication between this internal yolk-sac and the small intestine may be termed the ductus vitello-intestinalis internus.

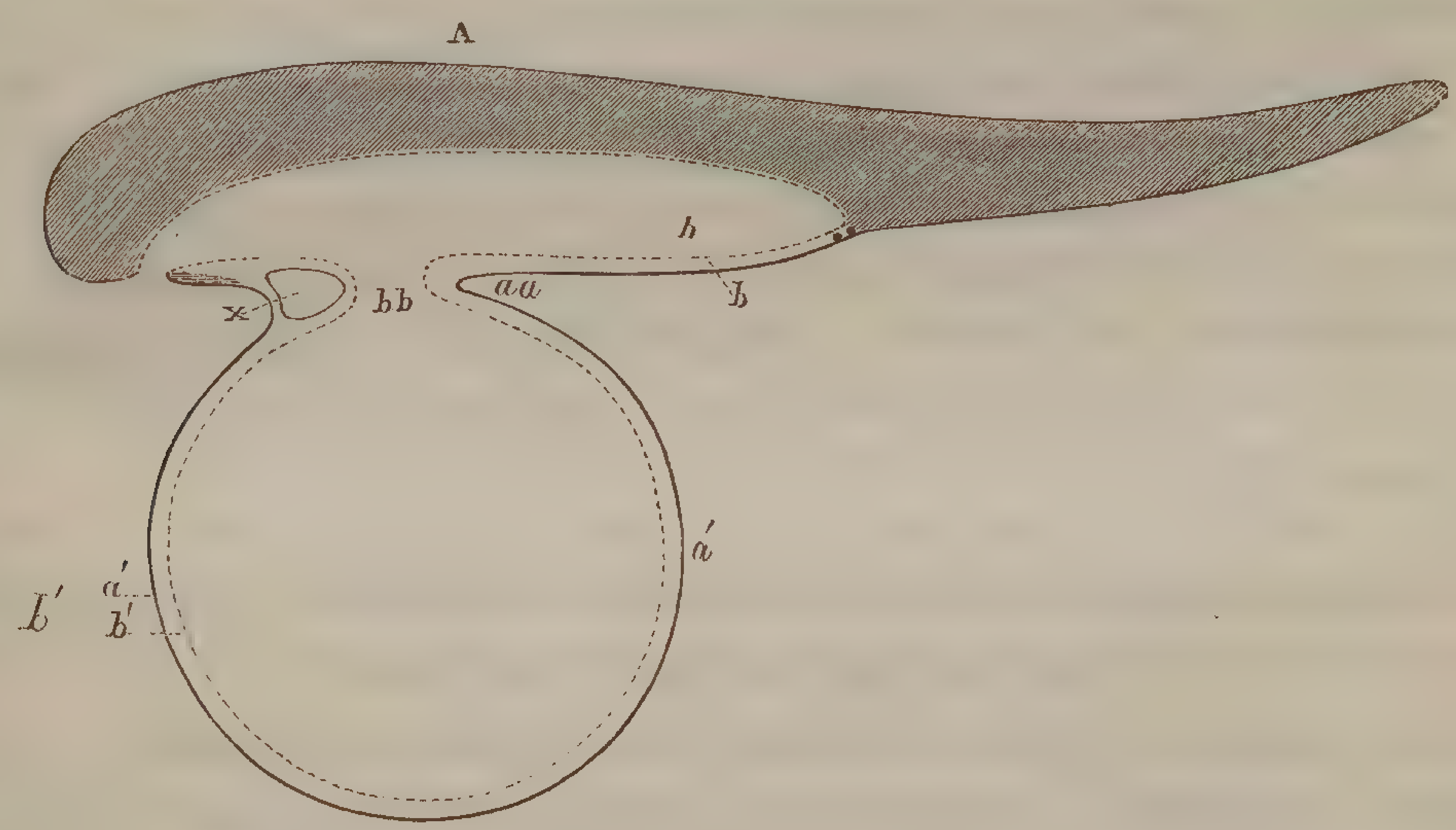
III. A third modification of the process of development is presented to us in those fishes which have an external yolk-sac, lying in front of the abdominal parietes of the embryo, and formed of a part both of the internal layer and of the external layer of the germinal membrane. Thus, in figure 175, A, marks the structures of the axis of the embryo; *a*, the abdominal parietes or plates; *a′*, the part of the external layer of the germinal membrane, which has become separated by a constriction from that part, forming the parietes of the body of the embryo, and which constitutes the external coat of the yolk-sac; *b*, that part of the internal layer of the germinal membrane which is converted into the intestine; *b′*, that part of the same layer which forms the yolk-sac;

Fig. 175.



and x, the situation of the heart between the animal, and the organic layer of the germinal membrane. In this form, therefore, the entire embryo, with the animal and organic parts of its trunk, become separated by a constriction from the remainder of the vesicle or sac formed by the germinal membrane; and as the separation by constriction gradually increases, the sac comes to hang as an appendage to the body of the embryo (see fig. 176). The sac is appended in this case to the most anterior part of the abdominal parietes, close beneath the heart. The external coat of this appended sac (a', in fig. 176) is called the

Fig. 176.



umbilical sac. The part at which it is connected with the particles of the abdomen is the umbilicus, *a a*. The internal layer or coat of the appendage is the proper vitellary sac, b', in which the yolk is contained, and from which the ductus vitello-intestinalis (in this case "externus"), *b b*, extends inwards through the umbilicus to the small intestine of the embryo. The part of the internal layer of the germinal membrane which passes through the umbilicus may be called the umbilicus-intestinalis. Such is the disposition of the parts, according to Rathke's researches, in Blennius viviparus, and Cottus gobio. Upon the yolk-sac are distributed the vasa omphalo-meseraica, which accompany the ductus vitello-intestinalis through the umbilicus. The umbilical sac, with the yolk-sac which it contains, diminishes in size in proportion as the embryo becomes developed, and is at length wholly absorbed.

IV. Another modification of the process occurs in the plagiostomatous fishes, the Sharks and Rays. At a certain period in the progress of their development the umbilical sac appended to their abdomen, generally by a long pedicle, contains a yolk-sac, and omphalo-mesenteric vessels. The duct of this yolk-sac, or ductus vitello-intestinalis, passes through the umbilicus, and unites with the superior extremity of the intestinum valvulare, into which, as Stenonis first observed, the bile likewise is poured. In most of the Sharks and Rays, however, whether they are developed within the uterus or not, there exist at a certain period in addition to this external yolk-sac an internal yolk-sac, which lies within the abdominal cavity.* This is a large cæcal diverticulum of the ductus vitello-intestinalis towards one side, which fills the greater part of the cavity of the abdomen.† When the embryo has attained its maturity, the umbilical sac, with the external yolk-sac which it contains, gradually diminishes in size, and at length disappears entirely by absorption. But in embryos which are fully developed the internal yolk-sac is still found, though its size has undergone diminution. In some of the Shark family the ductus umbilicalis is beset in its entire length with villi; this state was observed by Cuvier in Carcharias,‡ and by Leuckart in Zygœna. According to my observations the internal yolk-sac exists in addition to the external one in all Sharks and Rays, whether oviparous or viviparous, with the exception of those Sharks (the genus Carcharias), in which the external yolk-sac becomes transformed into a placenta fœtalis, and firmly connected with a placenta uterina of the parent fish.§

4. *The process of development exemplified in the formation of the principal organs in the embryo of the frog.*

In the foregoing pages we have given a concise exposition of the principal modifications of the general plan of development, which are met with in fishes and Amphibia. A detailed account of the process of development as it occurs in each of the classes of animals, corresponding to their modifications, would not accord with the object of this work. We must be content with illustrating the process by one example. Reichert's observations on the development of the embryo of the

* This internal yolk-sac had been seen by Aristotle. Speaking of the Sharks, he says, (Hist. Anim. 6. 10,) "In dissecting the fœtus we still find the egg-like mass of nutriment, even when the egg is no longer present." Ἡ δὲ τροφὴ ἀνατεμνομένου, κἂν μηκέτι ἔχῃ τὸ ὠὸν, ὠοειδής.

† This structure is represented by Collins, in his System of Anatomy, 1685. Tab. 33.

‡ Correctly Scoliodon (of Müller and Henle), a subgenus of Carcharias. In the Carcharias with serrate teeth (Prionodon of Müller and Henle), the umbilical duct is devoid of villi, and quite smooth.

§ On the development of the Amphibia consult Rusconi, Développement de la grenouille commune. Milan, 1826, et Amours des Salamandres Aquatiques. Milan, 1821; et Von Baer, in Burdach's Physiologie, Bd. ii. On the development of fishes see Rathke on the Blennius viviparus, in Abhandlungen zur Bildungs-und Entwickelungs-geschicte, ii. Leipz. 1833; Von Baer, Untersuchungen über die Entwickelungsgeschichte der Fische. Leipz. 1835; Rathke, Beiträge zur Geschichte der Thierwelt, iv. (Haifische); Dr. J. Davy, Philos. Transact. 1834, p. 2, (on the Torpedo); and J. Müller, in Bericht über die zur Bekanntmachunggeeigneten Verhandlungen der K. Acad. der Wisseusch. zu Berlin, 1839. Febr.

frog seem peculiarly adapted to furnish this illustration; for the researches of previous writers into the mode of development of fishes and Amphibia, though very valuable, were instituted before Schwann discovered the important part played by the organic cells in the formation of the embryo. Moreover, the process of development presents perhaps more peculiarities in the frog than in any other animal of the classes of fishes and Amphibia,—departs more from the general plan, and is consequently most interesting, as tending to show us what is, and what is not, essential to the process.

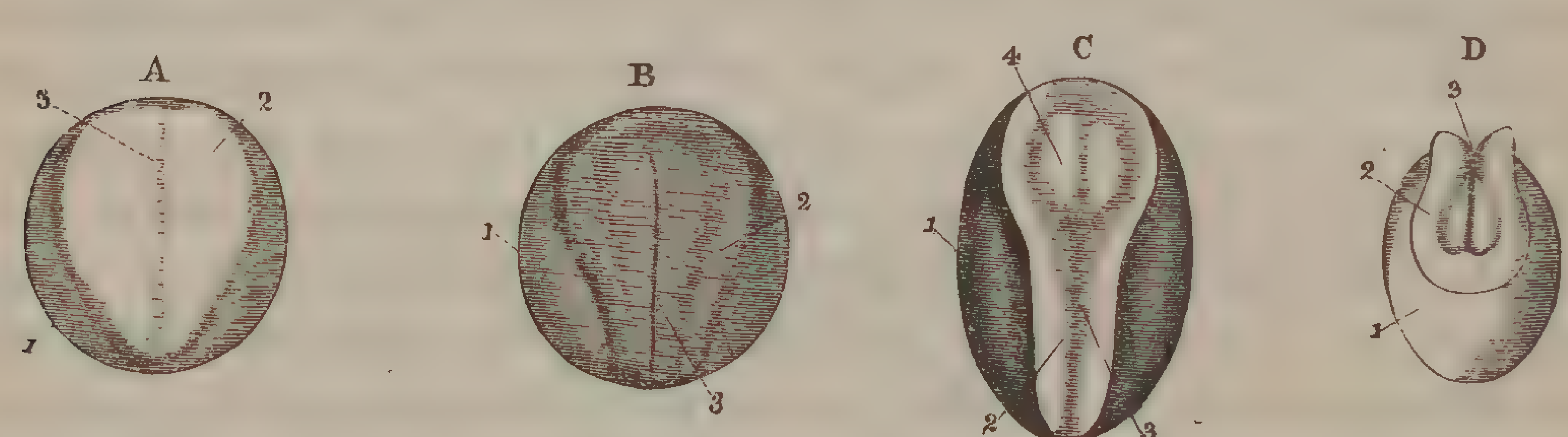
We shall find, however, that even in birds, according to Reichert's observations, the different systems of organs are not developed in such a regular manner, from different lamellæ of the germinal membrane, as has hitherto been supposed.

Reichert remarks in the first place, that "in following the series of metamorphoses presented by the embryo of the frog during its development, the observer must throw aside all preconceived notions derived from the history of the process of development in other animals, and that he must not expect to find a germinal membrane with a serous, a vascular, and a mucous layer, such as are ordinarily described. The first rudiment of the embryo is formed upon the cumulus germinativus described at page 1512, which corresponds to the cumulus germinativus or nucleus of the cicatricula in the hen's egg (see page 1468). The germinal disk from which the germinal membrane is afterwards developed in the ovum of the hen, does not exist in that of the frog. It may be remarked as a general law, that the development of an organ or system of organs in the embryo always takes place by the direct aggregation of those smaller cells of the yolk which are formed at first merely in the cumulus germinativus, but afterwards in the whole periphery of the yolk, so as to constitute its cortical layer. The cells composing the newly-formed structure of the embryo are therefore originally identical with those contained first in the cumulus germinativus, and afterwards in the cortical layer of the yolk. From the organisation of the yolk,—from the circumstance of the smaller cells adapted for the immediate construction of the embryo always existing merely at its surface,—it follows that the mass of the yolk must be gradually consumed in successive strata from without inwards. The first of the structures of the embryo which is developed from the yolk is the central part of the animal nervous system; the last is the mucous membrane of the intestine, the representative of vegetative or organic life.

Membrane investing the yolk during the development of the embryo.—The formation of this membrane is the first act of the process of development. It is produced by the separation of a single layer of cells upon the surface of the cumulus germinativus, from the mass beneath. In consequence of the deposition of a dark pigment in some of the cells composing it, it in the frog very soon appears coloured. This membrane rapidly extends beyond the limits of the cumulus, and has invested the surface of the entire yolk before any trace of the embryo is visible. Its extension is accompanied by the constant development of small cells upon the surface of the yolk, specially destined for its formation. Consequently when this investing membrane is completely formed, the periphery of the yolk has acquired a continuous stratum of those smaller cells which are prepared for the development of the embryo, and which are accumulated in larger number in the cumulus. By the time that this investing membrane is formed, the former vitellary membrane of the ovum has entirely disappeared.

Primary form of the animal system of organs.—As soon as the investing membrane is completed the development of the embryo from the yolk commences by the formation of the rudiments of the animal system. The chorda dorsalis, and on each side of it the rudiments of the central parts of the nervous system, first appear. These parts may be distinguished externally immediately over the cumulus germinativus, where the investing membrane was first formed. A space of nearly oval form is there seen, in which the investing membrane has a paler colour. Through the middle of this space which occupies about a third of the surface of the yolk, and which is rather wider at the end corresponding to the cephalic extremity at the future embryo, a narrow and shallow furrow runs in the longitudinal direction. (See fig. 177, A and B.)

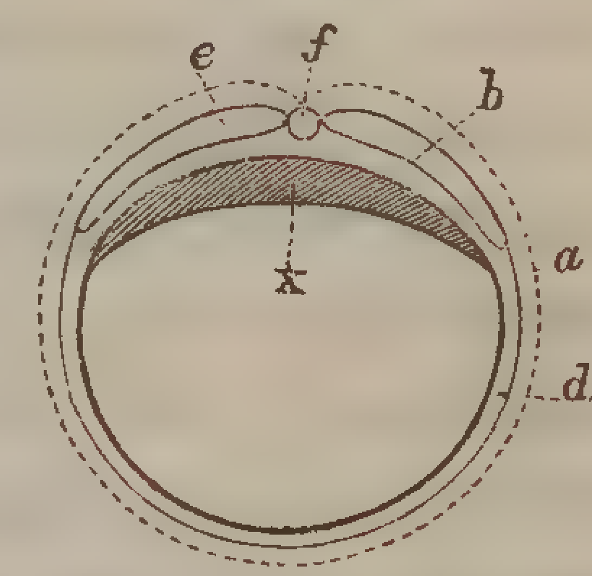
Fig. 177.*



This furrow indicates the course of the chorda dorsalis; and the parts of the surface which lie on each side of it correspond to the rudiments of the central organs of the nervous system. In a transverse section both these structures are seen to be formed of cells newly deposited at the surface of the cumulus germinativus, and in close contact with the "investing membrane." A distinct line of separation or cleft is visible between these rudiments of the embryonic animal system, and the rest of the cumulus germinativus; and this again is now seen to be separated from the central mass of the yolk by an apparent chasm, while at its circumference it still maintains a direct connection with the other yolk-cells.

* [Fig 177 represents the development of the rudimental nervous system in the ovum in the frog; after Reichert. 1, indicates the resisting membrane which has extended over the entire surface of the yolk. 2, the rudimental lateral halves of the nervous centres. 3, the median furrow. 4, part of the nervous centres corresponding to the future brain.]

Fig. 178.



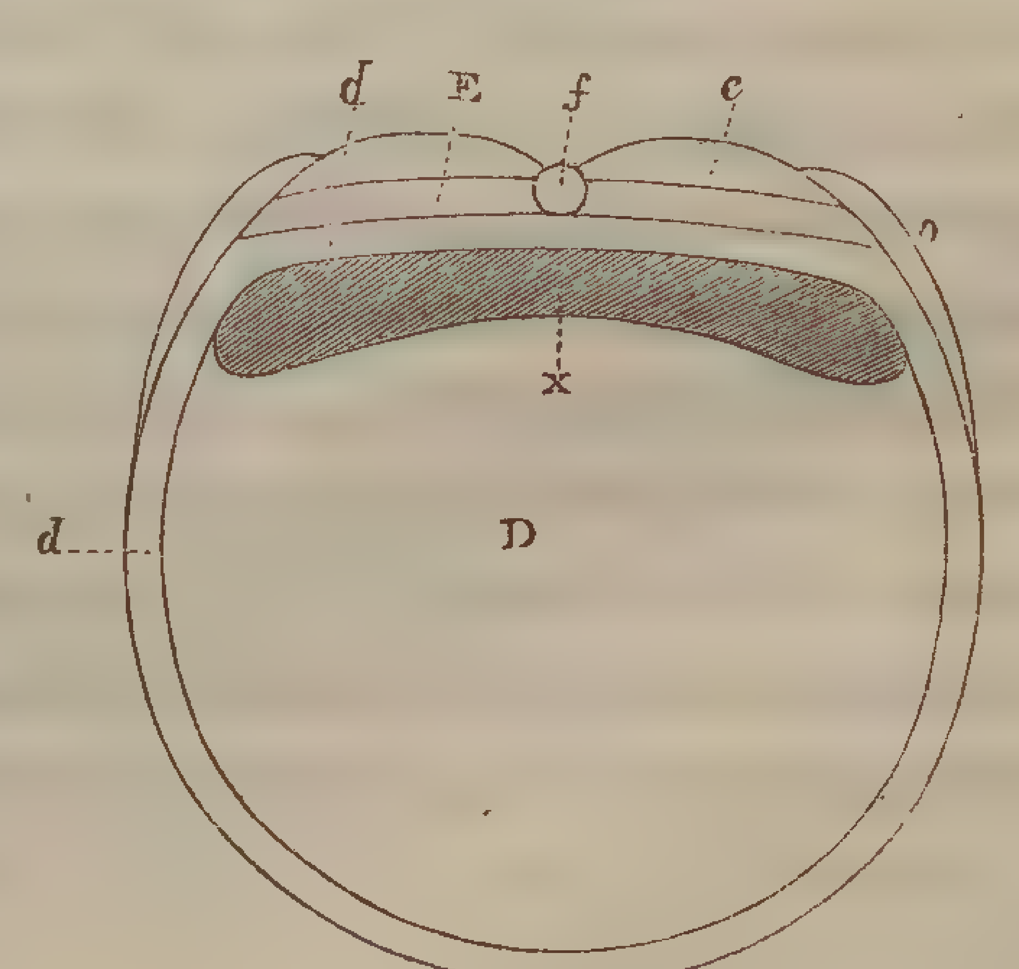
In figure 178, the dotted line *a* represents the investing membrane; *b*, the cumulus germinativus; *d*, the cortical layer of yolk-cells continuous with the cumulus; *e*, the rudiments of the central organs of the nervous system divided transversely; *f*, the chorda dorsalis; and x, the chasm in the yolk beneath the cumulus.

The cells composing these rudimentary structures of the embryo are all identical with the smaller yolk-cells, before described as being developed in preparation for the formation of the embryo. In the "investing membrane," and wherever they are deposited in a form approaching to that of a single membranous layer, they acquire the polyhedric shape.

As development progresses, the lateral halves of the rudimentary nervous centres, increasing in thickness, become drawn towards each other, and towards the median line of the embryo. (See fig. 177, C and D.) They thus form two ridges, one on each side of the chorda dorsalis, which gradually become more and more prominent, and render the median furrow proportionally deeper. These ridges have been erroneously regarded as the rudiments of the vertebral system, and have therefore been called the dorsal plates, while the depression which they bound has been named the dorsal groove. This groove, or furrow, is wider at the cephalic extremity of the embryo than posteriorly; for the lateral halves of the rudimentary nervous system diverge at the part where the brain is to be formed, and after describing an arch on each side, meet again in the middle line. In the dorsal furrow a delicate connecting membrane becomes visible; and soon afterwards, in the cephalic portion, the three main divisions of the brain appear. At each side of the brain, and intimately connected with it, two oval masses of cells are seen, placed one in front of the other. These are the first rudiments of the eye and ear.

Besides the structures here described, another part of the embryo has, at this period, become isolated from the cumulus germinativus, namely, the true vertebral system This, like the rudiments of the nervous centres, consists at first of two membrane-like laminæ of the cumulus, which lie at each side of the chorda dorsalis, beneath the central organs of the nervous system, and so concealed by the latter parts as not to be visible externally, and to be rendered apparent only by a transverse section. There are, as yet, no signs of vertebræ. In figure 179, *b*, is the cumulus; *d*, the cortical layer of the

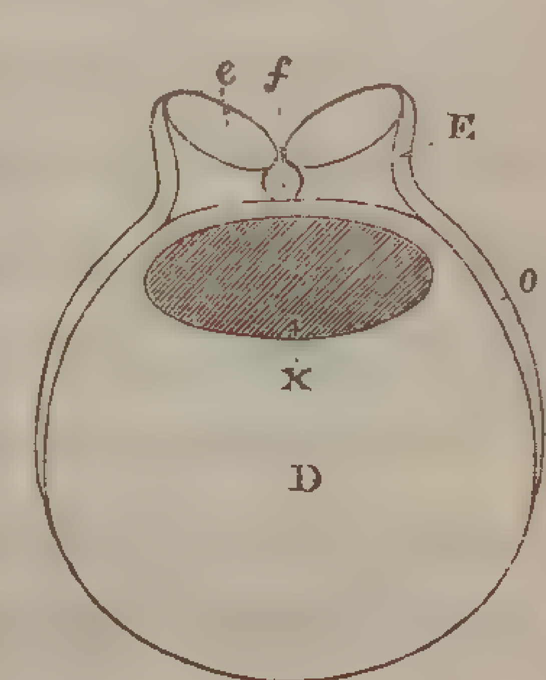
Fig. 179.



yolk; *e*, the nervous centres; *f*, the chorda dorsalis; E, the dorsal or vertebral plates; *x*, the chasm in the yolk beneath the cumulus germinativus; and D, the yolk.

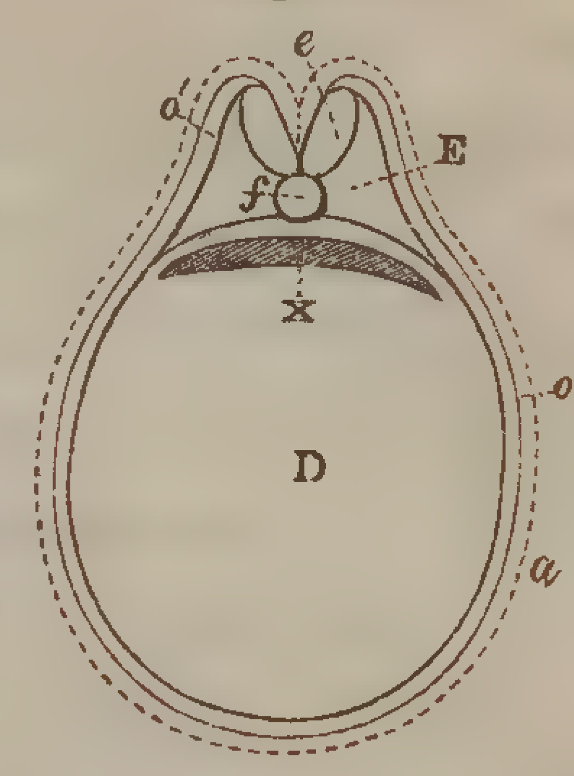
About the same time, also, the development of a system commences, which, after sundry metamorphoses, becomes at length the cutis of the animal. This may be called the cutaneous system, the precursor of the future parietes of the body, since it is of importance in the formation of the animal structures which constitute the parietes of the body of the embryo. This rudimentary cutaneous system lying beneath the "investing membrane" is seen most distinctly at that part where the external border of the rudimentary nervous centres on each side comes into relation with the rest of the yolk. It is indicated in figures 179 and 180 by the letter *o*. When it first appears, it forms a membranous layer of cells, which can be traced for a certain distance upon the external surface of the rudimentary nervous centres, as well as in the contrary direction over a small portion of the yolk; the cells composing it are polyhedral. The development of the cutaneous system commences at the external border of the cumulus germinativus, where this mass of formative cells is continuous with the other cells of the yolk; and it becomes extended inferiorly by the separation of the most superficial layer of cells from the surface of the yolk. Before the cutaneous systems of the two sides can meet, they have to extend by this mode of growth over a great extent of surface.

Fig. 180.



The ovulum gradually assumes a more and more elongated form: at the same time, the lateral halves of the rudimentary nervous centres approach each other more closely, and at length form a crest-like elevation upon the surface of the yolk, which has been regarded as the rudimentary vertebral column. The part of the embryo from which the true vertebral column is afterwards developed, lies beneath this crest. In proportion, however, as the lateral halves of the nervous centres become approximated, the rudimentary vertebral plates, increasing in size, become visible at their outer border. The vertebral plates thus come into relation with the cutaneous system, and, with the protection and aid of this system, proceed to the formation of the two tubes of the vertebral system, by the development of the dorsal and visceral plates. When the formation of these plates has commenced, they extend like two processes on each side from the body of the vertebral plate, one upwards and the other downwards. Soon afterwards the symmetrical segments of the vertebral column, the lateral halves of the vertebræ begin to show themselves in the rudimentary vertebral

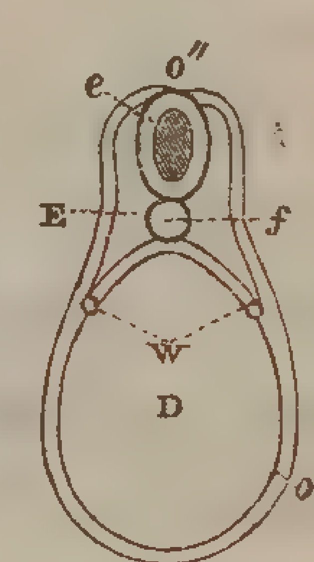
Fig. 181.



plates. In figure 181, the dotted line *a* represents (as in figure 178) the dark investing membrane of the ovum and embryo; *e*, the rudimentary nervous centres; *f*, the chorda dorsalis; E, the rudimentary vertebral plates, with their upward and downward prolongations, the dorsal and visceral laminæ; *o*, the cutaneous system; *x*, the chasm in the yolk beneath the cumulus germinativus; and D, the yolk.

The lateral halves of the rudimentary central nervous system now coalesce by their upper borders; their inferior borders had previously become united. The dorsal groove, with the black investing membrane lining it, is thus converted into a closed canal. At this period, therefore, the central nervous system has the form of a tube, which is wider at the cephalic extremity, where its cavity remains through life as the cerebral ventricles. The walls of this tube are thicker at the sides than above and below, and in its cavity are contained the remains of the portion of the dark investing membrane which lined the dorsal groove. In figure 182, *e* represents the central nervous system enclosing a canal; E, the vertebral system; *f*, the chorda dorsalis; and *o*, *o″*, the cutaneous system. The cutaneous system has extended beneath the investing membrane, over the whole surface of the yolk. Before the dorsal and visceral plates have met from opposite sides, so as to complete the upper and lower tubes, the cutaneous system serves to supply their deficiency; hence the part of the cutaneous system which unites the dorsal plates has received from Rathke the name of membrana reuniens superior; and that part of it by which the visceral plates of opposite sides are connected, the name of membrana reuniens inferior. In figure 182, *o*, is the membrana reuniens inferior; *o″*, the memb. reun. superior.

Fig. 182.



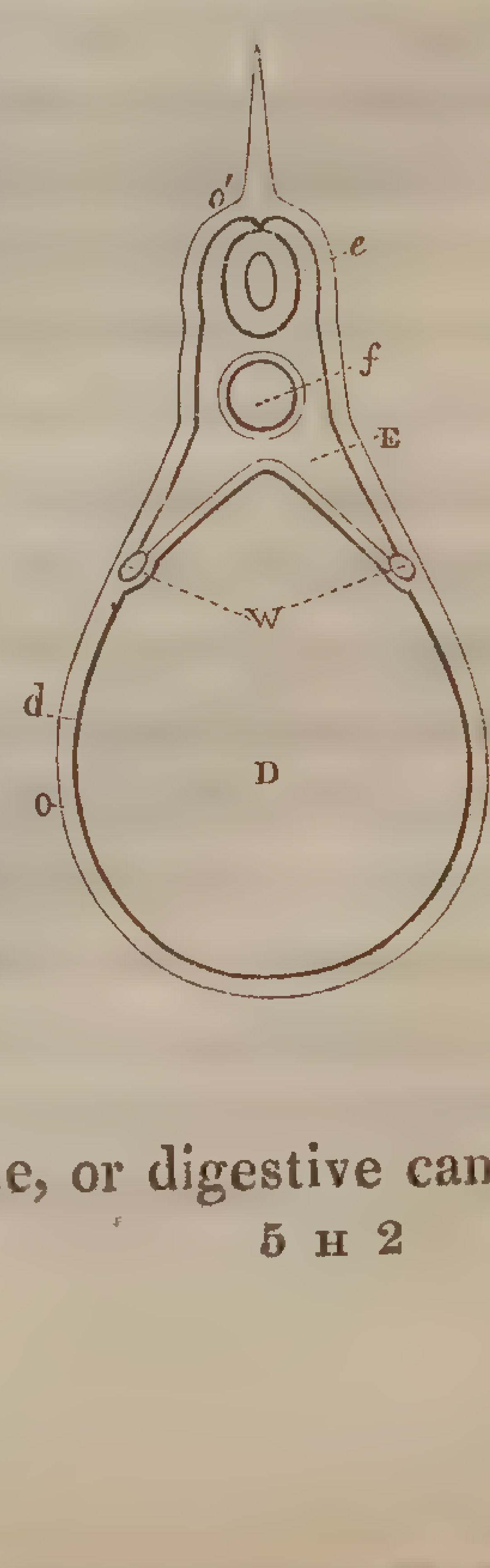
The embryo of the frog leaves the ovum at an earlier period than the fœtus of any other vertebrate animal; namely, as soon as the animal system of organs has been formed, though only in a rudimentary condition. The lateral halves of the rudimentary nervous centres have united, and the superior vertebral tube has become nearly closed in the trunk by the union of the dorsal laminæ, or arches, and the inferior vertebral tube at the head by two visceral laminæ, or arches; while in other parts these tubes are completed by the "connecting membranes." The tail of the tadpole is already distinctly visible. The entire embryo is invested by the cutaneous system, which plays so important a part in the early stages of development, and, externally to this, by the original "investing membrane." As a means of attachment, two suckers have been developed from the cutaneous system upon the first visceral arches.

Nutritive system for the organic life of the embryo. — Sanguiniferous system.—The development of the systems and organs destined for the common nutrition of the aggregated cells composing the embryo, does not commence until the animal system of organs, and thereby the external form of the embryo, are essentially completed. The development of the parts belonging to the animal system was effected by the mere vegetative endowment of the cells, without the aid of a vascular or sanguiniferous system, which is formed in the frog at a remarkably late period. The chasm already mentioned as existing in the yolk, immediately beneath the cumulus germinativus, persists as long as the rudiments of the animal system are being formed. Their development consumes so much of the cumulus, that afterwards only a thin layer of cells remains. The chasm in the yolk now disappears, and the remaining layer of the cells of the cumulus comes into close contact with the central mass of the yolk. The yolk then contained in the trunk of the embryo is entirely surrounded by an uniform, single, cortical layer of cells. In the head, on the contrary, the chasm is increased in size by the retreat of the yolk towards the abdomen, and the cavity of the mouth is thus formed. The single layer of cells which remained from the cumulus germinativus lies at the under surface of the basis of the cranium, and has also extended itself over the inner surface of the two visceral arches of the head. A complete lining membrane of the oral cavity is thus produced. A portion of the main mass of the yolk contained in the abdominal cavity projects more anteriorly than the rest of the mass, and is applied to the formation of the heart. The heart itself is developed from the middle of the lower part of this projecting mass, and the aortic arches at its sides. In their first rudimentary state these organs are solid masses; at a later period they acquire a tubular cavity, in which are seen the blood corpuscules or cells. The blood corpuscules are at this period quite round, and contain each a nucleus with nucleoli, and a granular matter in the cavity of the cell. A special cavity for the heart, distinct from that of the abdomen, and invested internally with a layer of epithelium (the pericardium), is also produced. With the aortic arches there are developed three branchial arches, which lie in the second visceral or, so-called, branchial cleft. From the formative substance of the branchial arches the branchiæ themselves are formed. These branchial arches and branchiæ are, together with the future cutis, produced from that embryonic structure which, in the preceding pages, has been termed the cutaneous system.

While the heart is connected anteriorly with the branchiæ through the medium of the aortic arches, its posterior extremity sends ramifications directly into the anterior part of the mass of yolk contained in the cavity of the abdomen. This part of the yolk is soon afterwards seen to isolate itself from the rest of that substance, and to become an independent body. It is the rudimentary mass from which the liver and pancreas are subsequently formed, but which as yet presents no indication of a division into two organs. The liver and pancreas are thus developed in the frog, from the mass of the yolk, before any trace of a digestive canal is perceptible in the abdominal cavity. The generation of young cells within parent cells is nowhere so distinctly manifest as in this formative mass of the liver and pancreas. The active development of cells which here takes place, is probably connected with the process of sanguification, since the phenomena, of which the area vasculosa of the germinal membrane of other animals is the seat, are not observed in the frog. The same direct aggregation of the yolk-cells contained in the abdominal cavity, which produced the liver and pancreas, also gives rise to the Wolffian bodies. These organs are situated in the place pointed out by Müller, close to the branchial apparatus, and their excretory ducts run along the abdominal cavity to the temporary anal opening formed by the cutaneous system. In figures 182 and 183 the situation of these ducts is shown; their transverse section being indicated by the letter W.

Further progress of the development of the animal system.—The embryo of the frog assumes first a fish-like form. The fin-like appendage and the horny plates in the mouth of the tadpole are developed from the cutaneous system. This system, however, is already reduced to little more than a protecting investment of the vertebral system, or of the animal parietes of the trunk. At the posterior part of the body merely, it still acts as membrana reuniens inferior, and forms the temporary anal opening. The central organ of the nervous system loses more and more the tubular form, in consequence of the thickening of its lateral halves; and the part of the dark investing membrane formerly contained in it disappears. The peripheral nervous system also becomes visible. In figure 183, *e* represents the central organ of the nervous system; *f*, the chorda dorsalis; E, the vertebral system, with its superior and inferior processes, the dorsal and visceral plates; *o*, *o*′, the cutaneous system, *o* being the membrana reuniens inferior; D, the yolk, contained in the simple abdominal cavity, no digestive canal being yet present; and *d*, the cortical layer of the yolk.

Fig. 183.



Digestive canal.—The development of the intestine, or digestive canal, does not commence in the frog until after the animal system is completed, and the sanguiniferous system has received its rudimentary form. In the earliest periods of development the globular matter contained in the formative cells themselves furnished the nutritive material; and afterwards, the liver and pancreas, or the rudimentary mass from which they are produced, conveyed the nutriment into the sanguiniferous system. No digestion was as yet required. The tadpole at this period appears on a superficial view fully formed. It is furnished with external gills and moves with great vivacity, but it takes no food. The intestinal canal, destined for the reception of foreign nutritive substances, is formed in the following manner:—The remaining mass of the yolk occupies now the great posterior division of the visceral cavity of the trunk, extending from the pharynx in front, and completely filling the rest of the cavity, with the exception of the space occupied by the rudiment of the liver and pancreas and the heart. Consequently, it lies in contact with the pharyngeal opening of the mouth, with the margin of the membrane investing the oral cavity, and with the rudimentary mass of the liver and pancreas anteriorly; with the cutaneous system, or the membrana reuniens inferior, posteriorly, inferiorly and laterally; and with the vertebral column, the visceral plates and the Wolffian bodies attached to them superiorly (see fig. 183). The yolk, however, lies quite free, and is not held together by any special membrane. All the cells of the yolk are now found to contain young cells in their cavity, and on the surface of the mass these young cells are set free and prepared for the development of fresh organs. In the frog and water salamander (Triton), and probably in all those lower vertebrate animals, in which successive layers of the yolk are employed in the development of the embryo, the intestine is first formed as a simple tube, destitute of mucous membrane; this membrane being subsequently added, as the last product developed from the yolk.

The membrane of the intestine.—The primitive membrane of the intestine is formed by the most superficial layer of the cells of the yolk on each side becoming separated in a membranous form. The membrane thus produced lies as an inclined roof-like covering over the yolk, and is firmly attached by its superior border along the vertebral column; so that there hang from the vertebral column two membranous laminæ (the parts described by Von Baer in the chick as the intestinal laminæ). Very soon these laminæ meet and unite inferiorly also, and thus include the whole yolk. The embryonic membrana intestinalis now forms a sac of a flattened oval shape in the abdominal cavity. Posteriorly, it communicates with the exterior by the temporary anal orifice in the skin, together with the excretory ducts of the Wolffian bodies. Anteriorly, it extends to the internal or pharyngeal opening of the oral cavity, and there becomes directly continuous with the lining membrane of that cavity.

The latter, consequently, must be regarded as the first-formed cephalic portion of the intestinal membrane. The primary membrane of the intestine is originally constituted of the simple cells of the yolk. Within these, young cells are afterwards developed. When the peculiar form of the intestine in the tadpole is tolerably distinct, the cells composing the intestinal membrane undergo two different kinds of changes: first, they become converted in the abdominal portion of the canal into primitive muscular fasciculi, which run for the most part transversely; and secondly, they are transformed into the glands, the secretion of which effects the digestion of the food. Lastly, a dense vascular net-work becomes developed in the parietes of the canal; and here also the blood-cells contain a finely granular matter, which is sometimes confined to the periphery of the nucleus, and sometimes occupies the entire cell.

The mucous membrane.—When the intestine has acquired the form of a small, spirally-convoluted tube, the remains of the yolk lie within the canal, forming a loose, but tolerably thick crust upon its internal surface, and leaving a small cavity in the middle of the canal. This crust is composed chiefly of the smaller yolk cells; the large cells of the yolk exist in it in very small number. It extends no farther than the abdominal part of the digestive canal. The yolk had retired from the cephalic portion of the cavity at a much earlier period, and the crust of cells is also not found there at the time of which we are speaking. As the intestine increases in length, the crust of cells on its inner surface grows thinner, and the cavity increases in diameter. At length this remaining yolk becomes so extended upon the inner surface of the intestine as to form only a single layer of yolk-cells; and this layer now becomes converted into the structure which must be regarded as the mucous membrane. The cells of this structure soon change their form; they become elongated in the direction of the radius of the cavity of the intestine, and acquire in part a conical, and in part a cylindrical shape, the apices of the cones being directed outwards. A nucleus is distinctly visible in each of these elongated cells; and by degrees they become filled with fat-like globules. This layer of the intestinal parietes is destitute of vessels. The intestine now consists of two tubes,—the tube of the muscular coat and that of the mucous coat, with a layer of glands between them. It is remarkable that this mucous or assimilating coat of the intestine exists only in the abdominal portion of the canal. In its structure it resembles most closely the so called epithelium of the intestine. But the term epithelium is here avoided, since this coat is evidently the assimilating organ of the intestine, no other mucous membrane existing in the intestine of the tadpole. Indeed, the cells of the so-named epithelium in fully-developed animals may have a higher function than that generally ascribed to epithelium; they may be the active elements in the processes of absorption and assimilation.

The mesentery.—At first no mesentery exists. The primary form of the digestive or intestinal sac corresponded to that of the mass of yolk contained in the abdominal cavity, and had a somewhat prominent border attached to the vertebral column. In proportion, however, as the digestive sac becomes elongated, the yolk and the intestinal membrane enclosing it must necessarily be removed from that part; and this is more particularly the case at the middle portion of the intestine which assumes the spirally-convoluted form. The two laminæ of the primary intestinal membrane which are attached along the vertebral column (mesenteric plates), gradually approach, and come into contact with each other to an extent corresponding with the distance to which the intestine is removed from the vertebral column, and then coalesce so as to form a band connecting those parts,—the mesentery. When the development of the different tissues in the primitive intestinal membrane takes place, a non-vascular layer of epithelium separates from the free external surface of that membrane. The same takes place on the surface of all the other structures in the abdominal cavity; and thus is produced the peritoneum. The formative mass between the two epithelium layers of the mesentery serves for the development of vessels, nerves, and the spleen. While, therefore, the non-vascular layers of cells seem to serve merely as a band of attachment, the principal mass of the mesentery represents the essential connexion between the systems of animal and vegetative life. The pericardium surrounding the heart, and the arachnoid, and all the serous sacs met with in other animals, are formed in the same way as the peritoneum.

When the intestinal canal is fully developed, the yolk is completely exhausted, and the tadpole organism of the frog perfect. The external gills have at the same time disappeared, and the internal gills have become developed. All the new parts which are developed during the subsequent metamorphosis of the larva, result from the production of new formative cells at determinate parts of the organism. Thus are formed the extremities of the young frog; the anterior pair of which lie concealed within the branchial cavity. This cavity is formed by the union of the membranous branchial operculum, developed for the protection of the branchiæ, with the anterior part of the body of the tadpole, except at one point, where a small round branchial aperture is left. The anterior extremities are not set free until the branchial apparatus becomes atrophied, and the pulmonary respiration commences. As soon as the vertebral system of the animal is fully developed, the "cutaneous system" retains no other function than that of forming the external investment of the whole animal. The fin-like appendages, the membranæ reunientes, the cutaneous temporary anal orifice, and the horny lamellæ of the mouth, cease to exist. The lungs do not arise from the same embryonic system which produced the branchiæ. The reduction of the cutaneous system to the mere cutis is attended by the atrophy and disappearance of the embryonic "investing membrane," and by the development of the epidermis, which may sometimes be detected beneath the "investing membrane." The development of the lungs commences at an earlier period, when the intestine has assumed merely a sigmoid curvature. They appear at the sides of that canal at the point where it enters the cephalic part of the larva; but they are not developed from the intestinal canal itself. The kidneys are formed about the middle period of larval life. The structure of the intestinal canal of the larva also undergoes great changes, connected with changes in the nature of the food taken. The generative organs are at first wholly wanting; their development commences simultaneously with that of the extremities."

CHAPTER II.

DEVELOPMENT OF BIRDS AND REPTILES.

We have seen that fishes and Amphibia are developed according to one type, from which they do not in any essential respect depart, and are distinguished from all the other vertebrata by the want of the Amnion and Allantois. In the same manner, birds and reptiles (including the serpents, lizards, crocodiles, and turtles and tortoises) agree in the main features of the process by which they are formed from the ovum, and all are furnished with both amnion and allantois. These membranes had been observed by Aristotle* in the embryo of birds. He distinguished a membrane which contained the yolk, a second which surrounded the embryo (the amnion), and a third which surrounded both the others, and also the fluid which existed between them. This third membrane he named the chorion. He recognised vessels also both in the membrane containing the yolk and in the chorion. In birds and reptiles there is no internal vitellary sac, as in some fishes, but the external vitellary sac is at length received through the umbilicus into the abdominal cavity. This fact also had been observed by Aristotle in birds. Moreover, it is peculiar to the animals of which we are now about to consider the development, that the umbilical sac, which in fishes contains the vitellary sac, and is continuous with the parietes of the trunk, is absent; the corresponding lamina surrounding the yolk being absorbed at an early period.†

* Hist. Animal. iv. 3.

† The physiological differences in the process of development between the Amphibia and Reptiles are sufficient to justify the complete separation of these two classes of animals, independently of the essential anatomical characters which distinguish them.—(See J. Müller, Tiedemann's Zeitschrift, iv. 2.)

The process of division and subdivision of the yolk, observed to precede the formation of the embryo in Amphibia and fishes, appears likewise not to take place in reptiles and birds.

The process of development in these classes will now be described more particularly, as it is presented to us in birds; the different stages of the process in this class having been followed most accurately by C. F. Wolff, Pander, and Von Baer.* The general view of the subject will be drawn from the classical works of those observers; but the account of the details of the process, and of the share which the cells of the yolk have in it, will be extracted from Reichert's manuscript statement of his more recent researches.

1. *General view of the process of development in birds.*

Development takes place in the ovum of birds under the influence of a temperature adapted to the life of a delicate warm-blooded animal,—namely, at a temperature varying from 95° to 104° Fahr. During the process of development, an evaporation of water, such as this temperature is calculated to induce, takes place from the surface of the egg; but this evaporation of water is not greater than would occur at the same heat were the egg not impregnated. As a consequence of this loss of its watery part, the white retires from the larger extremity of the egg, and a space is left there which becomes occupied by air entering through the pores of the shell. The air contained in this space has very nearly the same composition as common atmospheric air.

The first change which the "germ" presents in consequence of incubation, is its uniform extension at its margin. While thus enlarging, the "germinal membrane" for a time preserves its original thickness, and its outline remains circular. The influence of the developing germ upon the yolk gives rise to the appearance of several circular streaks — the "halones" — around the germinal membrane. These belong, not to the germinal membrane, but to the yolk itself. The "nucleus cicatriculæ," which lies beneath the centre of the germinal membrane, remains unchanged, and does not enter into any closer connection with that membrane. After the lapse of several hours, the middle portion of the germinal membrane becomes more transparent, and forms the "area pellucida." In this space, which at first has the form of an elongated ellipsis,

* The most important works on this part of the subject of development are: C. Fr. Wolff's Theoria Generationis, Halæ, 1759; and his treatise, Ueber die Bildung des Darmcanals, übersetzt von Meckel, Halle, 1812; Pander's Entwickelungs-geschichte des Hühnchens im Ei, Würzburgh, 1837; Von Baer's additions to Burdach's Physiologie, Bd. ii.; and his Entwickelungs-geschichte der Thiere; Valentin's Entwickelungs-geschichte; and Wagner's Physiologie.

but afterwards becomes more pear-shaped, the embryo appears. In figure 184, *a* indicates the "transparent area" or "area pellucida." All the surrounding portion of the germinal membrane is opaque. The entire germinal membrane is composed of cells, and increases by the formation of new cells. While the germinal membrane, in the direction of its superficies, separates into a central transparent and a peripheral opaque portion or area, it also undergoes a division in the direction of its thickness; for it is soon found to be composed of two layers, which, though not actually separate, yet have a different structure. The superior or external layer, which lies next to the vitelline membrane or proper membrane of the yolk-sac, is called the "serous layer;" the inferior or internal, in contact with the yolk itself, is named the "mucous layer." The structure of these two layers is as follows:—Schwann having folded the germinal membrane of an egg, which had been subjected during eight hours to the heat of incubation, in such a manner that its external surface was outwards, he found the folded margin, which of course was also formed by the external surface of the membrane, to be composed of extremely delicate transparent cells. These cells were of all sizes up to that of the globules which originally composed the germinal membrane before, and for a short time after, the commencement of incubation. They contained a transparent fluid and no nucleus; but in some there were seen a number of very small dark granules (fig. 185, A). In an ovum which had been subjected to sixteen hours' incubation, the mucous layer also was developed. The external surface at this period, according to Schwann, was formed of cells which had a nucleus attached to the inner surface of their wall with one or two nucleoli within the nucleus, and also a clear fluid with a few small granules (see fig. 185, B). These cells, owing to their being so closely pressed together, were polyhedral.* The internal

Fig. 184.

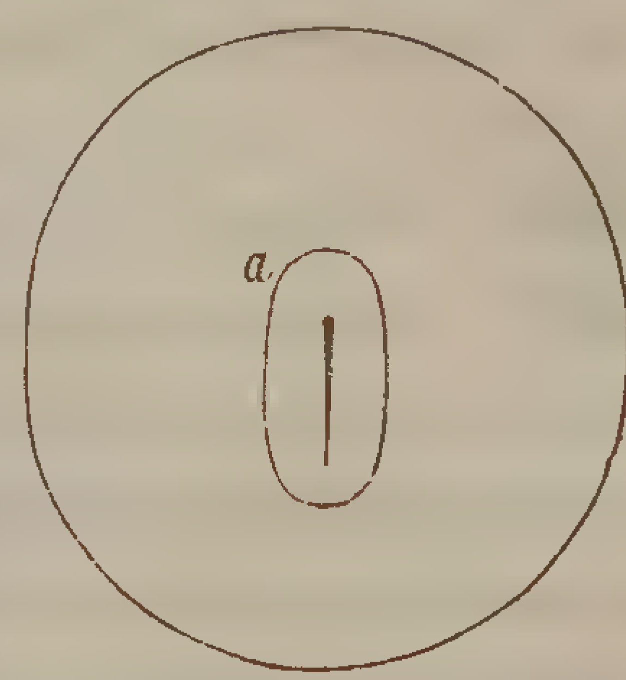


Fig. 185.†

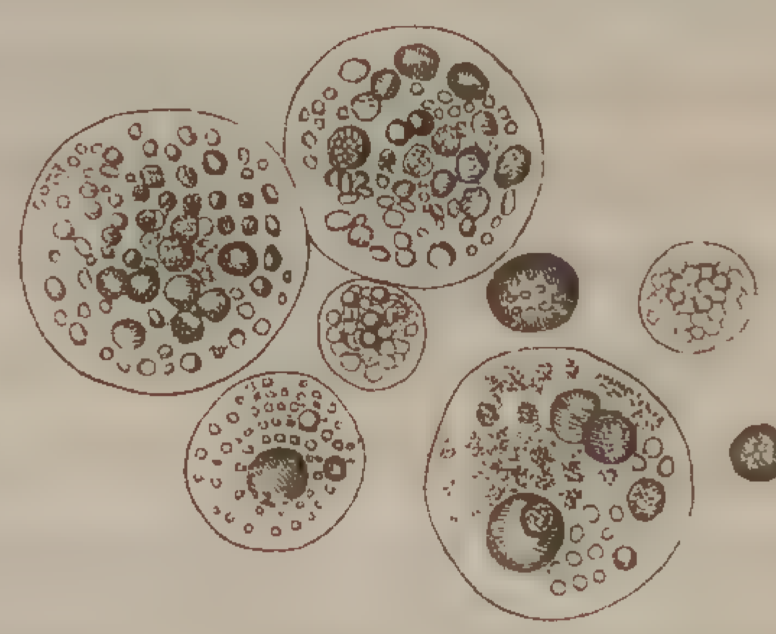
A B

* Compare Valentin's observations, Entwickelungs-geschichte, p. 287.

† [Fig. 185, A, represents a portion of the germinal membrane of an unincubated egg. At the points 1 and 2, the cavity of the cells could be distinguished. B, a portion of the germinal membrane, after sixteen hours' incubation, folded so that the serous layer forms the lower border. After Schwann.]

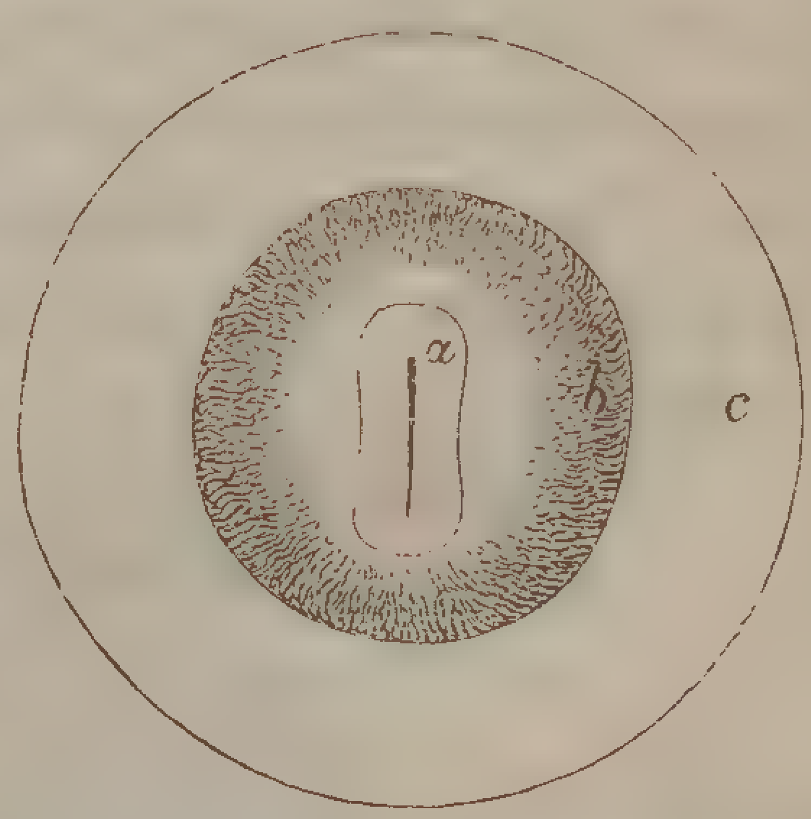
or mucous layer of the germinal membrane was formed, according to Schwann, of large cells which varied very much in size, and contained a transparent fluid and granules of different kinds. In almost every cell there was seen a globule distinguished by its dark circular outline, and sometimes there were several of these globules in one cell (see fig. 186). The cells of the mucous layer lie, not in very close contact with each other, in a structureless intercellular substance, their formative mass or "cytoblastema." This substance contains, besides the cells, a number of dark globules and smaller granules, a part of which are supposed by Schwann to be the nuclei of new cells. Within the area pellucida the cells of the mucous layer have a very different appearance. They are much smaller, and of pretty uniform size, very transparent, and containing, in place of a coarsely granular substance, only some very small globules. In these cells there is no nucleus; but the cells of the serous layer at the same part — the area pellucida — have a nucleus.

Fig. 186.*



The distinction between the area pellucida and the rest of the germinal membrane is not the only thing which presents itself for observation upon the surface of that membrane. Around the area pellucida two other distinct spaces soon become visible. These both have the form of a zone, and the boundary between them is a circle concentric with the margin of the germinal membrane. The space which lies within this circle, (*b*, in fig. 187,) and which is nearest to the transparent area (*a*), is called the "area vasculosa," because within it the blood-vessels form; and the space (*c*), which lies external to the same circle, is called the "area vitellina." This last zone extends itself more and more, and at a later period gradually encloses the whole yolk. The germinal membrane then becomes a closed sac containing the yolk, whilst the former vitelline membrane disappears.

Fig. 187.



The distinction between the area vasculosa and the area vitellina is produced by a change taking place in the substanceof the germinal membrane. A new deposit is formed between the external and internal layer of the membrane. The blood-vessels are first developed in this deposit; and hence it has been named the vascular layer, although it

* [Fig. 186 represents cells of the mucous layer of the germinal membrane, after Schwann.]

cannot be easily isolated as a distinct layer. This third layer of the germinal membrane extends no further than the inner margin of the area vitellina; and hence the distinction which is produced between the area vasculosa and area vitellina,—a distinction which is perceived about the middle of the third day of incubation.

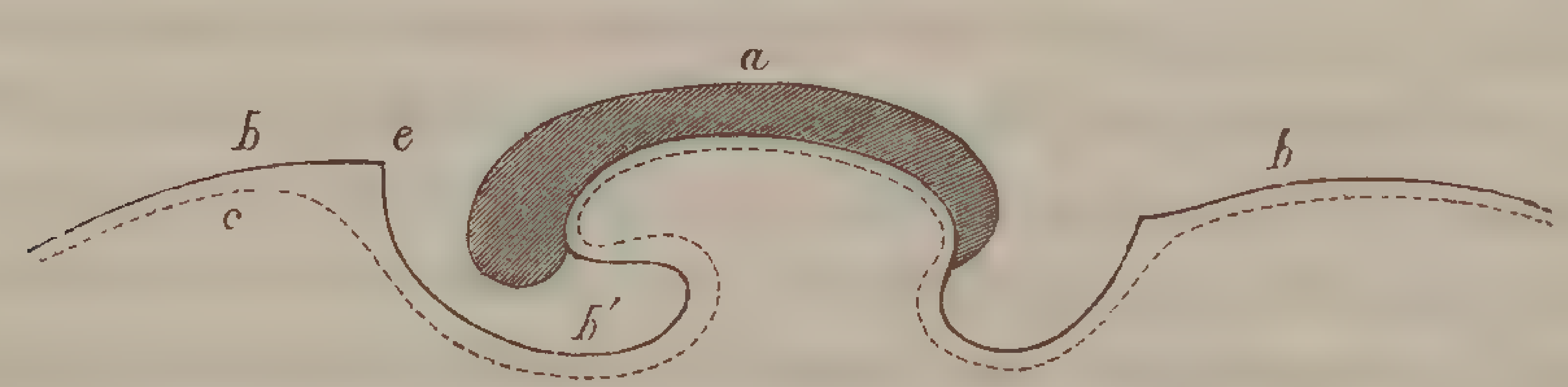
The first trace of the axis of the embryo becomes visible about this period in the form of a white streak, which occupies the middle line of the area pellucida. The long diameter of the transparent area is placed transversely to the axis of the egg, and this "primitive streak" has consequently the same position. The streak is thicker at its anterior or cephalic extremity, and tapers towards the opposite extremity. Von Baer regarded the primitive streak as the precursor of the vertebral column, — as a structure of only temporary persistence. To Reichert, on the contrary, it appeared to be no independent structure, but merely a groove. At the sides of this primitive streak, and parallel with it, two ridges or crests soon appear, — the "laminæ dorsales."

These ridges diverge slightly from one another, both anteriorly and posteriorly. According to the observations of previous embryologists, these parts are destined to embrace the rudimentary brain and spinal cord, by closing over them, and are, in fact, the rudiments of the vertebral column and cranium. But Reichert maintains that they are themselves the lateral halves of the central nervous system. Beneath the spinal cord lies the "chorda dorsalis," a delicate gelatiniform thread, first discovered by Von Baer. This may be regarded as the axis of the bodies of the vertebræ and of the cranium, but it is not itself converted into the bodies of the vertebræ. For the "rudiments of the bodies of the vertebræ" appear as a double row of quadrangular white dense spots, symmetrically arranged at the sides of the chorda dorsalis. (See fig. 191, page 1538.) These rudiments of the vertebræ subsequently become prolonged into the arch and into the body, so that at length the axis of the bodies of the vertebræ, or the chorda dorsalis, in the chick, is found to be embraced from below by these soft structures. At first only a few of these rudimentary vertebræ exist, but they afterwards increase in number. Malpighi observed this development of the vertebræ from two lateral halves.

These rudiments of the axis of the embryo are closely connected on all sides with the external layer of the germinal membrane, and at first lie in the same plane with it. Subsequently the embryo, together with the immediately contiguous part of the germinal membrane, elevates itself above the level of the rest of that membrane in the form of a small boat (see fig. 189), enclosing a cavity open beneath, which is the first condition of the cavity of the trunk of the future animal. By the bending inwards of the germinal membrane anteriorly, posteriorly, and at the sides of the rudimentary embryo, this cavity becomes more and more cut off from the general cavity of the yolk-sac, and acquires inferior and lateral walls. The cephalic end of the embryo, with the anterior part of the body, first bends forwards and downwards, and the germinal membrane follows this depression of the cephalic extremity of the embryo. The fold of the germinal membrane, thus bent inwards, extends from before backwards, until the cephalic part of the embryo no longer forms part of the walls of the cavity of the trunk. (See fig. 188.)

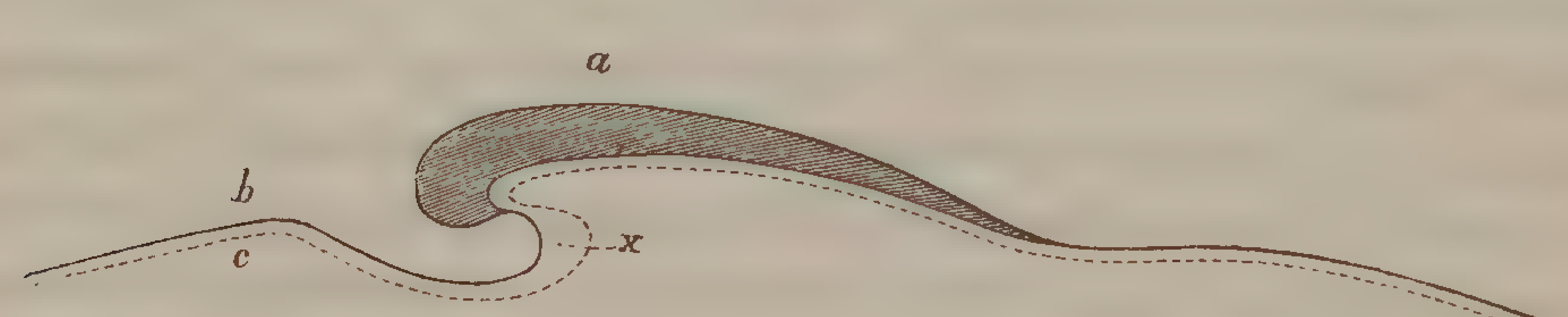
The portion of the germinal membrane thus bent or folded inwards is called the "involucrum capitis." It is to be observed as early as the first day of incubation, and appears first in the form of a transverse fold, which grows deeper and deeper. From the margin of this fold the peripheral part of the germinal membrane extends in its original direction.

Fig. 188.



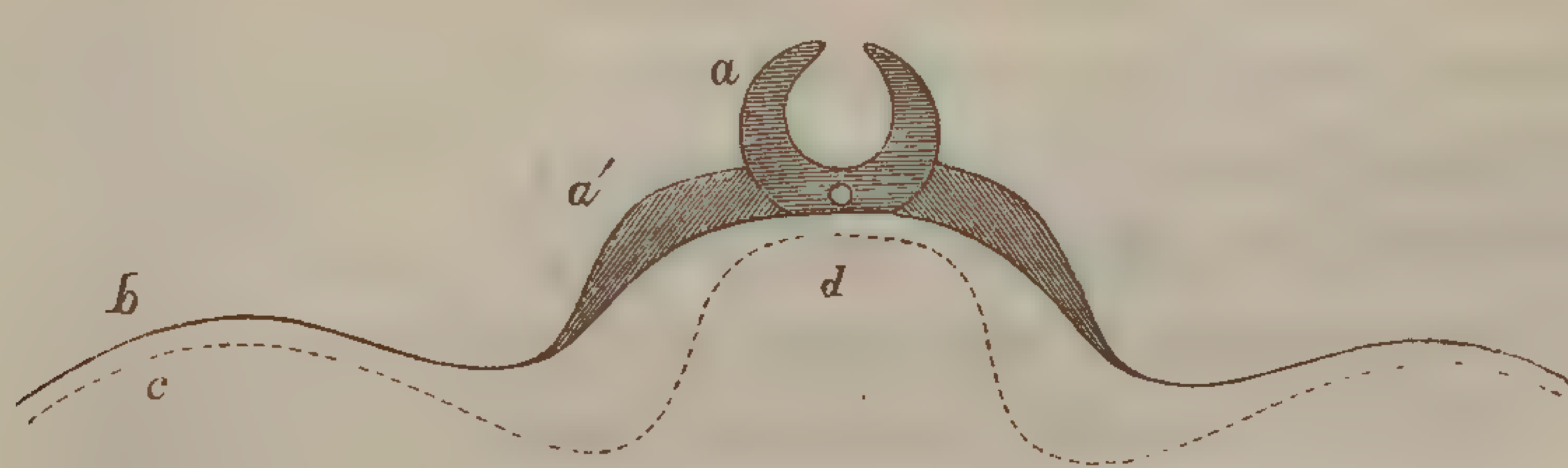
See figure 188, where *a* represents a longitudinal section of the embryo; *b*, the external layer of the germinal membrane, and *c*, the internal layer. During the second day of incubation a similar fold of the germinal membrane is formed at the caudal extremity of the embryo ("vagina caudæ"), and presses from behind forwards beneath it. (See fig. 189.)

Fig. 189.



These two folds are connected by that part of the boat-shaped embryo which passes off from the structures of the axis on each side into the expanded germinal membrane. In this way the embryo becomes in some measure separated by a constriction both anteriorly, posteriorly, and at the sides, from the rest of the germinal membrane, above the surface of which it elevates itself, with the cavity of its trunk, still in great part open, turned towards the yolk. The part of the internal layer of the germinal membrane which lines the cavity of the embryo is the primitive form of the intestinal canal. That part of the external layer of the germinal membrane, on the contrary, which descends on each side from the rudimentary axis of the embryo, and contributes to its boat-like form, is continuous with the rudimentary structures which are destined to form the parietes of the trunk, namely, the walls of the neck, chest, and abdomen. (Rathke's observations, however, have shown that the animal structures forming these parietes of the body are not wholly developed from the external layer of the germinal membrane.) In a transverse section of the embryo at this stage (in fig. 190) the external layer of the germinal membrane is seen to be continuous with those structures which form superiorly the "dorsal laminæ," the future envelope of the spinal cord, and inferiorly the "abdominal or visceral laminæ," destined to enclose the visceral system.

Fig. 190.



In fig. 190, *a* represents the dorsal portion, and *a′* the abdominal portion of the animal parietes of the cavities of the trunk; *b*, the peripheral part of the germinal membrane; *c*, the internal layer of the germinal membrane; and *d*, the organic part of the embryo,—the primitive form of the intestinal or digestive system.

The changes in the middle layer of the germinal membrane within the vascular area have in the mean time laid the foundation for the development of the "vascular system" and "the blood." At the circumference of the vascular area insulated spots and canals make their appearance, and these soon unite so as to form a network filled with a pale yellow transparent fluid. About the same time the "heart" is formed in the same layer of the germinal membrane, and at that part of it which is reflected downwards from the cephalic portion of the embryo, so as to enclose the anterior part of the cavity of the body. (See fig. 188, in which the letter *x* indicates the situation of the heart.) According to Schwann's observations, the blood-vessels are developed originally from nucleated cells. These cells, he states, send out processes; the processes from different cells unite; and in this way ramifications and a network are produced. Vessels extend from this network in the area vasculosa into the area pellucida, and join the rudimentary heart. The heart itself has the form of a long tube, which is prolonged inferiorly into two venous trunks, and superiorly into several "aortic arches" (at least three in number,) on each side. These aortic arches unite beneath the vertebral column, and form the "aorta." (See fig. 191.) The vascular layer now ramifies in the animal, as well as in the organic system of the embryo, and aids essentially in its further development. Some of the vessels or canals forming the network become enlarged into trunks, and when the heart begins to pulsate, a fluid circulates, which is at first colourless. Red "blood corpuscules," however, soon form in the area vasculosa. These corpuscules are at first globular, but at a later period they assume the elliptic form which characterises them in the adult bird. According to the observation of Schultz,† the nuclei appear first, and the red envelope subsequently. The primitive form of the embryonic circulation is as follows. The aorta divides into a right and a left branch, and these are continued as the "arteriæ omphalo-meseraicæ," (*a, a,* fig. 192,) into the germinal membrane, where they ramify and anastomose until they reach a circular venous canal (*s*) which surrounds the area vasculosa. From this venous canal, the "sinus terminalis," and from the vascular network of the germinal membrane, the blood is brought back by the "venæ omphalo-meseraicæ," (*v, v,*) which issue from the area vasculosa at points corresponding to the anterior and posterior extremities of the embryo. Subsequently other veins are developed in the vascular network, which follow the course of the arteries; and at length, when the germinal membrane has enclosed the whole yolk, the terminal sinus entirely disappears, and the whole yolk-sac becomes covered with blood-vessels.

Fig. 191.*

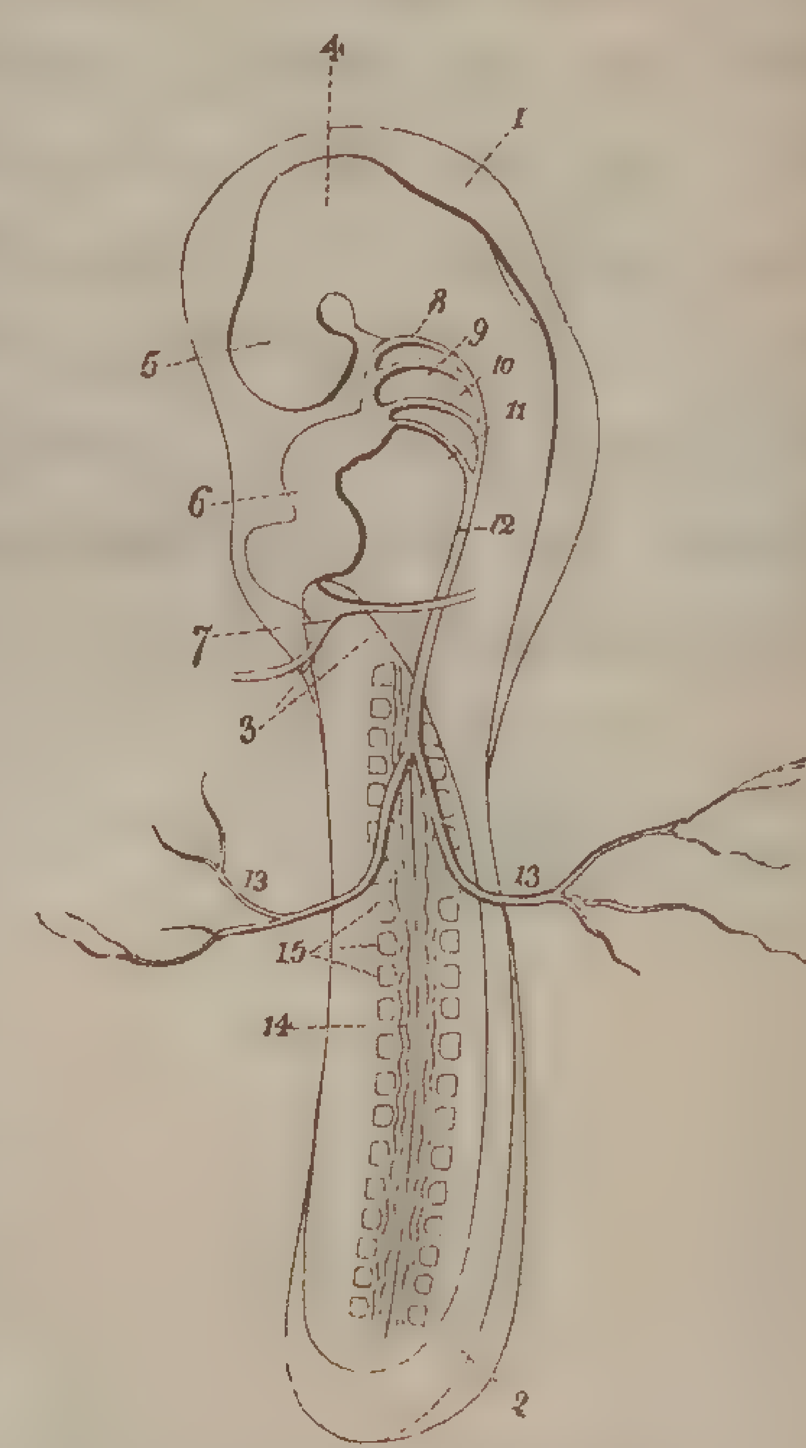
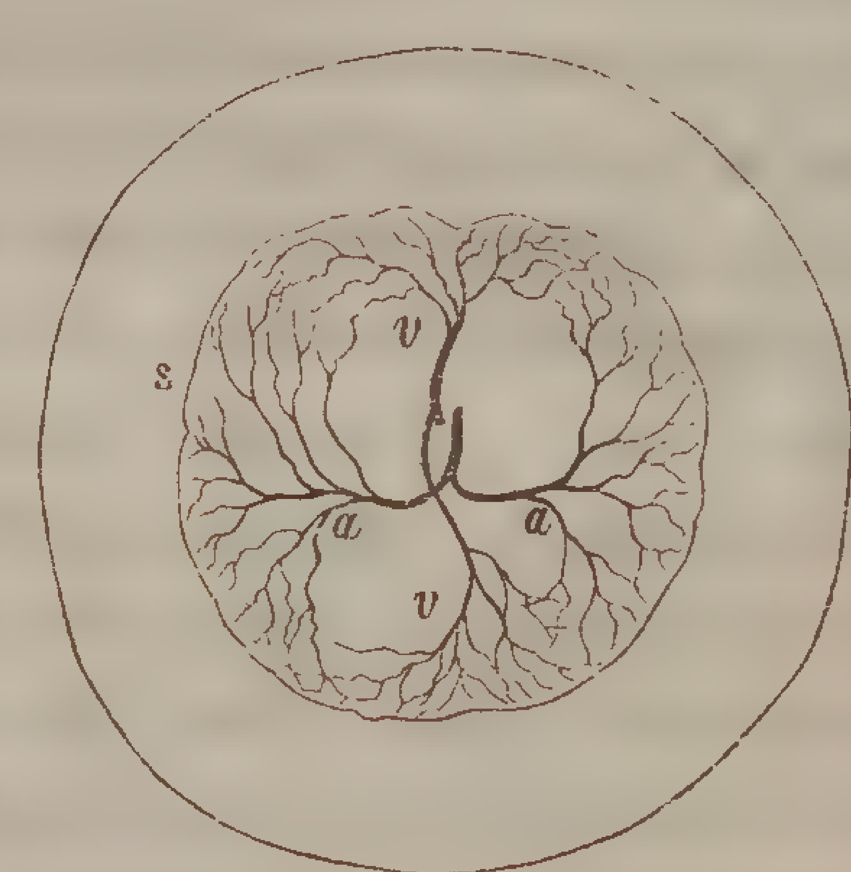


Fig. 192.



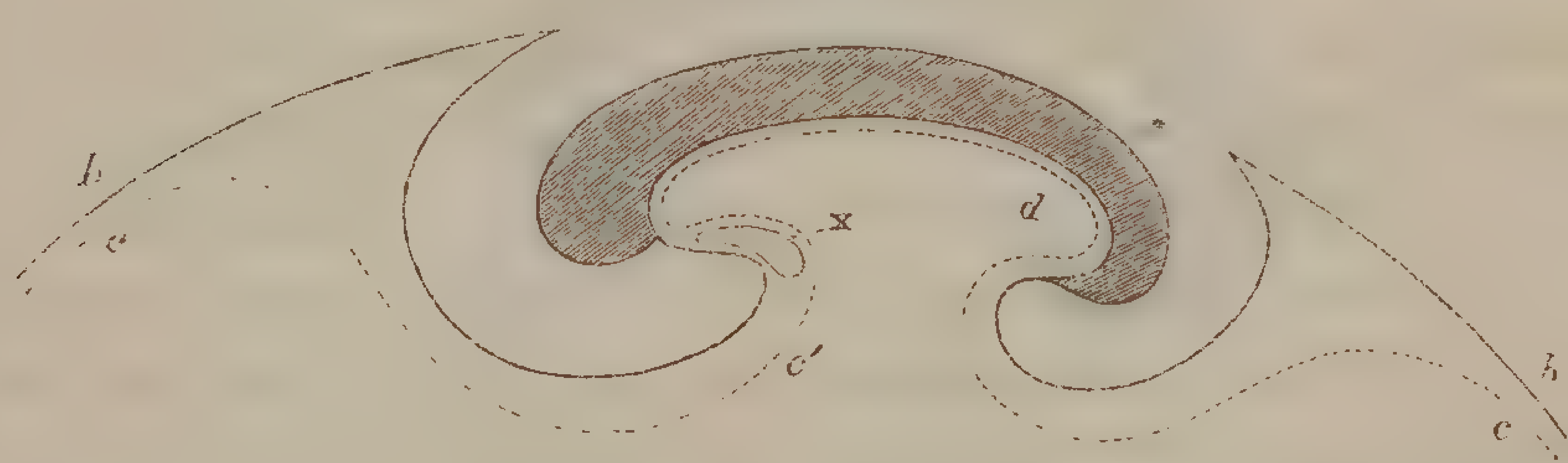
In the course of the third day of incubation the "amnion" is developed. It is formed by the external layer of the germinal membrane, which rises in the form of a fold around the embryo. This fold first becomes visible when the germinal membrance is drawn down to form the body of the

* [Embryo of the chick at the commencement of the third day, as seen from the abdominal aspect, and magnified. After Wagner. Icones Physiol. Tab. iv. 1. The involucrum capitis; 2. the involucrum, or vagina caudæ; 3. passage of the involucrum capitis into the lateral folds of the germinal membrane; 4. prominence of the corpora quadrigemina or optic lobes of the brain; 5. the anterior cerebral mass or hemispheres; 6. the heart; 7. entrance of the great venous trunks in the atrium cordis or auricle; 8, 9, 10, and 11. the four aortic arches; 12. the descending aorta; 13. the arteries of the germinal membrane; 14. the dorsal laminæ, rendered slightly wavy by the action of water; 15. the rudiments of the vertebræ.]

† System der Circulation.

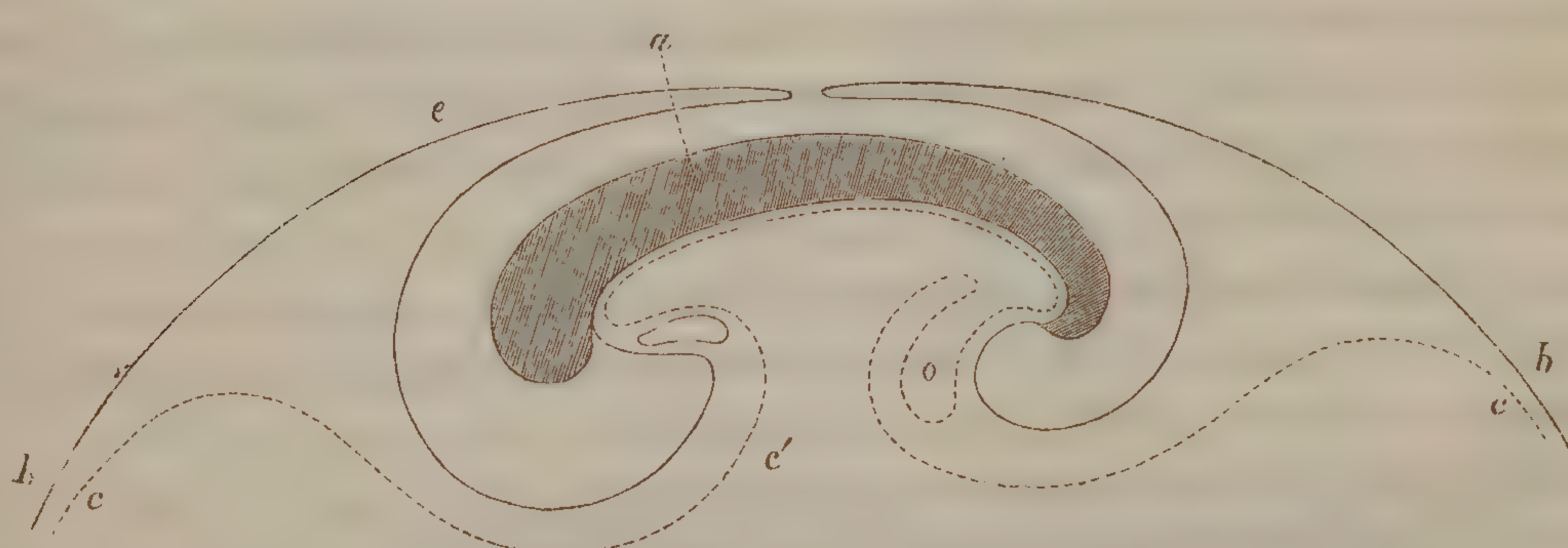
embryo (see fig. 189, page 1536). It forms a sort of hood over the cephalic end of the embryo, and then is reflected back in its original course.

Fig. 193.



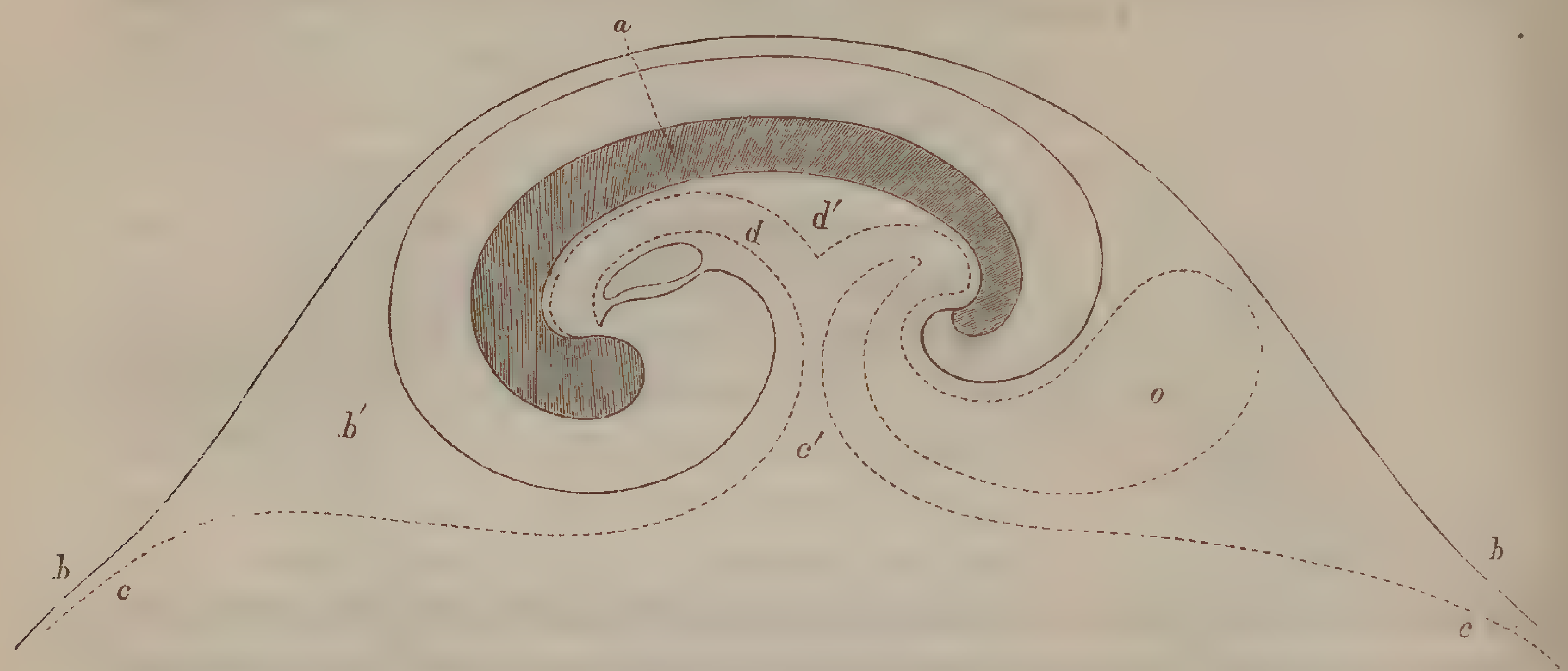
In fig. 193 this fold has increased; *b* and *c* here indicate the outer and inner layers of the germinal membrane; *d*, the cavity of the organic system of the embryo; and *c′*, the point of union of this system with the internal layer of the germinal membrane. From the external layer of the germinal membrane, *b*, a fold, *e*, is seen rising, and separating itself from the inner layer. This fold extends more and more over the cephalic portion of the embryo (see fig. 194, *c*), forming a complete sheath for it.

Fig. 194.



A similar fold rises from the same layer of the germinal membrane at the caudal end of the embryo, over which it extends, so as to form a similar sheath for it. (See figs. 193 and 194.) And a similar fold is formed at each side. These folds are all continuous, and, as they extend over the body of the embryo from its abdominal towards its dorsal aspect, they at length meet there and coalesce. (Fig. 195.) The embryo then lies completely enclosed in a non-vascular shut sac, the amnion, which contains a fluid, the "liquor amnios." The upper or external layer of the fold which produces the amnion is at this part of the ovum separated from the yolk and from the internal layer of the germinal membrane, with which it elsewhere lies in close contact, by the embryo. The true amnion formed by the inner lamella of the fold now constitutes a shut sac, which is continuous with the skin of the embryo at the former line of union of the parietes of its body with the external layer of the ger-

Fig. 195.



minal membrane. The parietes of the body of the embryo are therefore reflected upon themselves, as it were, so as to form the membrane of the amnion. The part at which the reflection takes place is the umbilicus. This at first is wide and long, but it gradually grows smaller. The inner layer of the germinal membrane remains continuous with the intestinal cavity. The constricted part at which the inner layer of the germinal membrane is continued into the wall of the intestinal cavity or tube (fig. 195, *c′*), is now called the vitelline duct, ductus vitello-intestinalis; the inner layer of the germinal membrane having at this period extended over the whole yolk, and become the vitelline sac. The communication between the yolk-sac and the intestines was pointed out by Stenonis; but it had previously been observed by Fabricius in the chick, after its escape from the egg. The vitelline duct passes through the umbilical opening; it is at first wide, but gradually diminishes in size.

The liver, as was first discovered by Rolando, is formed by the protrusion of a part of the primitive walls of the intestine. Von Baer observed the same fact, and their statements are confirmed by my own observations. For although I could not discover the protrusion of the walls of the intestinal tube in the Bufo obstetricans, either because I sought it at the wrong time, or because it does not take place in that animal, yet I saw it distinctly in the chick on the fourth day of incubation.* Valentin also has confirmed the accuracy of Rolando's observation. It is therefore very remarkable that neither the liver nor the lungs, which, according to Rathke, are developed by the same process, appeared to Reichert to be formed by protrusion of the intestinal walls.

Before the close of the third day the allantois also is formed (indicated in figs. 194 and 195 by the letter *o*). It is developed, according to the observations of preceding embryologists, by the protrusion of a

* Müller, De Glandul. struct. penit. Tab. x.

part of the walls of the terminal portion of the intestine. But it appeared to Reichert to be merely connected with the excretory ducts of the corpora Wolffiana, or primordial kidneys,—organs of which we shall treat in a future chapter. The allantois is an elongated vascular sacculus, which protrudes through the umbilicus, and increases in size until it becomes a large vascular sac. The pedicle of this sac is the urachus which passes with the ductus vitello intestinalis through the umbilicus, and is accompanied by the vasa umbilicalia, just as that duct is by the omphalo-mesenteric vessels. The allantois increases to such a size as to envelope the embryo, together with the amnion and yolk-sac. The vascular net-work which covers it serves the purpose of respiration.* The blood-vessels of the embryo will be described in the succeeding section.

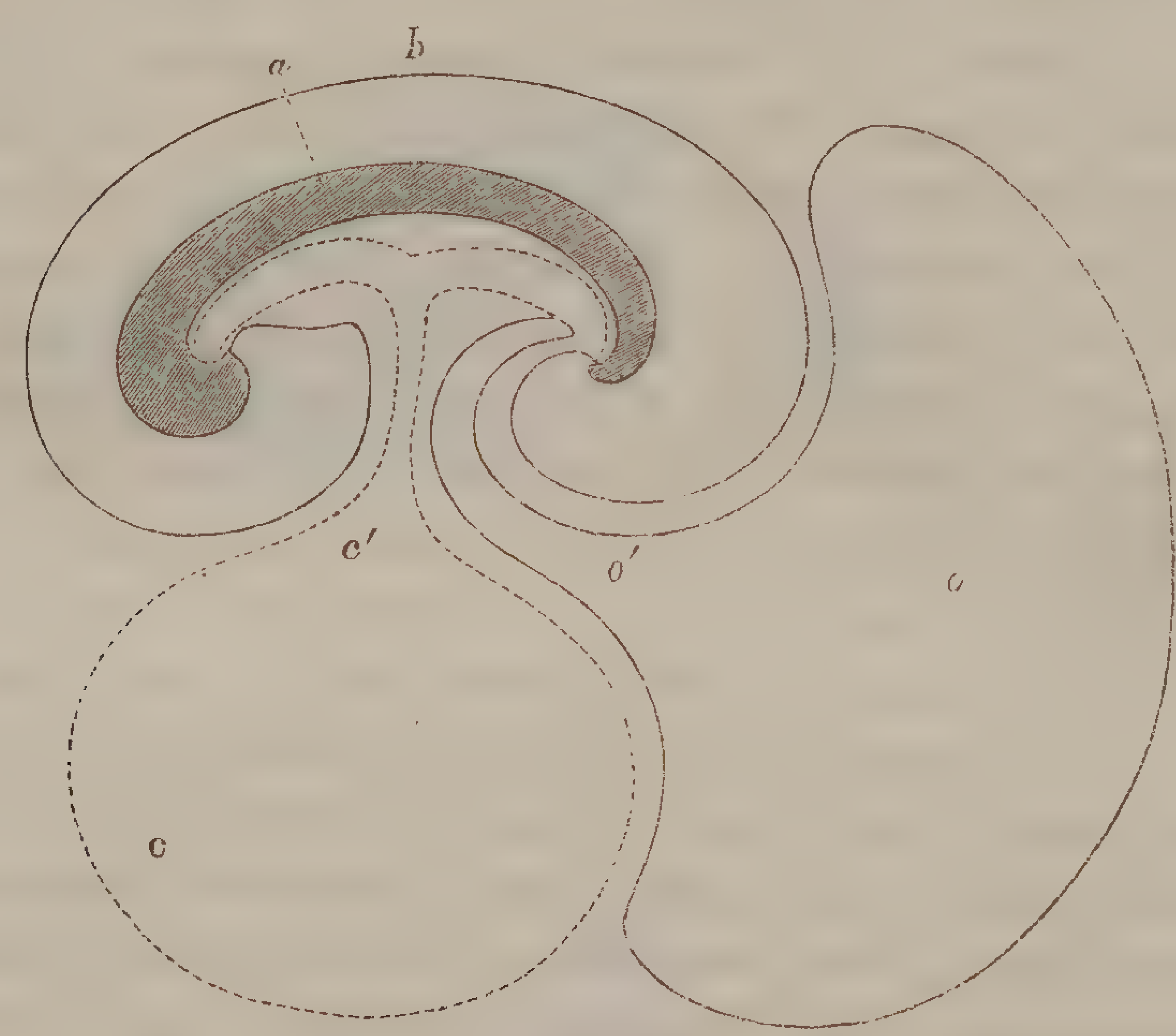
While the development of the embryo proceeds, and the structure and tissues of the different organs are perfected, the vitelline or yolk-sac gradually diminishes in size. At a later period it is received wholly within the abdominal cavity, and there remains connected with the intestine by the vitelline duct, while the umbilicus closes. The yolk-sac is still to be found within the abdominal cavity in birds and reptiles which have escaped from the shell. In fig. 196, *a*, represents the dorsal structures of the embryo; *b*, the amnion; *c*, the yolk-sac; *c′*, the vitelline duct; *o*, the allantois; and *o′*, the urachus.

The development of crocodiles, serpents, lizards, turtles and tortoises, seems to conform to the same general principles as those which regulate the process in birds. They all have a yolk-sac, which is origin-

* [Mr. Dalrymple, who has succeeded in making some very perfect injections of the allantois of the chick, has most kindly furnished the following account of the vessels of that membrane :—

" The allantois of the chick has a double order of vessels, which in some sort divides it into two proper membranes, artificially separable from each other. On the outer surface (that next the memb. testis) the larger arteries and veins ramify and inosculate under repeated angles, while on the inner surface is arranged a uniform layer of minute capillaries, constituting a most beautiful and regular system of pulmonary vessels. When this membrane has been minutely and thoroughly filled by injection, it presents an equally red surface that, viewed under a compound microscope with a half-inch object glass, shows the capillary vessels to be uniform as to size throughout, and so densely arranged, and so repeatedly anastomosing with each other, that the rhomboidal areas between them do not even equal the diameters of the vessels. The regularity of these spaces, both as to size and shape, their close approximation, and the minuteness of the capillaries themselves, indicate the extreme subdivision of the blood-vessels of this membrane, and resemble in a strikingly exact manner the vesicular lungs of the Batrachian and Saurian tribes. The arrangement of the vessels at the bottom of the pulmonary cells of the frog, with the single exception of the larger size of the capillaries, presents so complete a similitude as to justify us in considering the type of the distribution of the vessels of the allantois to be strictly pulmonary, and is a further confirmation of the so much disputed respiratory function of this membrane in the bird.—J. D."]

Fig. 196



ally connected with the intestine; but in serpents, according to the observations of Volkmann and Rathke, this connection ceases to exist at an early period. They have an amnion and an allantois.* All reptiles, however, are characterised by the presence of numerous looped and anastomosing vessels hanging from the inner surface of the membrane of the vitelline sac into the yolk. These are a further development of those convoluted vessels (the vasa lutea), which present themselves on the inner surface of the yolk-sac in the egg of the bird.†

2. *Development of the different systems of organs in the ovum of the bird.*‡

"The cells of the germ disk and those of the yolk-cavity alone contribute directly to the formation of the embryo. The cells of the substance of the yolk, on the contrary, appear at no period to aid directly in the formation of the embryonic structures. The nucleus of the cicatricula, or cumulus germinativus, which is to be regarded as merely the most superficial stratum of the cells of the yolk-cavity accumulated in the canal leading from that cavity to the germinal disk, cannot be entirely isolated from the disk either in a mature unimpregnated egg or in an egg in which development is commencing. When the first rudiments of the

* See Emmert and Hochstetter, über die Entwickelung der Eidechsen. Reid's Archiv. x. p. 84; Tiedemann über das Ei der Schildkröten. Heidelb. 1828; Volkmann, De colubri natricis generatione. Lips. 1834; Rathke, Entwickelungs-geschichte der Natter, Königsberg, 1839.

† [See the description of the yolk-sac and vasa lutea of the chick by Mr. Grainger, at the end of this chapter.]

‡ From Reichert's manuscript communication.

embryo are formed, the nucleus cicatriculæ is set free, and soon entirely disappears.

During the first epoch of the process of development all the structures of the embryo are formed by the direct apposition, in successive strata, first, of the cells composing the germinal disk, and subsequently of the neighbouring cells of the yolk-cavity; the rudimentary structures thus formed being enlarged by the addition of new cells of similar kind. No nutritive material is yet conveyed to these cells in any way. They increase for the purpose of giving the individual structure to the different rudimentary organs, at the expense of the abundant globular matter contained within them. This matter gradually disappears, while numerous young cells appear in some of the embryonic structures.

"*Investing membrane.*"—The first step preparatory to the development of the new organism from the ovum is in the chick, just as in the frog, the formation of an investing membrane, under the protection and by the aid of which the subsequent vital changes attendant on the development of the embryo proceed. This first product is seen upon the surface of the cicatricula or germ of every impregnated egg as soon as it is laid. It has the form of a circular disk, of the same size as the cicatricula itself. It is the first stratum of cells which assumes a distinctly membranous form upon the surface of the cicatricula, but it cannot during the first few hours of incubation be in any way separated artificially as a continuous membrane. Its presence is evinced by the distinctly circumscribed outline which it gives to the germ disk, and is recognised under the microscope by the microscopic cells of which it is composed. This new structure has hitherto been called the serous layer of the germinal membrane; but it has precisely the same functions as the dark "investing membrane" of the frog's ovum (see page 1521). It consists at this period, as Schwann has described it, under the name of the germinal membrane, (see page 1515,) of closely aggregated cells of various sizes, with a dark aspect, and globular contents. At first these cells have no visible membranous wall and no nucleus. The growth of this investing membrane advances constantly; with its centre fixed at the place of development of the embryo, it extends uniformly at its circumference between the yolk and the vitellary membrane. The first extension of the membrane takes place by the expansion of the cells originally composing it, these cells acquiring at the same time greater transparency, and their membranous wall becoming visible. Subsequently the investing membrane grows by the apposition of new cells of the yolk-cavity to its periphery, while a finely globular deposit takes place upon the nucleus of these cells, and renders them similar to the cells of the germinal disk. The "investing membrane" is one of those structures of the embryo which are entirely formed by the aggregation of the cells of the yolk-cavity, without any aid of the vascular system.

Primitive rudiments or foundation of the central nervous system.—The development from the yolk of those structures which belong entirely and peculiarly to the embryo, commences by the formation of the central organs of the nervous system. In the frog, the formation of these organs does not begin until the investing membrane has extended over the entire surface of the yolk; but, in the chick, that membrane has reached only a few lines beyond the circumference of the germ disk or cicatricula, before the commencing development of the structures proper to the embryo is evidenced, by the appearance of a whitish streak which traverses the centre of the circular disk, dividing it into two equal parts, without, however, reaching its circumference at either extremity. This primitive streak is the reflection of a shallow groove resulting from the formation of the lateral halves of the central nervous system on each side of the line which it occupies. Shortly afterwards the chorda dorsalis, distinguished by its white colour, is found running beneath the groove in its whole length; but the lighter colour of the groove is not due to the presence of this chorda dorsalis beneath it, for it disappears when the groove is obliterated by traction on each side, while similar white streaks may be produced by forming artificial grooves or furrows, at any part of the investing membrane. The natural form of the primitive groove may be seen very distinctly in transverse sections of the investing membrane. The rudiment of the central nervous system lies immediately around the primitive groove attached to the under surface of the investing membrane. Just as in the frog, it is formed of a membrane-like stratum of cells, which has separated itself from the germinal mass. When these parts are examined beneath the microscope, the cells of the "investing membrane," which have already become more transparent, and present a distinct membranous wall and sometimes a nucleus, are seen first, and beneath them the newly deposited cells of the rudimentary nervous system, as yet quite filled with globular contents. The primitive lateral halves of the nervous centres in their earliest condition have the form of two membrane-like layers of cells, deposited upon the under surface of the "investing membrane," at each side of the primitive groove, and uniting with one another before and behind, so as to form together an oval surface, which is traversed in the longitudinal direction by the primitive groove.

Membrana intermedia.—So soon as the layer of cells destined to form the rudimentary nervous centres has become isolated from the surface of the germinal disk, the second mass of cells destined to the formation of the structures of the embryo separates from the surface of the germ disk, in the form of a pretty firm, consistent membrane of circular outline, and thicker than the strata of cells which previously separated themselves. This membrane, at first, nearly equals in extent the investing membrane with which its upper or external surface is in close relation at its periphery, while at its centre it lies in contact with the rudimentary nervous centres. It extends beyond the limits of the area pellucida or germinativa. It is often possible to isolate this membrane, except at the point where it is in contact with the chorda dorsalis.

The membrana intermedia is of the greatest importance in the development of the higher vertebrata. Earlier observers have probably regarded it at first as the mucous layer of the germinal membrane, and subsequently as the vascular layer. It lies between the rudimentary nervous centres and the mucous membrane, which is soon afterwards formed. It is the common rudimentary mass from which are developed the vertebral, cutaneous, and sanguineous systems, and the intestinal or digestive system, with the exception of the mucous membrane, and it is the active medium of reaction or communication between the yolk and the rudimentary structures of the embryo which at this period exist, and which are merely the central nervous system and the mucous membrane.

The inferior tube or visceral cavity of the embryo is produced by the following process. Hitherto the central nervous system and the membrana intermedia formed a nearly plain surface, the only interruptions to which were the very slight convexities of the lateral halves of the nervous centres and the groove lying between them. These convexities, however, now increase, forming the parts hitherto designated the dorsal plates, and at length produce the superior vertebral tube, which is developed above the level of the surrounding part of the embryo and ovum. The inferior surface of the embryo, as yet plane, is formed by the membrana intermedia. This membrane now becomes bent downwards and backwards at a short distance in front of the central nervous system, and in a line corresponding to the almost semicircular outline of its cephalic extremity; whilst from the most posterior margin of this inflected part, the membrane again passes forwards and becomes continuous with its peripheral portion. This second returning part of the fold is the involucrum capitis of Von Baer. By this bending inwards of the membrana intermedia the anterior part of the embryo comes to enclose a hood-like cavity, which opens into the yolk-cavity, and which afterwards becomes the visceral cavity of the head and neck, with the structures belonging to those regions. The opening into this hood cavity is not in the place of the anterior orifice of the future digestive canal, but corresponds nearly to the situation where the stomach is afterwards placed. The mouth is developed at a later period, more anteriorly in the closed wall of the hood. The original opening into the hood-like cavity was not unaptly named by Wolff the *fovea cardiaca*.

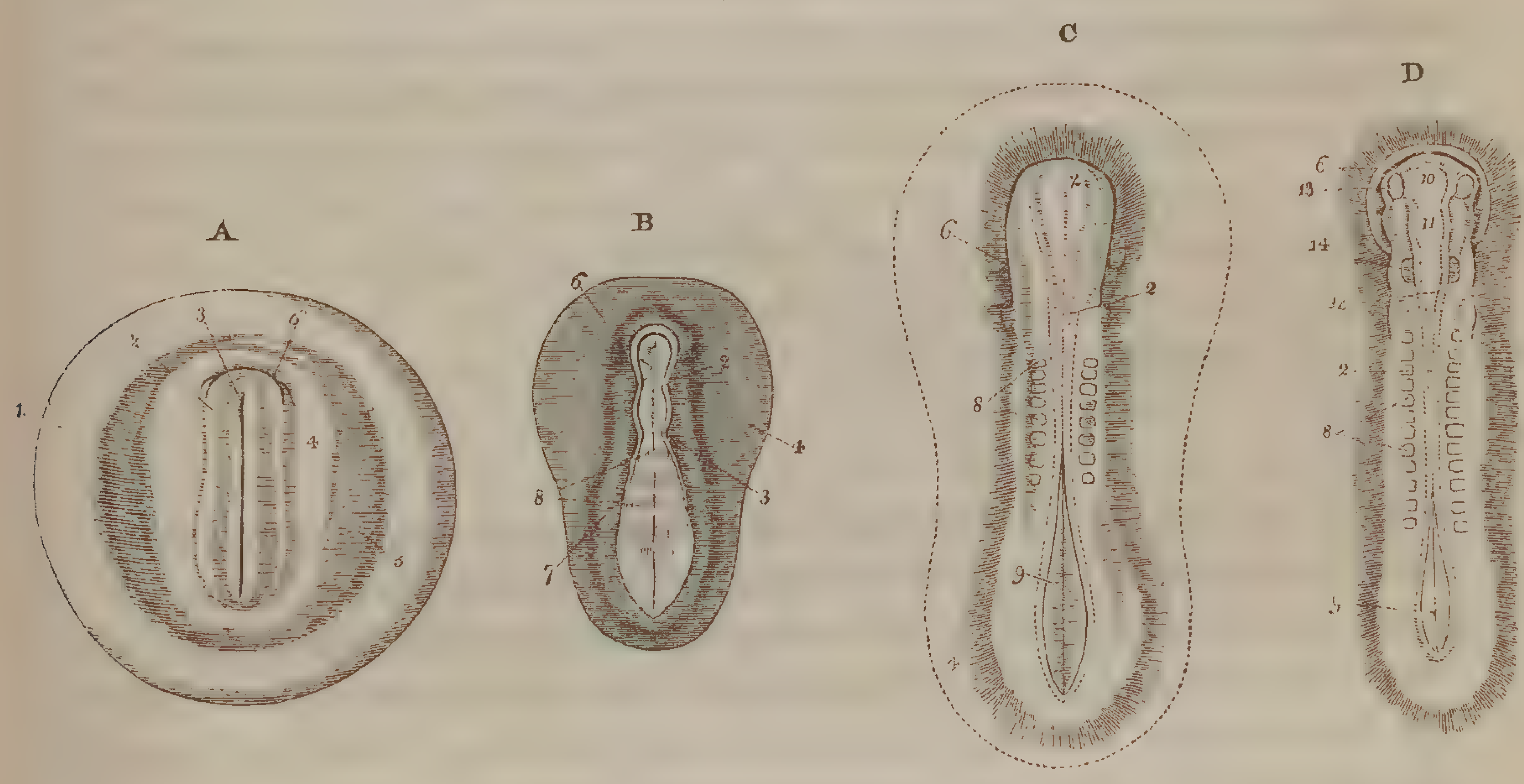
Development of the mucous membrane.—When the cephalic portion of the visceral tube of the embryo is formed, the last membranous layer of cells separates from the germinal disk, and forms the rudiment of the intestinal mucous membrane, at the under surface of the membrana intermedia. The rudiment of the mucous membrane is circular, like the germinal disk, and does not extend quite so far in circumference as the membrana intermedia. The latter membrane, as well as the "investing membrane" beyond it, is covered internally by a layer of the cells of the yolk-cavity which has extended from the circumference of the cumulus germinativus. This layer of cells, of white colour, appears to be directly continuous with the rudimentary mucous membrane; but differs from it both in function and elementary structure. The rudimentary mucous membrane is at this period composed of the same "cells of the yolk-cavity," filled with finely globular contents, which form the other structures of the embryo in their earliest condition. This layer of cells, composing the rudimentary mucous membrane, is not, however, at all points applied closely to the under surface of the membrana intermedia. On the contrary, that part of the membrana intermedia, which encloses the hood-like cephalic portion of the visceral cavity of the embryo, is withdrawn from immediate contact with the mucous membrane. For the latter membrane passes in a plain direction across the posterior opening into the hood. However, when the hood enlarges anteriorly, this septum stretched, as it were, across the opening, does not expand at the same time; but becomes atrophied or absorbed, so that an opening is formed in the mucous membrane, corresponding to the orifice of the cephalic visceral cavity. The part of the visceral cavity, just named, is, therefore, developed, independently of the mucous membrane, and the opening through this membrane forms the future œsophageal orifice of the stomach, where the central organ of assimilation commences.

When the rudiment of the mucous membrane is formed, the proper function of the germinal disk in the process of the development of the embryo ceases. Being a round disk, composed of the accumulated formative cells of the yolk-cavity, it was, up to this period, well fitted to form the membranous rudimentary structures of the embryo, by the separation of successive strata from its surface; but in the further development of the embryo it serves no purpose. It is true, there is seen for some time, beneath the embryo, a whitish mass of cells. This is the nucleus of the cicatricula, or the cumulus germinativus of earlier embryologists, which has become isolated, as it is said, from the rudimentary embryo. This mass of cells, however, consists only of the ordinary cells of the yolk-cavity, which have, for the most part, suffered no great internal changes; and it has no special connection with the embryo itself. It represents merely the cells of the yolk-cavity in the canal leading from that cavity to the germ disk, these cells appearing white, owing to their close aggregation, though in respect of the development of the embryo they have no greater importance than the other cells of the yolk-cavity.

During the development of the different rudimentary structures of the embryo just described, not only is the membranous wall of the cells observed to become manifest at the expense of the globular matter contained within them, but young cells are seen to be developed within parent cells.

The membranous lateral halves of the rudimentary nervous system now manifest a tendency to contract towards the middle line, and to unite, while the future envelopes of the nervous centres, developed from the membrana intermedia, rise simultaneously with them. When the union of the lateral halves of the nervous centres commences, their oval form undergoes a change; for a lateral indentation presents itself about the middle of their length. This is the first indication of the future distinction between the brain and spinal cord. (See fig. 197, A & B.) The process of union of the two lateral halves commences in the chick at the brain, and extends gradually to the spinal cord (fig. 197, B & C). During the contraction of the rudimentary nervous centres towards the median

Fig. 197.*

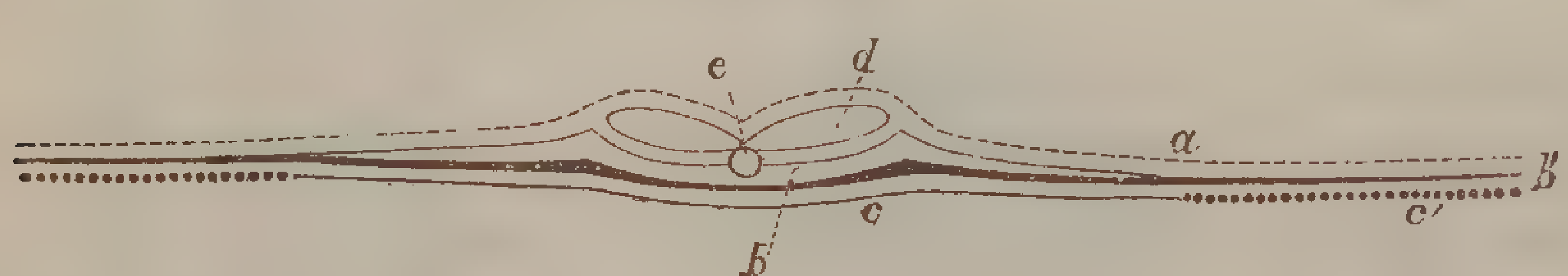


* [Fig. 197 represents the earliest stages in the development of the embryo, and more especially of the rudimentary nervous centres of the embryo of the common fowl. After Reichert. In all the views, 1, indicates the "investing membrane;" 2, the rudimentary nervous centres; 3, the primitive streak or groove; 4, the pear-shaped internal portion of the "membrana intermedia," which corresponds also to the "area pellucida;" 5, the peripheral portion of the membrana intermedia, which corresponds to the "area vasculosa;" 6, the fold which passes backwards and insulates the cephalic portion of the "membrana intermedia" and the head of the embryo; 7, the commencing cutaneous system; 8, the rudiments of the vertebræ, (in fig. B, still covered by the rudimentary nervous centres;) 9, part of the dorsal furrow not yet converted into

line, they increase somewhat in thickness; supported by their rudimentary envelopes which are rising beneath them, they elevate themselves by their outer margins and convert the primitive groove into a furrow, bounded by two ridges. Over this furrow lies the "investing membrane," and beneath are perceived the rudiments of the vertebra. The union of the lateral halves of the nervous centres consists in the coalescence of the outer margins of this furrow, which takes place first at the brain, and which, when completed, converts the central nervous system into a complete tube.

Central and peripheral parts of the membranous rudimentary structures of the embryo.—In the membrana intermedia a central and a peripheral portion are to be distinguished. The central portion has anteriorly formed the cephalic part of the visceral cavity; the peripheral portion continues in its original course beneath the investing membrane. This peripheral portion of the membrana intermedia forms a zone, corresponding to the circuit of the future area vasculosa. Beneath the central portion lies the mucous membrane, the peripheral prolongation of which is the cortical layer of the yolk. Near the embryo this cortical layer of the yolk lies in contact with the under surface of the peripheral portion of the membrana intermedia, but beyond this, at the inner surface of the "investing membrane." In the situation of the embryo itself, therefore, we find four strata arranged in the following order, taking them from without, inwards:—First, the investing membrane indicated in the

Fig. 198.



section, fig. 198, by the letter *a*; next, the central nervous system (*d*); next, the central portion of the membrana intermedia (*b*), with the chorda dorsalis (*e*); and most internally, the mucous membrane (*c*). More externally, in the circumference of the embryo, there are three layers, of which the most external is the investing membrane (*a*); the middle one, the peripheral portion of the membrana inter-

a closed canal by the arching over of the rudimentary lateral halves of the nervous centres; 10, the most anterior division of the brain, the vesicle of the third ventricle; 11, the second division of the brain, the vesicle of the aqueductus Sylvii; 12, the third division of the brain, or vesicle of the fourth ventricle; 13, rudiment of the optic nerve; 14, rudiment of the auditory nerve. In A, the lateral halves of the nervous centres are in their first and simplest condition; in B, their outer margins are becoming elevated; in C, the outer margins of the opposite halves have united in a great extent, converting the former groove into a canal; and in D, the three primary divisions of the brain are visible, and the rudiments of the higher organs of sense, are formed.]

media (b'), and the most internal, the cortical stratum of the yolk (c'), which is continuous with the mucous membrane (c). At a still greater distance from the embryo, and thence over the whole surface of the yolk, that is to say, from the margin of the membrana intermedia, only two layers are to be found, first, the investing membrane (a) and the cortical stratum of the yolk (c'). The cortical layer of the yolk, together with its central part, the rudimentary mucous membrane, constitutes what was termed the mucous layer of the germinal membrane by former embryologists. The cortical layer is composed of cells of the yolk-cavity, both in their simple form and in different states of metamorphosis. The nearer these cells are to the area vasculosa, the more advanced are these metamorphoses of development. Several lines from the area vasculosa there is a circle, in which the cortical layer of cells is distinguished by greater opacity and a whiter colour, and here a part of the cells have developed young cells in their interior. This state exists in a still greater degree beneath the area vasculosa. At the line of transition of the area vasculosa to the area pellucida, the cortical layer of the yolk is more transparent, and the cells composing it contain merely globules. It here is in relation with the cells of the mucous membrane.

Changes of development which take place in the membrana intermedia up to the formation of the sanguineous system.—In all the further stages of development of the embryo, the membrana intermedia plays the most important part. The great differences between the development of the ovum of the frog and that of the bird may in some measure be reconciled, by supposing that here the membrana intermedia takes the place of the vegetative and formative yolk of the former animal. Thus the central portion of the membrana intermedia gradually develops from its surface, (at first by its own vegetative power, and afterwards with the aid of the sanguineous system,) the auxiliary systems of the central organ of animal life, and then the sanguineous system itself, and lastly, after being pushed more and more downwards and inwards, becomes the intestinal system, which forms the support of the central organ of vegetative life, namely, the mucous membrane. The first products of the development of the centre of the membrana intermedia, without the aid of the sanguineous system, are the rudiments of the cutaneous system, and of the vertebral plates, and the formation of the sanguineous system which is essential to the further development of the embryo.

The rudiments of the cutaneous system and of the primitive plates of the vertebral system are formed nearly simultaneously at the period when the lateral halves of the central nervous system begin to contract towards each other for the purpose of uniting, and to elevate themselves from the level of the surrounding surface. The primitive plates of the vertebral system have then separated themselves as membranous laminæ from the membrana intermedia on each side of the chorda dorsalis, and are in their whole extent covered by the rudimentary nervous system, with which they correspond in length and breadth. The existence of the vertebral plates is evinced with the greatest certainty by the appearance of some of the segments of the vertebræ. The rudiments of the cutaneous system appear at each side of the vertebral plates upon the contiguous surface of the central portion of the membrana intermedia. The presence of the cutaneous system is rendered certain by the development of the membrana reuniens superior and inferior, which immediately follows. In proportion as the development of the cutaneous system proceeds, a new formation takes place in the membrana intermedia, corresponding to the growth of the visceral plates (?).

The rudiments of the vertebral and cutaneous systems form first the envelopes for the central nervous system; namely, the laminæ dorsales and the membrana reuniens superior. The walls of the visceral cavity are not produced until a later period, when the viscera themselves are developed. The sanguiniferous or vascular system manifests itself in the area pellucida or germinativa, by the formation first of the tubular part and afterwards of vessels. The situation where the heart is developed is the middle of the posterior margin of that fold, by the inflection of which the cephalic portion of the visceral cavity was formed. The mass of cells which constitute the rudimentary heart was separated from the under and inner surface of the membrana intermedia. The heart itself has the form of a cylinder, from both of whose extremities two branches are given off. The anterior branches lie in the side-walls of the cephalic visceral cavity, and there arch forwards and upwards towards the under surface of the vertebral tube. These are the rudiments of the first aortic arches. The branches given off from the posterior extremity of the tubular heart turn towards the free border of the fold, and then run outwards to the area vasculosa which occupies the peripheral portion of the membrana intermedia. These are the main venous trunks. The vessels as well as the heart are at first composed of free cells loosely aggregated together, and have then no cavity. By degrees their external surface becomes more solid, and the heart which has assumed a sigmoid flexure begins its contractions with a very slow rhythm. The cells lying loose in its cavity are by these contractions expelled into the first aortic arches, whilst new cells enter from the interior of the main venous trunks. The first blood-cells differ in no respect from the delicate cells which compose the different tissues; they are round, and have a nucleus with finely granular aspect and nucleoli. Their cell-cavity contains minute granules.

While the central part of the vascular system with blood-cells is formed in the area germinativa, a development of young cells within parent cells takes place in the peripheral part of the membrana intermedia which occupies the area vasculosa. Before the appearance of the bloody points in the area vasculosa, its peripheral part viewed with a magnifying power of 450 diameters, is seen to be composed merely of delicate cells uniformly disposed and separated by no intercellular substance. When the contractions of the heart commence, the blood-dots soon show themselves, and the peripheral part of the membrana intermedia presents under the microscope an irregular accumulation and distribution of the cells. Between the darker, irregular spots of the membrane, lighter parts are seen, in which the cells are arranged singly side by side, and have acquired an increased thickness of their wall, as if for the purpose of forming a membrane. By the time that vascular canals can be distinguished in the area vasculosa, the brighter parts have acquired a very transparent aspect; nuclei of cells can be distinguished here and there; but the walls of the cells have so completely coalesced, that the outlines of the distinct cells can no longer be distinguished. At the same time the darker and more irregular masses of cells are perceived to have become sanguineous canals filled with blood-cells,—the veins of the area vasculosa. About this period the smallest of the vascular canals always contain several blood-cells arranged side by side. Besides these venous trunks other canals are seen in the area vasculosa, running between the peripheral part of the membrana intermedia and the subjacent cortical stratum of the yolk. The walls of these canals are chiefly formed by the cells of this stratum of the yolk; these are the vitelline arteries. It is probable that the young cells produced within the yolk-cells form the blood-cells or corpuscules. The fully-formed cells of the yolk cavity are, however, four or five times larger than the blood-cells, which certainly are not formed directly from these so-called yolk granules.

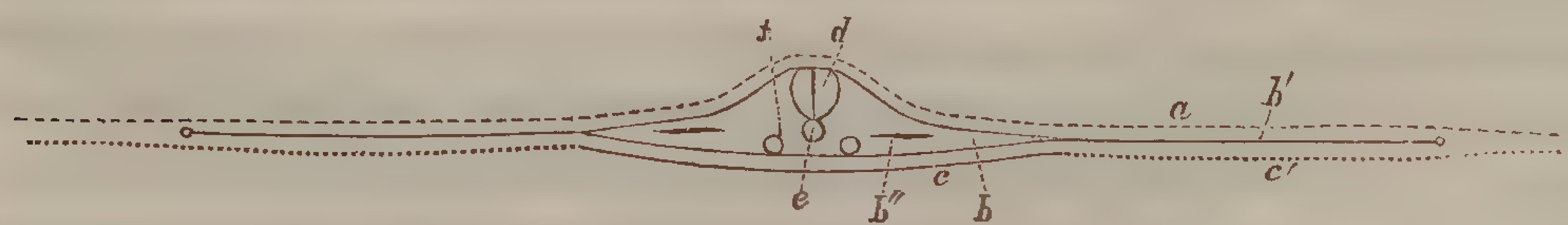
The aorta runs between the primitive laminæ of the vertebral system and the rest of the membrana intermedia, and soon divides into its two main branches. A short distance below the point of division these branches give off the vitelline arteries (arteriæ omphalo-mesentericæ).

The rudimentary mucous membrane receives no blood-vessels. The cells composing it increase in number by the development of young cells; but this process takes place slowly. The globules forming the contents of these cells is gradually converted into a transparent fluid, and young nuclei are formed, which develop small cells, and at length are converted into the cone-shaped cells of the mucous membrane of the perfect animal. After the closing of the superior vertebral tube by the membrana reuniens superior, a tendency to form the membrana reuniens inferior becomes manifest.

Amnion.—The Amnion is a part developed from the membrana reuniens inferior. It appears originally at the border of the involucrum capitis, where the inflected membranes again assume their original direction in their peripheral portion. It is not, however, formed by the rising of a fold of the serous layer of former writers (our "investing membrane"), but by a special lamina (B, fig. 200) separated from the membrana intermedia, which is merely invested by a fold of the "investing membrane." This new lamina rises so as at length to arch over the head of the embryo. In the mean time laminæ destined to form the amnion have separated from the membrana intermedia in the whole circumference of the abdominal portion of the superior vertebral tube. They meet at the posterior extremity and there form the caudal sheath. Thus in the whole circumference of the embryo a lamina derived from the cutaneous system bends upwards, over the back of the embryo, its reflection taking place at that part where it seems to be about to form the boundary of the abdominal cavity. The coalescence of these laminæ above the dorsal region converts the amnion into a closed sac.

Figures 199, 200, and 201, represent transverse perpendicular sections of the embryo. In fig. 199, *a*, indicates the "investing membrane;"

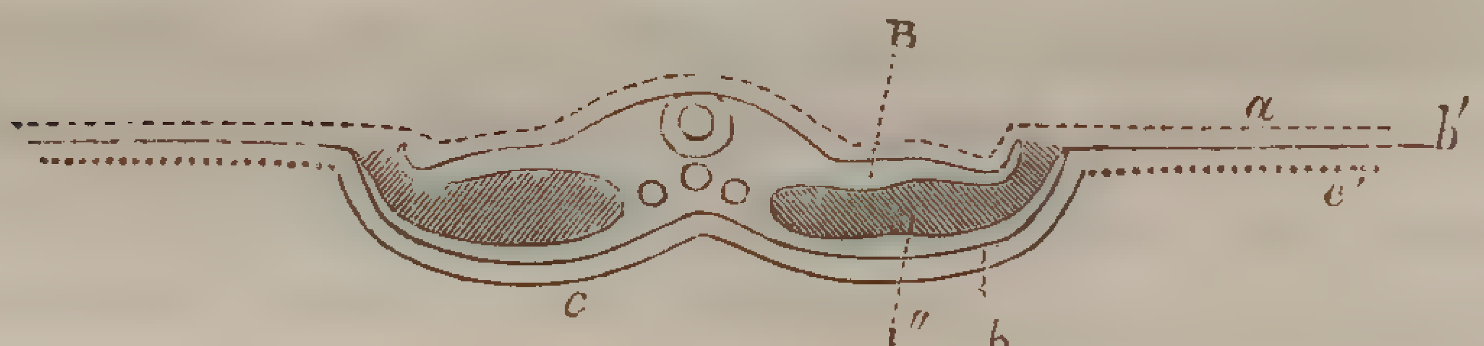
Fig. 199.



b, the membrana intermedia; *b′*, the peripheral part of that membrane; *c*, the mucous membrane; *c′*, its peripheral portion; *d*, the central nervous system; *e*, the chorda dorsalis; *f*, the two branches of the aorta; *b″*, the line showing the commencing separation of the lamellæ of the amnion from the membrana intermedia. In figs. 200 and 201, the separation of

Fig. 200.

Fig. 201.



the laminæ of the amnion is seen to become complete; and B indicates the membrana reuniens inferior, or lamina of the amnion, which in fig. 201 is turning upwards to form the amnion.

While the laminæ of the amnion are extending inwards to coalesce, the "investing membrane" forms a fold about their edge, and when they unite it is divided, just as happens when the two halves of the rudimentary nervous system coalesce by their upper edge (see figs. 202 and 203). The part which remains external to the amnion, and the continuity of which is again restored, forms the so-named serous tunic which retains the essential function of the investing membrane. The part included within the cavity of the amnion is still to be found there for a certain time, but it at length entirely disappears. The detachment of the laminæ of the amnion extends inwards to about the point where the great vascular trunks run between the rudimentary vertebral system, and the rest of the membrana intermedia. Here the connection between the animal system and the other structures not yet developed, but which are represented by the membrana intermedia, is still maintained. (See figs. 200 to 203.)

When the brain has become drawn down in nearly half its extent over the cephalic portion of the visceral cavity or tube, the visceral or abdominal laminæ begin to develop themselves, and to extend downwards from the same part of the rudimentary vertebral system from which the superior dorsal laminæ take their rise. At the cephalic part of the embryo they appear as the visceral processes (the so-named branchial arches), which extend downwards, and gradually unite to form the three visceral arches.

After the development of these arches, and of the three aortic arches connected with them, the brain, with its covering, becomes more and more dilated anteriorly; it is followed by the three visceral arches corresponding to the three cranial vertebræ; and the heart, with the aortic arches, in consequence of the development of the cervical portion of the embryo, appears to retire beneath the shoulders.

In figures 202 and 203, *a*, indicates the "investing membrane;" *b*, the membrana intermedia; *b′*, the peripheral part of that membrane; *c*, the mucous membrane; *c′*, its peripheral portion; *f*, the branches of the

Fig. 202.

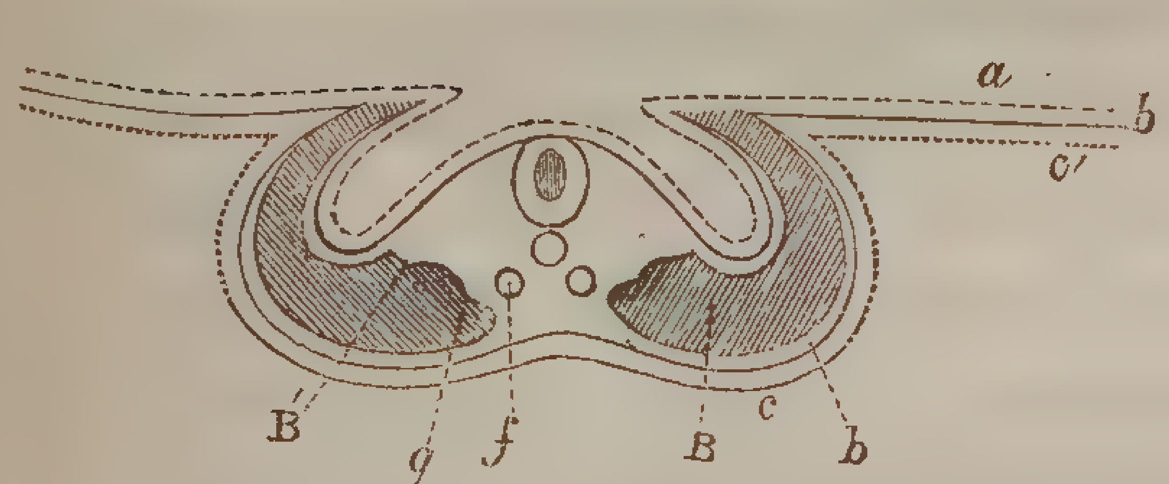
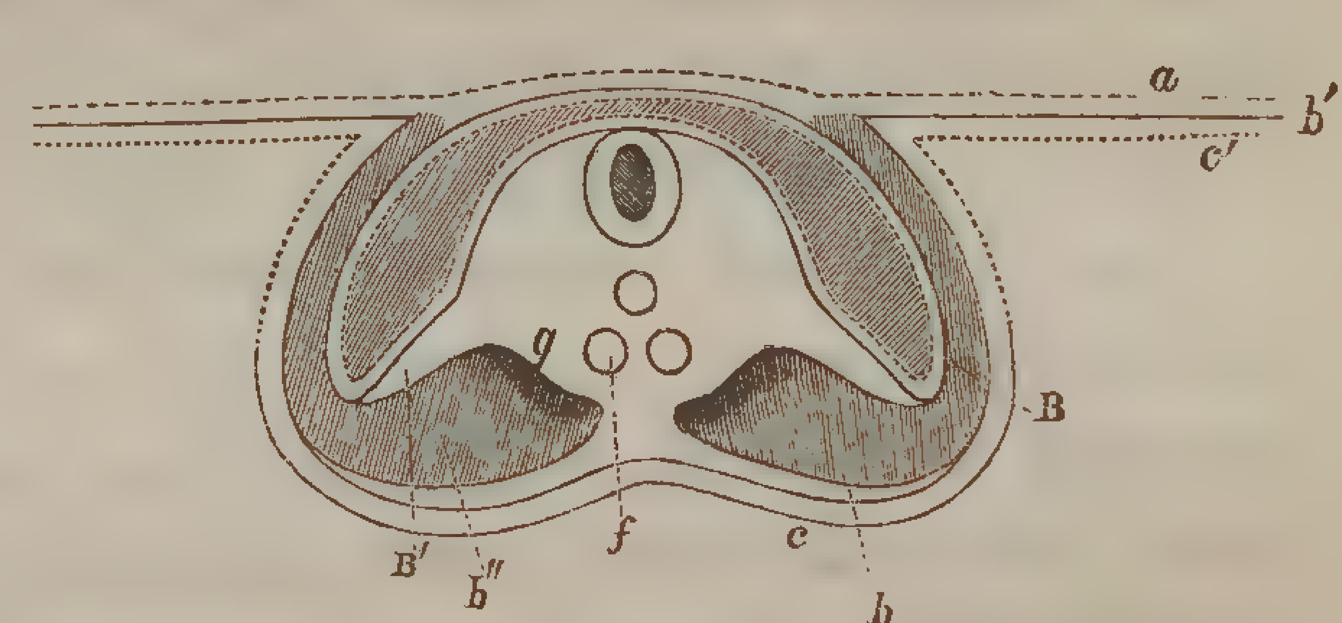


Fig. 203.



aorta; *b″*, the space left by the separation of the laminæ of the amnion from the membrana intermedia; B, the lamina of the amnion; B′, the visceral laminæ projecting downwards from the vertebral system.

The visceral laminæ remain closely applied to the cutaneous system which, as membrana reuniens, is continued into the membrane of the amnion. The appearance of the visceral laminæ is the first step towards the closing of the abdominal cavity, in effecting which the cutaneous system precedes the visceral plates. The basis of the amnion extends inwards so as to embrace all the viscera of the abdomen, which are formed, or are in the process of formation, and in this way produces the umbilicus. Through the medium of this opening, which gradually grows smaller and smaller, the yolk, surrounded by the peripheral portion of the membrana intermedia, communicates with the embryo. In the abdominal region, therefore, the cutaneous system assumes its original function of membrana reuniens inferior, and it is followed by the visceral plates. The heart also becomes more completely enclosed within the cavity of the trunk by the extension backwards of the basis of the vagina capitis. The extremities also make their appearance at the anterior and posterior extremities of the abdominal cavity in the form of elevated ridges on the exterior of the visceral laminæ.

The Wolffian bodies and the allantois.—The Wolffian bodies, or larval kidneys of the embryo, show themselves at the sides of the aorta and its two divisions, extending in their known elongated form from the region of the heart to the caudal extremity of the embryo. Their situation, as seen in a transverse section, is indicated by the letter *g* in the two foregoing figures. Their development causes a still greater narrowing of the connection between the membrana intermedia and the vertebral system: the extent of the connection being now limited to the space between the two corpora Wolffiana. The lateral portions of the membrana intermedia are at the same time pushed downwards, and hang in the form of inclined planes from the middle of the body. (These are the laminæ of the intestinal canal, pointed out in fig. 203 by the letter *b*.) At the period when the rudiments of the corpora Wolffiana are pretty distinctly marked out, the amnion already nearly closed, indications of the extremities visible, but the insulation of the intestinal membrane not yet commenced; then, at the posterior extremity of the Wolffian bodies, and between the visceral plates, which are continuous with each other at this part, and the membrana intermedia, which is now depressed to some distance from them, there appear two prominences, at first separated by the bending downwards of the caudal extremity of the embryo. These prominences are at this time perfectly solid bodies applied closely to the corpora Wolffiana, and at the inner border of the latter organs a delicate streak or thread can be traced down to each of the bodies in question. These threads are the excretory ducts of the Wolffian bodies; and the two solid bodies connected with them are the rudiments of the allantois. The latter bodies gradually approach each other and coalesce, forming a prominent mass, of which the surface is at first flattened. This mass increases in size rapidly, and becomes developed to a closed sac. The further changes which this sac undergoes, and the vascular system belonging to it, are already well known. In consequence of the development of the allantois, the "investing membrane" of the ovum and embryo is removed to a distance from the amnion, and from the peripheral part of the membrana intermedia, which, by degrees, extends so as to embrace the whole yolk. According to these observations, therefore, the allantois is produced neither from the mucous membrane, nor from any part of the intestinal system, which at this period is not at all marked off and formed, but is developed by the growth of cells at the posterior extremity of the corpora Wolffiana.

Rudiment of the liver and pancreas. — The mass from which the liver and pancreas are to be formed first shows itself when the central portion of the membrana intermedia begins to be separated by a constriction from the peripheral portion. This constriction of the membrana intermedia commences anteriorly, where the membrane is connected with the cephalic portion of the visceral cavity, which had become separated from the general cavity of the yolk-sac at an early period. It gives rise to the formation of a cavity, which afterwards is converted into the stomach. This cavity opens posteriorly into the yolk-sac; it is formed by the central portion of the membrana intermedia. Above it runs the aorta, and beneath it lies the posterior extremity of the heart. Also, inferiorly, but yet at the surface of the membrana intermedia, close to the place where the vitelline veins enter the heart, there appear two elevations,—at first of equal size,—the lobes of the liver; and besides these, also, the formative mass for the pancreas. These rudimentary masses have no kind of communication with the cavity of the central portion of the membrana intermedia, but are merely cellular growths from the surface of that membrane, from which they may be removed without its cavity being implicated. While the mass of the rudimentary liver and pancreas increases, and gains a connection with the main trunk of the vitelline veins, the membrana intermedia has gradually separated itself from that mass, and now proceeds to the last act of its formative power,—namely, to the development of the intestinal system. The original connection of the membrana intermedia with the rudimentary liver and pancreas ceases at an early period, and the development of those organs proceeds independently. In the liver the production of new cells is very active, and is the cause of its growth. But even at a later period, when the growth of the organ is only proportionate to that of other parts, this production of new cells continues, and in all parts of the organ cells are met with, which contain nuclei and young cells in all stages of development, just as in the frog. May not these young cells serve to increase the mass of the blood-cells?

At the same time with the liver, the lungs also appear in a rudimentary form. They are at first flask-shaped masses of cells, lying one on each side of the cavity already described as being formed within the central portion of the membrana intermedia, and above the liver near the vertebral column. They may be traced forwards to that part where the cephalic division of the visceral cavity ceases, and they are there lost in the formative substance. From the situation of these rudimentary lungs close to the free surface of the membrana intermedia in the abdominal cavity, they almost appear as if they had been developed from that membrane; but the real source whence they are produced is the posterior part of the cephalic division of the visceral tube.

Intestinal system.—We make a distinction between the mucous membrane, the central organ of vegetative life, and the system of membranes connected therewith. By intestinal system we here would designate the latter structures. In the earliest period of the development of the embryo, the cephalic division of the intestinal system was withdrawn from the influence of the mucous membrane by the folding in of that part of the membrana intermedia, and its separation from the general yolk-cavity by a constriction. The cephalic portion of the visceral system thus became placed under the exclusive influence of the animal system. The cavity of the cephalic portion of the visceral tube becomes the mouth, pharynx, and œsophagus, and into it the respiratory apparatus opens as an appended structure.

In the shallow groove which the visceral laminæ at first bound in the abdominal region, lies the central part of the membrana intermedia, continued anteriorly into the cephalic portion. Between it and the visceral laminæ on each side run the Wolffian bodies. The lateral halves of the membrana intermedia increase in thickness, and show a tendency to coalesce. Their union commences anteriorly, then takes place at the posterior part, and lastly at the intervening part. Previously the central portion of the membrana intermedia formed, together with the peripheral portion, merely a part of the general periphery of the yolk-ball; but when the process of development which we are describing commences, the centre of the membrana intermedia raises itself above the mass of the yolk in the form of a roof of two inclined planes. These planes meeting at an angle beneath the vertebral column of the embryo they are connected with it through the medium of the aorta and its two main branches. The lateral portions of the centre of the membrana intermedia gradually bend inwards at their lower margin, so as to convert the angular space or groove between them into a canal, which in the middle communicates by a wide opening with the yolk-cavity. By degrees the opening becomes narrowed, and at length is reduced to a very small passage, while the cavity of the canal (the intestine) grows larger.

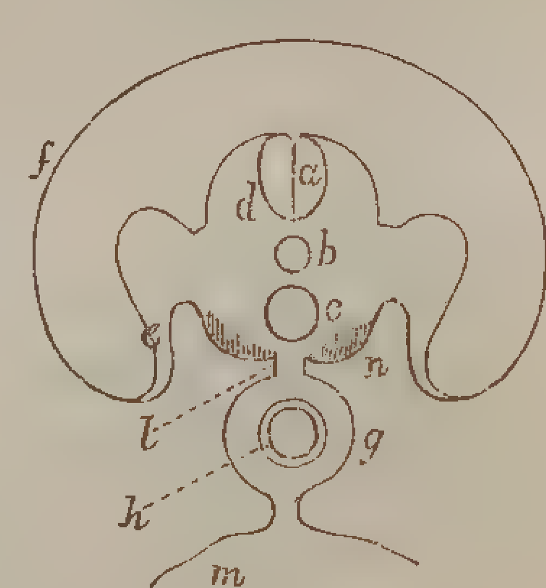
The formation of the intestinal canal and the narrowing of the orifice of communication between it and the yolk-cavity, are succeeded closely by the closing of the visceral cavity in the abdominal region. This is effected by the extension inwards of the base of the amnion, as membrana reuniens inferior, followed by the visceral laminæ. In this way is formed the umbilicus, at first of large diameter, from which the amnion now appears to take its rise.

Fig. 204.

In figure 204, *a* represents the central parts of the nervous system; *b*, the chorda dorsalis; *c*, the aorta; *d*, the parietes of the body continued superiorly into the dorsal laminæ; *e*, the visceral laminæ; *f*, the amnion; *g*, the intestinal membrane; *h*, the cavity of the stomach lined with mucous membrane; *i*, the liver; and *k*, the Wolffian bodies.

Figure 205 represents a section of the embryo in the neighbourhood of the upper extremities. *a* indicates the spinal cord; *b*, the corda dorsalis; *c*, the aorta; *d*, the dorsal laminæ; *e*, the visceral laminæ; *f*, the amnion; *g*, the intestinal membrane; *h*, the cavity of the stomach with the mucous membrane; *l*, the mesentery; *m*, the yolk-sac; and *n*, the Wolffian bodies.

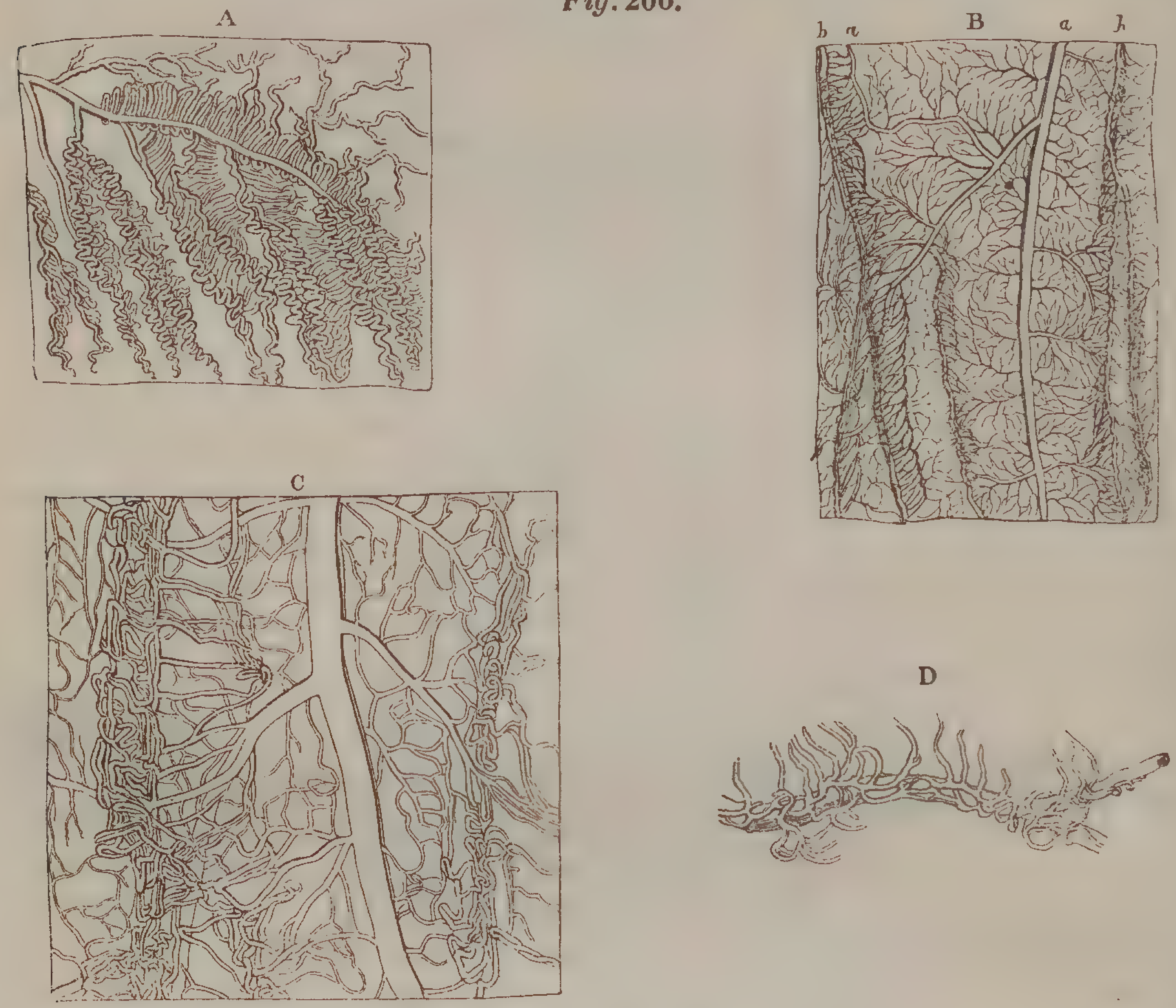
Fig. 205.



The mesentery is formed in exactly the same manner as in the frog. With the exception of the chorda dorsalis, of which the existence is only temporary, the mucous membrane is the only structure of the fœtus of equal importance, that is formed, extended, and even perfected independently of the vascular system. It receives its external investments from the central portion of the membrana intermedia. The peripheral portion of the latter membrane has gradually extended itself over the whole yolk, and invests it except at a small round spot. The cortical layer of the yolk becomes closely connected with the peripheral portion of the membrana intermedia. The vitelline arteries extend from this cortical layer into the yolk, forming the vascular loops known as the "vasa lutea." The function of the yolk itself is now reduced to that of mere nutritive matter, and the contents of the yolk-cells have undergone an essential change, since they yield under pressure a coherent fatty substance.

[The translator is indebted to Mr. Grainger for the following observations on *the structure and functions of the umbilical vesicle of the chick*. "When examined in the early days of incubation, the inner surface of the umbilical vesicle, composed, as it appears, of a highly organised mucous membrane, presents a surface uniformly extended, with no folds or inequalities perceptible by the naked eye, except those caused by its blood-vessels, which are most abundant. Subsequently an immense number of folds or valves, as they were termed by Haller, become visible, and on the ninth day of incubation they are very much developed, and project into the altered yolk. These folds become gradually more and more developed, and are doubled on themselves in a most intricate manner, especially after the chick has left the shell. (See fig. 206, A.)

Fig. 206.



In proportion as the vesicle diminishes in size, from the absorption of its contents, the folds are more crowded together. On the nineteenth day their extreme depth averages five-twelfths of an inch, gradually tapering off to a line or less in depth. When the inner surface of the vesicle is viewed under the microscope with a low power, it is seen to be covered both on the valves and in their intervals with an immense number of greyish-white corpuscules. Mr. Dalrymple has discovered that these globules may by careful washing be entirely removed, and that when this is done, after a successful injection of the omphalo-mesenteric vessels, the branches of these vessels, which form the folds above described (see fig. 206, B.) appear, so far as colour is concerned, like other blood-vessels; the peculiar colour which induced Haller to apply to them the name of *vasa lutea* being entirely dependent on the layer of granules covering them. I have lately had an opportunity, through the kindness of my friend Mr. Dalrymple, of examining some most perfect injections of the umbilical vesicle. The following is our joint account of the microscopic characters of the *vasa lutea*:—There are two classes of these vessels. The more simple form anastomoses on the plane part of the

* [Figure 206. The folds of the vitellary membrane and the vasa lutea, after drawings by Mrs. Holmes from injections by Mr. Dalrymple. A represents the wavy folds before the layer of nucleated cells has been removed; B shows the vessels of the folds and of the membrane between them, laid bare, and more highly magnified; C is a view, with a still higher magnifying power, of the internal surface of a portion of the vitellary membrane, in which the arrangement of the vessels forming the folds is more accurately seen. D, represents a portion of one of the venous trunks which lie in the free border of the fold, covered with its capillary network.]

umbilical vesicle, principally between the valves. The second set consists first of all of a trunk lying in the bottom (or free border) of the convoluted (wavy) fold or valve, closely covered on its walls by a reticulum of smaller vessels, and having appended to it simple vascular loops, which appear to arise from and return into the main canal. (See fig. 206, C and D.) These loops are in free connection with each other, having free inosculations. The intricacy of the vessels in the valves is much increased in consequence of each valve necessarily consisting of two layers, and being arranged in a waving or serpentine form. The general result of this organisation — that is, the frequent looping and anastomosis of the venules, and the folding of the valves — is to increase immensely the surface or extent of the venous system. That the vessels in question are veins is rendered very probable by their size, and by the functions known to be performed by the veins of the vesicle; indeed I have distinctly traced a direct continuity between the so-called vasa lutea and the omphalo-mesenteric vein. The microscopic measurements of the different vessels of the umbilical vesicle here described are, according to Mr. Dalrymple, as follows: — The main trunks of the naked vessels (the arteries), seen in figures B and C, and indicated by *a* in figure C, measured $\frac{1}{185}$ of an inch in diameter; the vessels of the capillary network of the plane or intervalvular surface of the membrane, $\frac{1}{1080}$ of an inch; the trunks of the vessels covered with capillaries (the veins), (see fig. 207, B, *b*, and D,) where they emerged from the folds, $\frac{1}{90}$ of an inch (one-fourth of this diameter being due to the covering of smaller capillaries); and the capillaries forming the network of the folds about $\frac{1}{900}$ of an inch. In these injected specimens, when the granular matter had been completely washed away, there certainly was nothing resembling a mucous membrane; the vessels, in some places especially, appeared quite free and uncovered towards the interior of the vesicle. It therefore is a question whether the granulated layer was the mucous membrane in an early stage of formation, a supposition which Mr. Dalrymple thought supported by the fact that some of the corpuscules were nucleated, and thus resembled the elementary condition of all tissues, or whether the mucous membrane had been destroyed in making the preparation."

"*Contents of the umbilical vesicle.* As incubation proceeds, the yolk becomes liquefied, and, as Prout has shown, and I have myself ascertained, chemically changed by an intermixture with the albumen, which probably enters the yolk-sac by endosmose. The liquefaction of the yolk always takes place at that part where it is covered by the vasa lutea; so that whilst a portion drawn out by a syringe in this situation is fluid, and does not coagulate by the ordinary tests, the yolk below is unaltered, and readily coagulates.

"*Functions.*—The umbilical vesicle is the organ on which the embryo of all classes is dependent for the materials of its development in the first period of existence, whilst in the oviparous and ovoviviparous animals the whole of the nutritive matter is derived from this source. The opinions which have prevailed respecting the mode in which the nutriment is introduced into the body of the embryo are extremely vague, and apparently erroneous. Some writers have attributed the nourishment, in part at least, to absorption of the albumen by the allantois; but all, with various modifications, contend for the introduction of nutritious matter into the intestine by the vitelline duct; whilst the agency of the vasa lutea is admitted, more or less, at one or other epoch of incubation. I believe it to be susceptible of proof, however, that instead of there being three different modes of nourishing the embryo, there is in the oviparous and ovoviviparous animals but one, that one consisting of the beautiful apparatus of the omphalo-mesenteric blood-vessels, with their appended plexus of the so-called 'vasa lutea.'

"The principal facts which support this view are, 1. that the vasa lutea do not disappear or decrease in proportion as the vessels of the allantois grow larger, but, on the contrary, become more and more developed, and at the end of incubation cover the whole yolk. 2. That they persist until the whole of the contents of the vesicle have disappeared, and are present after the ductus vitello-intestinalis has become impervious; the following being the order of disappearance of these parts; first, the vitelline duct; second, the contents of the vesicle; and last of all, the omphalo-mesenteric vessels. 3. That the action of these vasa lutea, consequently, continues until the whole of the process of development, so far as the egg is concerned, has come to a conclusion. 4. That the new nutritive compound formed within the umbilical vesicle by the union of the yolk and albumen, always accumulates at that part of the vesicle which lodges the vasa lutea. 5. That the opinion of the transmission of the contents of the umbilical vesicle into the intestine by the vitelline duct has apparently been adopted from two circumstances, namely, the open condition of that duct, and the supposed presence of yolk in the intestine of the embryo. But that these circumstances are inconclusive; in the first place, because the duct is closed before all the contents of the vesicle are absorbed, while its open condition, a necessary result of the organic formation of the intestinal canal from the upper part of the umbilical vesicle, no more indicates a functional action, than does the tube of the urachus resulting from the formation of the allantois and urinary bladder; and in the next place, because the presence of a substance resembling yolk in the intestine has been very rarely observed, and, in many of the instances in which it has been seen, has probably consisted of a mixture of bile and mucus like the meconium. 6. That the office of the allantois is, to serve the function of respiration, and not to absorb nutriment."]

CHAPTER III.

DEVELOPMENT OF MAMMIFEROUS ANIMALS AND MAN.

1. *Development of the ovum of Mammalia.*

THE transit of the ovum from the ovary into the Fallopian tube sometimes takes place within a few hours after the act of sexual union: thus, Dr. Barry found that the ovulum of the rabbit left the ovary within nine or ten hours after the coitus. In other cases the process occupies twenty-four hours, or even several days.

De Graaf* observed that the ovula of rabbits had been discharged from the ovary three days after the coitus. Cruikshank † found them in the Fallopian tube on the third day, and on the fourth day in the uterus. Coste found ova of rabbits in the uterus twenty-four hours after sexual union. Wharton Jones detected the ova of a rabbit in the Fallopian tube, two days after impregnation; while in a rabbit which he examined forty-one hours after its connexion with the male, no ova could yet be discovered either in the tubes or in the uterus. Prevost and Dumas, instituting an examination of two bitches eight days after impregnation, found ova in the uterus; and in one of the two a single ovum was also discovered in the Fallopian tube.

According to the researches of Bischoff, made on bitches, the period

* Opera Omnia, p. 215. † Phil. Transact. 1797.

of the escape of the ova from the ovary is very different in different cases. The earliest time at which he detected ova external to the ovary was thirty-six hours. In one bitch the ova had not left the Graafian vesicles nineteen hours after the act of sexual union. In another bitch, which fourteen days previously had ceased to have coitus with the dog, the ova had reached only the middle of the Fallopian tubes. A third bitch had refused the dog eleven days, and yet the ova had only just entered the uterus, and were very backward in their development. A remarkable fact, which seems quite unique, has been observed in the case of the ovum of the roe-deer. A very long period intervenes between the act of impregnation and the separation of the ovum from the ovary. The time of sexual union is August, while, according to the numerous observations of Pockels,* the ovum does not leave the Graafian vesicle and enter the Fallopian tube before December. The period of heat lasts from the end of July to the end of August. The ovum therefore remains about four months after its impregnation before its development commences.

The primitive changes which the ovum undergoes in the Fallopian tubes, and in the uterus, have been described by Cruikshank, Prevost and Dumas, Von Baer, Coste, Wagner, Wharton Jones, Bischoff, and Barry.

As early as 1672, De Graaf† detected ova in the Fallopian tubes of the rabbit, and observed that they had two coats. He says, "Minutissima ova quæ, licet perexigua, geminâ tamen tunicâ amiciuntur." In ova of the rabbit, taken from the Fallopian tube on the third day after impregnation, Cruikshank believed that he could distinguish three coats. The rudimentary condition of the embryo, in which merely the primitive streak and the area pellucida are visible, was first observed by Prevost and Dumas ‡ in the bitch. The last-named physiologists have given no accurate description of the very early ova which they discovered in the cornua of the uterus of the bitch; but in their drawings granules, containing each a nucleus-like point, are distinctly represented. These granules are stated to have existed at the upper surface of the ovum, but whether they were seated in its interior is uncertain, since Prevost and Dumas speak of the "decidua." They figure a round white spot as lying beneath the granules in question, and compare it to the "cicatricula." Von Baer examined ova taken from the uterus of the bitch before the formation of the embryo. They were composed of an external transparent coat, beset here and there with short villi or knots, the "membrana corticalis," and of an internal coat presenting circular markings, which, by a higher magnifying power, were seen to be circles of granules. (This appearance has been explained by Bischoff.) In

* Wiegmann's Archiv. 1835, 195. Müller's Archiv. 1836, 183.

† Op. Omn. 216.

‡ Ann. de Sc. Nat. III. Tab. v. Fig. 2, 3.

each ovum a round opaque spot was also visible. Von Baer regarded the internal coat on which the granules were seen as the vitelline membrane: it is the same tunic which Coste believes to be the germinal membrane. The opaque spot was supposed by Von Baer to be the germinal membrane or germ.

On the third day after impregnation, the ova found by Coste * in the uterus of the rabbit measured one line in diameter. Examined with the aid of the microscope, the external transparent membrane of the ovum, or the vitelline membrane, was perceived to be invested internally by a second granular membrane. The latter membrane enclosed the entire yolk, which at this period had become perfectly transparent. On the seventh day Coste detected the first rudiment of the embryo in the form of a spot composed of granular nebulæ, which lay at the surface of the granular membrane (the germinal membrane of Coste) and in its substance. The streak was distinguishable in this spot. In his more recent work,† Coste has related similar observations made on ova of the bitch, as well as of the rabbit, and has given drawings of the germinal membrane and the round embryo spot. He has also given similar representations of the germinal membrane of the sheep.

R. Wagner examined the ova of the rabbit at a very early period after impregnation, when they had reached the uterus but had not yet obtained any attachment. The ovum was of an oval shape, two lines in length, and one and a-half line broad. It was composed of two coats; of which the more external one was quite transparent, structureless, and thinner than the "zona pellucida" of the unimpregnated ovum in the ovary. The more internal coat, which after the ovum had been placed in water was separated from the external coat by a distinct interval, had a layer of small globules on its inner surface. In the middle of the ovum Wagner could distinguish a spot, composed of granules which seemed to have coalesced into a membrane. This description agrees entirely with that of the ovum observed by Gurlt, and likewise figured by Wagner. With respect to the external tunic of the ovum Wagner inclines to the opinion of Baer, that it becomes developed into the chorion, or the external membrane of the ovum in its more developed state. The second or internal tunic was regarded by Wagner as either the vitelline membrane or the germinal membrane, while he supposed the circular granular spot to be the germinal disk.‡

Wharton Jones found ova in the Fallopian tubes of a rabbit on the second day after impregnation. They were surrounded by a thick layer of gelatinous substance, which he found to exist even while the ovum was in the ovary, but which had not the form of a membranous invest-

* Recherches sur la Génération des Mammifères, Paris, 1834.

† Embryogenie Comparée, Paris, 1837.

‡ Abhandl. D. K. Baiersch. Akad. II. 1837.

ment until after impregnation. It is from this gelatinous layer, according to Wharton Jones, and not from the vitellary membrane, that the chorion is formed.*

Valentin† and Dr. Martin Barry‡ also describe the ovum found in the Fallopian tube to be invested by a thin membrane (see fig. 207), which subsequently becomes the chorion. This membrane, according to their observations, is formed during the passage of the ovum through the Fallopian tube; and the villi of the chorion gradually become developed from it. The vitelline membrane, according to Barry, disappears by liquefaction.§

The interesting researches of Bischoff have afforded us a complete view of the successive changes which the structure of the ovum undergoes in its passage through the Fallopian tube, and during the period immediately following its reception into the uterus.

All the ova which Bischoff || found in the Fallopian tubes bore a remarkable resemblance to the ova taken from the ovary: they still had the granular germinal disk, and the earliest had undergone no change of size. The germinal vesicle was sought for in vain, although it was still present in ova taken from the tumid Graafian vesicles of the ovary of a bitch nineteen hours after the first coitus. In its passage through the Fallopian tube the ovum gradually increases in size and the yolk in consistence. The granules of the yolk escape from the ovarian ovum when it is injured; while the yolk of impregnated ova may, according to Bischoff, be divided into two, four, or six solid portions. Bischoff further

* Phil. Transact. 1837.

† Repert. 3, 190.

‡ Philos. Transact. 1839, pt. ii. p. 339.

§ [It had been remarked by Valentin (Entwickelungs-geschichte, p. 39) that it would be interesting to know whether the mucous membrane of the Fallopian tube presents differences of structure at different parts for the secretion of albumen and chorion around the ovum, corresponding to the two divisions of the oviduct which secrete the albumen and membrane of the shell of the bird's egg. Mr. Grainger has observed that the Fallopian tube of Mammalia is really formed of two parts of very different structure. The following is an extract from an account of his observations communicated to the translator in writing:—"On slitting open the Fallopian tube of a sow a few days after conception, a decided difference was noticed in this canal. The part next to the uterus, 3¼ inches in length, had very thick coats like those of the vas deferens; the tube was very small, and was distinguished on its mucous surface by slightly elevated longitudinal rugæ. The second and more vascular part was 7½ inches long, and was suddenly enlarged, both as regards the outer surface and the canal within. It displayed a most beautiful and complex apparatus of folds or valves of the mucous membrane: these folds, like the striæ of the first portion of the tube, ran longitudinally, but owing to their great development had a plaited arrangement. I have since remarked the same difference, whenever I have sought it, in the tube of the cow, rabbit, and sheep." Lately Mr. Grainger has ascertained that it exists also in the human subject.]

|| Wagner's Physiologie, p. 95.

observed that the mass of the yolk had separated at parts from the inner surface of the vitelline membrane, and had assumed an angular figure. In several ova which had nearly reached the end of the Fallopian tube, a very delicate membrane was perceived closely surrounding the yolk; but Bischoff denies that an external coat, destined to become the chorion, is added to the ovum in the Fallopian tube.* At the period when the ova of the bitch and rabbit reach the uterus, they are, according to Bischoff, from five to six times as large as they are in the ovary. The vitelline membrane or external coat of the ovum grows thinner in the same proportion as the yolk increases in size; and the yolk itself becomes at length more fluid and transparent. On the surface of the yolk a connected layer of granules or, more correctly speaking, of cells is formed. This is the germinal membrane: it surrounds the entire yolk, and presents on one side of it a roundish opaque spot. Bischoff found the ova at this period lying quite free in the uterus, not surrounded by any decidua; and the discus proligerus was no longer visible. The germinal membrane, according to the observations of Bischoff made on the ova of the bitch, consists entirely of delicate cells, including granules. The embryo spot also consists of cells. The cells of the germinal membrane soon become so closely pressed together, that they assume, for the most part, the hexagonal form. In the middle of the cells smaller bodies (nuclei) are now seen, and around these an irregular granular substance.

Dr. Barry† has likewise observed these cells with nuclei and nucleoii. The first cells are, he says, large; but these are succeeded by smaller

* [A further remarkable observation has more recently been made by Bischoff (Müller's Archiv. 1841, p. 14) on the mammiferous ovum in the Fallopian tube. In four ova, found in the Fallopian tube of a rabbit shortly after impregnation had taken place, he saw the yolk perform regular and energetic rotatory movements within the cavity of the zona pellucida; and he also distinctly perceived that the surface of the yolk-mass was beset with delicate cilia. Bischoff has observed movements of the same kind, and also produced by cilia, in the ova of frogs, the yolk and embryo revolving within the vitellary membrane. The rotation of the embryo, by means of cilia in the ova of Mollusca and Polypi, has been long known; and the same phenomenon has been discovered by Ehrenberg and Von Siebold in the ova of Medusa Aurita. Bischoff's observations render it probable that the process is one common to all animals. Dr. Barry (Philos. Transact. 1839, pt. ii. p. 355) had previously described the rotatory motions of a mulberry-like object within a vesicle which he found attached to the lining membrane of the Fallopian tube. He compared this object to the structure of similar form which he has discovered to occupy the centre of the mammiferous ovum in certain stages of its development, and remarked that it remained to be discovered whether the latter structure also performs rotatory motions as the embryos of Mollusca and Polypi are known to do. But he regarded the revolving body observed by himself, and the vesicle containing it, as identical with certain pellucid vesicles which he had frequently seen under the mucous membrane of the uterus of the rabbit.]

† Edinb. Philos. Journal, 1839.

and more numerous ones. A continuous layer of cells forms at the inner surface of the membrane which surrounds the yolk; while a mulberry-like body is produced in the centre of the ovum. Dr. Barry has also instituted observations on the early stages of the development of the embryo, which seem to prove that the process in the Mammalia is in some measure peculiar.

[Dr. Barry's observations, of which Professor Müller had seen only a short abstract, appear to be not only highly interesting, but very important. In the account of his observations relative to the first changes succeeding fecundation (see page 1497), his description was followed up to the point where, the ovum having reached the middle of the Fallopian tube, the germinal vesicle disappeared, and was succeeded by two cells. The further changes which Dr. Barry has found the essential parts of the ovum to undergo, up to the formation of the embryo, are as follows:—Each of the twin cells (fig. 207, A) gives origin to two others, making four (fig. 207, B): each of these four in turn gives origin to two, by which the number is increased to eight (fig. 207, C); and this mode of augmentation continues until the germ consists of a mulberry-like object, the cells of which are so numerous as not to admit of being counted (see fig. 207, D, E, F). Together, with a doubling of the number of the cells, there occurs a diminution of their size. Every cell, whatever its minuteness, is found filled with the foundations of new cells into which its nucleus has been resolved. These foundations of new cells are arranged in concentric layers around a pellucid point. Each cell in fact exhibits the same process of cellular development as the original parent cell — the germinal vesicle (see page 1497). The foregoing changes usually take place in the ovum during its passage through the Fallopian tube. When it has entered the uterus, a layer of cells of the same kind as those forming the mulberry-like body makes its appearance on the whole of the inner surface of the membrane which invests the yolk (see fig. 207, F). The mulberry-like structure then passes from the centre of the yolk to a certain part of that layer (fig. 207, G); the vesicles of the latter coalesce with those of the former, where the two sets are in contact, to form a membrane — the future amnion; and the interior of the mulberry-like structure is now seen to be occupied by a large vesicle containing a fluid and dark granules. In the centre of the fluid of this vesicle is a spherical body, composed of a substance having a finely granular appearance, and containing a cavity filled with a colourless and pellucid fluid (see fig. 207, H). This hollow spherical body seems to be the true germ. The vesicle containing it disappears, and in its place is seen an elliptical depression filled with a pellucid fluid. In the centre of this depression (which appears to correspond to the area pellucida of the bird's egg) is the germ still presenting the appearance of a hollow sphere (fig. 207, I).

From the germ the embryo now begins to be formed. The germ separates into a central and a peripheral portion, both of which, at first appearing granular, are subsequently found to consist of vesicles. The central portion occupies the situation of the future brain, and soon presents a pointed process (fig. 207, J and K). This process becomes a hollow tube, exhibiting an enlargement at its caudal extremity, which indicates the situation of the future sinus rhomboidalis. Up to a certain period new layers of vesicles or cells come into view in the interior of the central portion of the germ, parts previously seen being pushed further out (see fig. 207, L and M).

According to Dr. Barry, there is no structure in the mammiferous ovum entitled to be denominated the "germinal membrane." The "amnion" (indicated by the cypher 4 in fig. 207, K, L, M), is formed, as has already been mentioned, from an epithelium-like layer of cells which lines the investing membrane of the ovum, and from the outer cells of the mulberry-like body, which together constitute a layer corresponding to the "lamina serosa" of authors. The "vascular lamina" of the umbilical vesicle arises as a hollow process originating from the germ and extending beneath the amnion so as to include the yolk.]*

The observations and drawings of Prevost and Dumas have shown that the formation of the embryo of Mammalia takes place according to the same plan as that of birds. For they have figured the "primitive streak," the "dorsal laminæ" bounding it on each side, and the pear-shaped "area pellucida," just as they appear in the incubated hen's egg; only the area immediately surrounding the area pellucida, and, without doubt, destined to form the "area vasculosa," is peculiar by its very elongated form corresponding to that of the area pellucida. Von Baer† saw the germinal membrane in a vascular state, in an ovum taken from the uterus of a bitch. Wagner represents the vascular area in an ovum‡ of the same animal of a circular form. The embryo bears the same relation to the entire sac-like germinal membrane in the mammiferous ovum as it does in the ovum of the bird. This was first shown by Von Baer, and the fact is illustrated by the beautiful drawings of Coste,§ taken from the rabbit, and of Bischoff,|| from the bitch. The "yolk-sac" of the mammiferous ovum communicates with the intestine of the embryo, at first by a wide opening, and afterwards by a duct or hollow pedicle, the "ductus omphalo-mesentericus," which is accompanied by the same vessels as in the bird, the "vasa omphalo-mesenterica." This yolk-sac of Mammalia is commonly called the "umbilical vesicle, or vesicula umbilicalis." According to Von Baer's researches, it has an external

* Philos. Transact. 1840, pt. ii. p. 536, et seq.

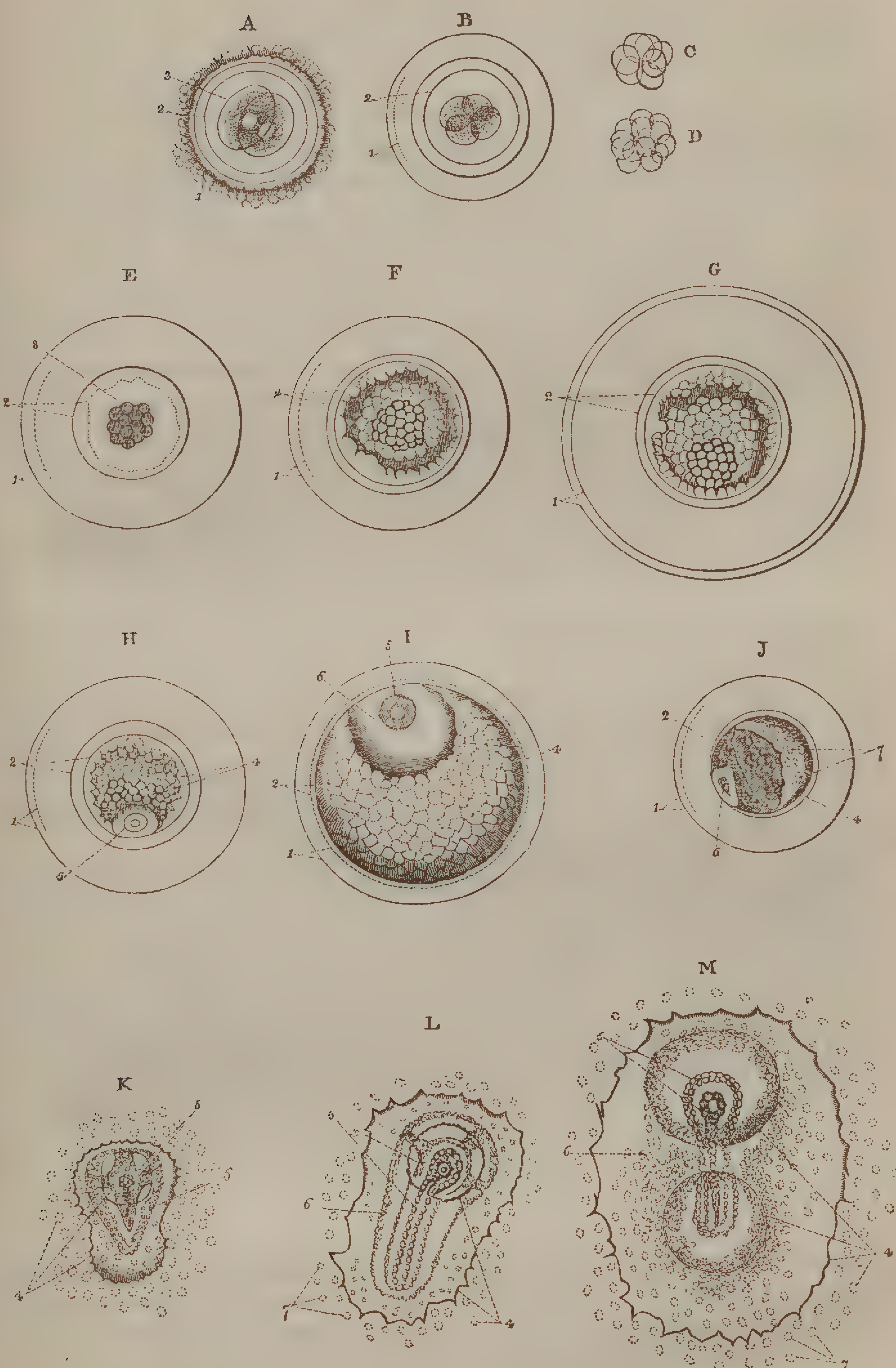
† De ovi Mammalium genere. Fig. vi.

‡ Icones Physiol. Tab. vi. Fig. 9.

§ Embryogenie. Tab. viii.

|| Wagner's Icones Physiol. vi. Fig. 11–14.

Fig. 207.*



[Fig. 207 illustrates the different stages in the development of the germ and embryo as described by Dr. Barry. A, B, C, D, E, are ova, or the mulberry-like bodies of ova, found in the Fallopian tube, between its middle and the uterus, at periods varying from 24 to 63 hours post coitum. F, G, H, I, and J, are ova taken from the uterus vascular layer, and an internal mucous layer, from which villous prolongations project into the yolk. These villi or folds, which are similar to those found in the yolk-sacs of birds, exist likewise in the umbilical vesicle of the human ovum. The "amnion" was observed by Von Baer to hold the same relation to the abdominal plates of the embryo, as in the bird; and it is doubtless developed in the same manner. The "allantois" also, is developed by the same process as in birds; its formation has been elucidated, more especially by the researches of Von Baer and Coste. Its blood-vessels are the "vasa umbilicalia."

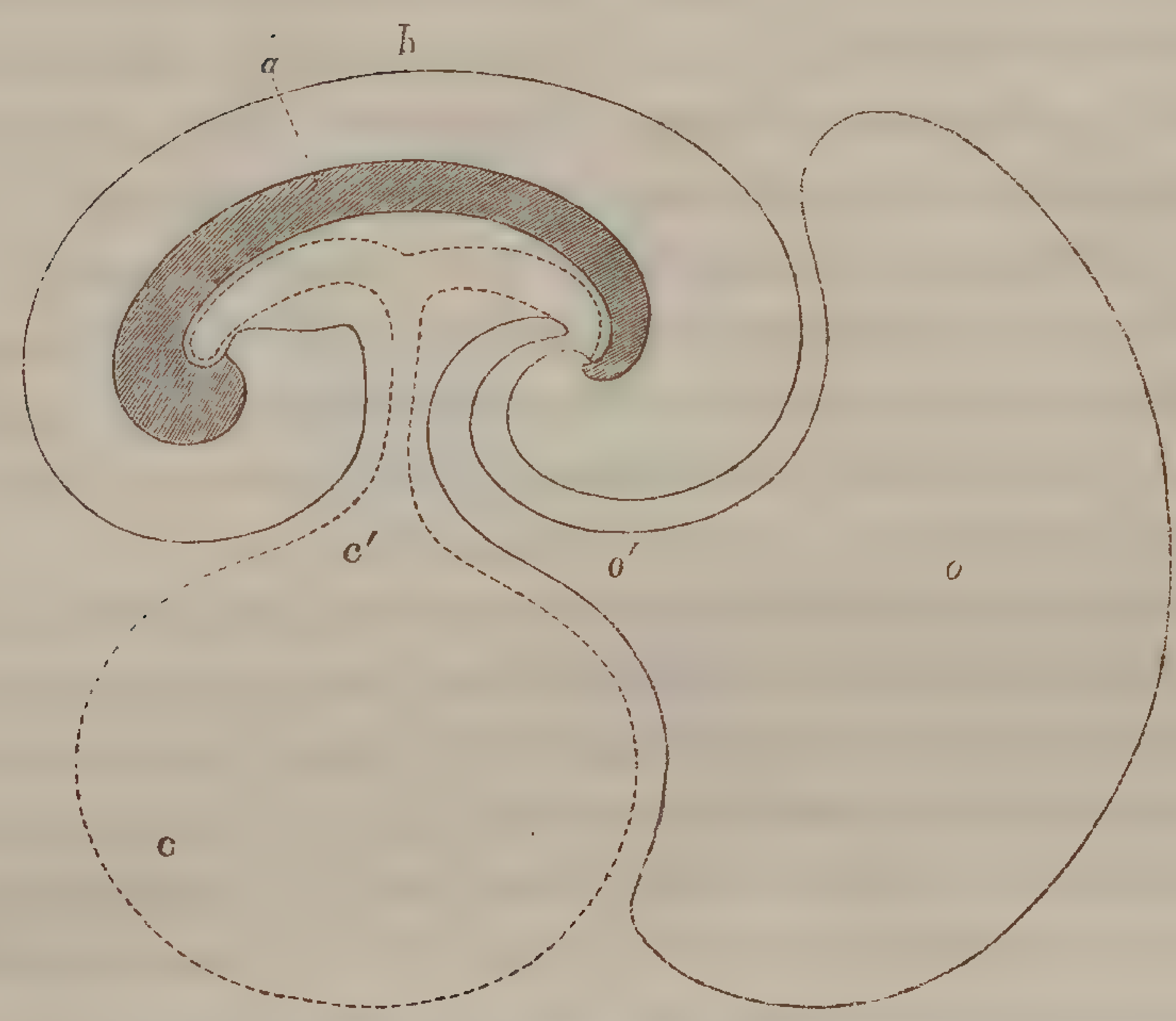
Before the formation of the urinary bladder, the allantois communicates with the common reservoir, into which the excretory ducts of the Wolffian bodies, the ureters, and the organs of generation open, which is called the "sinus urogenitalis." The urinary bladder is developed from the apex of this cavity; and for a certain period it is continued into the pedicle of the allantois or the urachus. The amnion passing off from the margin of the umbilicus, and forming a bladder-like investment for the fœtus, encloses, as a sheath, all the parts which issue from the umbilicus; namely, the pedicle of the umbilical vesicle or yolk-sac, the vasa omphalo-meseraica, the pedicle of the allantois, and its blood-vessels, the vasa umbilicalia. (See fig. 208.) These parts are thus united into a common cord, the "funiculus umbilicalis;" and the sheath of this cord, the "vagina funiculi umbilicalis," is consequently formed by the amnion. Through the medium of the vessels of the allantois, the vascular system of the fœtus reaches the "chorion," in the substance of which, and in its villi, the allantoid or umbilical vessels ramify.

While the ovum is undergoing the first changes of development in the uterus, it lies quite free in the cavity of that organ. But subsequently an exudation is poured out upon the inner surface of the uterus which is composed of cells, and constitutes the thin "membrana decidua" of the mammiferous ovum. Into this membranous uterine production, which is especially distinct in carnivorous animals,* the villi, growing from the chorion of the ovum, become inserted. At a still later period, the ovum enters into another kind of union with the uterus, by means of the placenta, the structure of which will be described hereafter.

at periods between 86 and 105 hours post coitum. K, L, and M, are embryos from ova of 111½ to 124½ hours. In all these figures, 1 indicates the incipient chorion; 2, the thick transparent membrane of the ovum or the zona pellucida; 3, the two cells into which the germinal vesicle and its contents become resolved, and the mulberry-like body which takes the place of those two cells; 4, the amnion; 5, the true germ; 6, (in fig. 1,) the space corresponding to the area pellucida; 6, (in figs. K, L, M,) the peripheral portion of the germ; 7, the cells of the layer which becomes the vascular lamina of the umbilical vesicle.]

* Bojanus, loc. cit.

Fig 208 *



The preceding description of the mammiferous ovum applies to the whole class of Mammalia, for in the ovum of all these animals there is an umbilical vesicle, an amnion, and an allantois. There is, however, a great variety in the relative development of the different parts in the different orders of the Mammalia. We will now briefly pass in review the most remarkable varieties of this kind; noticing, at the same time, the principal steps by which this branch of knowledge has been advanced.

Rufus Ephesius distinguished the amnion and its fluid from the allantois in the ovum of animals. Galen described, as existing in the ovum (of ruminants), an externa tunic, which he called the chorion; a second belonging to the fœtus itself, called by him the amnion; and a third lying between the two former, and connected with the urinary bladder, through the medium of the urachus, which he denominated the allantois. G. Needham discovered the umbilical vesicle, which he named the fourth membrane, together with its accompanying vessels, arising from the mesentery, in the ova of the dog, cat, and rabbit. The uniform presence of these membranes of the ovum in all the Mammalia, and their agreement with those of the bird's egg, was first correctly and completely recognised by Oken and Kieser. They also correctly asserted the direct connection of the umbilical vesicle or yolk-sac of the mammiferous ovum with the intestinal canal, a structure which had been denied

* In figure 208, *a* represents the dorsal structures of the embryo; *b*, the amnion; *c*, the yolk-sac or umbilical vesicle; *c′*, the vitelline duct or pedicle of the umbilical vesicle; *o*, the allantois; and *o′*, the urachus.

by many, the apparent connection having been supposed to be formed merely by vessels. Meckel afterwards refuted the opinion of Oken, that the cœcum was the point of connection of the umbilical vesicle with the intestine; but still the fact of that connection really existing may easily be verified in very young embryos. Bojanus* demonstrated the connexion of the vesicle with the small intestine in the dog. The same structure is uncommonly distinct in the ovum of ruminants in the earliest period of development (before the third week); and has been seen by Coste, as well as by Pockels, and myself. The hollow pedicle is, indeed, at this period, as wide as the elongated forked vesicle itself.

The varieties presented by the development of the different parts of the ovum in the various families of the class Mammalia, and their nature, have been elucidated by Oken, Kieser, Dutrochet, Von Baer, and Coste. Von Baer has treated most fully of this part of embryology; and we shall, therefore, here chiefly follow the account which he has given. The ovum of some Mammals rapidly assumes an elongated form at the commencement of its development. This takes place to the least extent in the Carnivora, as in the dog; to the greatest extent, in the Solidungula, in which the ovum is drawn out at each extremity into a long horn. The yolk-sac or umbilical vesicle of the Solidungula, as well as of the Ruminantia, and hog, consists of a pedicle connected with the rudimentary intestine, which is, at first, of considerable width, and of two exceeding long cornua passing off from this pedicle or neck in opposite directions. The cornua, at a subsequent period, become atrophied, and only the middle portion is left in an active state, and supplied with vessels; but of this portion, at length, only a trace remains. The yolk-sac of carnivorous animals changes from a spherical to an ellipsoid, and afterwards to a fusiform or spindle-like shape, which it preserves until birth, acquiring a large size and retaining its vascular network. The yolk-sac of rodent animals does not become elongated into cornua; but increases greatly in size, so that instead of being confined to the abdominal aspect of the embryo, it extends between the amnion and chorion, over the dorsum of the embryo to the opposite side of the abdomen; it is persistent until birth.†

The allantois is, according to Von Baer, composed of two layers, of which the internal one is a prolongation of the mucous membrane of the embryo, and the other, the external vascular layer in which the vasa umbilicalia ramify. In carnivorous animals this sac bears a close resemblance to the same part in birds; it extends entirely around the embryo, and invests the whole inner surface of the chorion, except at the part

* Nov. Act. Nat. Cur. x. pt. i. p. 141.

† See Von Baer, loc. citat. p. 191.

where the umbilical vesicle lies. That portion of the sac which lies in contact with the amnion, and which contains but few vessels, is the membrana media of earlier writers, and the "endochorion" of Dutrochet. The external portion of the sac, which is in relation with the chorion, is very vascular. The allantois of ruminants is from the first bicorned, and its cornua are developed in the same direction as those of the vesicula umbilicalis; but they retain their full size, while the cornua of the umbilical vesicle become atrophied. In the Solidungula the vascular layer of the allantois is separated from the mucous layer by an albuminous deposit; but in them, as well as in the Carnivora, where this separation does not take place, the vessels of the allantois ramify in the chorion. In rodents the allantois has its smallest size, and is confined to the abdominal aspect of the embryo; but its vessels soon leave it to ramify in the chorion. Here, therefore, as in other cases, the proper office of the allantois seems to be the conducting of the vessels of the embryo to the exterior envelope of the ovum, in which they ramify. Von Baer has demonstrated in the ovum of Mammalia a membranous layer lying beneath the chorion, which appears to correspond in origin to the serous layer in the egg of the bird. For it probably separates from the surface of the germinal membrane; then, as in the hen's eggs, grows in the form of a fold over the embryo, so as to form the amnion, and, after the completion and closure of the sac of the latter membrane, becomes isolated as a distinct lamella, enclosing the amnion, embryo, yolk-sac and allantois, and lying itself in close contact with the chorion. Between this lamella and the chorion there is, at first, a thin layer of albumen, the external albumen, which, however, passes by imbibition through the serous layer so as to collect beneath it, and then this layer appears to form merely a second lamella of the chorion. In ruminants, and in the hog, the allantois is free (as it in all cases is at first), and being rapidly developed soon reaches the serous lamella of the ovum and the chorion. It then extends into the long cornua of the ovum, and there at length bursts through the chorion, and protrudes, in the form of two cornua, externally. The extremities of the less elongated ovum of the Carnivora undergo the same change, and allow the cornua of the yolk-sac and allantois, still invested and held together by the serous covering of the ovum, to protrude. So soon as the vessels of the allantois have reached the chorion, they send minute branches into the villi of that membrane. Thus are formed the roots which henceforth extend from the surface of the ovum into the parietes of the uterus, and from which the placenta is afterwards developed.

Both the chorion and the amnion, according to the researches of Breschet and Gluge [and Barry], are composed of nucleated cells.

The fluid of the allantois contains the secretion of the primordial kidneys or Wolffian bodies, and of the true kidneys. Allantoin exists in it; and in that of birds Jacobson has discovered uric acid.*

2. *Development of the human ovum.*

The human ovum, in all probability, does not reach the uterus before the lapse of a week after impregnation. On the eighth day, Von Baer could detect no ovum either in the uterus or in the Fallopian tube. Home and Bauer state, that they found an ovum on the seventh day; but some doubt attaches to their observation. The ovum observed by E. H. and E. Weber was of the date of a week after impregnation. The earliest ova examined by Velpeau, belonged to a period between the tenth and twelfth days; they were already beset with villi, but presented no embryo. In an ovum of fourteen days Von Baer saw the embryo.

Before the ovum reaches the uterus, the formation of a new structure, the "membrana decidua," upon the inner surface of that organ, and corresponding, therefore, to its inner surface in form, has commenced. Ed. Weber observed it on the seventh day after coitus had taken place. It then resembled a layer of lymph, effused from the inner surface of the uterus, upon and between the enlarged vascular villi of that surface.† This membrane exists in animals also; but in a less highly developed form. It is sometimes formed in the uterus of the human female, in cases of extra-uterine fœtation, though not always; and in a case of development of the ovum in the Fallopian tube, the membrana decidua has been observed both in the uterus and in the tube. The membrana decidua is composed of a whitish grey, moist, and soft mass, similar to coagulated fibrin, and entirely formed of nucleated cells.‡ The vessels of the uterus are prolonged into this product. The thickness of the membrane sometimes equals from one to three lines. Its outer surface is intimately connected with the uterus, and when artificially detached, or separated spontaneously, is rough; while its inner surface is smooth. The relation which the decidua bears to the openings of the uterus is not always the same; it is sometimes closed at the lower

* The best figures of the ova of mammiferous animals will be found in the works of Von Baer and Coste, and in Gurlt's Anatom. Abbild. der Haus-säugethiere. The authors to be consulted on the subject of the development of this class are, Oken and Kieser, Beiträge Zur vergleichende Anatomie and Physiologie, 1806. Dutrochet, in the Mém. du Mus. d'Hist. Nat. T. iii. p. 82. G. Cuvier, ibid. p. 98. Bojanus, Nov. Act. Nat. Cur. x. p. 1. C. Mayer, ibid. xvii. 2. Coste, Recherches sur la Génération des Mammifères, Paris, 1834, et Embryogenie, Paris, 1837. Von Baer, Entwickelungs-geschichte der Thiere 2te Theil. Burdach, Physiologie, Bd. ii. Valentin, Entwickelungs-geschichte. R. Wagner, Physiologie and Icones Physiologicæ.

† Disq. Anat. uteri et ovariorum puellæ, vii. a conceptione die defunctæ.

‡ See a notice, by the Author, on the cellular structure of the decidua in Schwann's paper, in Froriep's Notiz. 1838. No. 112. p. 22. See also R. Wagner, Physiologie, p. 114, and Icon Physiol. Tab. xi. fig. 5 and 6.

orifices of the Fallopian tubes, and at the upper entrance of the cervix uteri; sometimes it is open at all these points or at one or other of them. R. Wagner* is quite correct in stating that all these varieties may occur. The cervix uteri is occupied by a mere gelatinous mucus.

When the ovum enters the uterus, it becomes imbedded in the structure of the decidua which is yet quite soft. The earliest ova which have been observed in connexion with the decidua, were not contained free in its cavity, but appeared to be implanted in it or pressed into it from without; the decidua, at the point of entrance of the ovum, being protruded inwards, and the ovum contained in a hollow of its external surface.† During the further growth of the ovum, the decidua becomes more and more inverted at this point, the inverted part being received into the cavity of the rest of the membrane. This inverted portion is called the decidua reflexa, while the other part of the membrane is called the decidua vera. The decidua vera and the decidua reflexa have the same structure, which differs totally from that of the mucous membrane of the uterus. They are, in fact, new products. It must not be imagined that the process by which the decidua reflexa is formed, is a mechanical one, that the ovum, as it enters the uterus, pushes the membrane before it; for, like all processes of the same kind, which occur in the animal organism, this one is effected by the vital vegetative action exerted in a determinate direction. The cavity of the decidua between the decidua vera and the decidua reflexa, contains an albuminous fluid, the "hydroperione" of Breschet. At the part where the uterine expansion of the decidua is interrupted by the reflexion inwards of the decidua reflexa, and where the ovum entered, the place of the former membrane is supplied by another mass similar to it, and connected at its margins with it, the "decidua serotina." When young ova are examined in the uterus both the decidua vera and the decidua reflexa are generally found; but in aborted ova this is seldom the case, a part of the decidua being most frequently retained in the uterus. As the ovum increases in size, the decidua vera and the decidua reflexa gradually come into contact, and in the third month of pregnancy the cavity between them has quite disappeared. Henceforth it is very difficult, or even quite impossible to distinguish the two layers. During the further growth of the ovum the decidua becomes still thinner, but is not entirely lost. At birth a part of it remains behind in the uterus, while a part comes away, forming a thin membranous covering of the ovum.‡

The first connection which subsists between the ovum and the decidua, consists in the ramified villi of the chorion becoming imbedded in

* Meckel's Archiv. 1830, and Physiologie, p. 114–117.

† See Bock, de Membranâ deciduâ. Bonnæ, 1831.

‡ Respecting the decidua of the mature ovum, consult Bischoff, Beiträge zur Lehre von den Eihüllen des menschlichen Fötus. Bonn, 1834.

the hollow canals which traverse the decidua. The villi extend through these canals in the manner of roots, and thus draw nourishment from a maternal structure without having any organic connection therewith.

According to the recent researches of E. H. Weber communicated to me in manuscript, the decidua is composed in greater part of the tubular follicles, which lie very closely arranged at the inner surface of the uterus, and of numerous blood-vessels ramifying upon, and between them. In animals, the long tubular follicles, here and there bifurcated, lie in the substance of the uterus itself, and open upon its inner surface by numerous orifices.* In the human subject they form the decidua.† When the inner surface of the decidua is examined, numerous filaments can be seen in its substance, tolerably regularly disposed, and directed towards the surface. These filaments resemble closely set villi, except that they do not lie free; the interspaces between them being filled with the substance of the decidua. If the cut surface of a divided uterus is examined in the bright sunlight, with a lens, these supposed villi are seen to be long and thin cylindrical tubuli, which become somewhat narrowed where they reach the free surface of the decidua, while at the attached or uterine surface of that membrane they become wider, are much convoluted, and appear to commence by closed extremities. If the substance of a pregnant uterus is compressed, a thick whitish fluid exudes upon the surface of the decidua, similar to the secretion which may be expressed from the uterine glands of animals. The decidua presents at its inner surface numerous orifices, which have been long known, and which appear to be the mouths by which two or more of the tubuli open. Besides these, however, there must be many orifices of single tubuli which are not visible. The tubuli are almost a quarter of an inch in length, and here and there bifurcate; the branches being as wide as the trunk of the follicle. This character completely distinguishes them from the blood-vessels which run in contact with them; for the blood-vessels form a net-work or loops, or at all events ramify, diminishing in diameter at each division. The diameter of the follicles is about $\frac{1}{17}$ of a Paris line; that of the capillaries $\frac{1}{104}$ of a Paris line.‡

* See E. H. Weber, in his Edition of Hildebrandt's Anatom. Bd. iv. p. 505. Burckhardt, Obs. Anat. de uteri vaccini fabricâ. Basil. 1834. E. H. Weber, Annot. Anat. 186.

† Engraved representations of the Decidua will be found in Dr. Hunter's Gravid Uterus, Plates 33 and 34; in Velpeau's Embryologie, Paris, 1833; in Seiller's Gebärmutter und das Ei des Menschen in den ersten Schwangerschaftsmonaten. Dresden, 1832; in Kilian's Geburtshülfl. Atlas. Tab. xxiv; and in C. Mayer's Icones Selectæ. Bonn, 1831. Tab. v. Figs. 6, 7, and 8.

‡ [Dr. Sharpey has been for some time engaged in investigating the structure and functions of the membrana decidua and the uterine glands, and has kindly favoured the translator with the following account of his observations :—

"The uterine glands alluded to in the text have now been ascertained to exist in

The development of the embryo, and the formation of the amnion and yolk-sac, are probably effected by the same process in man as in birds. The umbilical vesicle and its duct is known to have the same relation to the intestine as the yolk-sac and its duct have in the chick.

several orders of mammiferous animals, and from their enlarged size and augmented secretion during pregnancy, as well as the peculiar connection which is then established between them and the fœtal membranes, it has been inferred that they are in some important way subservient to the nutrition of the fœtus. The uterine cotyledons of Ruminants were very generally considered to be of a glandular nature by the older anatomists and as destined to supply a nutrient matter to the fœtus; indeed, it had not escaped notice, that these bodies actually yield a mucilaginous secretion; but besides the cotyledons, Malpighi discovered glands opening on all parts of the inner surface of the uterus of those animals, and recognised them as secreting organs; he has described them specially, in the gravid uterus of the sheep. (Opp. 1687, vol. ii. p. 220.) At a recent period the uterine glands of Ruminants were again observed by Baer, who also discovered similar glands in the sow, and although he erroneously supposed they were absorbent vessels, he described them well, and showed that they were connected in a peculiar manner with the ovum; the dilated orifices of the glands being attached to small vascular spots on the surface of the chorion, which, in the sow, he describes as formed by little circular or star-like elevations of the membrane surrounding a central depression. (Ueber die Gefaessverbindung zwischen Mutter und Frucht, 1828.) This arrangement was justly considered by Dr. E. H. Weber, who afterwards investigated the subject, as a provision for the accumulation of the secreted matter of the glands and for securing its effectual exposure to the blood-vessels of the fœtus. Weber also more fully described the glands in Ruminants, and observed glands of the same nature, though of a different form, in the uterus of the rabbit (loc. cit). Still more lately uterine glands have been discovered in the pregnant Porpoise, by Dr. Eschricht of Copenhagen, and in the gravid uterus of the cat the same observer found oblong cells lying under the mucous membrane, which he considers to be glandular cavities, though he could not discover their orifices on the inner surface of the membrane. (De organis quæ resp. et nutr. fœtus mammal. inserviunt. Hafn. 1837, p. 43.) Having had occasion to observe these glands in the uterus of the bitch, and having examined their condition in various stages of pregnancy as well as their relation to the membranes of the fœtus, I beg to subjoin an outline of my observations.

Fig. 209.*

Fig. 210.*

* Figs. 209 and 210. Uterine glands of the bitch magnified twelve diameters. Fig. 209, openings on the inner surface. Fig. 210, vertical section. 1, 1, simple glands; 2, 2, compound ditto.

Hence the vesicula umbilicalis and the yolk-sac are to be regarded as completely identical. The connection of the umbilical vesicle with the intestine in the human embryo cannot be demonstrated with great distinctness at the period when the duct of the vesicle has already become

The glands of the mucous membrane of the bitch's uterus are of two kinds, simple and compound. The simple glands, which are the more numerous, are merely very short unbranched tubes closed at one end (fig. 210, 1, 1); the compound glands, (2, 2,) have a long duct dividing into convoluted branches; both open on the inner surface of the membrane by small round orifices (fig. 209) lined with epithelium and set closely together. After impregnation the parts of the mucous membrane which come into immediate relation with the ova, together with the glands seated in those parts, undergo a remarkable alteration. In a uterus between three and four weeks after conception, at which period the dilatations or chambers (fig. 211) which contain the ova have attained the size of a walnut, we find, on laying open one of the chambers, that the lemon-shaped ovum is surrounded by a broad belt or zone of villi which rise from the surface of the chorion, and, becoming vascular, take part in the formation of the zonular placenta. Corresponding with this there is a zonular portion of the inner surface of the uterus (fig. 211, 3), somewhat raised above the rest, and perforated with small pits, into which the fœtal villi are received, and as this part of the membrane enters into the formation of the placenta and comes away with the ovum at parturition it is justly regarded as the decidua. The decidua is no new structure, however, it is merely a portion of the mucous membrane become more thick and vascular than the rest, and the pits on its surface which receive the fœtal villi are merely the glands already mentioned (fig. 209) somewhat enlarged and widened. While, however, the simple glands merely undergo a uniform enlargement, a change takes place in the compound glands of a much more remarkable character. The long excretory ducts of those glands (fig. 210, 2), immediately before they open on the inner surface of the membrane, become dilated into cells, one for each gland (fig. 213 and

Fig. 211.*

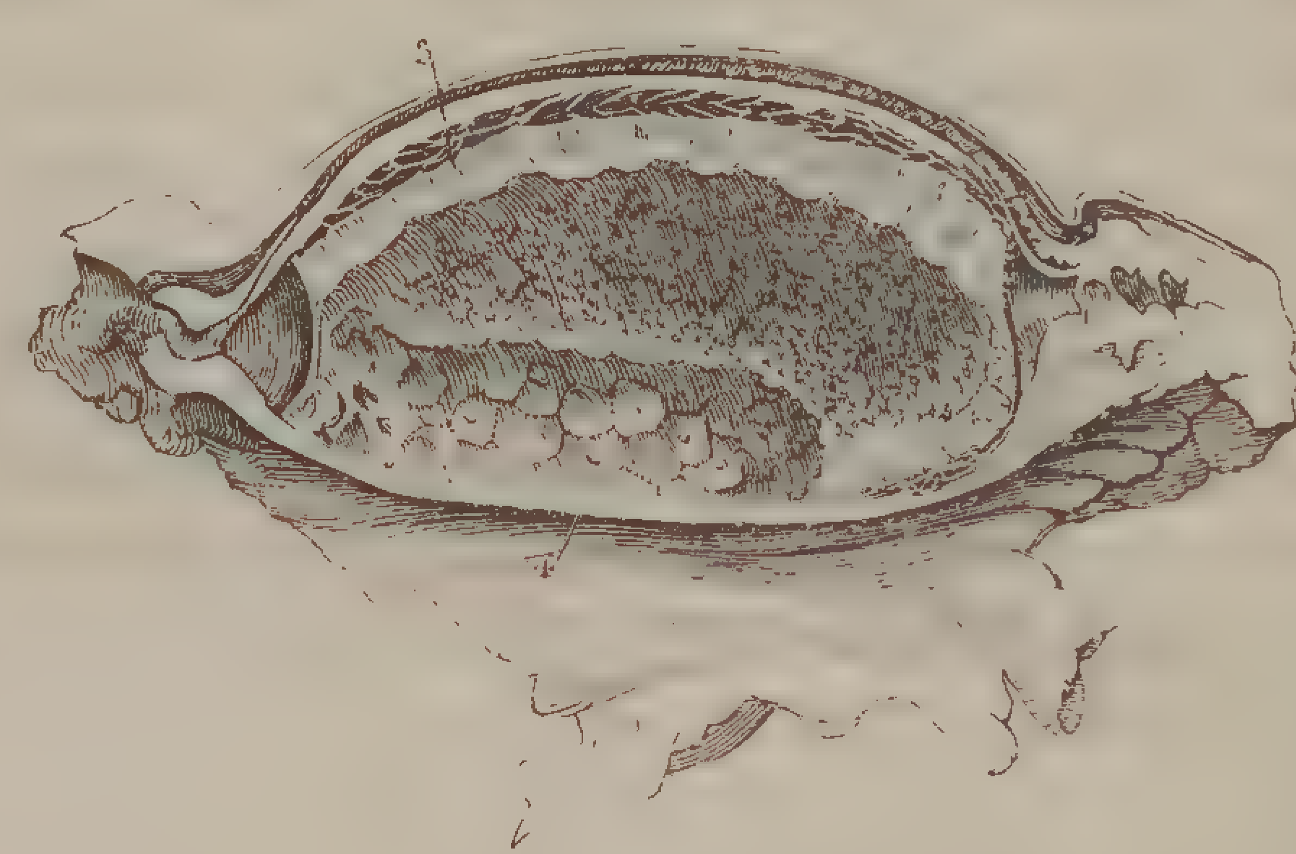
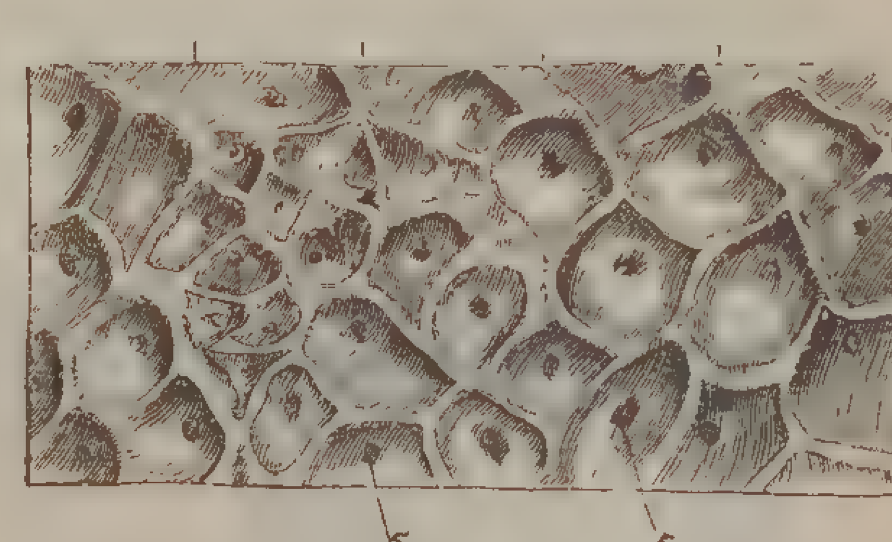


Fig. 212.†



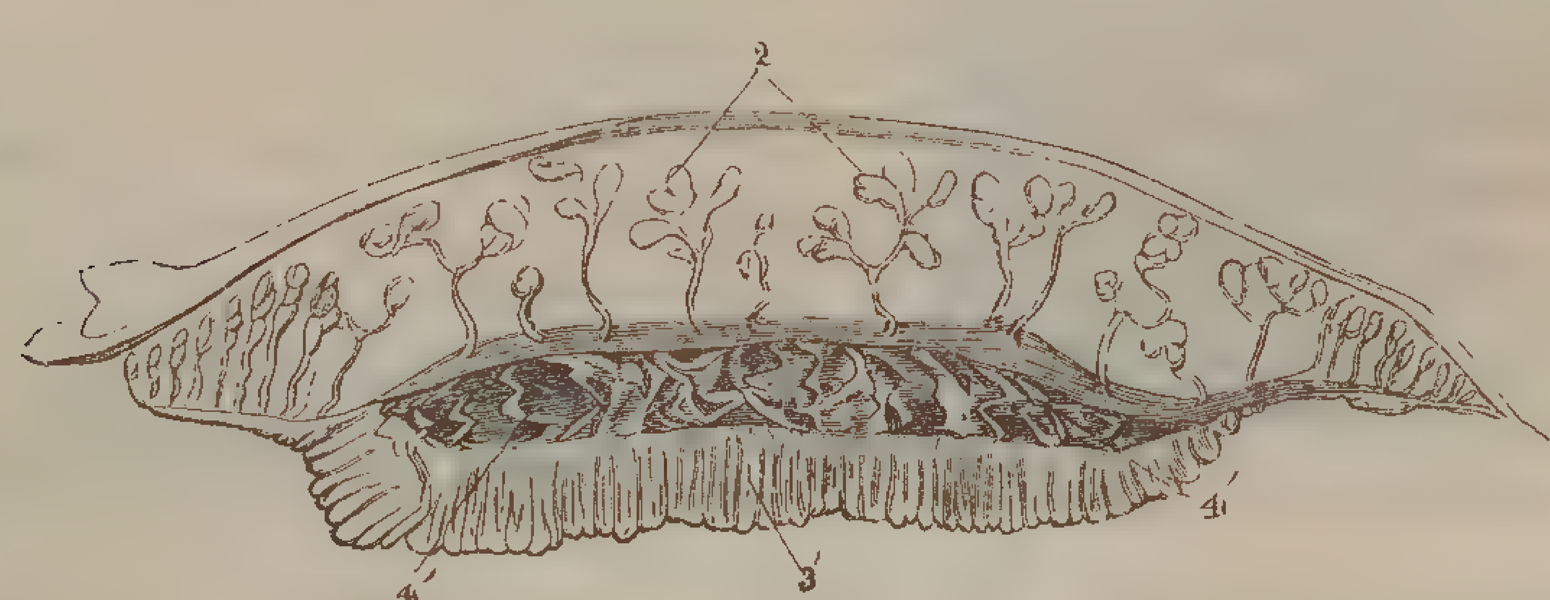
* Fig. 211. Natural size. A fœtal chamber of the uterus opened, the ovum removed. 3. Decidua with its perforations. At 4, part of the decidua has been removed to show the cellular dilatations of the glands beneath it.

† Fig. 212. Some of the glandular cells exposed as at 4 in former figure, magnified three diameters. 5, 5, the ducts opening into the bottom of the cells.

long and thin. Kieser* traced this duct to the intestine, and has given a representation of the structure. It was, however, the subject of much controversy, and the duct was by some anatomists regarded as a mere blood-vessel. In very young embryos, however, the fact may be demonstrated with certainty. In ova, in which the embryo measures

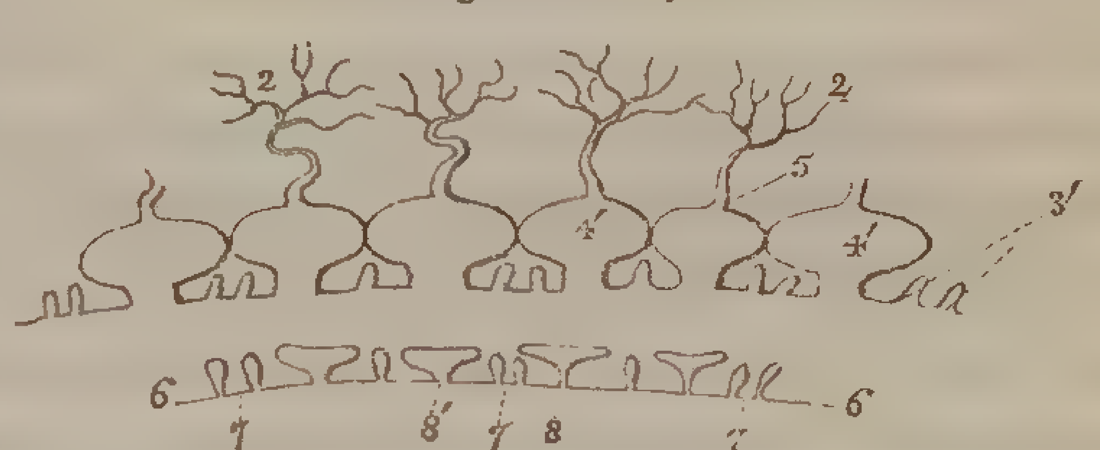
214, 4′), which are filled with a semi-fluid whitish granular secretion, and are lined with epithelium. These cells form a layer beneath the surface of the decidua (fig. 211, 4; fig. 213, 4′), and being crowded together assume a polyhedral form (fig. 212);

Fig. 213.†



at the bottom of each the tubular duct (figs. 212 and 214, 5) may be seen about to expand into the cell, and the cell again contracts at its orifice.

Fig. 214.‡



In a somewhat more advanced stage the glandular cells enlarge, their orifices expand and now membranous processes (figs. 214 and 215, 8, 8′), rise from the surface of the ovum and enter the glandular cells, passing a little way beyond the orifices, by the circumference of which they are embraced. These fœtal processes are prolonged from the chorion (6) and its vascular lining or endochorion (6′) and hence contain ramifications of the umbilical vessels. They are for the most part hollow or saccular, at least at first, and some of them present, for a time, a small aperture of communication (8′) between their cavity and the general sac of the chorion, or rather of its vascular lining, but this is soon obliterated; ultimately, they come to resemble much the villi in structure, differing only in size and form. As pregnancy advances the parts described enlarge, the villi become more complex by ramification, the fœtal processes also give off numerous lateral offsets; but their broad flattened tops which close the mouths of the glandular cells are smooth and even, and are covered with a prolong-

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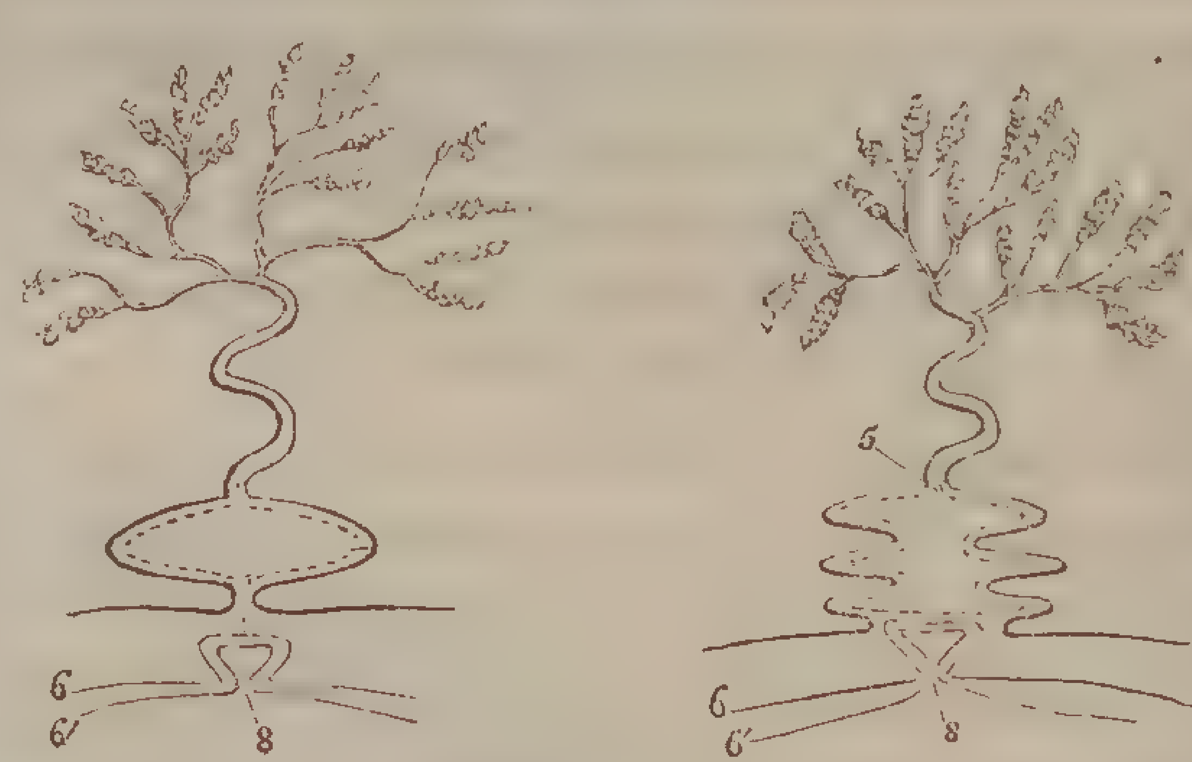
* Die Bildung des Darmcanals aus der Vesicula Umbilicalis. Götting. 1810.

† Fig. 213. Nat. size. Vertical section of parietes of a fœtal chamber somewhat more advanced than 211. At 2, the membranes have been drawn asunder to show the compound glands spread out. 3′, decidua. 4′, 4′, glandular cells.

‡ Fig. 214. Diagram of part of the decidua and ovum separated, to show their mutual relation. 2, 3, 4, 5, as in the former figures. 6, chorion. 7, villi. 8, 8′, fœtal processes of the chorion.

only from two to three lines in length, the duct of the umbilical vesicle is very short and wide, and its walls are distinctly continuous with those of the rudimentary intestine. I observed this relation of the parts in an ovum which I described some time since.* Similar observations

Fig. 215.



ation of the same epithelium which lines the cells (fig. 215 dotted line). The maternal or decidual vessels are everywhere closely applied to the surface of the villi and fill up the intervals between them; they also closely embrace the fœtal processes, except at their expanded summits, which, as before stated, are in contact with the secretion of the glandular cells. The maternal vessels in proceeding from the uterus first ramify on the parietes of the cells, by which they are supported; but as they approach the villi and surface of the ovum they form an abundant network, the branches of which are unsupported by membranous structure, seemingly as if the intermediate tissue of the decidua had disappeared, its vessels alone remaining in the later periods of pregnancy. At parturition the decidual vessels come away with the ovum, the parietes of the now greatly enlarged glandular cells also separate in great part from the uterus, leaving merely the bottoms with the round openings of the glandular ducts in their centres. After separation of the ovum and placenta, numerous truncated and somewhat shriveled vessels project from the inner surface of the uterus; they are chiefly veins, and they may be seen for a considerable time after parturition on those parts of the uterus to which the ova had been attached.

From the description given, then, it follows, that in the placenta of the bitch there is an arrangement by which a matter secreted from the enlarged glands of the uterus is brought into proximity with the vessels of the fœtus, and seeing that a provision of a similar nature is found in various other instances, it is not improbable that in viviparous animals generally a matter deposited from the maternal system by means of a glandular apparatus may be absorbed into that of the fœtus and serve for its nutrition; but this is a question which can be determined only after a more extended investigation. As connected with this subject the source of the well known green-coloured deposit found at the borders of the placenta of carnivora would naturally become an object of inquiry, but on this point I cannot as yet speak with certainty.

Human Decidua.—These observations on the decidua of the dog led me to examine anew the human decidua, and more especially its relations to the mucous membrane of the uterus, and I shall now briefly state the result, although I find I have been in a great measure anticipated by Weber, as appears from the statement of Professor Müller in the text. It is right to mention, however, that the results were arrived at quite independently of Weber's observations, and, indeed, before the original of the pages of this work in which they are noticed reached me.

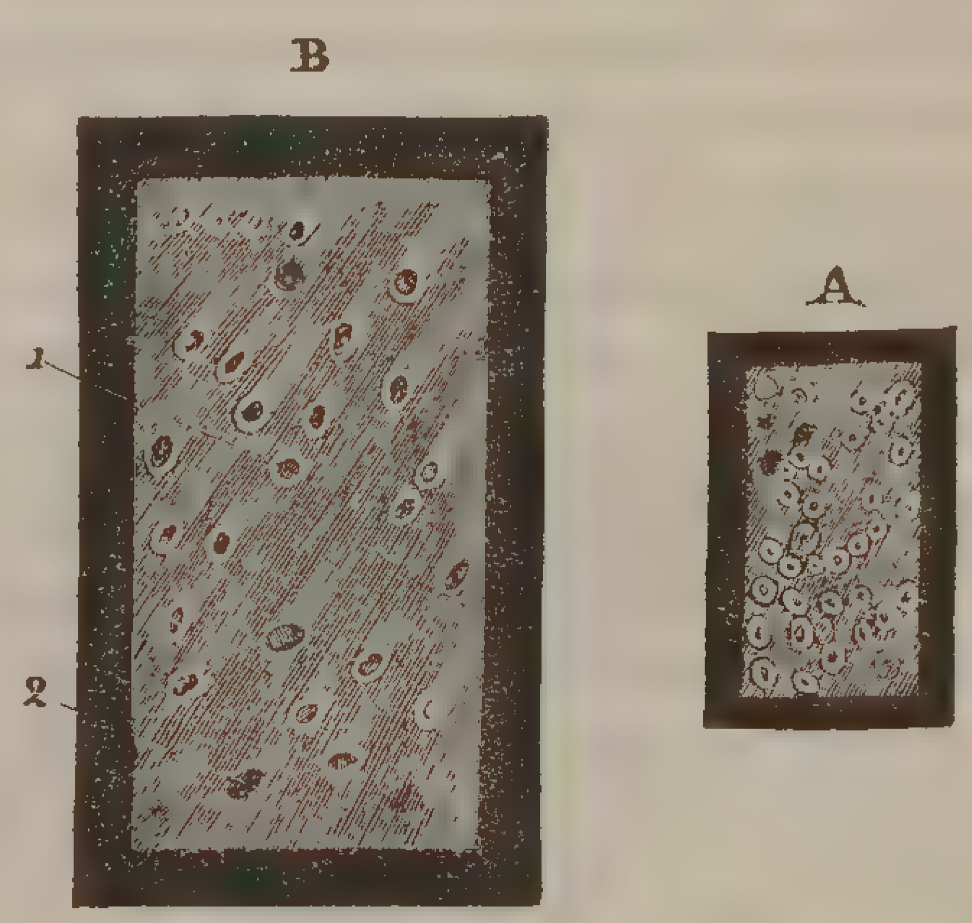
In various instances in which there was reason to believe that impregnation had recently taken place, and in which the ovary contained a recent corpus luteum and the uterus a distinct decidual lining, though no ovum had been discovered, the decidua, in some places $\frac{1}{10}$th of an inch thick, seemed obviously to consist of the thickened mucous membrane. Its surface presented a multitude of small round apertures (fig. 216)

* Müller's Archiv. 1834, p. 8.

have been made by Wagner and Dr. Allen Thomson. The latter anatomist has indeed seen the umbilical vesicle at so early a stage of development, that its walls were, without any constriction, directly continuous

which, on a vertical section, were seen to belong to the tubular glands of the mucous membrane, elongated, and enlarged. These tubes were lined with a white epithelium, (as at 1,) which rendered them very conspicuous; they were much waved and contorted towards their deep and doubtless closed extremity, and at various parts they appeared to be implanted at some depth in the tissue of the uterus. Whether any of them divided into branches I could not determine. In a specimen belonging to Dr. John Reid, the uterus contained an early ovum, considered as dating little more than fifteen days after conception. The decidua vera was somewhat corrugated on the surface, it had the usual cribriform aspect and the pits were for the most part wider than in the earlier examples; but the smaller orifices still presented the character of the tubular glands, and others showed an obvious transition between these and the larger ones. On making a section parallel with the surface, it appeared that many of the pits had a comparatively wide cavity with a narrow orifice. From these and other observations of a similar kind I was led to conclude that the apertures on the decidua which give to that membrane its well known cribriform character, however much they may be modified in the later stages of pregnancy, are originally nothing else than the openings of the glands of the lining membrane of the uterus, and that, as in the bitch, the mucous membrane is really converted into the decidua, and discharged from the uterus at parturition; an opinion, it may be remarked, adopted on other grounds by various continental physiologists. In a uterus supposed to have been recently impregnated, and in which the vessels had been minutely injected with vermilion, the lining membrane or commencing decidua appeared everywhere pervaded by a network of blood-vessels, in the midst of which the tubular glands were seen, their white epithelium strongly contrasting with the surrounding redness. In more advanced stages the veins of the decidua form large ramifying canals in the substance of the membrane, which freely communicate with the uterine veins. On inflating these venous canals of the decidua with a blowpipe, the air will frequently pass out at the openings on the surface of the membrane which we have considered as the orifices of the enlarged uterine glands, and it might hence be concluded that there is a natural communication between the two. I am nevertheless disposed to think that the venous canals and glandular recesses form two separate systems of cavities within the decidua, divided from each other by very thin parietes which are easily ruptured. I am inclined to adopt this opinion in consequence of repeated examination, in various ways, of the structure

Fig. 216.*



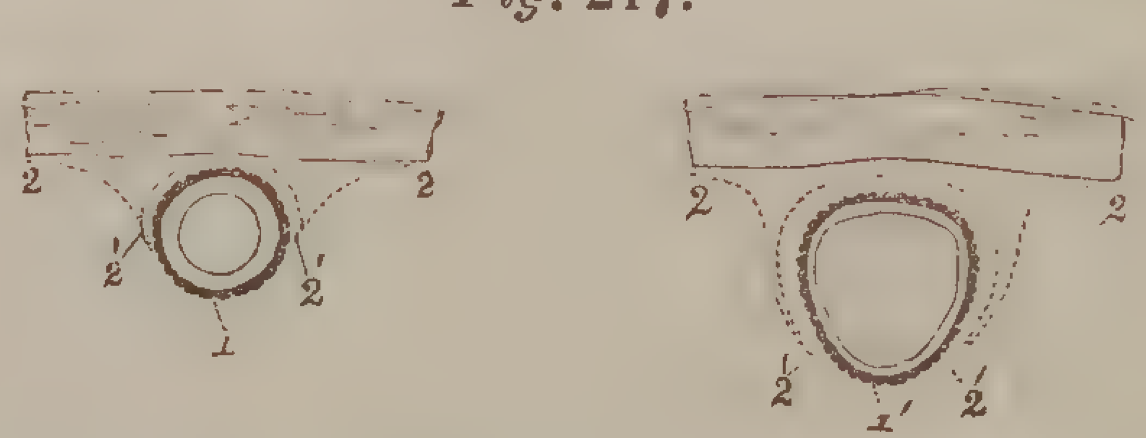
* Fig. 216. Two thin segments of human decidua after recent impregnation, viewed on a dark ground; they show the openings on the surface of the membrane. A is magnified six diameters and B twelve diameters. At 1 the lining of epithelium is seen within the orifices, at 2 it has escaped.

with the borders of the carina of the embryo. In a drawing of a very young embryo, which has been sent to me by Professor E. H. Weber,

in question (though I must admit that the result has not been always favourable), and also from considering that the pits in the decidua appear, as already stated, to be merely the enlarged uterine glands, which, when observed in earlier stages, seem to have the same relation to the surrounding blood-vessels of the decidua as is known to subsist between glands and blood-vessels in general.

An objection to the opinion that the decidua is merely the altered mucous membrane of the uterus which will naturally occur, is the difficulty of accounting on that view for the investment of the ovum by the decidua reflexa, which is continuous with the uterine decidua and is believed by most, though not by all physiologists, to have a similar origin. At the same time the force of this objection is lessened by the fact, that the decidua reflexa, though continuous with the vera, does not, usually, at least, present the same character as the vera throughout its whole extent; for, without laying stress on the differences generally pointed out by authors, I may state, that in various conceptions which I have examined the decidua reflexa in a great part of its surface was destitute of the small orifices which characterise the vera, and that these were confined chiefly, though certainly not entirely, to a zone of the membrane adjoining the angle of reflexion, that is, to the part next the decidua vera. Now, if this observation be found to hold good generally, it will not be necessary to suppose that the lining membrane of the uterus is extended over the whole surface of the ovum to form the decidua reflexa; and although I am not prepared on such limited observation to offer a decided opinion, especially on a question of acknowledged difficulty as this is, still, as at least a possible explanation, it might be suggested that the minute ovum on its entrance into the uterus is covered with exuded lymph (1 in diagram), either entirely or on that part of its surface which does not adhere to the inside of the uterus; that as the ovum enlarges, a circular fold (2′ 2′) of the altered mucous membrane (2) (decidua) is drawn up upon it, all round its adhering part, enveloping the ovum to a greater or less extent, and afterwards forming the cribriform zonular portion of the decidua reflexa, whilst the remaining thin smooth portion of the latter membrane, which is more distant from the line of reflection, and is destitute of apertures, is formed by an extension of the covering lymph (1′). Or perhaps the following more simple explanation might not be inadmissible; viz. that the minute ovum on reaching the uterus becomes imbedded in the substance of the then soft and pulpy mucous membrane, and that in its subsequent enlargement it carries along with it a covering of the membrane, which is expanded into the decidua reflexa.

Fig. 217.



Are the cells observed in the human decidua, by Dr. Montgomery, identical with the dilated uterine glands? Dr. M. occasionally found them to contain "a milky or chylous fluid," but he does not describe them as opening on the inner surface of the membrane.

In acknowledging the kindness of my friend, Dr. John Reid, now Professor of Medicine, in St. Andrews, in freely placing at my disposal some very valuable specimens in his collection, I deem it due also to that gentleman to state that he had previously observed the tubular structure of the mucous membrane of the uterus, and was led, by an examination of recently impregnated uteri, to infer that one of the earliest changes which occur after impregnation was an increased development of the tubular strucnot only the duct of the umbilical vesicle, but its blood-vessels also are seen.*

ture, and this he conceived was connected with the formation of the decidua: at the same time he did not suppose that the mucous membrane was converted into the decidua, but was disposed to think that the decidua was secreted by the tubes of the mucous membrane."]

* [The blood-vessels of the umbilical vesicle (omphalo-mesenteric vessels) are beautifully shown in the preparation of a human embryo belonging to Dr. Sharpey, who has allowed a drawing of the preparation (plate iii.) to be made for the use of this work. Figure 218 is an outline copy of the plate referred to. The aborted ovum measured about $1\frac{1}{2}$ inch. Abundant and large villi extended from the chorion (1) to the decidua at the part where the cord was attached. The amnion (2) is laid open, and the fœtus is seen lying at the bottom of its cavity. The extreme length of the fœtus was $1\frac{1}{20}$ of an inch; the length of the head from the vertex or highest point to the indentation beneath the jaw was $\frac{1}{2}$ an inch. The vesicula umbilicalis (3), rather more than $\frac{1}{10}$th of an inch in diameter, was left adhering to the outside of the amnion when the chorion was separated. The length of the pedicle from the vesicle itself to the point where it entered the umbilical cord was $\frac{7}{10}$th of an inch. On laying open the abdomen of the fœtus and the cord, it was found that the intestine (4) on leaving the stomach made a turn to the right; then after a retrograde bend it passed through the umbilicus into the cord, at first straight (5), then making three coils in the cord, then returning straight again (6) into the abdomen,

Fig. 218.

and terminating at the lower end of the body. This straight returning portion was the large intestine, as was indicated by the commencing cæcum which appeared at the point where the coils within the cord terminated. (See fig. 5, plate iv.) The umbilical vein (7) could be easily traced in the cord, and in the abdomen could be seen entering the lower part of the liver (9), being there connected with the intestinal vessels (vena porta? 8). The umbilical arteries also (12) were easily seen. On tracing back the fine pedicle of the umbilical vesicle towards the fœtus, it was seen, on approaching the intestine, to consist of two filaments which were separated by the coil of intestine. After a nice dissection, one of these (11) was traced back to the small intestine in the

In young ova the chorion is separated by a large interval from the amnion, which at that period closely embraces the fœtus. This space is filled with a substance which is sometimes of a fluid consistence, at others gelatinous,—the " corps reticulé " of Velpeau (see fig. 224, page 1589). A thin layer of membrane (the Endochorion) may be readily separated from the inner surface of the chorion ; so that the gelatinous or fluid body just described appears to be included in a special sac. Sometimes reticulated filaments traverse the gelatinous mass, being connected on the one hand with the endochorion, and on the other with the amnion. Many anatomists,—for example, Velpeau among the more recent writers, — have regarded this substance with its including membrane as the allantois of the human ovum, it being placed between the amnion, umbilical vesicle, and chorion, nearly in the same position as the allantois of Mammalia. This view has never been confirmed by observations on the development of the human allantois ; and it is, moreover, in itself improbable. The " corps reticulé " appears to be a mere albuminous secretion; while the allantois very probably, like the same part in the ovum of rodent animals, is developed merely as a narrow vesicle which elongates itself till it reaches the chorion, and is only destined

abdomen which it joined almost immediately below the stomach, enlarging somewhat at the point of its junction. This seems to be the omphalo-mesenteric vein. The other filament (10), also after a nice dissection, was found to proceed from the mesenteric vessels. These vessels appeared to arise by a thick tapering origin near the first turn of intestine which embraced them in its concavity ; they then passed forwards to the part of the intestine contained in the cord, dividing into three or more chief branches, and from the middle one of these branches the second filament of the umbilical pedicle (the omphalo-mesenteric artery) proceeded. This origin of the omphalo-mesenteric artery is displayed in fig. 5, plate iv. A part of the sheath of the cord is seen in plate iii. and in fig. 218 (13). The other anatomical facts observed in this fœtus were the following :—The eyeball (14) was surrounded by the circular border — the orbit—but was destitute of eyelids. The external ear (15) presented, faintly marked, the helix, antihelix, tragus, antitragus, and concha, but was scarcely elevated above the surface. There was no prominent nose. The nostrils were two round apertures less than $\frac{1}{20}$th inch apart, *from each of which a white line* extended downwards and a little outwards to the mouth, — a large transverse slit $\frac{2}{10}$ths of an inch long, and nearly on a level with the external ear. The limbs were distinctly divided into arm and fore-arm, thigh and leg ; the fingers and toes appearing as rounded lobes at the broad edge which terminated the limb, while higher up they were separated by grooves.

In another, younger fœtus (measuring $\frac{6}{10}$ths of an inch in length) also dissected by and in the possession of Dr. Sharpey, the filament which appears to be identical with the omphalo-mesenteric vein has been traced further into the abdomen, — namely, beneath the intestine to the membrane, and probably to the vessels, which lie in the concavity of the first intestinal turn. This fœtus is represented in fig. 4, plate iv. The canal of the intestine has been cut transversely, and the minute filament or vessel is seen passing beneath it.

The above description of the embryos and corresponding figures is derived from Dr. Sharpey's notes].

to conduct the umbilical vessels to that membrane. This view is supported by the observations of several embryologists,* who have seen two vesicles with narrow necks projecting from the abdomen of the early human embryo. (See fig. 220, page 1585.) The short and thick cord also which passed from the caudal part of the embryo to the chorion in the ovum, described some years since by myself,† appears to have been the allantois. (See figs. 1, 2, and 3, plate iv.) This cord was not composed of vessels, but appeared to be a simple structure. The same body is more distinctly seen in the ovum figured by Wagner.‡ (See fig. 222, page 1587.) In many cases the end of the allantois seems to dilate a little at the point where it is inserted into the chorion. Von Baer says that in all the ova of the first and second month which he has examined, he found a very small flattened vesicle at the point of attachment of the umbilical cord to the chorion, which communicated more or less distinctly with a duct contained in the cord. The vessels ran in contact with this duct which could be traced into the Cloaca.

Von Baer proposes two modes of explaining the connection of the allantois with the chorion. The vascular layer of the allantois may separate from the mucous layer and apply itself in the form of a distinct membrane to the external tunic of the ovum or the chorion; while the mucous layer remains in the form of a canal; in which case the albuminous mass found between the chorion and amnion would be a deposit between the vascular and the mucous layer of the allantois, such as takes place at a later period of development in the Solidungula. According to the other view, this separation of the layers of the allantois, does not take place; but the umbilical vessels extend from the small allantois, and implant themselves in the chorion; while the allantois itself undergoes no further development, and at length entirely disappears, leaving merely its pedicle—the urachus. If this were the process, the albuminous mass would be a deposit formed beneath the external tunic of the ovum; while that membrane assumed the character of the chorion. There are instances of the occurrence of both these processes in different mammiferous animals. Von Baer regards the latter as the more probable explanation; and I am myself of the same opinion, chiefly on the ground that Wharton Jones and Allen Thomson have observed the presence of the albuminous or reticulated mass in ova, where the embryo was not yet attached to the chorion, and the allantois consequently not de-

* Pockels, Isis, 1825. Tab. xii, xiii. Coste, Embryog. Tab. iii. figs. 4 and 5. Seiler. Tab. x. Von Baer's Entwickelungs-geschichte. Tab. vi. figs. 15 and 17; and in Siebold's Journal, No. xiv. figs. 7 and 8. A. Thomson, Edinb. Med. and Surg. Journal, No. 140, fig. 3, plate iii.

† Müller's Archiv. 1834, p. 8; and 1836, p. 167.

‡ Icon. Physiol. Tab. viii. fig. 2 and 3.

veloped. According to this view, the lamella lining the inner surface of the chorion would probably be the membrana serosa already described. (See page 1571.)

When the embryo by means of its vessels has gained a vascular connection with the chorion, the allantois can no longer be discovered, the urachus of the urinary bladder,—a filament extending into the umbilical cord,—being its only remains.

The successive changes which the ovum undergoes may be referred to the following stages: — The first stage extends to the appearance of the embryo, elevating itself above the surface of the yolk-sac. The changes which occur during this period are the least known; but the villi of the chorion are at this time developed. This stage is illustrated by an observation of Mr. Wharton Jones.* The ovum which he describes had the size of a pea, and was stated to be aborted in the third or fourth week after impregnation, but may have become detached at a much earlier period. It lay imbedded in one side of the uterine decidua. One side of its external surface was smooth, the other beset with villi. The whole cavity of the chorion was filled with a gelatinous tissue, in which towards one end of the ovum a small round body, — the vesicular germinal membrane, — was imbedded. The embryo was not yet visible.

In the second period the embryo becomes separated by a constriction from the yolk-sac, and the amnion and allantois are developed; but the embryo is not yet attached to the chorion by means of the latter membrane. Two ova, observed by Dr. Allen Thomson,† belong to this period. Both these ova were beset with villi of the chorion. One measured one-quarter of an inch, the other one-half of an inch in diameter. In the smaller one the yolk-sac or umbilical vesicle occupied the greater part of the cavity of the chorion, but did not entirely fill it, the space between them being occupied by a thin tenacious web of albuminous filaments. The embryo, one line in length, lay with its abdominal side nearly flat on the surface of the yolk-sac, with which it formed a common cavity.

In the second ovum (fig. 219) the cavity of the chorion was in proportion to the embryo very large, and was filled with the above-mentioned filamentous tissue. The embryo and yolk-sac were connected to the chorion by a part of this tissue which was more dense than the rest. The embryo was not attached to the yolk-sac by a narrow pedicle, but lay nearly flat upon it, its sides passing uninterruptedly into the parietes of the yolk-sac. In this embryo the dorsal laminæ were remarkably dis-

* Philos. Transact. 1837, p. 339. [See also an account of an early ovum observed by Volkmann, in Müller's Archiv. 1839, p. 248.]

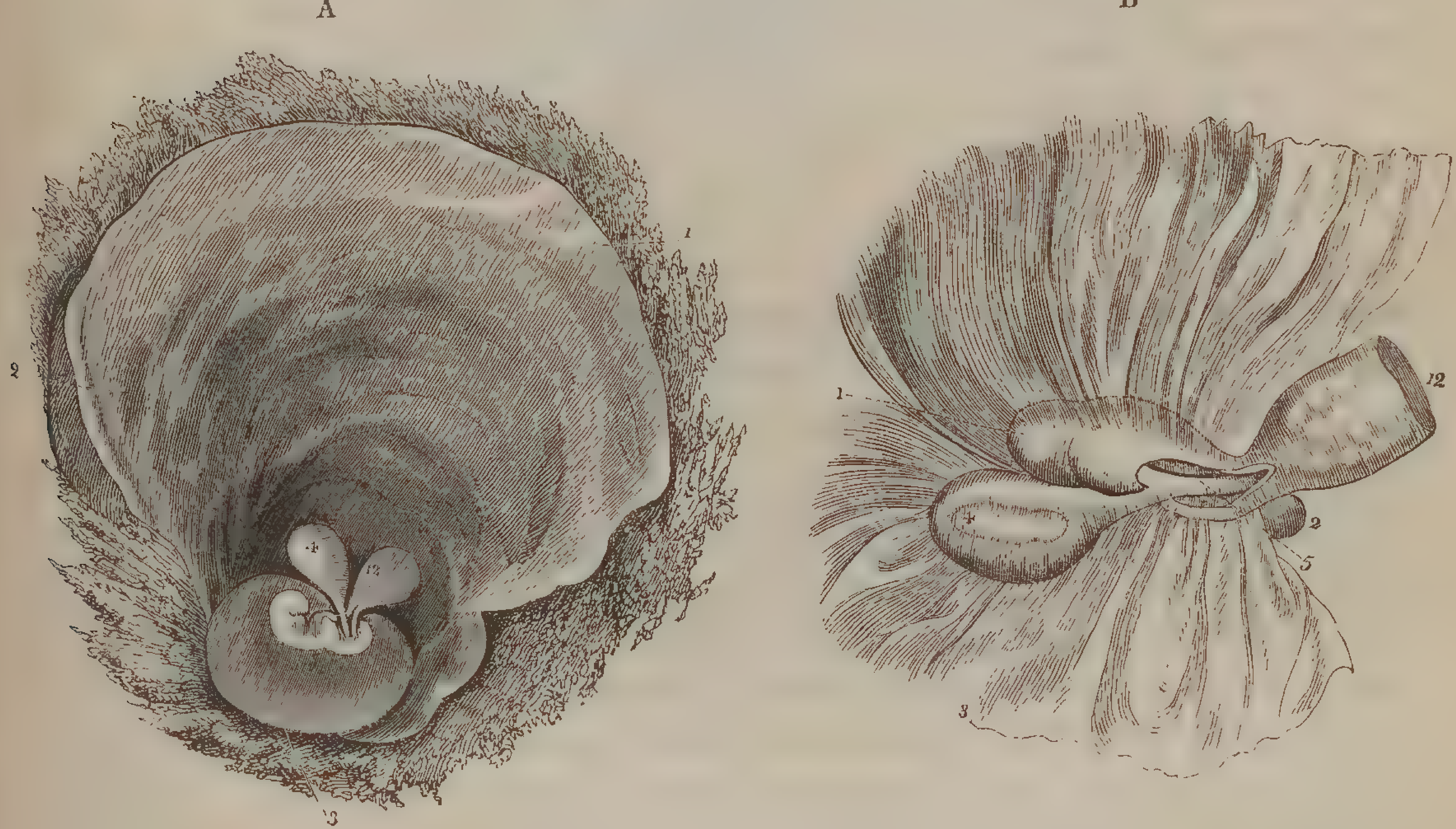
† Edinburg Med. and Surg. Journal, No. 140, figs. 1 and 2.

tinct, they not having united at this period. Neither allantois nor amnion were present.

Fig. 219.*

To the same period are to be referred several ova in which the allantois has been observed in the progress of development. In these ova,—for example in those described by Pockels and Coste (see fig. 220),—two pedunculated vesicles project from the abdomen of the embryo, but neither is attached to the chorion.

Fig. 220.†



* [Fig. 219. The second ovum described by Dr. A. Thomson, and dating little more than fifteen days from conception. A, the cavity of the chorion laid open, showing in its upper part the yolk-sac with the embryo lying across it. B and C, the yolk-sac and embryo magnified ten diameters. The cephalic extremity of the embryo is uppermost: 1, indicates the open vertebral canal; 2, the folds of the intestinal groove; 3, the situation of the heart; 4, a piece of membrane which may be connected with the formation of the chorion.]

† [Fig. 220. A, An ovum belonging to a period between the 16th and 20th day, described and figured by Coste. "It is magnified to the extent of four diameters. The decidua, 1, and the chorion, 2, have been partially removed; and the embryo is dis-

A third stage of development extends from the period of the attachment of the ovum to the choroid by means of the allantois, to the complete formation of the umbilical cord. The amnion, however, has not yet formed a sheath to the umbilical cord, enclosing all the parts which issue from the abdomen of the embryo. This stage also is illustrated by an observation of Dr. Allen Thomson. The fœtus in this ovum (Fig. 221) was $\frac{1}{8}$ of an inch in length. The heart hung from the anterior aspect of the body in the form of a looped vessel. The intestine was a straight canal, the mouth being present, but the anus not open. At the middle of the body the intestine opened by a wide orifice into the yolk-sac, or umbilical vesicle, which was beginning to become narrowed at its lower part. From the more posterior part of the fœtus a pear-shaped body projected, which attached it to the chorion. Two branchial clifts were visible. The amnion was already not present (probably from the development of the ovum having been

Fig. 221.*

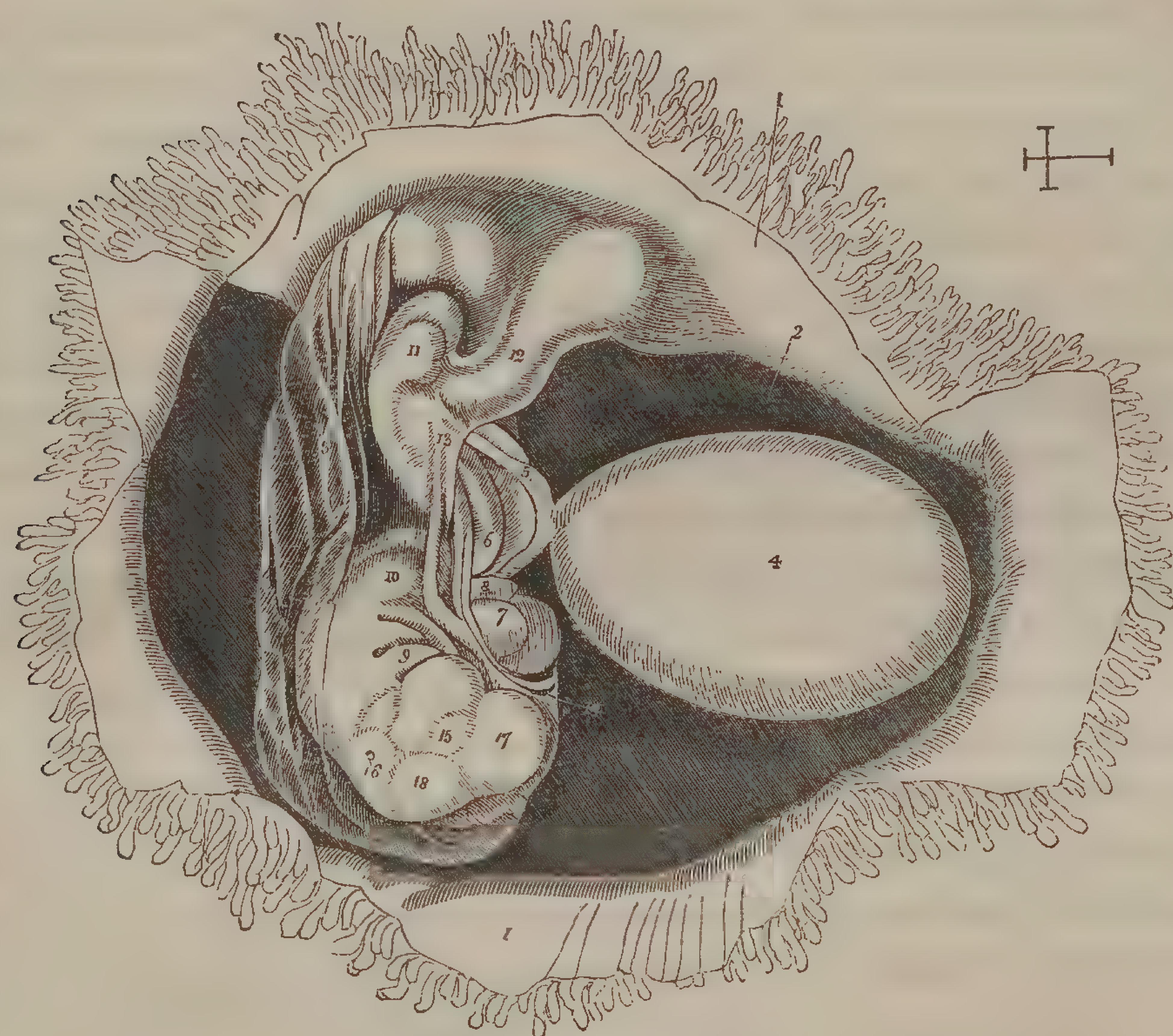
tinctly seen enveloped in the amnion, 3; the umbilical vesicle, 4, projects from the middle of the body; and the allantois, 12, situated nearer to the posterior extremity of the embryo, is beginning to apply itself to the chorion. The pedicles of both enter the umbilical aperture, but are quite distinct from each other."

B. "The embryo from the same ovum magnified ten diameters. The cephalic extremity of the embryo, 1, is seen through the transparent amnion, 3; 2, is the caudal extremity of the embryo. The umbilical vesicle, 4, communicates directly with the intestinal tube, 5; and the allantois, 12, flattened at its extremity, by which it was in contact with the chorion, is continued laterally into the future abdominal parietes of the embryo; whilst its middle part dips down into the pelvic cavity, where it communicates with the intestine."]

* [Fig. 221. The third embryo described by Dr. A. Thomson, and dating five or six weeks from conception. 1,1,1, indicates the head, body, and caudal extremity of the embryo; 2. the heart in the form of a bent tube; 3. two branchial slits; 4. the umbilical vesicle or yolk-sac; 5. the pyriform part, connecting the caudal extremity of the intestine and embryo with the chorion (6). The fœtus has been removed from the ovum along with the umbilical vesicle of a portion of the chorion, and represented magnified eighteen diameters.]

abnormally modified). Next in order to this ovum we must place two ova, precisely similar to each other, which have been observed, one by Wagner (Fig. 222), and the other by myself. The latter is the one

Fig. 222.*



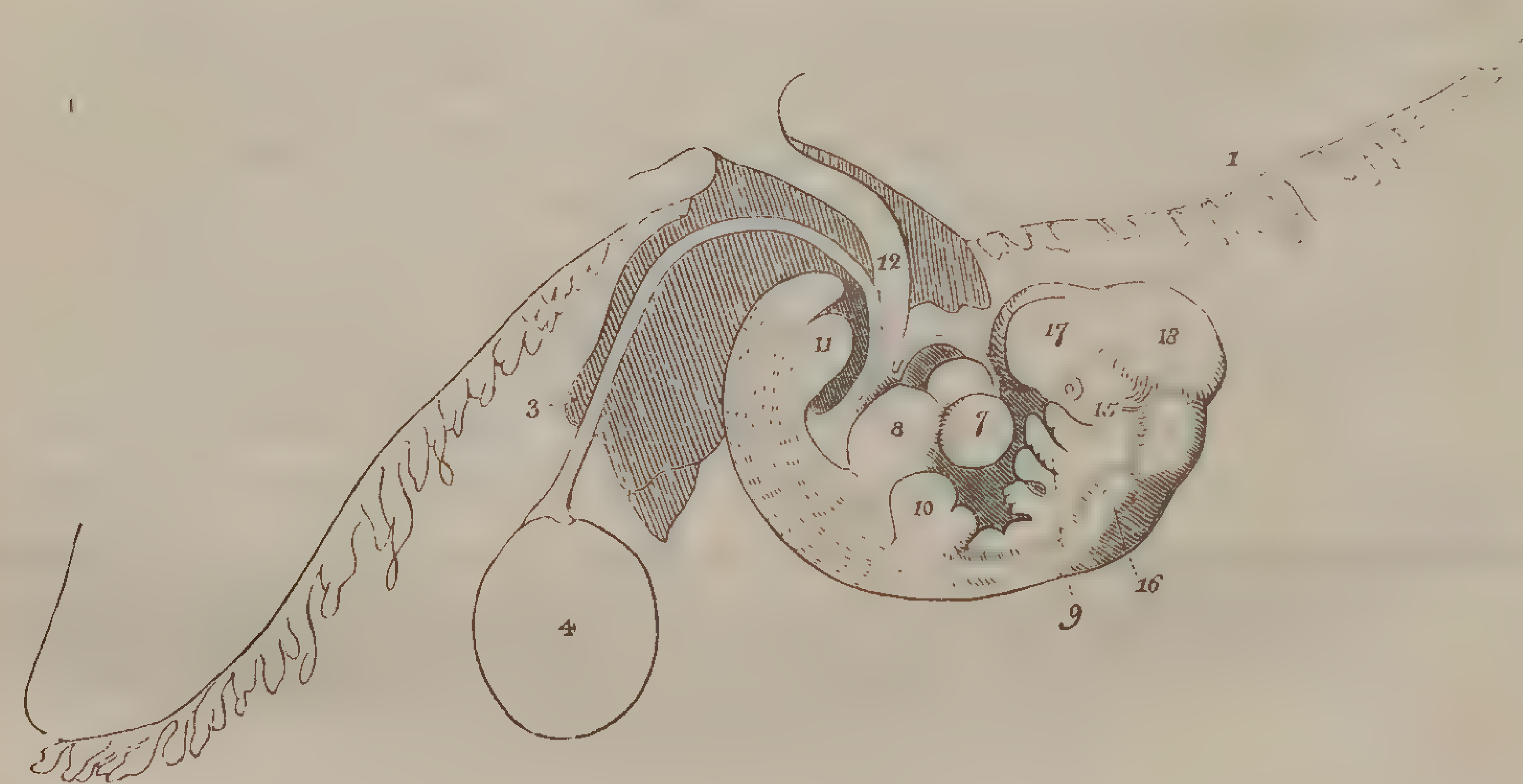
mentioned at page 1583. This ovum measured from seven to eight lines in diameter. It was sent to me by Dr. Wolff of Bonn. Figures 1, 2, and 3, Plate III. are copies of a drawing of the ovum and embryo, which Prof. D'Alton had some time since the kindness to make for me. The embryo is $2\frac{1}{2}$ lines in length; the thick umbilical cord measures $\frac{2}{3}$ of a line, and the umbilical vesicle $1\frac{1}{2}$ line in diameter. The amnion is so closely applied to the embryo as to be scarcely distinguishable with the naked eye. It is continued from the lamina abdominalis at the margin of the wide abdominal opening, and has become united with the whole length of the umbilical cord at its lower surface. The intestine is a canal occupying the cavity of the embryo, and opening directly by a

* [Fig. 222. The ovum and embryo described and figured by Wagner, and belonging to the third week (about the 21st day) from conception. The natural size of the embryo is shown at the side. 1. the chorion opened and reflected back; 2. the space between the chorion and amnion; 3. the amnion; 4 the umbilical vesicle or yolk-sac; 5. the intestine; 6. the corpus Wolffianum; 7. the heart; 8. the liver; 9. the inferior maxilla; 10. the anterior extremity; 11. the posterior extremity; 12. the allantois; 13. and 14. the points where the amnion is reflected back over the cephalic and the caudal extremities of the embryo; 15. the rudiment of the eye; 16. the ear; 17. the cerebral hemispheres; 18. the corpora quadrigemina.]

very wide orifice into the umbilical vesicle, at the point where the abdominal lamina is reflected into the amnion; so that in the situation of the future duct of the umbilical vesicle there is merely a slight constriction. The cervical region of the embryo presents three pairs of branchial clefts and arches, behind which, in the middle line, the tubular heart projects from the anterior face of the embryo. This ovum is particularly interesting from the time at which the coitus took place being accurately known. It was on the 2nd of December; at the next menstrual period, namely the 25th of December, the menses did not appear: on the 27th the coitus was repeated, and on the 5th of January abortion took place. If we were guided simply by these data, the age of the ovum must be either thirty-four or nine days. I regarded the latter view as improbable. (Von Baer and Wagner were incorrect in attributing to me the contrary opinion.) Von Baer conjectures that the ovum became separated during the second coitus, and, consequently, that it should be referred to the twenty-fifth day of development: Wagner is of the same opinion.

The ovum of three weeks' development, which is represented by Wagner (fig. 222) is in a very similar stage of formation. The rudiments of the extremities are just perceptible in the form of leaf-shaped projections. The different parts of the ovum are represented in so similar a state and form in the drawings of these two ova, that we seem to be justified in assuming them both to be in the normal condition.*

Fig. 223.



* [Figures 223 and 224 represent the human embryo at stages of development somewhat further advanced. Figure 223 shows an embryo of the fourth week, described and figured by Müller in Meckel's Archiv. 1830. The length of the embryo was 3½ lines. The ovum was open and the amnion torn, when it was obtained by Prof. Müller. 2. is the chorion; 3. a remaining part of the amnion, which was firmly attached to the chorion at the point of insertion of the umbilical cord; 4. the umbilical vesicle from which the long pedicle passed, enclosed in the

The space between the chorion and amnion filled with albumen exists only during the first and second months of pregnancy. In consequence of the growth of the amnion, the two membranes come into close relation with each other; although they are still separated by the tunica media, so accurately described by Bischoff.

The umbilical vesicle, which at first communicates with the intestine by a wide and short passage gradually, like the yolk-sac in birds, acquires a long and delicate pedicle, the "ductus omphalo-entericus," which is accompanied by the vasa omphalo-meseraica. This duct and the accompanying vessels then form part of the umbilical cord, the contents of which are held together by the reflected tube of the amnion, the "vagina funiculi umbilicalis." The umbilical vesicle, filled with a yellowish white yolk, is then found constantly lying between the chorion and amnion, at a varying distance from the insertion of the umbilical cord into the placenta. About the third month the vesicle, which has

umbilical cord, into the abdomen of the embryo; 7. the heart; 8. the liver; 9. the visceral arch destined to form the lower jaw; beneath which are two other visceral arches separated by the so-called branchial clefts: 10. is the rudiment of the upper extremity; 11. that of the lower extremity. 12. is the umbilical cord; 15. the eye; 16. the ear; 17. the cerebral hemispheres; 18. the optic lobes or corpora quadrigemina.

Fig. 224.

Fig. 225.

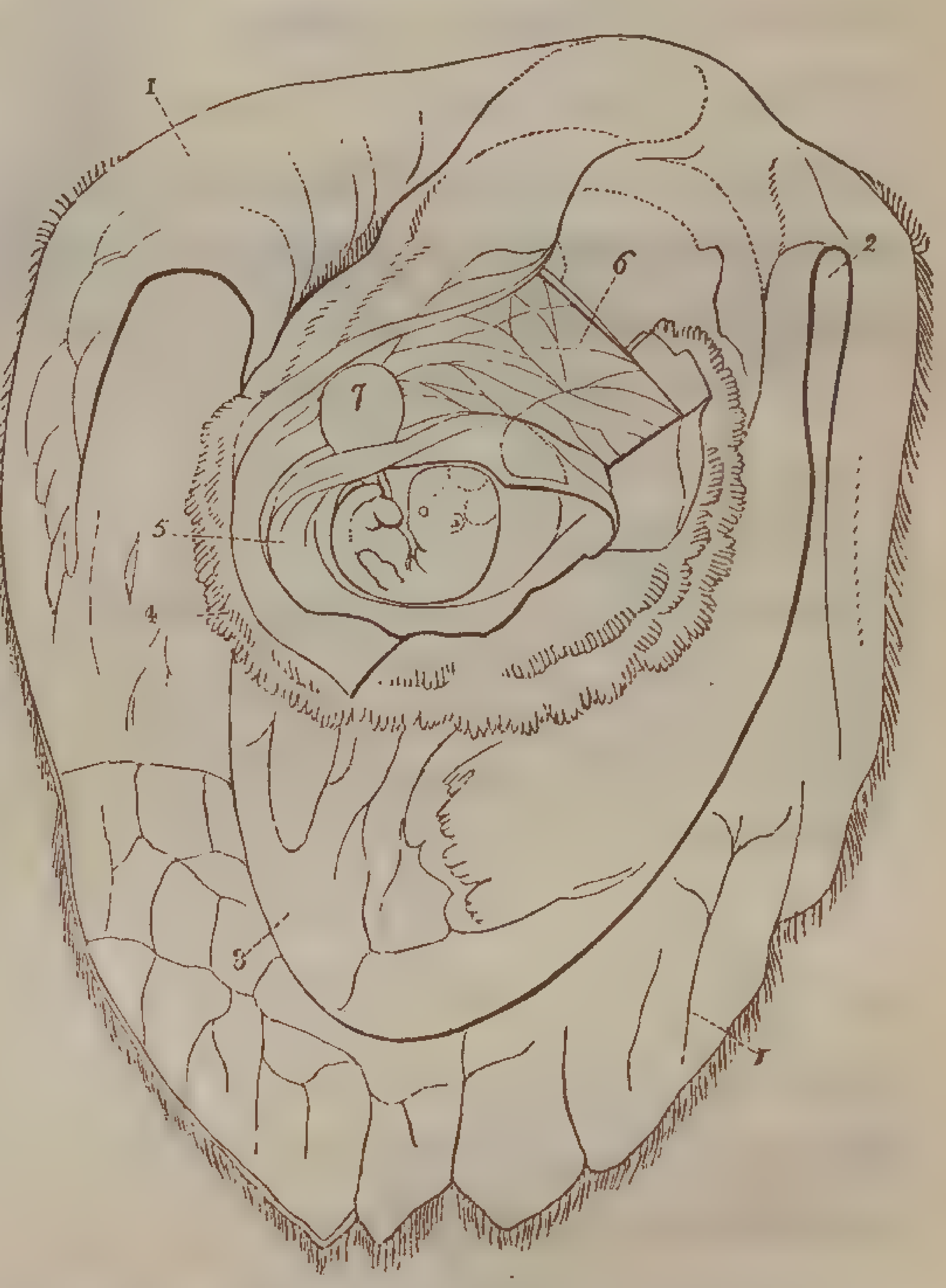


Fig. 224 represents an aborted ovum and embryo of five weeks, described and figured by Wagner, Icones Physiol. Tab. VIII. Figs. V. and VI. The various parts of an ovum at this period are well seen, and all are in their normal state except the decidua reflexa. Fig. 225 the same in outline. 1. indicates the decidua vera reflected at 2, into the decidua reflexa (3.) which is thickened by the infiltration of blood; 4. the villi of the chorion; 5. the amnion laid open; 6. the "corps-reticulé;" 7. the umbilical vesicle.]

acquired the diameter of four or five lines, begins to become atrophied. The same is the case with its duct or pedicle. Sometimes however, as Mayer has shown, both the vesicle and delicate thread-like pedicle can be detected even in ova of the full period of gestation.

When the Amnion and Chorion have come into close relation with each other, the ovum undergoes very little further change, except that the villi of the chorion become accumulated at one spot in order to the formation of the "placenta," and that the vessels of the chorion extend at this spot only into those branched processes or villi with clubbed extremities which, like the rest of the membrane, are composed of nucleated cells. The villi, however, do not disappear from the other parts of the chorion, but merely the interspaces between them become greater in consequence of the growth of the entire ovum. Even in ova of the full period these villi are still found upon the chorion.

During the development of the embryo the umbilical cord undergoes a constant increase in length.

In the fully formed ovum (fig. 226), the following membranes are found in passing from without inwards, closely applied to each other; first the decidua (3, 5), next the chorion (6), and last the amnion (9); the amnion being reflected upon the inner surface of the chorion at the point of insertion of the umbilical cord (11), of which it forms the sheath, while at the umbilicus it becomes continuous with the inte-

Fig. 226*

* [Represents a perpendicular section of a uterus with a fully formed ovum. A plug of lymph (1) occupies the cervix uteri; 2, indicates the opening of the Fallopian tube of one side; 3, the decidua vera; 4, the cavity of the uterus nearly filled by the ovum; 5, the decidua reflexa; 6, the chorion; 7, the decidua serotina (see page 1573); 8, the allantois and the situation of the future placenta; 9, the amnion; 10, the umbilical vesicle; 11, the umbilical cord. This diagram is copied from Wagner's "Icones Physiologicæ." Tab. vii. fig. x.]

gument of the embryo. The cord invested by this tubular sheath of the amnion, contains the following parts:

1. The remains of the ductus omphalo-entericus, or pedicle of the umbilical vesicle; accompanied by

2. The vasa omphalo-meseraica, branches of the mesenteric vessels of the fœtus;

3. The urachus; and,

4. The vasa umbilicalia, which in the later period of uterine gestation constitute the principal part of the umbilical cord. In mammiferous animals there are generally two umbilical veins as well as two arteries; but in the human subject there is but one umbilical vein and two umbilical arteries. The umbilical arteries are the main branches of the arteriæ hypogastricæ. They convey the blood of the fœtus into the placenta, or rather into the vessels of the aggregated villi of the chorion, which form the greater part of the placenta. In these villi which are imbedded in the decidua of the uterus or the uterine placenta, the blood of the umbilical arteries passes through loop-shaped capillaries into small veins, which by their union form the vena umbilicalis. The vena umbilicalis, of which the persistent vena abdominalis of reptiles and amphibia is the analogue, pours its blood partly into the vena portæ and partly through the ductus venosus Arantii into the vena cava.

The *liquor amnii* of the human ovum contains, according to the analysis of C. Vogt,* an alcoholic extract with lactate of soda, chloride of sodium, albumen, and sulphate and phosphate of lime. The liquor amnii of an ovum of 3½ months' gestation had a specific gravity of 1·0182; that of an ovum of 6 months, a specific gravity of 1·0092. In the former 1000 parts contained 10·77 parts of albumen; in the latter only 6·67 parts.†

Having thus passed in review the general changes which the human ovum presents in the progress of its development, I proceed to the consideration of a question which has been hitherto only incidentally mentioned;—I mean the question,—what import should be attributed to the resemblances observed to subsist between the embryos of different classes of animals. Not long since it was supposed and seriously affirmed by many naturalists that the human embryo previously to arriving at its perfect state passed through the different stages of development which are permanent conditions of other animals. This was a

* Müller's Archiv. 1837, p. 69.

† For representations of ova belonging to the different periods of utero-gestation I refer to the works of Soemmering, Leiler, Velpeau, and R. Wagner.

The writings which treat on the same subject are those of Kieser, Pockels, Burdach, Leiler, Velpeau, Bischoff, Valentin, Mayer, Coste, Von Baer, Wagner, and Thompson, which have been already referred to; also Wrisberg's Descriptio Anatom. Embryonis, Gött. 1764; Autenrieth's Suppl. ad Hist. Embryon. Hum. Tub. 1797, and the paper by the author in Meckel's Archiv. 1830. p. 411.

very bold hypothesis, and one that is by no means correct. Its falsity was well demonstrated by Von Baer. The human embryo in fact, at no period resembles a radiate animal, or an insect, a molluscous creature, or a worm. These animals are constructed after a plan which is totally different from that which regulates the formation of the vertebrata. Man, therefore, being a vertebrate animal, and being constructed according to the general type of the vertebrata could at most in the progress of his development present resemblances to other vertebrate animals. But it is not true even that he resembles at one time a fish, at another time one of the amphibia or reptiles, and at another time a bird; he merely bears the same resemblance to a fish which he does to a bird or reptile, namely, the resemblance which all vertebrate animals bear to each other. In their first condition, the embryo of all these animals have in the highest degree the most general and simple characters of the type according to which they are formed, and hence at this period they all resemble each other so closely, that it is often difficult to distinguish them. At first, therefore, the fish, the reptile, the bird, the mammal, and man conform very closely to the common type, but in the progress of their development they gradually depart from it; the extremity, for example, which was at first the same in all, by degrees assumes the form of a fin, a wing, a paw, or a hand. Hence we may understand how it happens that all embryos have at first arches separated by clefts at the sides of their neck, the parts unaptly termed branchial arches; these being merely an expression of the general plan of structure, and having as yet none of the attributes of branchiæ. In all animals these arches contain branches of the aorta, which reunite posteriorly to form the descending aorta; but it is only in fishes that they undergo a progressive metamorphosis, consisting of the development of branchial laminæ upon some of the arches, and of the conversion of the aortic vascular arches into a system of blood-vessels with a pinnate arrangement, and distinct arterial and venous trunks; the latter of which unite to form the descending aorta. The same process takes place in the Amphibia; but their branchiæ dwindle away at the time of the metamorphosis from the state of larvæ. The branchial vessels are reduced to the primary unbranched aortic arches; while their branchial arches for the most part disappear, and as happens at an earlier period in reptiles, birds, mammals, and man, are converted into other persistent structures. In the embryos of the latter animals the aortic arches also which are expressions of the common, simple type of the vertebrata, in greater part disappear, and there remain in the reptiles only two, or at most four arches, and in birds, mammals, and man, only one.

The process of development of the embryo itself will be described more minutely in the following section, in which the development of the different organs are treated of separately; but some of the principal changes in its form and size will be here recounted. *At the commencement of the second month* the length of the embryo extends to a few lines, or half an inch. The extremities are then visible in the form of leaf-like appendages; and the cavity of the mouth exists and is wide open; the anus is developed somewhat later; the coccyx is very prominent. The branchial clefts have not yet disappeared, though they soon afterwards become closed; the head acquires a considerable size; the eyes, which are at first placed laterally, assume a more anterior position, and the nasal cavities soon become developed. The attachment of the umbilical cord is yet very near to the posterior extremity of the trunk; but in the progress of development it moves more forwards, and at length occupies the middle point of the abdomen. *During the second month* the sheath of the umbilical cord is formed; the intestine, at first a straight canal, receives an angular bend with the apex of which the umbilical vesicle is connected, and this bent or loop-like part of the intestine is at this period received into the commencement of the vagina funiculi umbilicalis. (See fig. 4, Plate IV.) *Towards the end of the second month* ossification also commences at several points, and the rudiments of the muscular system are formed. The heart is covered in, and its septum begins to be developed; the aortic arches are reduced in number to two, which unite posteriorly to form the aorta descendens, and one of which subsequently becomes the pulmonary artery. The glandular viscera, the lungs, liver, and the Wolffian bodies exist. The formation of the last named organs is soon followed by the development of the rudimentary kidneys, and the testes or ovaries. The external organs of generation make their appearance in the form of a wart-like prominence in front of the cleft which leads to the sinus urogenitalis. The urinary bladder is formed at a later period by a part of the sinus just named, leading in the direction of the urachus, being separated from the rest by a constriction. At this time the oral and nasal cavities are not separated; the eyelids and external ear, however, are beginning to be formed; the different parts of the extremities become perceptible, and the hands and feet present marks of the division into the digits. The embryo is now about one inch in length. *In the course of the third month* the fœtus acquires the length of two and a half or three inches; *in the fourth*, during which the sex becomes distinguishable, it reaches to four inches; and *in the fifth* to twelve inches. At this period occur the formation of the fat, and the further development of the rudimentary horny structures, the nails and the down, lanugo, which appears over the whole surface, and the eyelids coalesce. In the fifth month, also, the movements of the embryo are felt by the mother. A fœtus born during the *sixth month* breathes, but does not continue to live. In the *seventh lunar month* the embryo acquires the length of 16 inches or more, and if expelled from the uterus is sometimes capable of living; its skin is red. In the *eighth lunar month* its length is $16\frac{1}{2}$ inches; the testes at this period descend from the abdominal cavity through the inguinal ring into the scrotum, which had hitherto the form of empty folds of skin; and the eyelids become free. In the *ninth month* the hair appears on the head, and the embryo measures 17 inches in length. In the *tenth lunar month* its length reaches 18 or 20 inches. At this period, or even during the eighth or ninth month, the membrana pupillaris disappears; and the skin, no longer so red, is covered by an unctuous matter, the "vernix caseosa," which, according to R. Wagner, consists of the desquamated scales of epidermis. In other animals the skin seems to throw off the epidermis in the form of a continuous membrane, and hence the body of the embryo has been frequently seen enveloped in this free epidermal membrane, whilst the hairs which had been formed subsequently were growing beneath it.

CHAPTER IV.

OF THE DIFFERENCES PRESENTED BY THE PROCESS OF DEVELOPMENT IN OVIPAROUS AND VIVIPAROUS ANIMALS.

The development of the ova of different animals takes place under very different conditions. Sometimes the ova are expelled from the system of the mother, and undergo development independently of it, the requisite nutriment being contained within themselves. Such is the case in oviparous animals. In other instances the ova are developed within the body of the mother, but yet lie free in the cavity of the uterus, with which they have no organic connection. Here also they derive for the most part no nutriment from without, although they may appropriate for their growth the fluid secreted by the uterus. I propose to apply the name of "Vivipara acotyledona" to all those viviparous animals, the ova of which are not connected with the uterus by means of vascular cotyledons or a placenta. The third class of animals are those in which such a connection with the uterus, destined for the assumption of nutriment, exists. These are "Vivipara cotylophora." In all these animals the ovum when it enters the uterus is very small, it not being necessary that it should contain a supply of nutriment within itself.

I. *Ovipara.*

The greater number of animals, invertebrate as well as vertebrate, are oviparous. The oviparous vertebrata comprehend the majority of fishes, reptiles, and birds. Few of the plagiostomatous fishes (the Sharks and Rays), however, are oviparous; namely, among the sharks only the family Scyllium, with seven genera, and amongst the rays only the family Raia. The ova of the oviparous sharks and rays, and of the Chimæræ, have a very firm horny shell of a flat form; and the gland destined for the formation of the shell is in these animals remarkably developed. One mammal, the Ornithorynchus, has been supposed to be oviparous; but, according to Mr. Owen, the correctness of this supposition is very much to be doubted.

The ova of oviparous animals, when deposited, in some cases undergo their further development in the water, in other cases on land. The development of the ova of fishes takes place invariably in the water, whilst among reptiles and Amphibia there are some of which the ova are developed in the water, others in which this is effected on land. The ova of Amphibia generally undergo the changes of development in the water, and their external investment, the analogue of the shell, imbibes the water so as to become greatly swollen. The ova of Alytes obstetricans, however, are developed in the ground, and the male sitting close to the female in the loose earth of a declivity bears the strings of ova wound around his feet. The ova of this animal have a hard horny shell, which is continued in the form of a thread from one ovum to another. In the Pipæ the ova, after they have been spread by the male over the back of the female and impregnated, are developed there, each in a cavity of the skin, which surrounds the ovum in the manner of a membrana decidua. The ova of several species of Syngnathus are developed in a furrow or groove at the surface of the abdomen or tail. The development of the ova is sometimes effected spontaneously, under the influence merely of the general conditions of nature, at other times, as in birds, with the aid of the parent which supplies the temperature required for the process.

II. *Vivipara Acotyledona.*

Very frequently the ova undergo complete or partial development in the oviducts of the parent animal. In the ova of Lacerta agilis the process has already advanced some extent at the time of their discharge. In Lacerta crocea the entire development of the embryo is completed in the oviduct. The poisonous serpents are viviparous, whilst the harmless species are oviparous. In both, the shells of the ova are of the same thickness; but in the former they are soft, in the latter hard, containing more calcareous matter. The true or land salamanders are viviparous; the tritons or water salamanders are oviparous. Amongst the osseous fishes the viviparous species,—such as Anableps and Zoarces,—are rare in comparison with the oviparous. Amongst the cartilaginous fishes the reverse is the case; for the Sharks and Rays are for the most part viviparous,—namely, the families Galei, Musteli, Zygænæ, Alopeciæ, Spinaces, Scymni, Squatinæ, &c. amongst the Sharks, and the families Pristides, Rhinobatides, Torpedines, Trygones, Myliobatides, and Cephalopteræ amongst the Rays. The coverings of the ovum in the viviparous Sharks and Rays are remarkably thin; and the ova increase in size by the absorption of a peculiar fluid secreted by the uterus; for Dr. J. Davy has observed that a developed embryo of the Torpedo is absolutely much heavier than an undeveloped ovum of the same animal. Before the appearance of the embryo the ovum of a Torpedo weighed 182 grains, and an ovum in which the embryo was visible weighed 177 grains, whilst the weight of a mature fœtus was 479 grains. This fact is important, since it shows how nearly allied are the viviparous generation without connection between the fœtus and uterus, and the form of viviparous generation in which that connection subsists.

Amongst the Mammalia also there are vivipara acolytophora, — that is, viviparous animals in which the ovum is not connected to the uterus by means of a placenta. Mr. Owen has given the following description of the embryo and membranes of the ovum of a Kangaroo, which had passed through half the usual period of gestation,—38 days. The membranes consisted of an amnion, a yolk-sac, and a very thin, non-vascular chorion. The allantois and placenta were wanting. In a uterine fœtus of a Kangaroo, the development of which was further advanced, and which has been described by M. Coste, as well as by Mr. Owen, the umbilical cord extended about three lines beyond the surface of the abdomen, the amnion forming a sheath for it. The cord then divided into two sacs. Of these sacs one, very vascular, was, like that seen in the former fœtus, the analogue of the yolk-sac, and was accompanied by the vasa omphalo-meseraica. The second sac had not more than one-sixth of the size of the one just described, was pear-shaped, presented numerous ramifications of the vasa umbilicalia, and formed a true allantois. This sac, however, had no connection with the uterus.*

The fœtus of the Kangaroo is expelled from the uterus at an extremely early period, when it measures scarcely more than an inch in length. It is then placed by the mother in the marsupial pouch, and applied to one of the nipples, attached to which and sucking, it passes through the further stages of its development. This natural premature birth is one extreme amongst the varieties of the process; the other extreme, a case of protracted birth, occurs in the Pupiparous insects, Hippoboscus, Melophaga, &c. which pass through their entire larval condition within the body of the parent, and are born in the state of Pupæ. A phenomenon somewhat analogous to this last mentioned is that presented by the Rana Pipa, in which the embryos are developed in cavities of the skin of the female, and do not escape thence until they have quite passed through the condition of larvæ.

* See Owen, in Loudon's Magazine of Natural History. New Series, vol. i. p. 471. Coste, in Comptes Rendus, Fevr. 1838.

III. *Vivipara Cotylophora.*

A placenta exists only in the human subject, in Mammalia and in some genera of sharks. The connection between the fœtus and the mother usually consists in the very close contact of the corresponding surfaces of a placenta uterina and a placenta fœtalis; the vascular folds or villi of the latter being inserted in the manner of roots into depressions or cavities of the former. The placenta fœtalis is sometimes formed by the yolk-sac, namely in some Sharks. In this case the vessels which ramify in the fœtal placenta, and convey the nutritive materials from the uterine placenta to the fœtus, are the vasa omphalo-meseraica. Generally the placenta fœtalis is formed by the chorion, and its vessels are the vasa umbilicalia, which are conducted to the chorion by an allantois. This is the structure existing in those vivipara cotylophora which have an allantoid or vasa umbilicalia and vascular chorion, namely in the Mammalia and Man.

always Contact [illegible]

a. Connection of the fœtus with the uterus by means of a placenta in some genera of sharks.

Aristotle was acquainted with the remarkable varieties in the mode of development of the ovum presented by the Sharks. In the tenth chapter of the sixth Book of his Natural History, amongst many other observations worthy of consideration respecting the cartilaginous fishes, he says that there are both oviparous and viviparous sharks, and that in some of the latter the fœtus is connected to the uterus just as in Mammalia. The oviparous are the family Scyllium, whilst the Squalus, Vulpes, and Squalus acanthias are viviparous.

"But in those sharks which are smooth and are called 'λεῖοι,' the ova lie as in the Scyllium between the oviducts. When they separate from the ovary they enter each of the two oviducts, and the embryos are there developed, an umbilical cord connecting them with the walls of the uterine cavity; so that after the ovum (the yolk) is consumed, the embryo appears to have the same relation to the parent as in quadrupeds. A long umbilical cord is connected to the lower part of the uterus by means of a body like a placenta, whilst at its other extremity it is attached to the embryo about the middle, where the liver lies."*

The term Galeus lævis has been fixed as applicable to a particular species of shark by the ichthyologists of the sixteenth century, — Belon, Salviani, and Rondelet. Salviani and Rondelet, contemporaneous but independent writers, both regarded the shark with ray's teeth, the

* Aristotle, Hist. Animal. vi. p. 10. See also De Generat. Anim. ii. p. 3.

Squalus mustelus of Linnæus, as the γαλεὸς λεῖος of Aristotle; and Rondelet represents that shark with an umbilical cord passing from the sexual orifice of the mother to the navel of the young fish. Fabricius, Tyson, Collins, and Camper observed the embryo of a shark which they called Galeus lævis; but it is doubtful whether this was the shark with teeth like those of the ray. Here no connection of the fœtus to the uterus by means of a placenta was observed; but, on the contrary, there was attached to the navel merely the simple yolk-sac, — as in the oviparous, and the other viviparous, sharks. At that period Galeus lævis was a term applied to any shark which was not rough, and more especially to any which had no spines on the dorsal fins. Cavolini associates the Squalus mustelus of Linnæus (or the shark with teeth like those of the ray), the embryo of which he had seen, with the γαλεὸς λεῖος of Aristotle. When speaking, however, of the generation of the cartilaginous fishes, he does not allude to Aristotle's observation.

On the other hand some facts have been accidentally observed which, although they were not originally adduced in confirmation of the assertions of Aristotle, yet agree therewith. Stenonis* described the embryo of Galeus lævis or Pesce palombo, which was connected with the uterus by means of a placenta. The placenta was hollow, and its cavity communicated with the valvular intestine of the fœtus through the medium of a tubular canal contained in the umbilical cord. This fish was not so described that its identity could be determined; all that is known of it being that it had an intestine with a spiral valve.

Dutertre† described a Requiem shark which, according to the description and drawing of it given by him, must have been a Carcharias. Dutertre says that its young were fixed by means of a cord to a large membrane. Cuvier‡ also says briefly in his great work on fishes that in the Carcharias the yolk-sac is attached to the uterus as firmly as a placenta. "Toutefois le vitellus fort réduit des fétus des requins prêts à naître m'a paru adhérer à la matrice presque aussi fixément qu'un placenta." The yolk-sac of this fœtus was also beset with villi. Neither Stenonis, nor Dutertre, nor Cuvier refers to the old observations on this subject.

The fish examined by Cuvier was of the genus Carcharias, but not the Carcharias with saw-like teeth (Prionodon of Müller and Henle); for in the latter species the interior of the yolk-duct is destitute of villi and quite smooth. This villous structure, however, exists in the subgenus Scoliodon of Müller and Henle. But the Carcharias, with saw-like teeth, in which the yolk-duct is devoid of villi, has,

* Act. Med. Hafn. Bartholini, 1673, vol. ii; Hafn. 1675, p. 219.

† Histore des Antilles.

‡ Hist. des Poissons. T. i. p. 341.

according to my observations, as well as the Scoliodon, that connection with the uterus by means of a placenta, which Aristotle discovered.

The Galeus lævis of Stenonis does not belong to the genus Carcharias. It has an intestine with a spiral valve, as described and represented by Stenonis. But all the species of Carcharias have an intestine with a straight though waving valve. New researches have shown that two species of the genus Mustelus, with teeth like the rays, differ physiologically from each other in the circumstance that in one the fœtus, as in the genus Carcharias, is firmly connected to the uterus by means of a placenta, whilst the other has a yolk-sac which is quite free and unattached. The former, Mustelus lævis, (as Aristotle would have called it,) is distinguished by the narrowness of its thoracic fins, the form of its teeth, the position of the first dorsal fin behind the thoracic fins, and a dark spot passing through the posterior border of the tail. Of the second species, Mustelus vulgaris, there is a white-spotted variety and one destitute of spots, which in colour does not differ from Mustelus lævis.*

The placenta fœtalis of these fishes is formed by the plicated yolk-sac. The folds of the placenta are much more complex in Carcharias than in Mustelus lævis; and in the former genus the free portion of the yolk-sac forms several cœcal diverticula. The sharks of the genus Carcharias are also to be distinguished from the Mustelus lævis by the anatomical peculiarity of the trunks of the blood-vessels entering the interior of the yolk-sac before they are distributed in the folds. We will now describe more fully the placenta formed by the yolk-sac in the Carcharias, and will illustrate it by some diagrams.

Fig. 227.

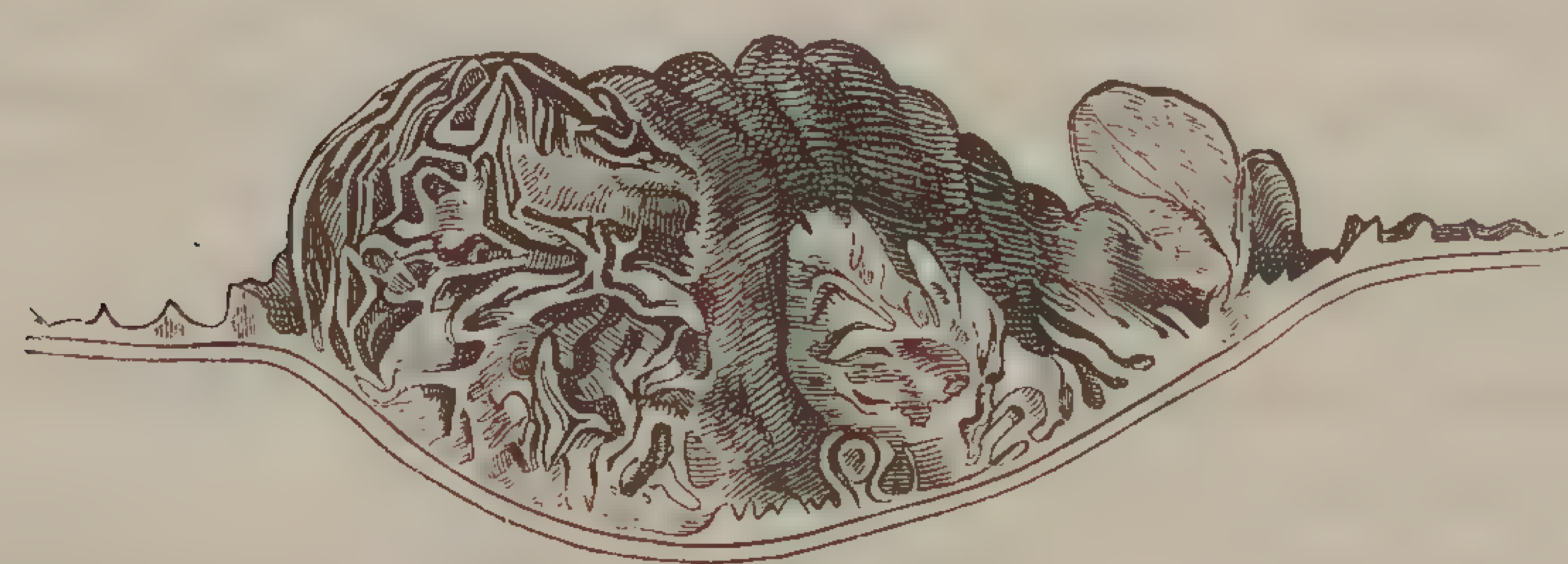
The yolk-sac (fig. 227), as usual, possesses two coats, an internal vascular coat which is continuous with the intestine, through the medium of the yolk-duct, and an external non-vascular coat, which extends as a sheath over the yolk-duct and the omphalo-meseraic vessels, and is continuous with the skin of the fœtus at the anterior part of the abdomen, the ordinary point of insertion of the umbilical cord in fishes. For the formation of the placenta fœtalis both membranes of the yolk-sac are thrown into a mass of folds of different sizes. The interior of the yolk-sac is thus converted into a very irregular cavity with a large number of recesses. These wrinkled folds, at the side cor-

* See the Monats-bericht der Akad. der Wissensch. zu Berlin, 6 Aug. 1840.

responding to the uterus, are most closely connected with that organ, and cannot be separated from it without some force. The part of the yolk-sac which is turned from the uterus presents merely freely floating diverticula (see fig. 227). As far as the yolk-sac enters into the formation of the placenta its two membranes are in the closest contact with each other; but at that part of it which forms the free and hollow diverticula, the membranes are separated from each other by a distinct interval. Both membranes, however, are closed at all parts.

The placenta uterina (fig. 228) is constituted by very prominent

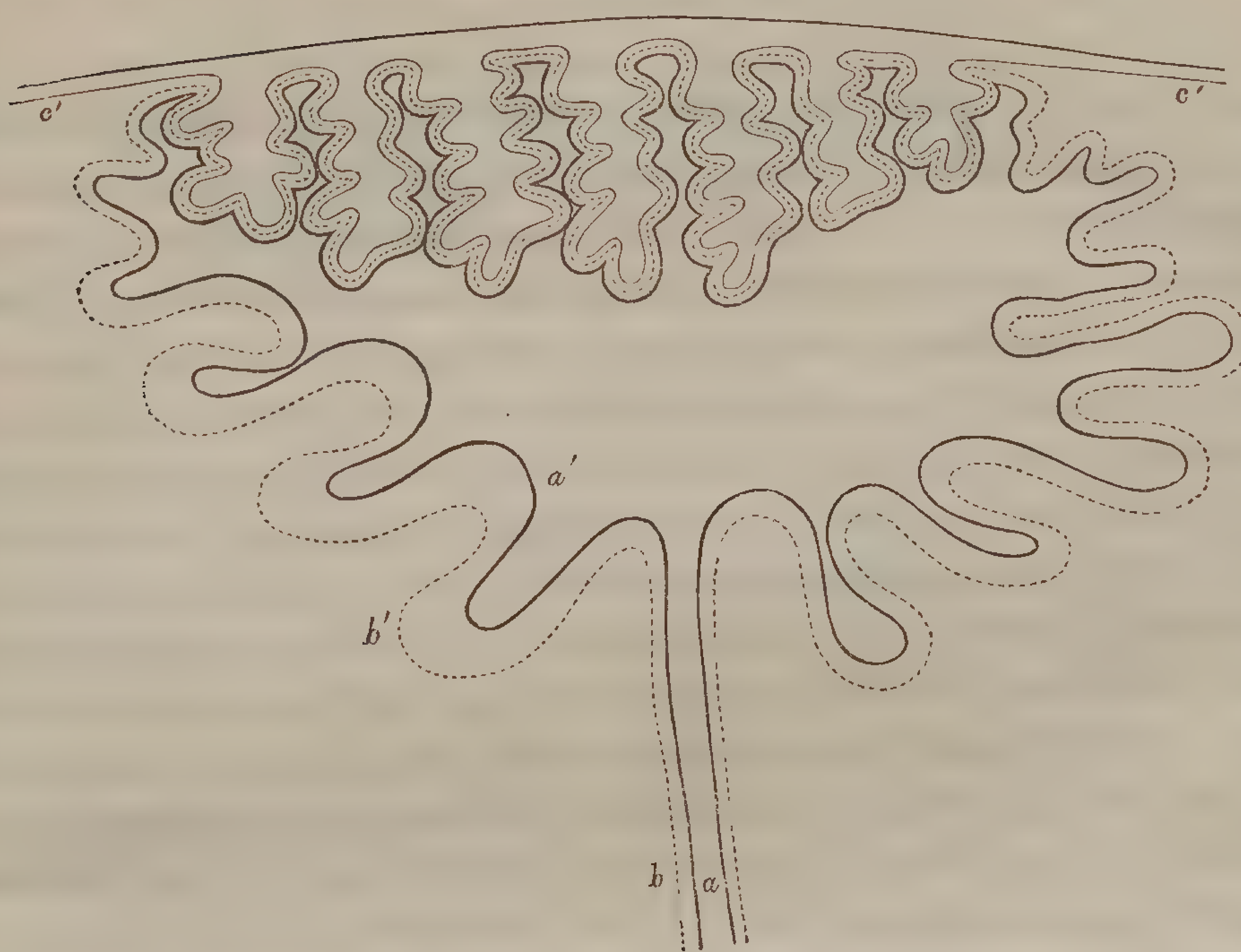
Fig. 228.



wrinkled folds of the inner membrane of the uterus, which accurately correspond to those of the placenta fœtalis. The folds of both are interposed between each other, and are as closely and firmly attached as are the placenta uterina and placenta fœtalis of any mammiferous animal. The extremely delicate and structureless external membrane of the ovum passes between the folds of the two placentæ at the line where they meet, but where they are actually in contact seems to be dissolved; for when the two placentæ are forcibly separated the membrane in question cannot be detected, although by slowly and carefully withdrawing the numerous and very complex folds of the placenta from one another, the fœtal and maternal portions can be separated without suffering any injury. The following figure (fig. 229) represents an ideal but much simplified section of the organ. *a* indicates the yolk-duct; *b* the sheath of the umbilical cord; a′ the internal membrane of the yolk-sac; b′ its external membrane; and c′ the internal coat of the uterus, which forms the placenta uterina.

The placentæ uterinæ receive their blood-vessels from the vessels of the uterus, which are of large size, and run to the seat of the placentæ at the lower part of the organ. The vessels of the placenta fœtalis are the extraordinarily large vasa omphalo-meseraica, which are here proportionally of as great size as the vasa umbilicalia of mammalia. The trunks of these vessels lie with the vitelline or yolk-duct in the sheath of the umbilical cord; but when they reach the yolk-sac they penetrate into the interior of the proper yolk-sac or internal membrane of the hollow placenta fœtalis, projecting nearly into the middle of its cavity, and are

Fig. 229.



thence distributed in a number of branches to the membrane of the yolk-sac, its folds, and diverticula.*

The minute structure of the placenta fœtalis and that of the placenta uterina are the same. The most external layer of the placenta uterina, which lies in immediate contact with the placenta fœtalis, consists like the decidua of the human uterus of microscopic nucleated cells. The substance of the membranes of the yolk-sac, the more external of which is destitute of vessels, has the same structure.

The organic relation of the placenta fœtalis and the placenta uterina to one another is the same here as in Mammalia. They lie in immediate contact, and this contact subsists over an immense surface of folds; but the vascular system of the parent is restricted to the uterine placenta, that of the fœtus to the placenta fœtalis. The organic attraction of matters from the maternal blood is probably effected by means of the microscopic cells.

The fœtus continues thus united to the uterus in the Carcharias and Scoliodon until it is fully developed. These vivipara cotylophora amongst the plagiostomatous fishes have the peculiarity of not possessing the internal vitelline sac within their abdomen. There are no vivi-

* The vitelline duct is inserted into the intestine, as in the other sharks and rays, which have merely a simple yolk-sac at the upper extremity of the valvular gut, where the hepatic and pancreatic ducts likewise open into the canal. This upper end of the valvular gut is destitute of valvulæ and is the part called by Ente the "bursa," and by Collins the "bursa Entiana," while more recent writers, not considering that Ente had not examined a fœtal shark, have applied the name of "bursa Entiana" to the internal yolk-sac, or even to the external yolk-sac of the Sharks.

para cotylophora amongst the Rays. The true rays (Raia) are oviparous, and all the other allied genera are vivipara acotyledona.

*b. Connection of the fœtus with the uterus in Mammalia and Man.**

The ovum appears to have a firm connection with the uterus in all Mammalia, with the exception of the Marsupialia and Monotremata. The means of attachment are always either vascular villi or folds of the chorion, and the chorion receives its blood-vessels from the vasa umbilicalia of the fœtus, which are distributed upon the allantoïs, and by it are conducted to the chorion. The villi are sometimes distributed over the whole surface of the chorion, as in the Hog family, the Solidungala, the Camel family, and the Cetacea; sometimes they form a zone around the ovum, as in Carnivora; at other times they are collected into several masses scattered over the chorion, the cotyledons, as in most Ruminantia; and lastly, in man and some other animals they form a single placenta upon one side of the chorion. The double placenta sometimes observed in the Rodentia approaches closely to the last form. Corresponding to the vascular villi of the fœtal chorion and placenta there are depressions upon the inner surface of the uterus in which the villi are imbedded like roots in the soil. When the villi are aggregated together at particular points of the chorion so as to form cotyledons, the uterus has at corresponding points maternal cotyledons,—projecting cup-like bodies, pierced by innumerable tubular cavities, which receive the villi of the fœtal cotyledons. In the human subject the placenta uterina is a growth of the decidua uterina, which at the part corresponding to the fœtal placenta undergoes an excessive development, and penetrates the substance of the fœtal placenta, passing between the tufts of villi even as far as the chorion. In all cases, whether the villi are scattered over a wide surface, or aggregated into masses, the object attained is a great increase of the surface of contact between the chorion and the uterus. Two principal modifications of the form in which this increase of surface is given, are to be observed, namely, the development of ramified villi imbedded in the uterus, and the formation of folds on both chorion and uterus, which are interposed between each other.

The varieties of structure will now be examined more in detail with relation to the different orders of animals.

In the Pachydermata, the placenta extends over the whole surface of the chorion, with the exception of the appendages of the ovum, and the chorion is uniformly beset with vascular villi. The placenta uterina in like manner extends over the inner surface of the uterus, which

* Writings on the subject. Von Baer, Untersuchungen über die Gefässverbindung zwischen Mutter und Frucht in den Säugethieren. Leipz. 1828. E. H. Weber in Hildebrandt's Anatomie, Bd. iv. p. 496, in Froriep's Notiz. 1835, Bd. 46, p. 90. and in Wagner's Physiologie, p. 124. Eschricht, de organis, quæ respirationi et nutritioni fœtus animalium inserviunt. Hafniæ, 1837.

assumes a cellular structure, containing innumerable depressions or excavations for the reception of the villi of the chorion. A slight approach to the formation of distinct masses of villi is here presented by the less numerous larger depressions of the uterus, through which glandular tubuli open, and the corresponding circles of villi upon the ovum, which Von Baer has observed. The surface of the chorion in the dolphin is, according to Eschricht's researches, covered with rugæ and villi. The latter are separate from each other about the distance of half a line; they have not the form of folds as in the hog, nor of feathery cones as in the ox, but constitute numerous branched cauliflower-like round masses seated upon narrow pedicles. Hence the crowns of these villi are closer to each other than their bases. Their size varies; the largest measure about a line in length, and at their crown about one-fourth of a line in diameter. The crowns of these villi present an extremely beautiful net-work of capillaries. The inner surface of the uterus, likewise, has rugæ and also cells, which form sheaths for the villi. The walls of these cells are covered with capillary vessels. The Cetacea also have, like the Pachydermata and Ruminantia, uterine glands which secrete the fluid destined for the nutrition of the fœtus.

In the Carnivora the placenta forms a zone around the ovum. The placenta of the cat has been shown by Eschricht to be formed of very thin laminæ, rising perpendicularly from the chorion, and plicated and disposed in an irregular manner. When the placenta is injected from the parent and from the fœtus with different coloured matters, the inner surface of the placenta appears completely variegated. On more accurate examination, it is found that this appearance arises from the intermingling of the laminæ of the chorion and those of the uterus, while the capillaries of one set of folds enter into no communication with those of the other. The laminæ reach through the entire thickness of the placenta, being two lines in depth; whilst they are extremely thin, their diameter not much exceeding that of blood corpuscules. At each margin of the lamina is a vessel of larger size than the capillaries of the general network. Eschricht shows that the uterine portion of the placenta of the cat is a vascular membrane, quite distinct from the mucous membrane of the uterus. For when it was removed, together with the fœtal portion of the placenta, the mucous membrane remained quite entire beneath, the blood-vessels only appearing torn. [See the observations of Dr. Sharpey on the placenta of the bitch at page 1575.]

The Ruminantia are divisible into two classes in respect of the structure of the placenta. In one which embraces the camel and lama, the chorion is universally beset with numerous scattered villi. In the other class, comprehending the giraffe, according to Mr. Owen, as well as the ox, sheep, goat, stag, &c. the villi are collected together so as to form cotyledons, which are distributed over the chorion, whilst the surface between them is destitute of villi. Each cotyledon consists of numerous tufts of ramified vascular villi. The cotyledo uterinus, which is here persistent even in the intervals of pregnancy, forms a prominence on the inner surface of the uterus, and has sometimes the shape of a sort of cup, with thick prominent borders, as in the sheep; sometimes that of a slightly elevated rounded mass, with a contracted basis. On the surface of the cotyledo uterinus are seen the openings of the canals, which correspond to the tufts of villi of the fœtal cotyledon, and the walls of which are covered by a very close network of capillaries belonging to the maternal system.

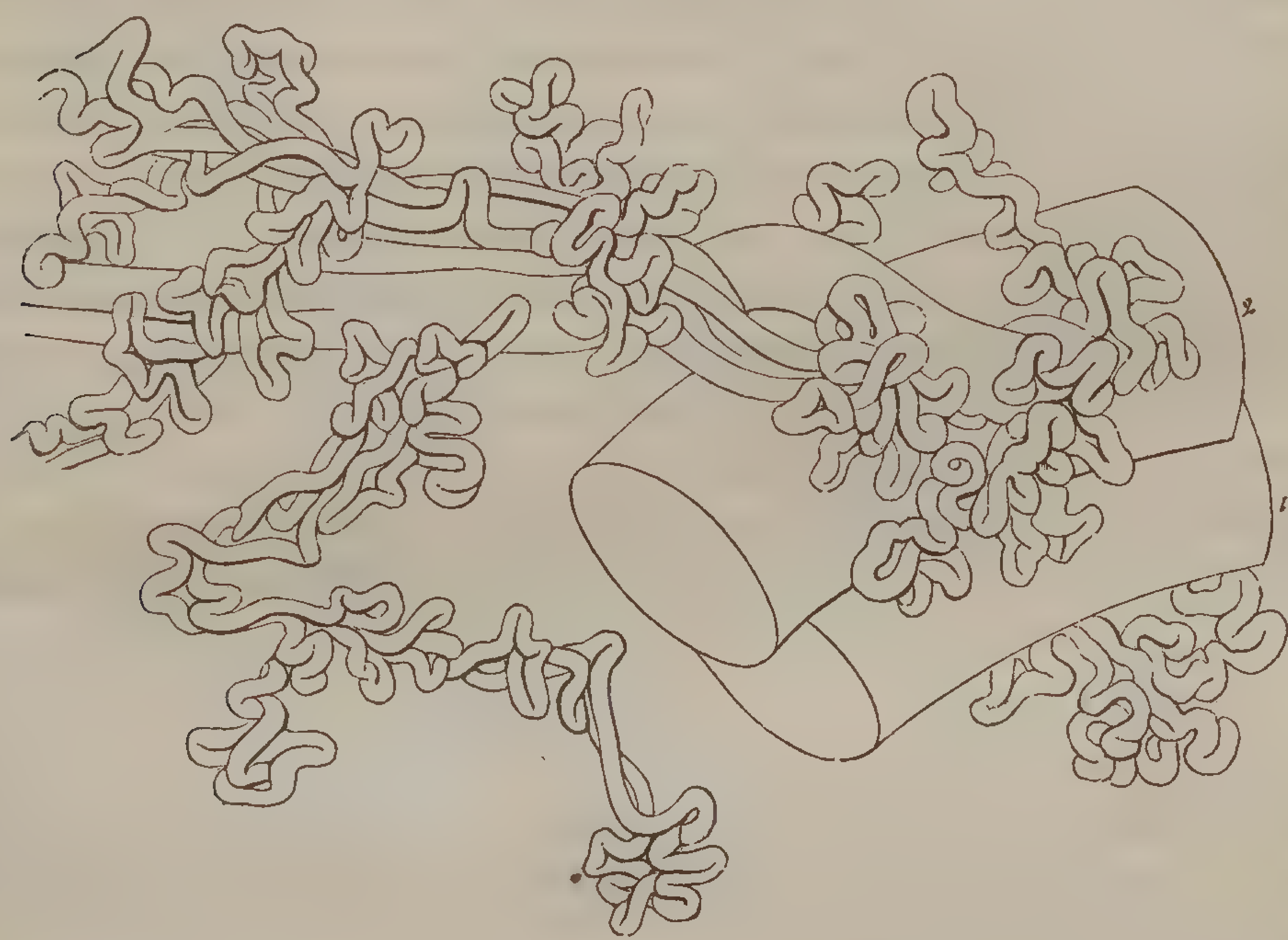
The ovum of the sloth also has separate lobular cotyledons, but they lie near each other at one part of the chorion.* In the Rodentia and Insectivora the placenta has a concentrated form. The Rodentia have frequently two placentæ lying near each other, frequently also only one. The ovum of the rabbit, except in the situation of the placenta, is smooth and free from villi. Even where it is thus smooth it is provided with blood-vessels; but these, according to Von Baer, are not branches of the umbilical vessels which go to form the placenta, but are derived from the vasa omphalo-meseraica, it being the yolk-sac, and not the allantois, which extends over the greater part of the ovum. The allantois of the rat was observed by Eschricht to be thrown into a labyrinth of folds in the situation of the placenta. The placenta itself is composed of laminæ of the chorion and uterus, interposed between each other. In the mole, Eschricht was able to separate the fœtal from the uterine portion at the margin of the round placenta, and found the former composed of villi, the latter perforated with canals. In the apes also the placenta is single, and in this respect, as well as in the small size of the umbilical vesicle, these animals resemble man; but they are distinguished by having two umbilical veins. (Such is the structure in Cebus, Mycetes, and Hapale, according to Rudolphi.)

The human placenta is throughout composed of two elements, the parts of the placenta fœtalis and those of the placenta uterina intermingled. The fœtal placenta consists entirely of dense tufts of branched vascular villi, whilst the uterine placenta is formed of the substance of the decidua, which penetrates between the villi of the fœtal placenta even to the surface of the chorion, and completely encloses them. The exact relation which the two parts bear to each other is, however, according to Professor E. H. Weber, very different in man and in Mammalia. In Mammalia the vascular villi of the fœtus are received into the vascular sheaths of the uterine placenta,

* Rudolphi, Abhandl. der Akademie zu Berlin. J. 1828. The urachus of the sloth does not open at the fundus but near the neck of the urinary bladder.

so that the capillaries of the fœtal and those of the maternal system come into contact with each other, and suffer an interchange of the matters which they contain. In the human subject, on the contrary, the vascular villi of the fœtus dip into wide blood-vessels, which arise from the uterine system, and which permeate the whole uterine portion

Fig. 230.*



of the placenta; the looped capillaries of the fœtus being thus surrounded and bathed, as it were, in the maternal blood. The ends of the villi are formed by the inosculating loops of the minute arteries and veins of the fœtus; which, however, have the distinguishing character that the same vessel makes several turns from one loop into another before it enters the nearest venous trunk. (See fig. 230 and 231.) The vessels belonging to the maternal system, which penetrate the uterine portion of the decidua and in all parts contain villi of the fœtal portion, may be readily filled with injection from the arteries of the uterus. Eschricht inclines to the

Fig. 231.†

* [Fig. 230 represents the villi of the fœtal portion of a mature human placenta, magnified 100 diameters; after E. H. Weber. The capillary vessels are perfectly filled with injection, and their diameter varies from $\frac{1}{115}$ to $\frac{1}{170}$ of a French line. 1, the artery: 2, the vein.]

† [Fig. 231 is the extremity of a villus, taken from a recent placenta, in which the vessels were still filled with blood, magnified 200 diameters; after Weber. The loop, 1, is filled with blood; the other loop, 2, is empty; 3, is the margin of the pellucid villus.]

opinion, that in man as in Mammalia, only the capillaries of the decidua come into contact with the looped vessels of the villi. Weber, on the contrary, maintains that the uterine arteries and veins on entering the spongy substance of the placenta, no longer ramify and give off branches and twigs, but take the form of a net-work, the canals of which are much larger than the ordinary capillaries. The extremely thin parietes of these canals, according to Weber, apply themselves to all the branches and capillary loops of the vessels which form the fœtal villi, so that even here the structure consists essentially in two sets of vessels being brought into the closest possible contact.*

[The recent observations of Dr. J. Reid (Edinb. Med. and Surg. Journ, No. 146,) agree in the most important points with those of Weber, but yet differ from them in some particulars. Dr. Reid's views are illustrated by figures 232, 233, and 234. According to Dr. Reid, the blood sent from the mother to the placenta is poured by the curling arteries of the uterus (1, fig. 232 and fig. 233) " into a large sac (3, fig. 233), formed by the inner coat of the vascular system of the mother, which is intersected in many thousand different directions by the placental tufts (3, fig. 232), projecting into it like fringes, and pushing its thin wall before them in the form of sheaths, which closely envelope both the trunk and each individual branch composing these trunks (fig. 233). From this sac the maternal blood is returned by the utero-placental veins (2, fig. 233) without having been extravasated, or without having left her own

Fig. 232.

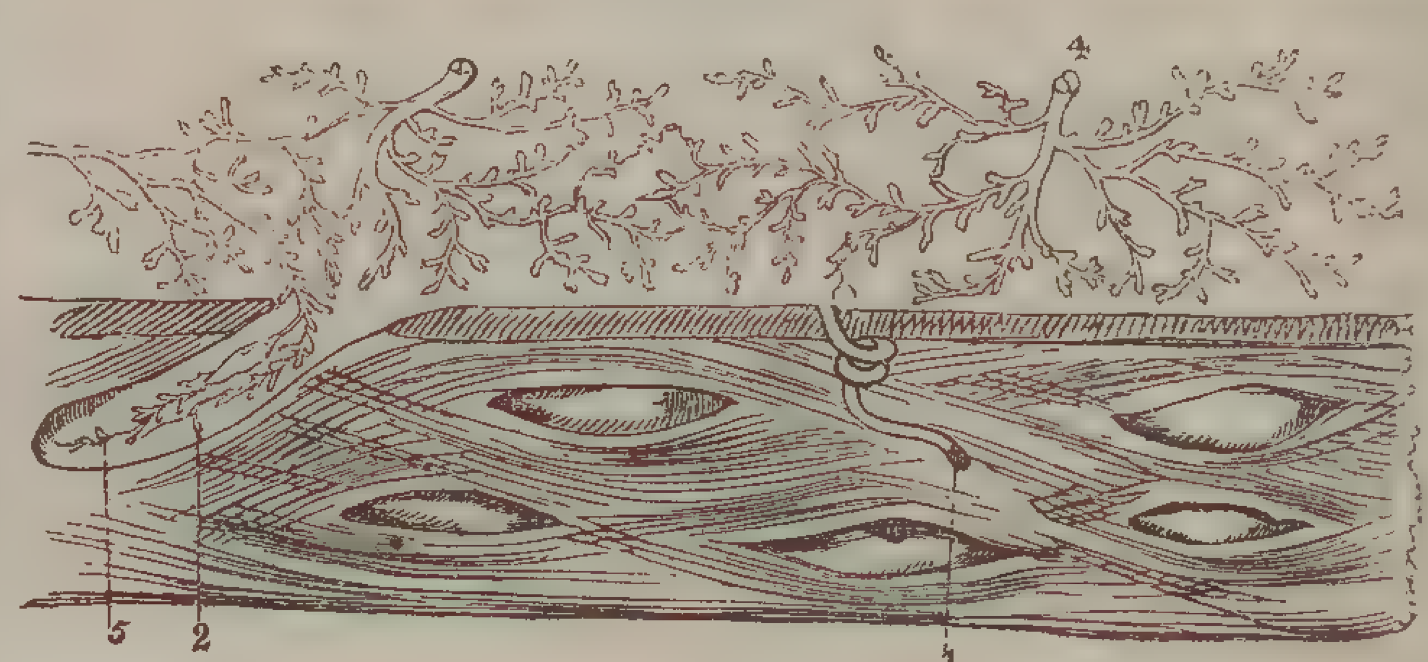


Fig. 233.

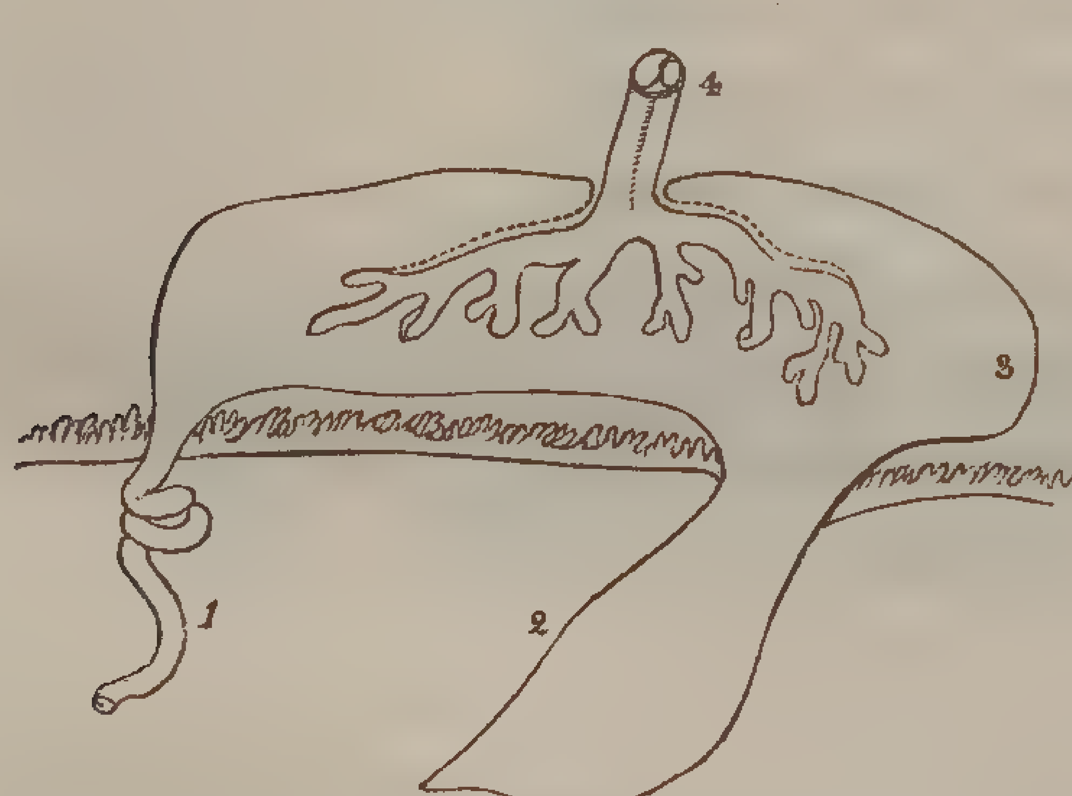
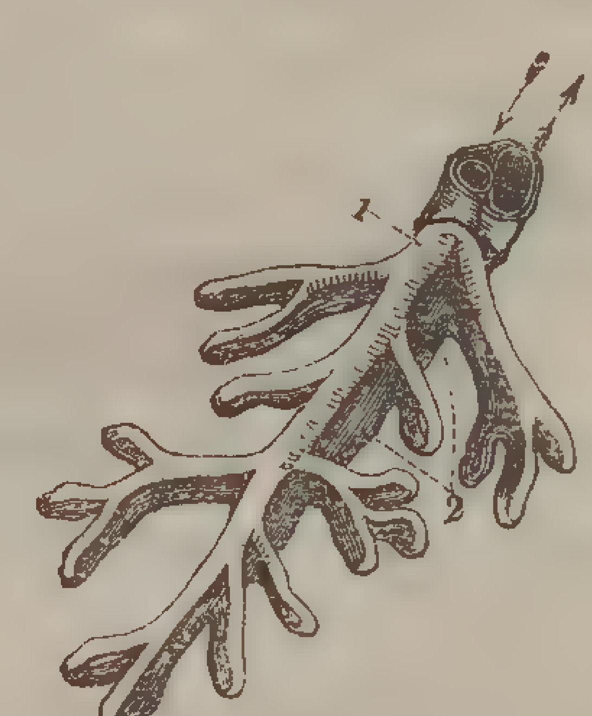


Fig. 234.



system of vessels." The uterine vessels, therefore, according to Dr. Reid, do not form a network in the substance of the placenta as de-

* See the account of Weber's more recent researches in connection with this subject in Wagner's Physiologie, p. 124.

scribed by Weber. Further, Dr. Reid has observed, that the tufts of the placental vessels are prolonged into some of the uterine sinuses (2 and 5, fig. 232), a fact not noticed by Weber. Dr. Reid states also, that in the placental tufts each branch of the umbilical artery is bound up with a branch of one of the umbilical veins, and that both of them divide and subdivide exactly in the same manner, and terminate by inosculation with each other at the blunt extremities of the branched tufts. (Fig. 234; where 1 is the arterial, and 2 the venous twig.) It appears, however, that this description of the structure of the placental tufts is erroneous. In a paper on the structure of the placenta, recently sent in to the Royal Medico-chirurgical Society by Mr. Dalrymple, most satisfactory confirmation is given to Weber's account of the mode of termination of the fœtal vessels in the placental tufts. Several drawings, made by Mr. Dalrymple before he had seen the figures given by Weber in Wagner's Icones, (and copied at page 1605, figs. 230 and 231), bear the most remarkable resemblance to those figures. The minute arteries and veins are not bound up together, two and two; but the same capillary tube, arising from an arterial trunk, makes several convolutions and forms several loops before it terminates in a vein.]

In the human subject, as in Mammalia, there is no passage of blood from the vessels of the mother into those of the fœtus, and *vice versâ*. When the placenta is injected from the vessels of the mother, as can be readily done, only the vessels of the maternal portion of the placenta are filled. And, on the other hand, the passage of injected matters from the umbilical arteries, or vein, of the fœtus into the vessels of the uterus, by no means proves the existence of a communication between the two sets of vessels; for the injected mass becoming extravasated from the vascular loops of the fœtal placenta, must pass directly into maternal vessels, and if forced onwards necessarily fills the veins of the uterus.

The placenta fœtalis and the placenta uterina can be separated in some animals with great ease, and without injury to either; but in other animals and man they cannot be detached from each other without laceration. Von Baer remarks that the fœtal cotyledons of the Ruminantia, when they are only slightly developed, adhere so firmly to the maternal cotyledons which form sheaths for the villi, that it is impossible in their fresh state to withdraw them uninjured. But after a short period has elapsed they are easily separable, and then, according to Von Baer, there is always found between the embryonic and the maternal part of the cotyledon a mass of thickish consistence, the origin of which is a matter of doubt. It may be derived either from the sheaths of the maternal cotyledon, or from the villi of the fœtal cotyledon, or from both. It has probably formed a layer of active organic cells, which played an important part between the two systems of vessels. When the cotyledons of the ruminants separate at the time of birth, the vascular tufts of the villi remain uninjured. The Mammalia present great varieties in the process of the separation of the placenta. E. H. Weber divides these varieties into two classes. To the first class belong those cases in which the two placentæ (the fœtal and the uterine) are so loosely connected that they separate without either receiving any injury. The uterus here suffers no lesion, and the uterine placentæ remain after birth, and merely diminish in size: this is the process in the ruminants, horses, and hogs. The second class includes those instances where the two portions of the placentæ are so intimately united that the uterine portion is torn away, together with the fœtal portion, at the time of birth. Here the uterus receives a wound, and the placentæ are deciduous organs, which must be renewed at each gestation. This class is exemplified in man, the Carnivora and the Rodentia.*

Nutrition of the fœtus. — There is a period in the growth of the ovum which precedes the development of blood-vessels. Since the chorion and its villi are composed of nucleated cells, similar to those which are the active agents in the growth and vegetative changes of the primitive structures of the embryo, previous to the formation of vessels and the circulation of blood, the growth of the villi of the chorion long before the development of the blood-vessels is an intelligible phenomenon. These villi then attract matters from the surrounding fluids, and, like the cellular structures of plants, convey them onwards, transmitting them from one cell to another, until they accumulate in the interior of the ovum. This is the essential process in all organic absorption, even when blood-vessels and lymphatics exist; for even in the intestines the vascular villi are invested by a sheath formed of nucleated cells, which exert the same action as the cortical cells of the spongiola of the roots in plants. When the blood-vessels of the embryo have reached the chorion and its villi, these blood-vessels which have been developed from cells and participate in the active properties of cells, absorb the nutriment. The nutritive matters thus absorbed are supplied either by the blood of the mother in which the villi float, as in the human placenta, or as in Mammalia by the white secretion of the uterine glands. The absorbed nutriment enters directly into the blood of the fœtus. The process thus maintained between the fœtal and the maternal blood supplies the process of respiration to the fœtus, or an equivalent for that process.

There is no other mode of nutrition to which great importance can be ascribed. It is true, the amnion may, by the organic action of its cells, absorb fluids from the chorion, and deposit nutriment in the form of a small quantity of albumen in the liquor amnii. The liquor amnii enters the mouth of the fœtus, and certainly reaches the intestinal canal as well as the trachea. For in the stomach of the fœtus of the human

* See Froriep's Notiz. 46 Bd. p. 90. Compare Eschricht, loc. cit.

subject, as well as of mammiferous animals, there have been found hairs derived from the lanugo or first hair of the fœtus, which falls out and becomes mixed with the liquor amnii. But this mode of nutrition by means of the liquor amnii can at most be of trifling and very inadequate amount.

SECTION III.

Of the development of the organs and tissues in the fœtus.

CHAPTER I.

DEVELOPMENT OF THE SYSTEMS OF ORGAN AND ORGANS.

In the preceding section the object held in view has been to give a succinct statement of the most important general phenomena of development presented by the ovum, and of their most remarkable varieties in the different classes of animals. The mention of numerous particulars, which would have obscured the general view of the subject, has been intentionally avoided. It remains now to consider in succession the development of the several systems of organs, so far as accords with the purpose of this work, and is rendered possible by the present state of our knowledge.*

The development of determinate parts from a homogeneous mass presupposes the existence of a formative substance endowed with plastic power, which contains within itself in the potential or virtual state all that is actually produced from it by development. The germ was potentially the entire animal; and the first rudimental mass of an organ bears the same relation to all the structures afterwards to be formed within it,—with this difference, that the potential germ being supplied with nutritive matter acts independently of any other power, whilst the plastic force which effects the development of the particular parts and tissues in an organ is controlled by the organic force of the whole organism to which the organ belongs, and is, as it were, delegated to the organ by the general organic force. This blastema of a part in the state of formation has, therefore, nearly the same relation to the whole system as the

* The works treating generally of the development of the different systems of organs, are Burdach's Physiologie Bd. ii; Rathke's Abh. zur Bildungs-und Entwickelungs-geschichte, Leipzig, 1832, 1833; Von Baer's Entwickelungs-geschichte der Thiere, Bd. i. und ii.; Valentin's Entwickelungs-geschichte; and Von Ammon's Chirurgische Pathologie in Abbildungen, H. i. Leipz. 1838. The principal treatises on the development of special systems and organs will be mentioned in the course of the present section.

part when fully developed. In the lower animals the special part acts as a delegated part of the whole as long as it is connected therewith, but can be separated from the rest of the system or organic being and its controlling influence; it may then even become the foundation or germ of a new being, as we have seen exemplified in the Hydra and Planaria. (See page 1431.) Hence in those more simple animals the blastema of a part which by the organic plastic force of the being is caused to assume the structure and properties of a special organ, would probably, if withdrawn from that influence by separation from the rest of the being, in process of development become the stock of a new animal.

The "blastema" must not, however, be regarded as a mere soft, plastic, gelatinous mass devoid of structure or composed only of globules, such as it appears to the naked eye or with low magnifying powers; for according to the researches of Schwann, it consists partly of a fluid, partly of granules which spontaneously change into the nuclei of cells and into cells, and partly, also, of such nucleated cells already formed. Such, be it remembered, is the substance which will be spoken of in the following pages under the designation of the "blastema" of the different organic systems; although the phenomena of the development and metamorphosis of cells in the formation of the different parts will not at present be described.

1. *Vertebral column and cranium.*

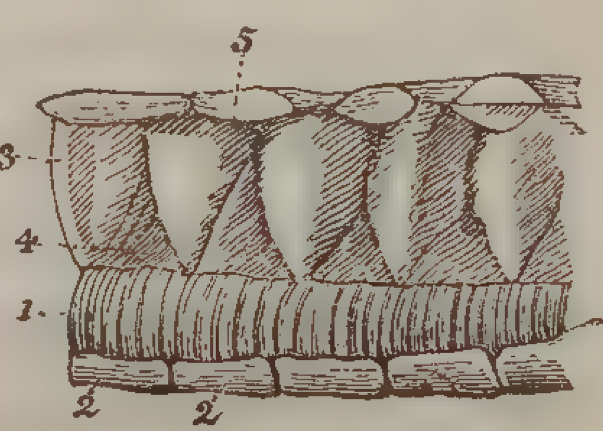
The persistent conditions of the vertebral column in many fishes, which have been described by G. Cuvier, C. A. S. Schultze, Von Baer and myself, offer some very remarkable points of comparison with the fœtal state of the vertebræ in the higher animals.

The primitive part of the vertebral column in all the vertebrata is the gelatinous chorda dorsalis which consists entirely of cells. This cord tapers to a point at the cranial and caudal extremities of the animals. In the progress of its development it is found to become enclosed in a membranous sheath which at length acquires a fibrous structure, composed of transverse annular fibres. (See fig. 235 and 237.) The chorda dorsalis is to be regarded as the azygous axis of the spinal column and in particular of the future bodies of the vertebræ, although it never itself passes into the cartilaginous or the osseous state, but remains enclosed as in a case within the persistent parts of the vertebral column which are developed around it; being permanent, however, only in a few animals, whilst in the majority it disappears at an early period.

The cartilaginous or osseous vertebræ are always first developed in pairs of lateral elements at the sides of the chorda dorsalis. From these lateral elements are formed the bodies and the arches of the vertebræ. In some animals, however, the lateral elements of the vertebræ undergo no further development, and it is in these that the chorda dorsalis is persistent through life.

In the myxinoid fishes the spinal column presents no vertebral segments, and there exists merely the chorda dorsalis with the fibrous layer surrounding its sheath, which is the layer in which the skeleton originates. This fibrous layer also forms superiorly the membranous covering of the vertebral canal. In the Petromyzon the same fibrous layer contains cartilaginous plates of the rudiments of the arches of the vertebræ, whilst as yet, no trace of the bodies of the vertebræ exists. In the Chimæra and Sturgeon there are cartilaginous plates upon the chorda dorsalis or its sheath both above and below,—in other words, the fibrous layer has developed superior and inferior symmetrical parts of vertebræ. (See fig. 235.) The superior lateral portions form the superior arches; the inferior form the transverse processes, and in the caudal part of the column in the Sturgeon unite below so as to form inferior arches in which the extreme portion of the aorta lies. The superior and inferior parts of the vertebræ have not become united in these animals except at the most anterior part of the column, where such a union has taken place and the chorda has become wholly enclosed in cartilage.

Fig. 235.*



The vertebræ of fishes, therefore, appear to be formed by the coalescence of four symmetrical portions, the upper pair of which embrace the spinal cord, whilst the lower pair enclose the aorta in the caudal region, and in the trunk support the ribs. From the coalescence of these four rudimentary portions the bodies of the vertebræ enclosing the chorda dorsalis and its sheath at first sight appear to arise. But such is not the case; for in fishes the conversion of the sheath itself into cartilage or bone has a share in the formation of the bodies of the vertebræ. It is true that in the Sturgeon this sheath remains throughout life fibrous, but in the Chimæræ it becomes ossified. In these animals the chorda remains persistent as the base of the vertebral column; but at the same time its thick sheath, on which the symmetrical cartilaginous portions of the vertebræ rest, presents thin ossified rings much more numerous than the vertebral segments. (See fig. 235.) The sheath of the chord preserves its membranous structure only internally towards the gelatine mass and on its exterior. We have evidence, therefore, in these instances, that the body of the vertebra in fishes is composed of a central and a cortical portion which have very different modes of origin. In the Sharks and Rays and the osseous fishes the same fact is equally distinct; and here the vertebræ have

* [Fig. 235. Part of the vertebral column of Chimære monstrosa. 1, chorda dorsalis with its sheath; 2, rudiments of the transverse processes of the vertebræ; 3, rudiments of the arches of the vertebræ, or cartilaginous crurales; 4, cartilaginous inter-crurales; 5, small cartilages completing the spinal canal above, and interposed between the pairs of arches. After Müller, Anatomie der Myxinoiden, 1834.]

undergone more or less complete ossification. In the embryos of sharks and rays the chorda dorsalis is at a certain period quite uniform in outline, whilst the superior and inferior pairs of vertebral elements in a cartilaginous state rest upon its thick sheath (fig. 236, A). Subsequently this sheath becomes constricted at

Fig. 236.*

intervals corresponding to the distances of the future vertebræ, begins to be divided into distinct segments, and assumes the cartilaginous or osseous state. The chorda in this way becomes constricted at successive points and divided into a series of rounded masses resting in the concave facets of the interposed vertebræ, through the centre of which they frequently communicate with each other. The layers of the vertebræ which form the facets originated in the sheath of the chorda, and constitute the central portion of the body of the vertebra in the fish. The external layer or cortical portion is produced by the coalescence of the four primitive lateral elements. (See fig. 236, B.) The mode of development of the vertebra is essentially the same in the osseous fishes. In many families, as the Cyprini and Salmonidæ, a suture can be distinguished at each side of the body of the vertebra, and in the third or fourth vertebra in Cyprini it is possible, even in the adult condition, to separate the four lateral elements or the cortical portion from the central portion of the body of the vertebra.

In the Swordfish there is no lateral suture; but a space in which ossification has not taken place exists between the cortical and central parts of the bodies of the vertebræ. The chorda itself lies within, constricted in the situation of each vertebra, while its larger portions rest on the facets of the contiguous vertebræ.† The vertebral column is not, however, developed in all classes in the same manner.

In Amphibia and Reptiles the inferior pair of lateral elements of the vertebræ are not developed, except in the caudal region, where they form inferior arches. The development of the body of the vertebræ is effected in very different ways, in relation to the chorda dorsalis, in these classes of animals. In the frog-like Amphibia (Anoura) two principal varieties of the mode of development of this part have been observed by Dugès. In the genus Pelobates (P. cultripes seu Rana

* [Fig. 236. Part of the vertebral column of a fœtal Acanthias vulgaris. A, lateral view. 1, superior vertebral elements or arches; 2, sheath of the chorda dorsalis undergoing division into the bodies of the vertebræ; 3, inferior vertebral elements. B, the same seen in a transverse section. After Müller, Vergleichende Neurologie der Myxinoiden. Abhandl. der k. Ak. der Wissen, zu Berlin, 1838.]

† See J. Müller, Vergleichende Anatomie der Myxinoiden, Abhandl. der Akad. d. Wissensch. zu Berlin. J. 1834, and the more recent paper, Die Vergleichende Neurologie der Myxinoiden. Ibid. J. 1838, p. 232.

cultripes, Cuvier; Cultripes provincialis, Müller; and P. fuscus, Wagl.; Bufo fuscus, Cuvier; Cultripes minor, Müller) the chorda dorsalis is not surrounded by the bodies of the vertebræ; but the superior pair of lateral elements merely have been developed, constituting the arches, and have coalesced beneath the chorda, so as to form the body of the vertebra. The chorda, therefore, lies in a groove upon the upper surface of the bodies of the vertebræ; but it gradually wastes and disappears. The same structure exists, according to my observations, in the genus Pseudis (Rana paradoxa).

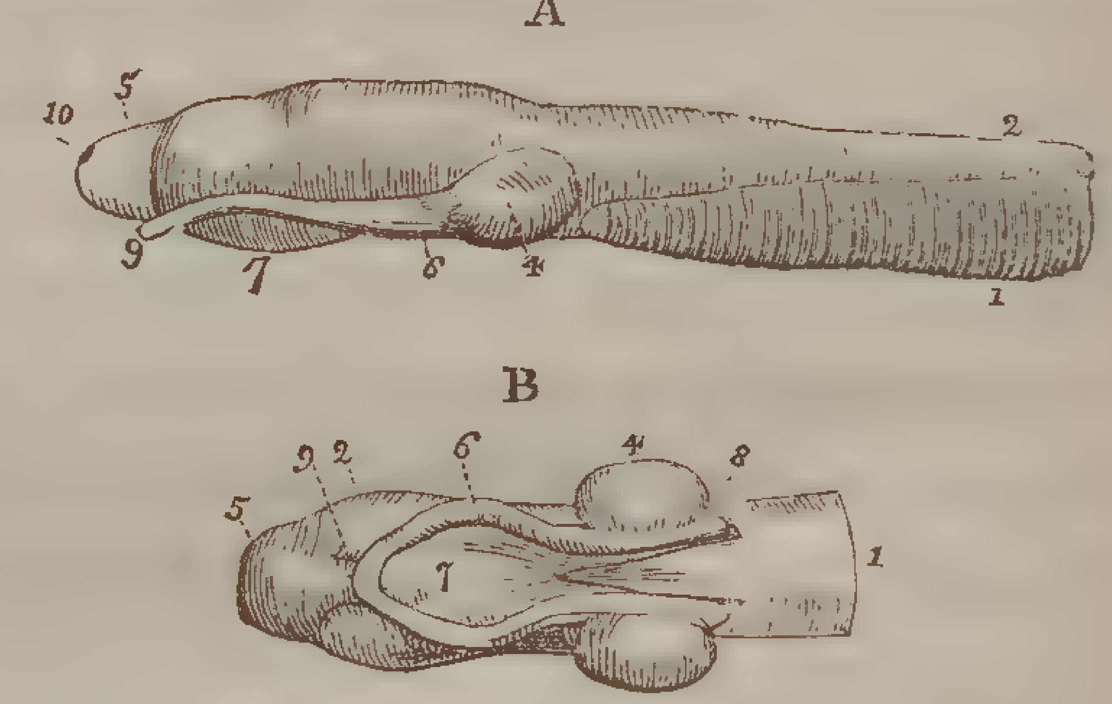
In other frog-like Amphibia, and the Salamandrinæ, the mode of origin of the body of the vertebræ is totally different. The sheath of the chorda itself becomes the seat of ossification in annular segments corresponding to the successive vertebræ, and remains membranous only in their intervals. Hence, at a certain period of the life of the larva, the chorda dorsalis is enclosed in a number of thin ossified rings, which, however, gradually grow thicker and take the place of the chorda. In this case the body of the vertebræ is not formed by two symmetrical elements, and the superior pair of lateral elements of the vertebra, forming the arches, merely becomes united to the ossified rings.

In reptiles, birds, and mammals the type of formation of the vertebræ seems to be again different. The peculiarity of this type is, at all events, distinct in the class of birds. Here the vertebræ in that part of the spinal column which belongs to the trunk, are developed from a single pair of elementary parts. When the formation of these parts from the blastema commences, there appear at each side of the chorda dorsalis a series of quadrangular figures, the rudiments of the future vertebræ. (See fig. 191, page 1538.) These gradually increase in number and size, so as to surround the chorda both above and below, sending out at the same time superiorly processes to form the arches destined to enclose the spinal marrow. In this primitive condition the body and arches of each vertebra are formed by one piece on each side. At a certain period these two primary elements, which have become cartilaginous, unite inferiorly by a suture. The chorda is now enclosed in a case, formed by the bodies of the vertebræ, but it gradually wastes and disappears. Before the disappearance of the chorda the ossification of the bodies and arches of the vertebræ begins at distinct points.

The ossification of the body is first observed at the point where the two primitive elements of the vertebræ have united inferiorly. The form of this centre of ossification is bilobed; only in the sacral vertebræ of the bird have I seen it in the form of two distinct ossifying points. Those vertebræ which do not bear ribs, such as the cervical vertebræ, have generally an additional centre of ossification in the transverse process, which is to be regarded as an abortive rudiment of a rib. In the fœtal bird these additional ossified portions exist in all the cervical vertebræ and gradually become so much developed in the lower part of the cervical region as to form the upper false ribs of this class of animals. The same parts exist in Mammalia and man. Those of the last cervical vertebra are the most developed, and in children may, for a considerable period, be distinguished as a separate part on each side, like the root or head of a rib. Hence, it follows, that the lower of the nine cervical vertebræ of the Sloth, which bear rudiments of ribs, are not on that account to be regarded as dorsal vertebræ, but that this animal has really nine true cervical vertebræ. The transverse processes of the lumbar vertebræ seldom present distinct points of ossification, forming false ribs; but, in the hog, at a certain period of fœtal life this is an ordinary appearance. Of the same nature are the two portions of bone which, in man and other animals, unite the sacral vertebræ on each side to the ilia. In crocodiles, tortoises, and turtles these parts of the skeleton are so elongated that the pelvis is clearly seen to be connected with the vertebral column by means of vertebral ribs.*

The true cranium is a prolongation of the vertebral column, and is developed at a much earlier period than the facial bones. Originally, it is formed of but one mass, (in which condition it remains as the cerebral capsule in the Cyclostomatous fishes, the Sharks and the Rays,) the chorda dorsalis being continued into its base and ending there with a tapering point. This relation of the chorda dorsalis to the basis of the cranium is persistent through life in the Cyclostomata and Sturgeon family; the acuminated extremity of the chorda reaching to about the middle of the base of the cerebral capsule. The sheath of the chorda extends to its very point. The first appearance of a solid support at the base of the cranium, which I have observed in the Ammocœtes, consists of two elongated bands of cartilage, one on the right and the other on the left side, which are connected with the cartilaginous capsule of the auditory apparatus, and united with each other in an arched manner anteriorly beneath the anterior end of the cere-

Fig 237.†



* See the Vergleichende Anatomie der Myxinoiden, loc. cit. p. 303.

† [Fig. 237. The rudimentary parts of the cranium in Ammocœtes branchialis; A, viewed from the side; B, seen from below. 1, internal sheath of the chorda dorsalis; 2, tube of the spinal marrow; 3, cerebral capsule; 4, auditory capsule; 5, nasal capsule; 6, palatal bands of cartilage; 7, the palatal palate or lamina, united at its borders to the palatal cartilages; 8, cartilage of the basis cranii; 9, anterior commissure of the palatal cartilages; 10, the nasal orifice. After Müller Vergleichende Anat. der Myxinoiden.]

bral capsule. (See fig. 237.) The same cartilages are present in the Myxinoid fishes, and are persistent; the facial cartilages also proceeding from them. In Ammocœtes and Myxine these basilar cartilages have the cephalic portion of the chorda dorsalis between them. In Bdellostoma the process of development has gone a step further; for here the two cartilages have wholly coalesced posteriorly and have formed a simple basilar cartilage, in which the chorda is enclosed. Hence we see that in the cranium, as in the spinal column, there are at first developed at the sides of the chorda dorsalis two symmetrical elements, which subsequently coalesce and may wholly enclose the chorda. Rathke has recently observed, in the embryos of serpents and other animals, before the formation of the proper cranial vertebræ, two symmetrical bands of cartilage, similar to those which I discovered as a persistent structure in the simplest state in Ammocœtes.*

At a later period the basis cranii of vertebrate animals contains three parts analogous to the bodies of vertebræ, the most anterior of which, in the majority of animals, is generally small and its development frequently abortive, whilst in man and mammiferous animals the three are very distinct. These parts are developed by the formation of three distinct points of ossification, one behind the other, in the basilar cartilage. The three ossified portions become united by sutures, and in mammals form a rod-like body tapering towards its anterior extremity and giving attachment at its sides to the lateral parts of the three vertebræ. The bodies of the three cranial vertebræ are the os basilare occipitale, the os basilare sphænoideum posterius, and the os basilare sphænoideum anterius, which in all mammals are very clearly defined. The lateral parts of the vertebræ, developed in the cerebral capsule, are: 1, the lateral parts of the occipital bone; 2, the alæ majores of the sphenoid bone; and, 3, the alæ minores of the same bone. The superior part or squama of the occipital bone, the parietal bones, and the frontal bone are developed in the cerebral capsule and complete the arches of the three vertebræ. Between the parietal bones and the occipital squama there are developed in some animals ossicula Wormiana, analogous to those bones which lie between the arches of the vertebræ in Sharks and Rays. Similar bones are developed also at the basis of the vertebral column, as in the sturgeon, and at the base of the cranium. Of this nature are apparently the ossa petrosa also, which have no exclusive connection with the auditory apparatus, and in birds and the animals below them in the scale, share with other bones the function of enclosing the labyrinth.

The squamous part of the temporal bone in man and the higher animals contributes to the formation of the true cranium, from which it is in reptiles, amphibia, and fishes more or less excluded. The proper

* See Rathke, über die Entwickelung des Schädels. Königsburg, 1839.

function of this bone is to support the lower jaw. In birds, reptiles, amphibia, and fishes, several other parts, as the os quadratum and the os zygomaticum, aid in the composition of the suspensor of the lower jaw.* In young mammiferous animals two other parts can be distinguished in connection with the temporal bone, namely, the annulus tympanicus and the bulla tympani, which Hagenbach could distinguish as separate parts in some mammals. Platner saw an annulus tympanicus in several birds; and frogs also have a rudiment of the same part.

2. *The facial portion of the skull and the "visceral arches."*

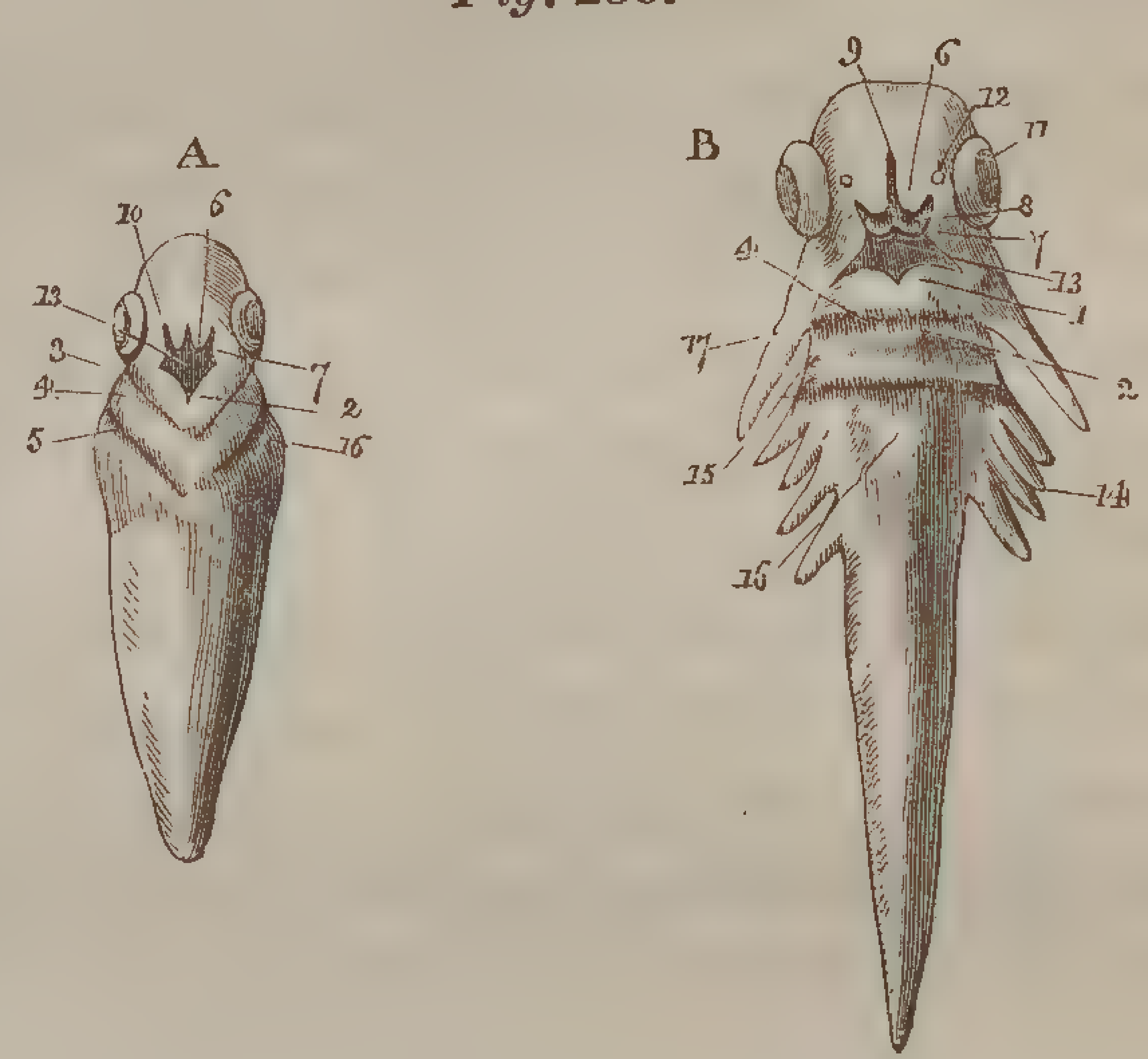
The facial region of vertebrate animals consists of the organs of sense, nose, eye, and ear, which are appended to the cranium and the cerebral vesicles contained within it, and of the upper and lower jaws and their muscles. The upper jaw, or maxillary apparatus, according to the general plan of the Vertebrata, is, in its most perfect form, composed of five bones, namely, the os intermaxillare, the vomer, the os maxillare, the os palatinum, and the os pterygoideum seu palatinum posterius. In some animals all these bones exist on each side of the face, and they may all bear teeth; but certain of them are in many animals destitute of teeth, and abortive in their developments; as are, for example, in man and mammalia, the vomer, the os palatinum, and the os pterygoideum, or internal ala of the processus pterygoideus of the sphenoid bone, which, in several animals, is developed as a distinct bone, and forms a continuation of the palate backwards. In its most fully developed form the superior maxillary apparatus reaches, through the medium of the os pterygoideum, to the lower jaw; and then the upper and the lower maxillary apparatus form together a fork-like body suspended from the temporal bone. Of these parts only an imperfect palate exists in the cyclostomatous fishes, neither upper nor lower jaw being present. The organs of sense of the Vertebrata have frequently special bones provided for them, which form parts of the skeleton; such are the ethmoid bone, the nasal bones, the supra-orbital bones of Lizards and the Python, the infra-orbital bones of fishes, and the tympanic ring. In many animals also there extends between the temporal bone and the upper jaw an arch which is completed by the malar or jugal bone.

The mode of development of the facial part of the head has of late years been investigated by Von Baer, Rathke and Reichert. Before the development of the face, the visceral cavity of the cephalic region is formed superiorly by the primitive rudimentary structure which contains the encephalon, the cerebral capsule; whilst the lower and lateral walls of that

* For information respecting the comparative anatomy of these parts the reader may refer to Hallmann's valuable treatise: Vergleichende Osteologie des Schläfenbeins. Hannover, 1837.

cavity are formed by the anterior "visceral arch." At this period there is no nasal cavity, and the visceral cavity of the head extends uninterruptedly from the first visceral arch to the cerebral capsule. In birds and mammiferous animals there are three visceral arches, and also three visceral clefts. The first cleft becomes converted into the external auditory passage, the tympanum and the tuba Eustachii; the second and the third are obliterated. The face is originally formed of a middle portion proceeding from the forehead, Von Baer's frontal process, and of a lateral portion on each side derived from the superior extremity of the first visceral arch. These parts are at first separate. The lateral and the inferior parts, destined to form the superior and inferior maxillary apparatus, are both, according to Reichert, derived from the first visceral arch, in which an angular bend appears; the part above this bend being converted into the superior maxillary mass, and that below it into the inferior maxillary apparatus. (See fig. 238.) The superior maxillary mass, in its growth, approaches the frontal process and unites with it; a cavity being left beneath that process and between the two superior maxillary masses, which becomes the nasal cavity. By the union of the superior maxillary masses (the superior maxilla and palate bone) of opposite sides beneath this cavity the separation of the nose from the mouth by the palate is produced. Attached to the elongated frontal, or nasal process of the forehead, there soon appears the substance of the superior intermaxillary bone, whilst at the lower part of the visceral arch, from which the lower jaw is formed, a partly detached portion presents itself, which Reichert calls the inferior intermaxillary rudiment. It is not yet known whence the rudiment of the superior

Fig. 238.*



* [Fig. 238. Development of the parts of the face in the embryo of Triton tæniatus. A, an embryo four lines long, magnified: B, another embryo further advanced in development. After Reichert. 1. The first visceral arch, or inferior arch of the first cephalic vertebra (incorrectly marked 2 in the figure A); 2. the second visceral arch; 3. the second visceral process; 4. the first visceral cleft; 5. the second visceral cleft; 6. the nasal or anterior frontal process; 7. rudiments of the superior maxilla; 8. rudiments of the superior intermaxillary bone; 9. the cleft between the nasal or anterior frontal processes; 10. the external nasal opening; 11. the eye; 12. the small elevation of the lachrymal bone; 13. the opening of the cephalic visceral cavity or mouth; 14. the external branchiæ; 15. the membranous branchial operculum; 16. elevated ridge pushed forwards by the heart and its aortic arches.]

intermaxillary bone is first derived; for although the blastema of this part is first observed between the nasal processes on the part of the face derived from the forehead, yet it is very possible for it to have been derived originally from the nasal processes themselves, and from the immediately contiguous superior part of the first visceral arch. This latter view appears to me more accordant with comparative anatomy, since the superior maxillary apparatus, in its most complete form, comprehends the os intermaxillare, the vomer, the os maxillare, and the ossa palatinum et pterygoideum. There would then remain merely the middle part of the face which belongs to organs of sense, and is attached to the anterior part of the skull; and this part, in the Plagiostomatous fishes, is united with the skull, whilst the parts belonging to the upper jaw are detached from it. On the other hand, however, there are facts in comparative anatomy which favour the contrary view; for the vomer, although it arises in the middle line, yet belongs to the general category of the maxillary apparatus and dentiferous bones. In man and mammals its development is abortive, but in fishes and batrachian amphibia it contains teeth. The intermaxillary bones therefore may, very possibly, like the vomer, differ entirely from the other parts of the upper jaw in their origin. In the monstruosity called harelip, in which the upper jaw bones and palate bones of opposite sides do not meet, the right and left intermaxillary bones are united, and instead of being attached to the upper jaw bones of their respective sides, remain in the middle line; the cleft of the palate being prolonged forwards on each side between the maxillary and the intermaxillary bone, so as to leave the latter with the incisor teeth suspended to the vomer. It will be evident from the preceding description, that the palate dividing the nasal from the oral cavity does not exist during a long period of fœtal life; this septum between the two cavities not being formed until the superior maxillary masses, extending inwards from each side, meet in the middle line.

The mode of development of the face not only affords an explanation of the abnormal cleft palate and the congenital cleft between the upper maxillary and the intermaxillary bone; but also seems to throw light upon those congenital fissures which pass between the intermaxillary bone and upper jaw as far upwards as the orbital cavity. Congenital clefts of this kind, which correspond to primitive conditions of the parts, are called results of the arrest of development. But in applying this extremely fruitful theory, which Meckel's researches have rendered so important, to fissures of the integuments, some caution is necessary. The harelip, or cleft of the upper lip in the situation of the junction between the os maxillare superius and the os intermaxillare, certainly is dependent on arrest of development, but not entirely: for the upper lip is at no period of normal development cleft in this manner, but grows from its attached border uniformly at all points at the same time. The arrested development of the deeper-seated parts seems, however, to give rise to an imperfect formation of the lip.

The transformations which the visceral arches undergo in mammalia are, according to Reichert's observations, as follow: the "blastema" of the first visceral arch produces, as special structures, the superior maxillary apparatus, the under jaw, and a part of the ossicula auditûs, namely, the malleus and the incus. It was discovered by Meckel, that in the fœtus of the human subject and of mammiferous animals the malleus is prolonged at the inner side of the lower jaw bone as far as the chin, where it forms an arch by its union with its fellow of the opposite side. There are formed therefore, in the first visceral arch, both an inferior maxillary arch and an arch of the malleus. Reichert shows that the latter is formed first. After the development of the lower jaw, the long process of the malleus lies at the inner side of the first solid rudiment of that bone; and when the lower jaw is in greater part developed and ossified, the prolongation of the malleus begins to suffer atrophy.

From the second visceral arch are formed the suspensory apparatus of the hyoid bone and the stapes of the ear. The suspensory apparatus of the os hyoides in the human subject is at its upper part osseous, consisting of the processus stiloideus, which is at first isolated, but subsequently becomes anchylosed with the temporal bone; in its middle portion it is ligamentous, where it constitutes the ligamentum stilo-hyoideum; while most inferiorly it is again osseous, and forms the smaller cornu of the os hyoides. In most mammals nearly the whole of this suspensory apparatus becomes ossified, and constitutes the numerous segments of the anterior cornu of the os lingualis seu hyoides. The posterior cornua and the body of this bone are developed from a cartilaginous band contained in the third visceral arch.*

3. *The Extremities.*

The extremities are developed in an uniform manner in all vertebrate animals. They appear in the form of leaf-like elevations from the parietes of the trunk (see fig. 223, page 1588) at points where more or less of an arch will be produced for them within. The primitive form of the extremity is nearly the same, whether it be destined for swimming, crawling, walking, or flying. The primitive rudiment is formed according to the general type of the vertebrata, and is subsequently moulded into the specific forms. In the human fœtus the fingers are at first united by the blastema as if webbed for swimming; but this is

* For an account of the metamorphoses which the "visceral arches" undergo in birds, reptiles, and amphibians, Reichert's work already cited, and his Vergleichende Entwickelungs-geschichte des Kopfes der nackten Amphibien, Königsberg, 1838, may be consulted.

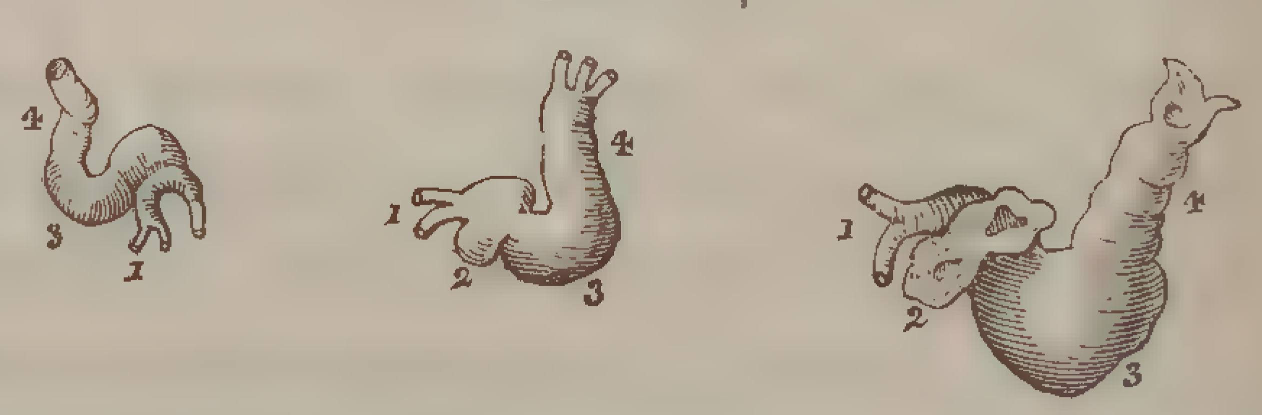
to be regarded not so much as an approximation to the form of aquatic animals, as the primitive form of the hand, the individual parts of which subsequently become more completely isolated.*

4. *The vascular system.*

The first development of the vascular system and heart in the germinal membrane has been already described. The earliest form of the circulation presents itself in the area vasculosa bounded by the sinus terminalis, to which the blood is distributed from the heart and aorta by means of two transverse arteries, and from which it is again returned to the heart by two veins running in opposite directions from the upper and lower parts of the area vasculosa. (See figs. 191 and 192, page 1538.) This arrangement of vessels subsequently undergoes a change; the veins above described are replaced by others which are developed from the vascular network of the area vasculosa and accompany the transverse arteries; the sinus terminalis ceases to exist, and the vessels extend over the whole surface of the yolk-sac.

The Heart.—The heart is originally in all animals a simple undivided canal, which at its lower extremity receives the venous trunks, and at its upper extremity divides into the arterial trunks or aortic arches. This canal becomes curved in a horse-shoe form, and at the same time becomes divided into three cavities (fig. 239). Of these three cavities which are developed in all vertebrata, the posterior is the simple auricle; the middle one the simple ventricle; and the most anterior the bulbus arteriosus. These three parts of the heart contract in succession. The division of the heart into three cavities is observed in the chick about the second or third day. The auricle and the bulbus arteriosus at this period lie at the extremities of the horse-shoe. The bulging out of the middle portion inferiorly gives the first indication of the future form of the ventricle. (See fig. 239.) The great curvature of the horse-shoe by the same means becomes much more developed than the smaller curvature between the auricle and bulbus; and the two extremities, the auricle and bulb, approach each other superiorly, so as to produce a greater resemblance to the later form of the heart, whilst the ventricle becomes more and

Fig. 239.†

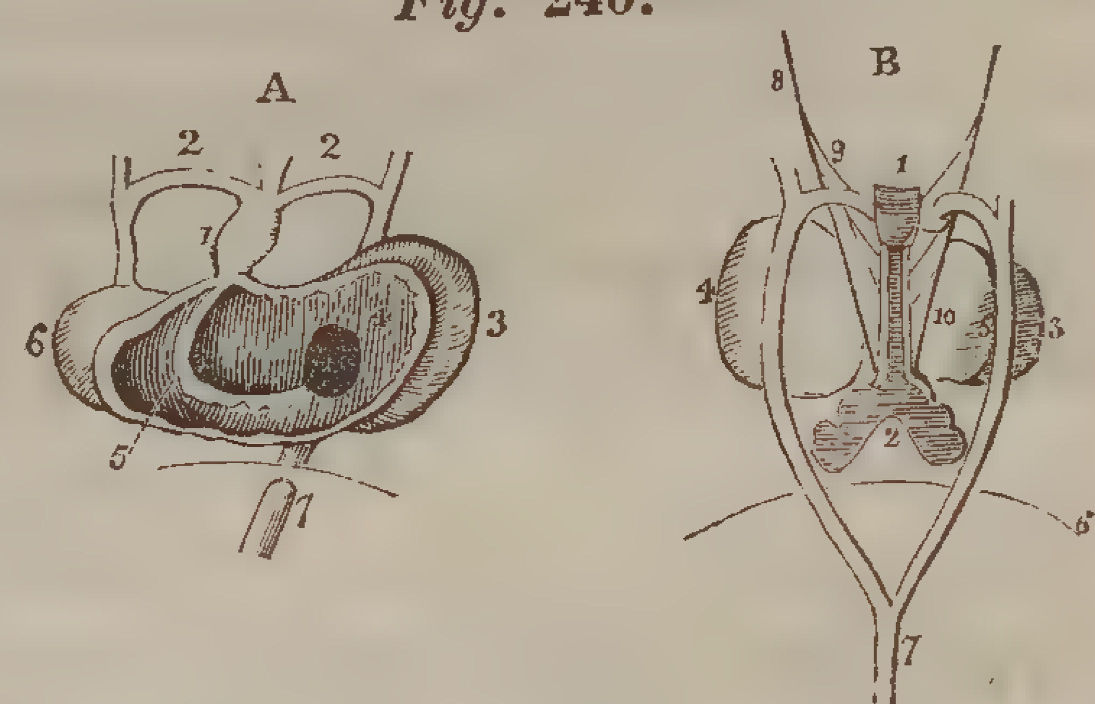


* An account of the special development of the osseous system must be sought in the more extended works on the subject of fœtal development. A complete account will be found in Valentin's "Entwickelungs-geschichte."

† [Fig. 239. Heart of the chick at the 45th, 65th, and 85th hours of incubation. 1, indicates the venous trunks; 2, the auricle; 3, the ventricle; 4, the bulbus arteriosus. After Dr. Allen Thomson, Edinb. New Phil. Journ. vol. ix. pt. ii.]

more developed inferiorly. The heart of fishes (see fig. 5, p. 160, edit. 1; p. 172, edit. 2) retains these three cavities, no further division by internal septa into right and left chambers taking place. In the amphibia also the heart throughout life consists of the three muscular divisions which are so early formed in the embryo; but the auricle is divided internally by a septum into a pulmonary and a systemic auricle (fig. 10, p. 165, edit. 1; p. 176, edit. 2). In reptiles, not merely the auricle is thus divided into two cavities, but a similar septum is more or less developed in the ventricle. In birds, mammals and the human subject both the auricle and ventricle undergo complete division by septa; whilst in these animals, as well as in reptiles, the bulbus aorta is not permanent, but becomes lost in the ventricles. The division of the auricle and ventricle into right and left cavities begins in birds about the 60th or 70th hour. The septum dividing the ventricle, according to Von Baer, commences at the apex and extends upwards. (See fig. 240.) A communication between the two ventricles was observed by Dr. Allen Thomson still existing after 7½ days' incubation. Subsequently this opening is closed, and at the same time a septum is developed in the bulbus aortæ separating the roots of the proper aorta and the arteria pulmonalis. The septum of the auricles is developed from a semilunar fold which extends from above downwards. The left auricle, which is at first very small, is found in connection with the pulmonary veins after the sixth day. In man the septum between the ventricles, according to Meckel, begins to be formed about the fourth week, and at the end of eight weeks is complete. The septum of the auricles in man and all animals which possess it, remains imperfect throughout fœtal life. When the partition of the auricle is first commencing, the two venæ cavæ have different relations to the two cavities. The superior cava enters as in the adult into the right auricle; but the inferior cava is so placed that it appears to enter the left auricle, and the posterior part of the septum auricularum is

Fig. 240.*



* [Fig. 240. Heart of a human embryo of about the fifth week. A, the heart opened on the abdominal aspect. 1 indicates the bulbus arteriosus; 2, two aortic arches which unite posteriorly to form the aorta; 3, the auricle (which is at this period almost quite a simple cavity); 4, the opening from the auricle into the ventricle (6), which is laid open; 5, the septum rising from the lowest part of the cavity of the ventricle; 7, the vena cava inferior. B. The same heart viewed from behind. 1, the trachea; 2, the lungs; 3, the ventricle; 4, 5, the large atrium cordis or auricle; 6, the diaphragm; 7, the aorta descendens; 8, the nervus vagus; 9, its branches; 10, continuation of the nervus vagus. After Von Baer, Siebold's Journal, Bd. xiv, and Entwickelungs-geschichte der Thiere, Bd. ii.]

formed by the great Eustachian valve, which extends from the point of entrance of the inferior cava. Subsequently, however, the septum, growing from above downwards, becomes directed more and more to the left of the vena cava inferior. During the entire period of fœtal life, however, there remains an opening in the septum auricularum, which the valvula foraminis ovalis, developed in the third month, imperfectly closes.*

Aortic arches and pulmonary vessels.—In the early embryos of all vertebrate animals the blood is distributed from the bulbus aortæ towards either side, and after passing round the circumference of the visceral cavity is again collected in front of the vertebral column into a single vessel, the aorta descendens. According to Serres, the aorta descendens in the chick about the 40th or 50th hour is double in its whole length. Dr. Allen Thomson observed this condition about the 36th or 40th hour; but found the two vessels already united in a considerable extent at the 48th or 50th hour. According to Reichert there is a small transverse communication even at the earliest period. The aortic arches are always several in number, and at first lie in connection with the visceral arches. In those animals which breathe by branchiæ, and in which the visceral arches partly serve for the formation of the branchial apparatus, each of the aortic arches is resolved into two parallel vessels, one arterial, which comes from the heart and ramifies wholly in the branchiæ; and the other venous, which arises in the branchial laminæ and unites with the veins of the other branchiæ in front of the aorta to form the descending aorta. In the amphibia the same structure exists for a certain period; but afterwards the branchial vessels are again transformed into three aortic arches, which when the branchial apparatus has ceased to exist sink deeper into the thoracic cavity and become permanent.

The Sharks and Rays and the Amphibia have either fœtal or larval branchiæ. These are distinguished from permanent branchiæ, being filaments or tufts, projecting or depending externally from the branchial cavity and containing vascular loops. The external gills of the Sharks and Rays do not exist during the whole period even of fœtal life, but disappear at a certain time, no trace of them being found in the more advanced fœtus.† The external branchiæ of some amphibia, as the Bufo obstetricans and Salamandris terrestris, are fully developed even during fœtal life, and receive blood-vessels. In frogs the external branchiæ are provided for the first few days of the larva condition, they

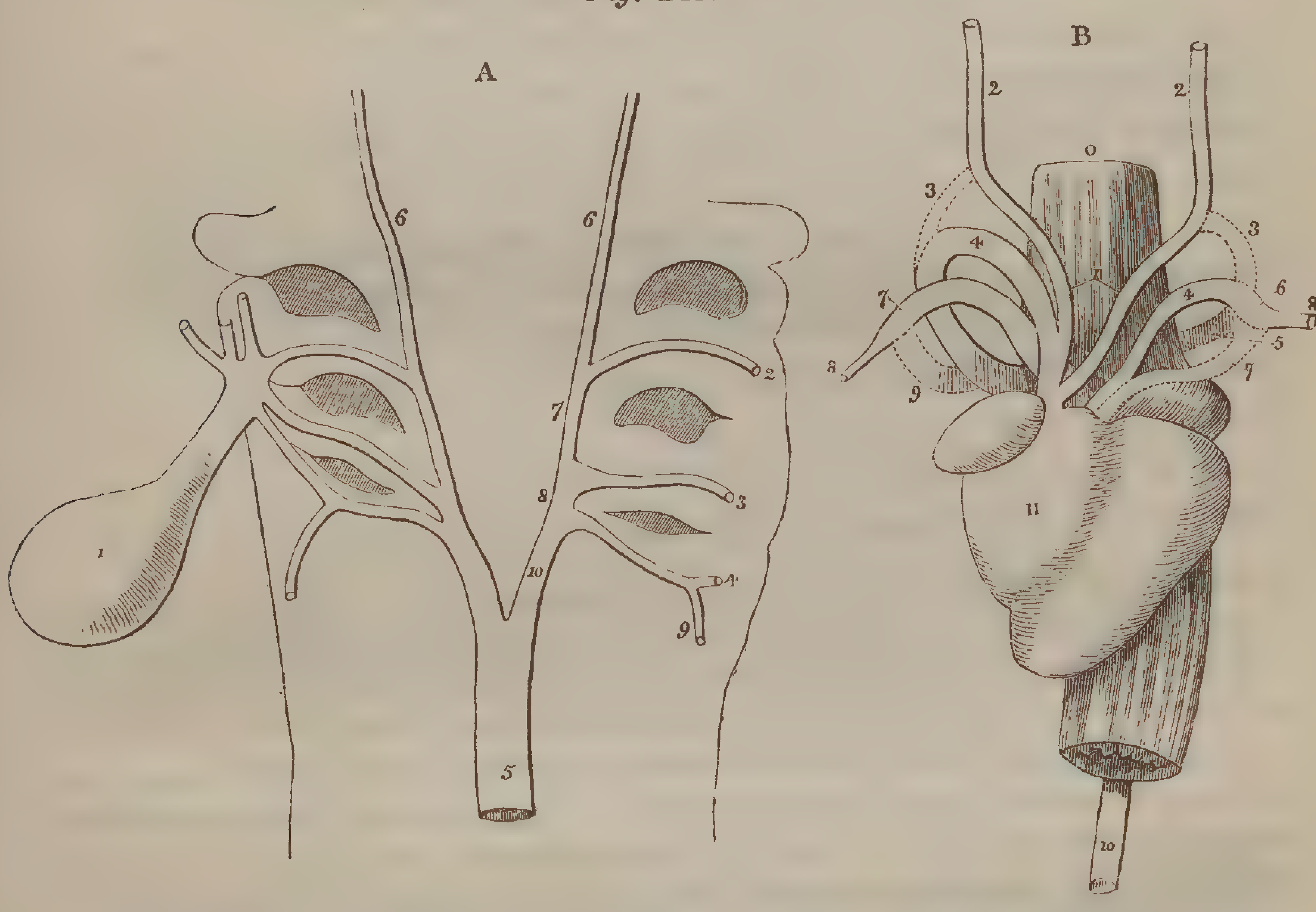
* The authors to be consulted on the development of the heart are, Meckel, Archiv. ii. p. 402; Kilian, über den Kreislauf des Blutes im Kinde, welches noch nicht geathmet hat. Karlsruhe, 1826; Allen Thomson, Edinb. New Philos. Journ. Oct. 1830; Von Baer, op. cit.; and Valentin, op. cit.

† Leuckart, über die Aeusseren Kiemen der Embryonen von Rochen und Haien. Stuttgardt. 1836.

then disappear whilst the internal branchiæ take their place. When the lungs of the frog have become developed, the pulmonary artery on each side is a branch of the most inferior aortic arch, whilst the posterior portion of this arch resembles a persistent ductus arteriosus. In the Reptilia no branchiæ or branchial vessels are developed on the visceral arches, and the several aortic arches are received into the thoracic cavity, yet continue to exist in part throughout life. The lizards have four permanent aortic arches, two on each side; whilst the tortoises, and turtles, the crocodiles, and the serpents, have only two, one of which gives off the vessels for the upper part of the body, while the other furnishes the artery for the viscera. (See fig. 6, p. 161, edit. 1; p. 173, edit. 2.) The pulmonary artery of these animals arises independently from the ventricle; but in the adult turtles and tortoises it is possible to distinguish traces of two other aortic arches which are now obliterated, but which previously had the relation of ductus arteriosi to the vessels sent from them to the lungs.

In birds there exist at a certain period of fœtal life six aortic arches. Of these the two superior furnish the arteriæ anonymæ of the upper

Fig. 241.*

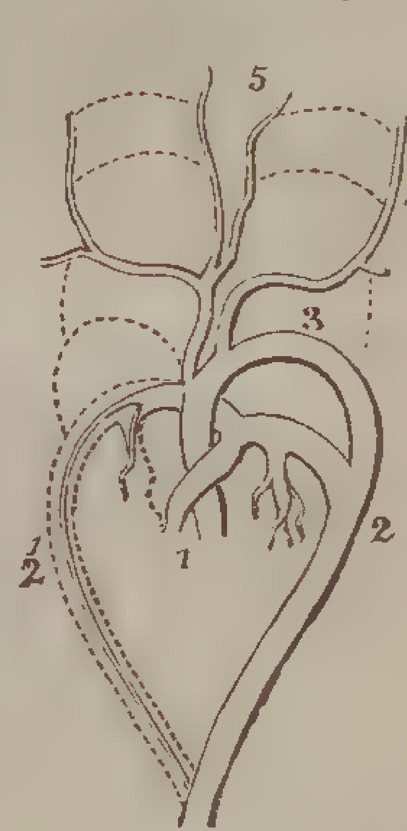


* [Fig. 241. From Huschke, Isis, 1828. A. Neck of an embryo chick at the end of the fourth day of incubation cut open in front, and the lateral halves spread out so as to show the aortic arches and the descending aorta: 1, the heart; 2, 3, and 4, the branchial arteries or aortic arches; 5, the descending aorta; 6, the arteria anonyma; 7, 8, the anastomotic branches between the first and second and between the second and third aortic arches; 9, the artery to the lungs; 10, the future ductus arteriosus. B. Plan showing the changes by which the adult condition of the great vessels arising

parts of the body. The posterior parts of this pair of arches become atrophied. The most inferior pair of arches supply the pulmonary arteries, and form two ductus arteriosi terminating in the aorta descendens, which are not obliterated until the development of the fœtus is completed. The pulmonary arteries then become independent vessels, and arise from the right ventricle of the heart by a distinct trunk, which had at an early period become separated from the aorta by a septum dividing the interior of the bulbus aortæ. Of the two middle aortic arches only the right one remains, the left being obliterated early in fœtal life.*

In Mammalia, according to Von Baer's observations, the aortic arches are soon reduced to three, one of which is the persistent arch of the aorta, whilst the other two are the ductus arteriosi of the pulmonary artery. Of these ductus arteriosi the right also disappears; so that during the remainder of fœtal life only two aortic arches exist, one arising from the right, and the other from the left ventricle. (Fig. 242.) The former of these gives off the arteries to the lungs, the latter the vessels to the upper parts of the body. These two arches are of equal size, and so remain until the fœtus has attained its maturity. After birth the posterior portion of the arch which arises from the right ventricle (the ductus arteriosus Botalli) rapidly becomes narrowed, and in the course of the first few weeks after birth its cavity is entirely obliterated. The anterior portion of this arch now becomes the trunk of the independent arteriæ pulmonales. At the same time the closure of the foramen ovale takes place.

Fig. 242.†



In birds the arch of the aorta is a right aortic arch, — that is to say, it passes to the right of the trachea

from the heart is produced from the embryonic structure: 1, 1, the first pair of aortic arches in the embryo, giving off the arteriæ anonymæ (2, 2); 3, branches of communication between the first and second aortic arches (obliterated in the process of development); 4, 4, the second pair of aortic arches. That of the right side becomes the persistent arch of the aorta; that of the left is the future left pulmonary artery; 5, the ductus arteriosus which becomes obliterated; 6, anastomosis between the second and third aortic arch of the left side; 7, the third aortic arch. That of the left side becomes obliterated; that of the right side forms the right pulmonary artery; 8, 8, the pulmonary arteries; 9, branch of communication between the third and second arch of right side; 10, descending aorta; H, heart; O, œsophagus.]

* See the excellent papers of Huschke in the Isis, 1827, p. 401; and 1828, p. 161. Compare Allen Thomson's observations in the Edinb. New Phil. Journ. January, 1831.

† [Fig. 242. Plan of the transformation of the system of aortic arches into the permanent arterial trunks in mammiferous animals; after Von Baer. 1 indicates the situation of the original single trunk which arose from the single ventricle and which

and œsophagus in its way to the vertebral column. In man and Mammalia it is a left aortic arch passing to the left side of the parts just mentioned.

Veins.—It appears, from Rathke's excellent researches, that the conformation of the venous system also is at first the same in the embryos of all vertebrate animals, and subsequently departs in various ways from the common primitive type. In the original condition there are two anterior venous trunks (the jugular veins) and two posterior trunks, which Rathke names the cardinal veins. One of the anterior trunks, and one of the posterior unite on each side and form a transverse canal, — the ductus Cuvieri. The two ductus Cuvieri unite beneath the œsophagus to form a shorter main canal which enters the auricle,—at that time a simple cavity. The cardinal veins are originally formed by the caudal veins, branches from the kidneys and Wolffian bodies, and others from the dorsal parietes of the trunk, which are at a later period the intercostal and lumbar veins; and in animals which have lower extremities the two cardinal veins also receive the venæ crurales. This system, as it exists in all animals, may be designated the venous system of the simple auricle. It persists in most vertebrate animals as long as their heart resembles that of fishes. In fishes themselves it continues to exist throughout life. (See fig. 5, p. 160, edit. 1; p. 172, edit. 2.) In the Amphibia and Reptilia the cardinal veins become the venæ advehentes of the kidneys, which convey the blood to those organs from the hinder extremities. The common canal, formed by the union of the two ductus Cuvieri, is at a still earlier period absorbed into the cavity of the originally simple auricle in all animals above fishes; and after the septum auricularum is formed, the two ductus enter separately the right auricle. The venæ subclaviæ unite with the venæ jugulares. The ductus Cuvieri in birds and some mammals remain as two venæ cavæ superiores, or anteriores, entering the right auricle separately. In other mammals the right duct alone remains as the superior or anterior vena cava. In serpents, lizards, birds, and mammals, there is formed a distinct system of vertebral veins, the posterior of which are the vena azygos, and vena hemi-

has become divided into two tubes. The single trunk gave off five pairs of aortic arches which terminated in the two roots of the aorta (2, 2′). Those of the arches which are obliterated at a very early period are marked by dotted lines. The first arch of the right side with the root of the aorta of that side (2′) which remains longer and forms the right ductus arteriosus, is drawn as a very narrow vessel with a dotted line on each side. The vessels which still exist at birth are drawn of the full size. These are the first arch of the left side, constituting the ductus arteriosus Botalli, which is in greater part obliterated soon after birth, and the second arch of the left side, constituting the permanent arch of the aorta (3). The subclavian arteries (4) and the carotid arteries (5) are seen to be formed from parts of the other primitive aortic arches. After the obliteration of the left ductus arteriosus the pulmonary arteries are the only remains of the first pair of aortic arches.]

azygos (more correctly venæ conjugatæ, since they are perfectly symmetrical branches of a single trunk, which is a true vena azygos). The blood of the anterior and posterior vertebral veins is poured into the superior vena cava.

The omphalo-mesenteric vein, vena omphalo-meseraica, which receives the vein of the mesentery, is a primitive structure common to all vertebrate animals. It passes with the two ductus Cuvieri, originally between them, but as a separate vessel to the auricle. When the liver is formed, this vein gives branches to it, and receives from it others, the venæ hepaticæ, in birds and mammals. Between the two sets of hepatic veins the trunk of the omphalo-mesenteric vein becomes obliterated, and then the vena portæ is formed as an independent vessel conveying blood to the liver, while the same blood is carried out of the organ by the distinct venæ hepaticæ.

In fishes there is no inferior cava. In birds and mammals that vessel arises between the Wolffian bodies, and originally enters the omphalo-mesenteric vein in front of or above the liver; and hence, after the hepatic circulation is established, this vena cava receives the hepatic veins. There is no vessel in fishes analogous to this vein. In Reptilia and Amphibia the inferior vena cava receives, not only the venæ hepaticæ, but also the blood of the kidneys and organs of generation. (See fig. 12, p. 169, edit. 1; p. 180, edit. 2.) In birds and mammals the blood of most of the animal structures of the posterior part of the body enters the vena cava inferior. In rare cases of abnormal formation the vena cava fails to be developed, and then the blood from the lower parts of the body is conveyed to the superior cava through the system of the vena azygos.*

The umbilical vein is to be regarded as the product of the combination of the veins of the allantois with an anterior vein of the abdominal parietes, vena abdominalis, which is permanent in the Reptilia and Amphibia, and joins the vena portæ. The vena abdominalis anterior exists alone in the Amphibia, since they have no allantois; but in the Reptilia both vena abdominalis anterior and the veins of the allantois exist in the fœtus.

It is probable that the veins of the anterior parietes of the abdomen and the allantoic veins are at first distinct, and become united during the further development of the allantois. On this supposition, we may explain the enigmatical fact that the umbilical vein (the vein of the allantois) terminates in the vena portæ, which lies in a part of the body very distant from that at which the allantois was developed. Rathke adduces arguments in favour of this view. In man the vena umbilicalis receives branches of the epigastric vein.†

* Stark, de Venæ azygos Naturâ. Lips. 1835.

† Burow, in Müller's Archiv. 1838, p. 44.

The umbilical vein in birds and mammals originally terminates, according to Rathke, in that part of the omphalo-mesenteric vein which is about to enter the heart, and which subsequently forms the most anterior or superior part of the vena cava inferior. At a later period the umbilical vein, like the omphalo-mesenteric vein, sends branches to the liver, and the anastomosis between the umbilical vein and the inferior vena cava, the ductus venosus arantii, is produced.*

The circulation of the fœtus is essentially distinguished from that of the adult human subject by the mingling of the blood of the two auricles, which takes place through the opening in their septum, also by the further mixture of the blood of the two sides of the heart which is effected through the medium of the ductus arteriosus Botalli, and further by the circumstance of part only of the blood of the right ventricle being sent to the lungs. All the blood of the body, or all the blood which the two ventricles emit, except the small quantity which the lungs receive from the right ventricle is returned to the right auricle. The blood of the left ventricle is sent to the upper parts and also to the lower parts of the body; that of the right ventricle passes chiefly through the ductus Botalli, and supplies the lower parts of the body. All this blood returns to the right auricle. Only the fractional portion which the right ventricle sends to the lungs is collected from those organs in the left ventricle. If we suppose that both ventricles emit the same quantity of blood, — since all the blood from the one and a part of that from the other return to the right auricle,—the right auricle must receive more than half the whole mass of blood, — that is, more than the right ventricle emits; whilst the left auricle must receive less than half and less than the corresponding ventricle emits. And hence it follows that a part of the blood of the right auricle must flow through the foramen ovale into the left auricle.

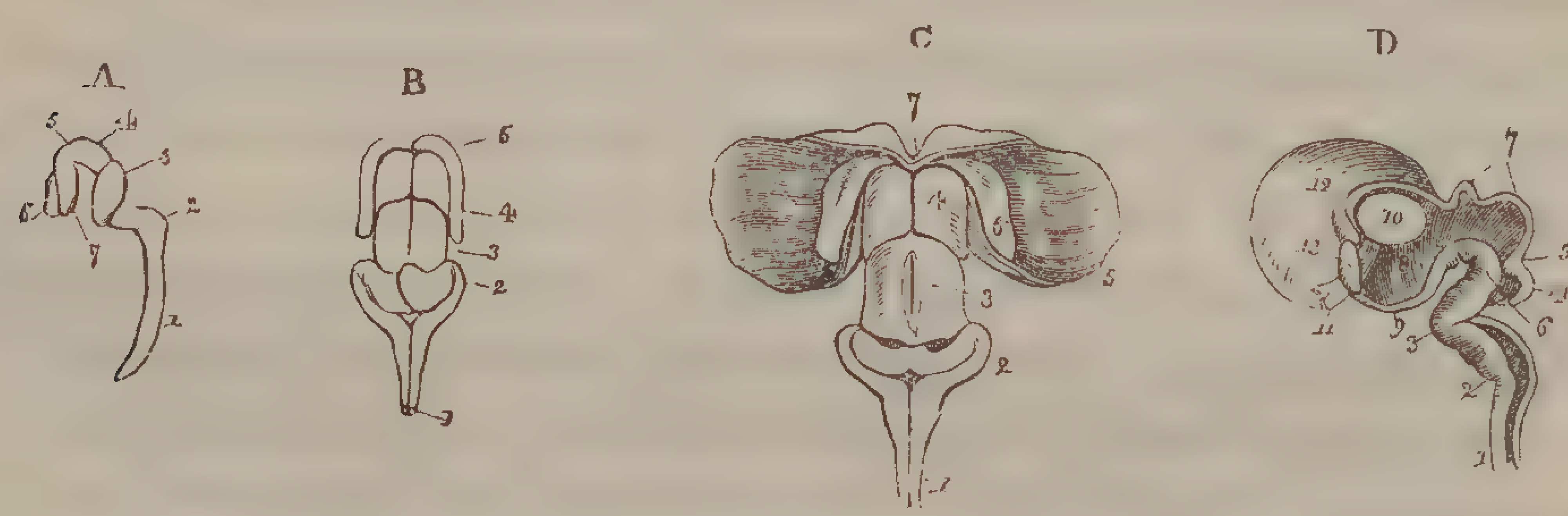
5. *Nervous System.*

The nervous system in its rudimentary form consists, according to Reichert, of two laminæ meeting in a central groove, the outer borders of which gradually become elevated, and then unite so as to form a tube. In the situation of the medulla oblongata this canal seems to remain open, unless the cleft is formed again after being once closed. Between this part, the medulla oblongata, and the most anterior extremity of the canal, several vesicular enlargements, the vesicles of the brain, are developed. (See fig. 197, page 1547.) The cerebellum was observed by Von Baer immediately in front of the medulla oblongata as early as the fourth day. To produce the cerebellum the laminæ of the spinal cord, after having formed the fourth ventricle, meet

* Rathke, über den Bau und die Entwickelung des Venensystems der Wirbelthiere. Königsburg, 1838.

again superiorly and anteriorly and enclose a short canal leading into the vesicle of the optic lobes or corpora quadrigemina, which is the largest of the cerebral vesicles. The vesicle in front of that of the optic lobes is the vesicle of the third ventricle, the first formed, and at first the most anterior of all. In front of this, however, are developed the vesicles of the cerebrum, which are at first very small. (See fig. 253, A and B.) The nerves of special sense are originally hollow processes of the ventricles, the auditory nerve arising from the fourth, the optic nerve from the third, and the olfactory nerve from the lateral ventricle. The most essential parts of the organs of sense are, therefore, in their origin, diverticula, or parts protruded from the brain. After the sixth day Von Baer could no longer detect a cavity in these nerves. After a certain period the vesicle of the corpora quadrigemina does not

Fig. 243.



increase in size equally with the other parts, whilst the cerebral hemispheres become most rapidly developed, and extend so as to cover the parts situated behind them. (See fig. 243, C, D.) The great cerebral ganglia are produced by thickening of the walls of the primary vesicles; the corpora striata in the most anterior or cerebral vesicles, and the optic thalami in the vesicle of the third ventricle. (Fig. 243, C.) On the sixth day of incubation the vesicle of the

* [Fig. 243. Early forms of the brain in the embryo, after Tiedemann. A, Brain and spinal cord of an embryo of the seventh week. 1, the spinal cord; 2, enlargement of the spinal cord where it makes a bend forwards; 3, the cerebellum; 4, the optic lobes; 5, the optic thalami; 6, the membranous hemispheres of the cerebrum; 7, prominence analogous to the corpus striatum. B, Brain of an embryo of the ninth week. 1, the spinal cord; 2, the cerebellum; 3, the optic lobes; 4, the optic thalami, enclosing the third ventricle; 5, the cerebral hemispheres. C, Brain of an embryo of the twelfth week, viewed from above, the membranous walls of the hemispheres being reflected to either side. 1, the spinal cord; 2, the cerebellum; 3, optic lobes; 4, the optic thalami, between which the third ventricle lies; 5, the walls of the hemispheres; 6, the corpora striata; 7, commencement of the corpus callosum. D, Perpendicular section of the same brain. 1, the spinal cord; 2, bend of the cord forwards; 3, second bend of the cord upwards; 4, cerebellum; 5, thin laminæ connecting the cerebellum with the optic lobes; 6, crura cerebri; 7, optic lobes or corpora quadrigemina; 8, cavity of the third ventricle; 9, the infundibulum; 10, optic lobe; 11, optic nerves; 12, margin of the fissure leading into the lateral ventricle; 13, the corpus callosum, at this period perpendicular in its direction.]

third ventricle was seen by Von Baer with a wide opening at its anterior part, the medullary mass having already receded from this part during the days preceding. The cerebrum, which is divided into two halves by the sinking down of its roof, being originally a part protruded from the vesicle of the third ventricle, which it overlaps, has through this cleft an indirect communication with the exterior. The great transverse fissure which subsequently leads between the optic thalamus and the fornix into the interior of the cerebrum probably is produced from the same cleft of the third ventricle by the division extending laterally, in such a manner as to leave the fornix forming the margin of the fissure, as it does in the adult. Von Baer regards as the primitive rudiment of the fornix, the boundary between the cavity of the vesicle of the third ventricle and the two cavities of the lateral ventricles; and if the cleft of the third ventricle already existing be supposed to be extended towards either side through the boundary here indicated, the great transverse fissure of the cerebrum will be produced. The borders of this fissure will then be on one side the thickened walls of the vesicle of the third ventricle (the optic thalamus), and on the other the border of the vesicle of the lateral ventricle, namely, the posterior pillar of the fornix. The glandula pinealis is, according to Von Baer, the elevated and subsequently shrunken roof of the third ventricle. The origin of the corpus callosum of Mammalia, only a trace of which is met with in other animals, is not yet known with certainty. Von Baer regards the anterior pillars of the fornix as identical with the original central depression of the cerebrum, and supposes that the walls of the hemispheres again apply themselves to each other and unite superiorly, since otherwise the ventricle of the septum lucidum could not be formed. The spinal marrow of the fœtus differs from that of the adult in containing a trace of the primitive canal, and in reaching much lower in the cavity of the spinal column.*

Among the permanent forms of the brain in the animal kingdom those of the Petromyzon and Ammocœtes are remarkable for their resemblance to the form of the fœtal brain in the higher animals, Amphibia, reptiles, birds, and mammals. The brain of these fishes possesses a special vesicle of the third ventricle, with an opening in its roof, and also a vesicle of the corpora quadrigemina. Both of these primitive parts are, in the osseous fishes, united into one large vesicle, which consequently cannot be compared to any single division of the brain of the higher vertebrata.†

The nerves are probably developed simultaneously in their whole

* Von Baer, Entwickelungs-geschichte I. und II. Compare Meckel, Archiv. 1815. Tiedemann, Anatomie und Bildungs-geschichte des Gehirns, Nürnberg, 1816.

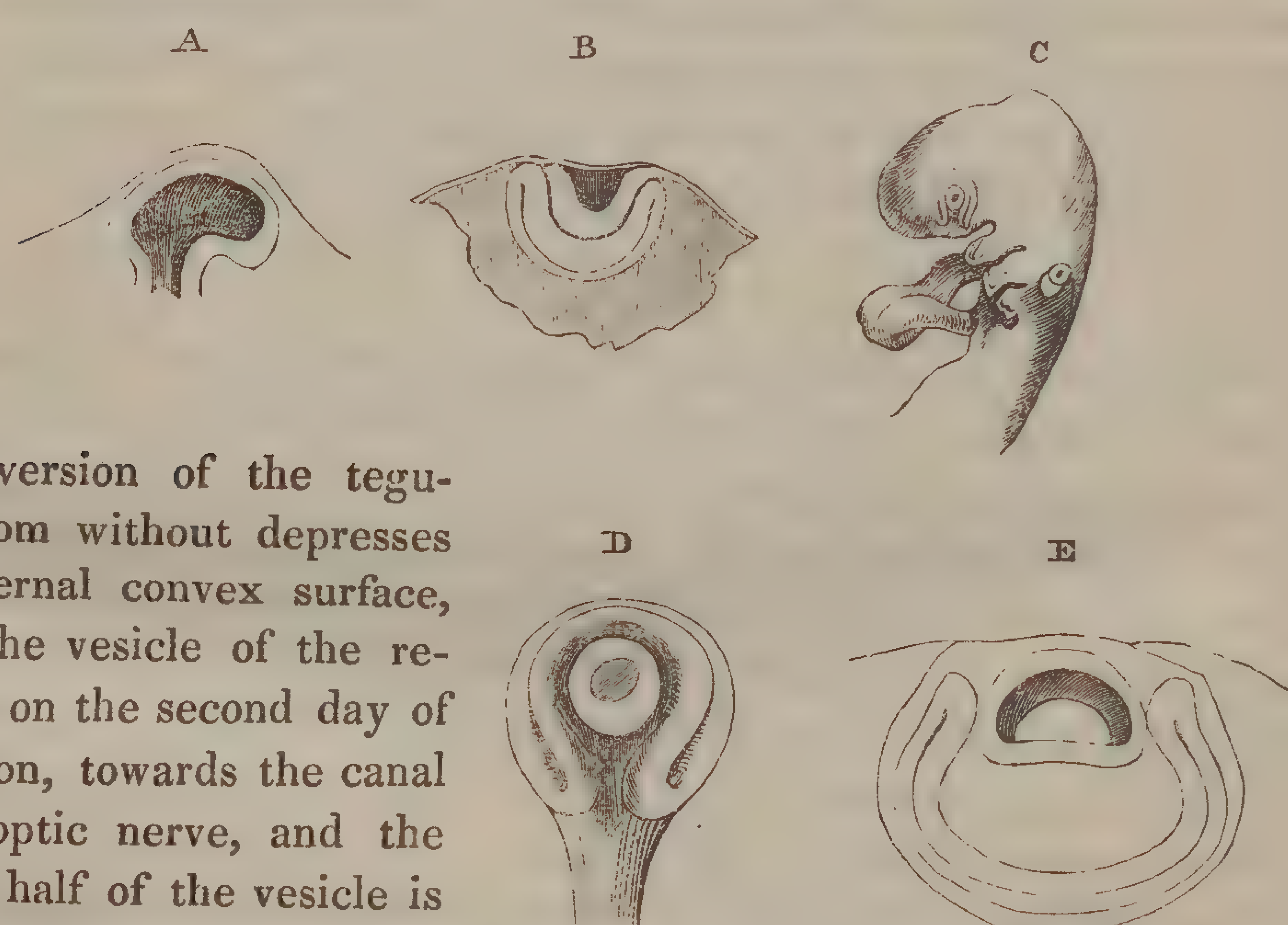
† J. Müller, Vergleichende Neurologie der Myxinoiden.

length, from the centre to the organs for which they are destined. The reality of either a centrifugal or a centripetal development of the nerves can by no means be demonstrated.

6. *Organs of Sense.*

The eye is in part developed as a protruded portion of the vesicle of the third ventricle of the brain, and it contains part of the membranes of the brain, namely, the fibrous and the vascular tunic. At a certain period of development there is observed at the inner side of the eye in all animals a fissure, which was regarded by Von Baer as an attenuated part of the retina, but which has been demonstrated by Huschke to be a real fissure. In the eye of fishes the retina presents throughout life a cleft running from the centre towards the anterior border. The retina is originally a vesicle-like protrusion of the brain, with the cavity of which it communicates through the medium of the tubular optic nerve (fig. 244, A). According to Huschke's more recent researches the cavity of the optic vesicle in the fœtal chick begins to diminish from the second day of incubation, and subsequently is reduced to the space which exists between Jacob's membrane and the retina (fig. 244, B). The sac of the transparent media which the eye afterwards contains at no period communicates with the cavity of the brain. The capsule of the lens appears, from Huschke's observations, to be developed from an inverted portion of the common integuments, and consequently is at a certain period open externally (fig. 244, B).

Fig. 244.*



The inversion of the tegument from without depresses the external convex surface, which the vesicle of the retina has on the second day of incubation, towards the canal of the optic nerve, and the anterior half of the vesicle is thus reflected inwards upon

* [Fig. 244. Development of the eye; after Huschke. A. Longitudinal section of an eye of an embryo chick of two days, enlarged thirty times. The cavities of the

itself in the manner of a serous sac. The inverted layer becomes the future retina; the external layer, the membrana Jacobi. The true cleft in the bird's eye, according to Huschke's present view, is not formed until the third day,—not before the lens is developed; and he regards it as a consequence of the inversion of the retina. The depression produced by the pressure of the capsule of the lens upon the primitive optic vesicle is nearly round, but becomes elongated towards the canal of the optic nerve and towards the middle line of the body. This part of the depression becomes converted into a furrow (fig. 244, C, D). The apparent cleft is merely the appearance produced by this furrow or depressed fold, its margins consisting on each side of two laminæ. Consequently, it does not lead into the cavity of the tubular optic nerve.*

The iris appears to be at first wanting at the anterior border of the membrana choroidea, unless this border of the choroid itself should be regarded as the rudiment of the iris. In the human embryo the margin of the choroid at its inner and lower side, which afterwards becomes the lower side, is originally notched or fissured; but the circle of the iris is complete at its first development. The coloboma iridis or cleft of the iris at its lower part is so far a malformation resulting from arrest of development, as its origin is connected with the existence of this primitive fissure of the choroid. But the connection of the fissure of the iris with the original arrest of development appears to be similar to that which subsists between the fissure in hare-lip and the imperfect development of the more deeply seated structures; for the coloboma seems to arise from the imperfect development of the iris in the situation of the fissure in the choroid.†

retina and optic nerve are seen, the whole being covered by the external tegument. C, the cephalic part of an embryo chick of the first half of the third day of incubation, magnified seven times; showing the eye with the capsule of the lens still open, surrounded by the retina, which is folded so as to consist of two layers, and presents the cleft inferiorly. There are also seen the tubular looped heart, three branchial or visceral arches, and the labyrinth of the ear still open. B, is a section of the eye of the same embryo, through the middle of the lens, enlarged thirty times. The semicircular layers of membrane are seen. The most internal is the very thick capsule of the lens; the next is the true retina, the most external is the external layer of the retina or Jacob's membrane. D, is the eye of a chick of the third day of incubation, showing the same parts as figure C on a larger scale. E, is the section of an eye at the fourth day of incubation of the chick, magnified thirty times. The capsule of the lens is now closed, is covered with conjunctiva, and contains a conical nucleus, the lens. The vitreous humour is developed between the capsule of the lens and the retina, external to the two layers of the retina is the sclerotic coat.]

* Von Baer, op. cit.; Huschke in Ammon's Zeitschrift für Ophthalmologie, 1835, p. 272.

† Compare Seiler, über die Ursprünglichen Bildungs-fehler des Auges. Dresden, 1833.

The eye of the fœtus of Mammalia and Man is characterised by the possession of a delicate membrane closing the pupil, the membrana pupillaris, the blood-vessels of which are derived from the anterior surface of the iris. The latter circumstance and the attachment of the membrane not exactly at the margin of the iris, but somewhat in front of the margin and rather to its anterior surface, render it probable that this membrana pupillaris is continued over the anterior surface of the iris, and perhaps lines the whole anterior chamber of the eye. From the pupillar margin of the iris there likewise extends backwards the vascular membrana capsulo-pupillaris, which connects the margin of the capsule of the lens with the margin of the iris. The blood-vessels of this membrane are derived from the capsular branch of the arteria centralis retinæ, which penetrates the vitreous body, and reaching the posterior wall of the capsule of the lens gives off a number of twigs which radiate towards its circumference. These radiating vessels, however, do not belong to the lenticular capsule itself, but are prolonged into the vessels of the membrana capsulo-pupillaris, which at the margin of the pupil anastomose with the vessels of the pupillary membrane and iris. By maceration the membrana capsulo-pupillaris can sometimes be separated from the proper pupillary membrane, which in these cases appears to have a distinct posterior lamella belonging to the structure of the former membrane. This lamella with the capsulo-pupillary membrane and the vascular membrane investing the anterior concavity of the vitreous body, forms a shut sac, to the posterior wall of which the capsule of the lens is applied, while between the anterior part of the sac, which is united with the pupillary membrane and the capsule of the lens, the posterior chamber of the eye lies. Both the vessels of the pupillary membrane and those of the capsulo-pupillary membrane communicate with the vessels of the iris.*

The eyelids of the human subject and mammiferous animals, like those of birds, are first developed in the form of a ring. They then extend over the globe of the eye until they meet and become firmly agglutinated to each other. But before birth, or in the Carnivora after birth, they again separate.

The ear likewise consists of a part developed from within and of one formed externally. The labyrinth is developed upon the hollow protruded part of the brain which forms the auditory nerve. It appears first in the form of an elongated vesicle at the hinder part of the head of very young embryos above the second so-named branchial cleft. In the Cyclostomatous fishes this primitive form of the labyrinth is retained, at least by its hard parts. According to the researches of Valentin the

* Henle, de membranâ pupillari, Bonnæ, 1832. Reich, de membranâ pupillari, Berol, 1833. Valentin, Entwickelungs-geschichte. B. Langenbeck, de Retinâ. Gott. 1836. Krause, in Müller's Archiv. 1837, p. xxxv.

labyrinth of the fœtus appears first as a separate body of a roundish but somewhat elongated form. The inner end of the cavity of this body soon becomes more elongated, and while it begins to make a circular turn forms a second roundish vesicle which is the rudiment of the cochlea. The convolutions of the cochlea are then formed in the following manner. The wall of the primary vesicle of the cochlea becomes, as it were, excavated from the interior, first in the direction from the vestibule towards the basis of the cranium, and afterwards in a spiral course, till it reaches the point which becomes the summit of the perpendicular axis or modiolus. In this way are produced the external form resembling that of a turbinated shell, and internally a deep furrow or half-canal, the walls of which in their windings approach each other more and more closely by their inner borders, and at length coalesce, so that they surround a cylindrical or rather a conical body, the axis of the convolutions. The conversion of the groove of the cochlea into a complete tube takes place in different animals at different periods of development. The semicicular canals of the internal ear of Mammals are produced, according to the same observer, as diverticula of the vestibule, which terminate again communicating with the same cavity.*

The Eustachian tuba, the cavity of the tympanum and the external auditory passage, according to the observations of Huschke,† are remains of the first so-named branchial cleft. The membrana tympani divides the cavity of this cleft into an internal space the tympanum, and an external meatus. The systems of tegumentary structures, the mucous membrane of the mouth, which is prolonged in the form of a diverticulum through the Eustachian tuba into the tympanum, and the external cutaneous system come into relation with each other at this point, the two membranes being separated only by the proper membrane of the tympanum. The origin of the ossicula aûditus has already been mentioned (page 1619). Their ossification commences in the human subject as early as the fourth month.

The development of the nose is described at page 1617.

7. *Alimentary or digestive canal.*

The alimentary canal is at first an uniform straight tube, which gradually becomes divided into its special parts, stomach, small intestine, and large intestine. The stomach originally has the same direction as the rest of the canal; its cardiac extremity being superior, its pylorus inferior. The first changes of position which the alimentary canal undergoes consist in the stomach assuming an oblique direction, in the small intestine taking a new course from the stomach towards the navel, and, after making an abrupt bend there, returning towards the

* Valentin, Entwickelungs-geschichte, p. 206.

† Isis, 1831, p. 951.

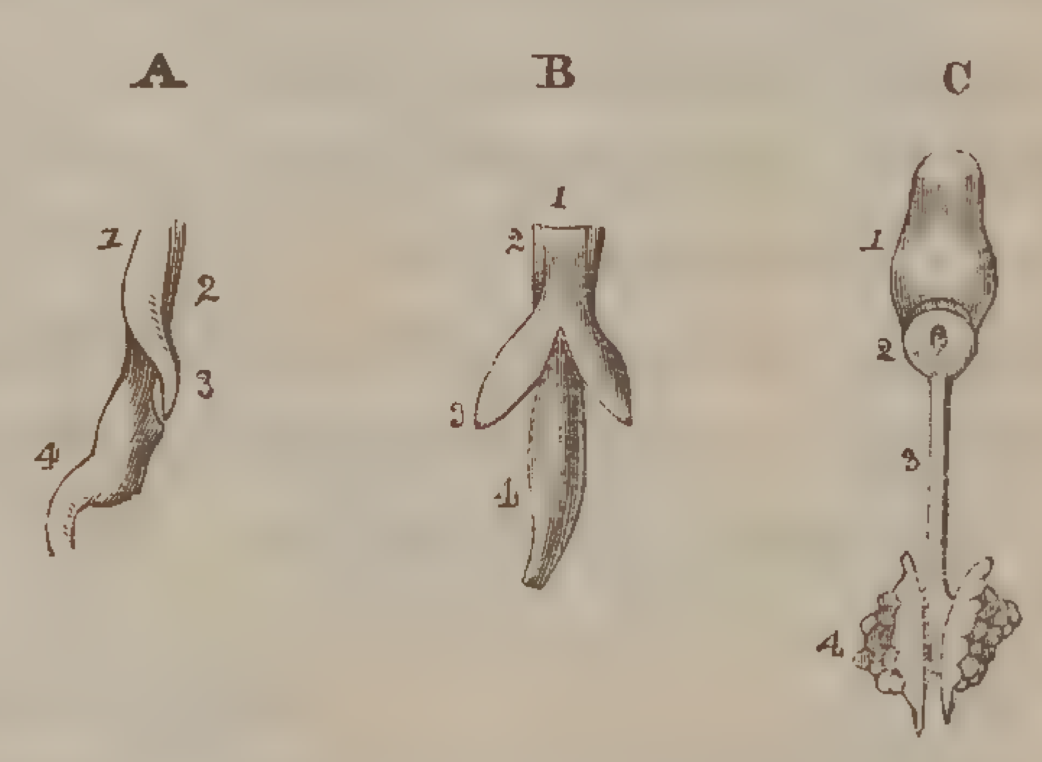
middle of the body in order to make its final curve to reach the anus. The limit between the small and the large intestine lies in the part returning from the umbilicus, the ductus omphalo-entericus being connected with the lower part of the small intestine. (See plate iv. fig. 4.) At this point of the intestine the canal frequently presents a diverticulum in the adult, and the existence of this abnormal structure has a relation to the original communication subsisting between the intestine and the duct of the umbilical vesicle. The small intestine where it approaches the umbilicus gradually becomes elongated and convoluted (see plate iii), and at the same time the large intestine rises so as to form its great arch around the greater part of the small intestine.* The mode of development of the peritoneum and mesentery has been described at page 1530.

The mesentery has at first, like the intestinal canal, a straight direction, and the stomach has then its mesogastrium extending from its greater curvature to the middle line of the posterior wall of the abdominal cavity. The process by which this mesogastrium together with the stomach itself acquires a transverse position, is converted into the great omentum, and subsequently becomes connected with the transverse colon, has already been detailed. (See p. 497, edit. 1; and p. 544, edit. 2.) It has also been shown that the spleen is originally developed within the mesogastrium, and consequently is, no less than the mesenteric glands, a symmetrical organ.†

8. *Respiratory apparatus.*

The lungs, whose origin has already been pointed out (at p. 1556), appear as small tubercles on the abdominal surface of the œsophagus. They are united at the anterior part of their circumference, and here a pedicle is formed which becomes elongated into the trachea. (See fig. 245, A, B.) Soon afterwards the lung is seen to consist of a

Fig. 245.‡



* See Meckel's Archiv. 1817. Müller, ibid. 1830.

† The development of the liver, pancreas, and salivary glands is described at pages 446 to 452, edit. 1, and pages 488 to 494, edit. 2.

‡ [Fig. 245 illustrates the development of the respiratory organs. A, is the œsophagus of a chick on the fourth day of incubation with the rudiments of the trachea and the lung of the left side, viewed laterally. 1, the inferior wall of œsophagus; 2, the upper wall of the same tube; 3, the rudimentary lung; 4, the stomach. B, is the same object seen from below, so that both lungs are visible. C, shows the tongue and respiratory organs of the embryo of a horse. 1, the tongue; 2, the larynx; 3, the trachea; 4, the lungs viewed from the upper side. After Rathke.]

mass of cæcal tubes issuing from the branches of the trachea. (Fig. 245, c.)*

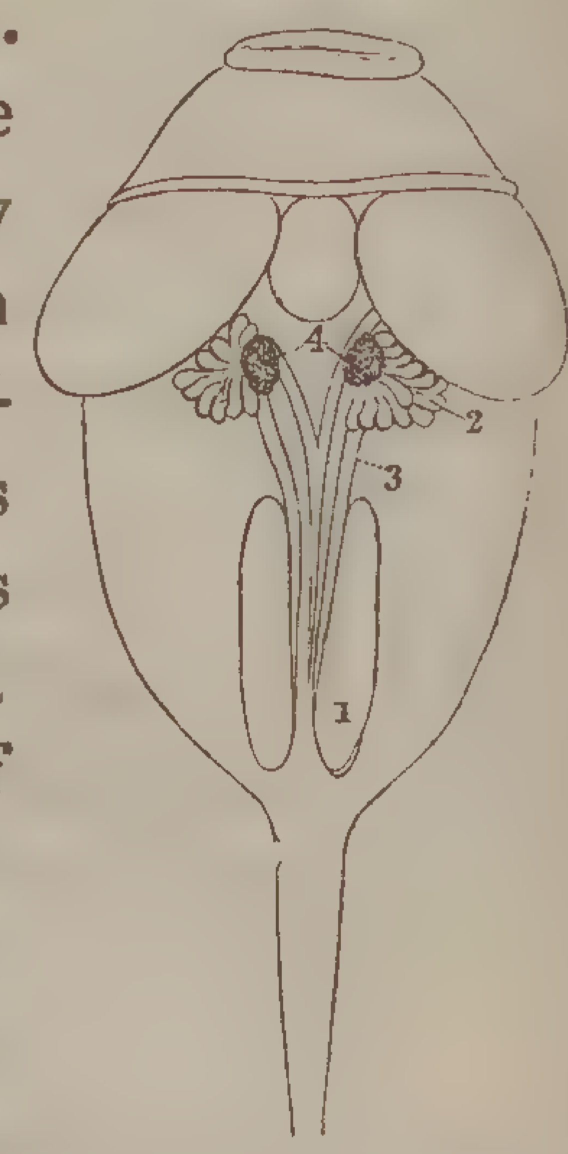
With respect to the diaphragm, it has been observed by Von Baer that the earlier the period of development at which it is examined the nearer is its position to the anterior part of the body. For example, in fœtal pigs half an inch in length in which the heart lay but just within the trunk, he found the superior border of the diaphragm attached at the most anterior part of the trunk, apparently to the first dorsal vertebra. Von Baer was able to recognise the diaphragm distinctly when the yet undivided ventricle of the heart was scarcely received into the cavity of the trunk.

9. *The Wolffian bodies, urinary apparatus, and sexual organs.*

The Wolffian bodies were first discovered by C. Fr. Wolff, but were regarded by him as rudiments of the kidneys. Oken recognised their existence in Mammalia. Meckel also observed them in the human subject; but was not aware of their true nature and compared them to the epididymis. Rathke afterwards examined them in birds, mammals, and reptiles, and ascertained that the kidneys were independent of them, but still believed that they became the epididymis in the male, while in the female they disappeared. They appeared to be absent in fishes and amphibia, while they were found in all animals which had an allantois and an amnion, and hence their existence seemed to be in some way connected with the presence of these membranes. It is quite true that they are absent in fishes; but I have detected them both in the fœtus and in the larva of batrachian amphibia. Here they have a distinct excretory duct and a position so far removed from the organs of generation as well as from the kidneys, (namely, in the most anterior part of the abdominal cavity close beneath the branchiæ), that they seem to be quite independent of both of those systems of organs, and in mammals I have found the epididymis likewise independent of the Wolffian body, lying between it and the testicle in connection with which it is developed. The Wolffian bodies are without doubt secreting organs, since they have excretory ducts which open into the cloaca; and in the fœtal bird I have seen within their secreting tubes and their excretory duct a whitish yellow matter which could be pressed from one part of the tubes to another. The observation of Jacobson, also, that uric acid can be detected in the fluid of the allantois of the bird's egg at a very early period of incubation, whilst the kidneys are not visible before the sixth day, renders it probable that the Wolffian bodies have the same function as those organs,—that they are primary or temporary kidneys bearing the same

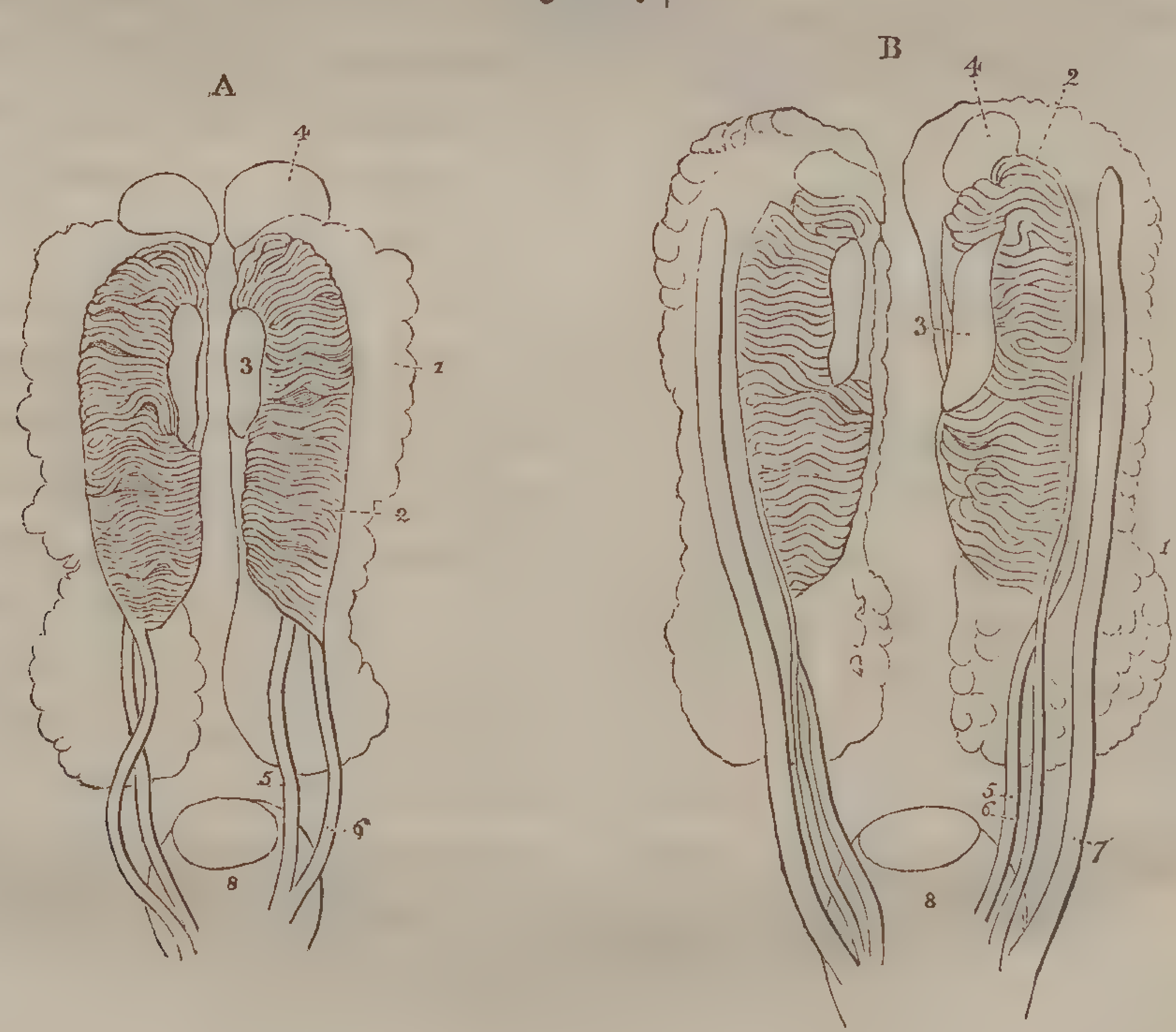
* The process of the development of the trachea and larynx is minutely described by Von Baer, op. cit.; Rathke, Nov. Act. t. xiv. pt. i. p. 162; and Valentin, op. cit. p. 49.

Fig. 246.*



relation to the persistent kidneys as the branchiæ of Amphibia do to the lungs which succeed them. The presence of the Malpighian corpuscules of the kidneys in the corpora Wolffiana, as observed by Rathke, is favourable to the same view. The duration of the existence of the Wolffian bodies is very different in the different classes of Vertebrata. It is longest in the Amphibia. In the larvæ of the frogs and Salamanders each of these organs consists of a bunch of cæca situated at the most anterior part of the abdominal cavity, from which an excretory duct passes backwards along the side of the vertebral column. (See fig. 246.) Here they exist during the whole period of the larva state. In birds the Wolffian bodies are developed on the third day of incubation. They extend from the heart to the posterior extremity of the body of the embryo, and consist of cæcal tubes united by one excretory duct which opens on each side into the cloaca. (See fig. 247.) Behind the Wolffian bodies are formed the kidneys, and above these the

Fig. 247†.



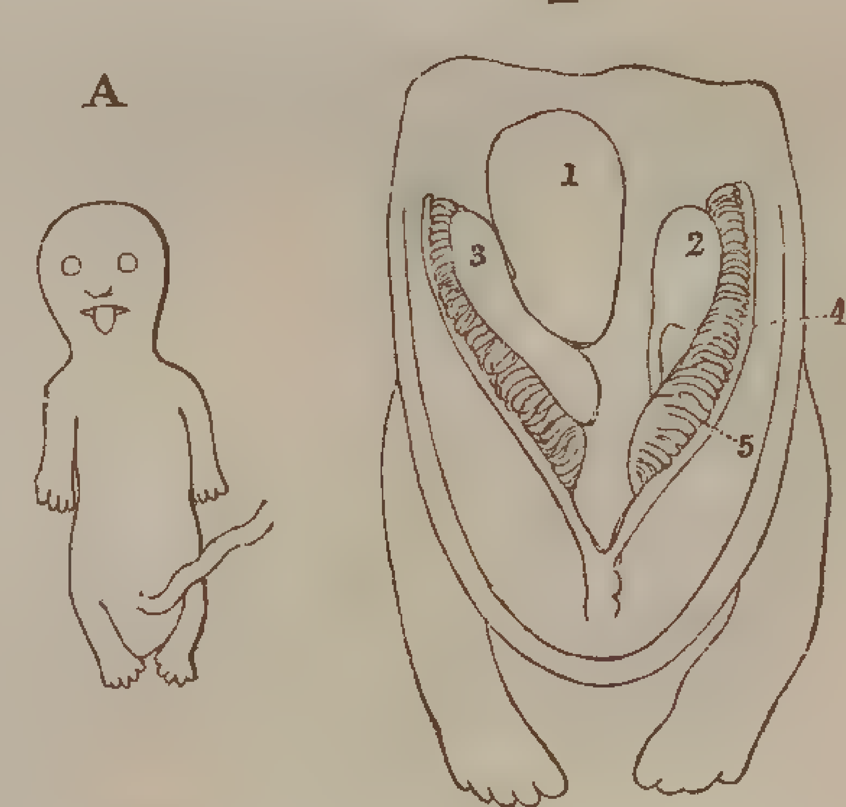
* [Fig. 246. Larva of a frog. View of the posterior part of the cavity of the trunk. 1, the kidneys; 2, the Wolffian bodies; 3, its excretory duct. After Müller.]

† [Fig. 247, shows the Wolffian bodies, kidneys, and organs of generation in a male (A), and in a female embryo of a chick (B). The parts indicated by cyphers are the following:—1, the kidneys; 2, the Wolffian bodies; 3, the testis in the male and the ovary in the female; 4, the supra-renal capsules; 5, the ureters; 6, the ducts of the Wolffian bodies; 7, the Fallopian tube; 8, the cloaca. After Müller.]

supra-renal capsules. While the kidneys increase in size, the Wolffian bodies gradually grow smaller. The testicles or ovaries are developed in front of them, and in the female or hen-bird there is always seen an oviduct* distinct from the duct of the Wolffian lobe. (See fig. 247, B.) In the male I have been able to detect no vas deferens distinct from the excretory duct of the corpus Wolffianum; but on the contrary the testicle and the excretory duct of the former body seemed to become connected by means of vasa efferentia. (See fig. 247, A.) As development advances the Wolffian bodies diminish in size, and after the chick is hatched merely the remains are found lying upon the kidneys.

In mammalia the Wolffian bodies are bean-shaped, and are composed of transverse cæca. (See fig. 248, B, 4.) The kidneys (2) and supra-renal capsules (1) are developed behind them. Their size is at first so great, that they entirely conceal the kidneys; but in proportion as the latter bodies increase in size, they grow relatively smaller, and come to be placed more inferiorly. Their excretory duct leads from the lower extremity of the organ to the sinus urogenitalis of the fœtus. Along the outer border of the gland runs the efferent part of the generative apparatus (5), viz. the Fallopian tuba or the vas deferens, which at first have the same conformation, and terminate by a free extremity; whilst the testicle or ovary (3) is formed independently at the internal excavated border of the organ. Subsequently the efferent tube and the testicle in the male become connected by transverse vessels, whilst in the female the extremity of the efferent tube merely acquires an open mouth. In both sexes the Wolffian bodies entirely disappear, and are not converted into any other organ. The epidydimis is developed independently, that part which consists of the coni vasculosi being formed of the communicating tubes which connect the efferent tube with the testis, and the rest being constituted by the convolutions of the efferent tube itself. All that part of the efferent tube of the generative apparatus which is thrown

Fig. 248.†

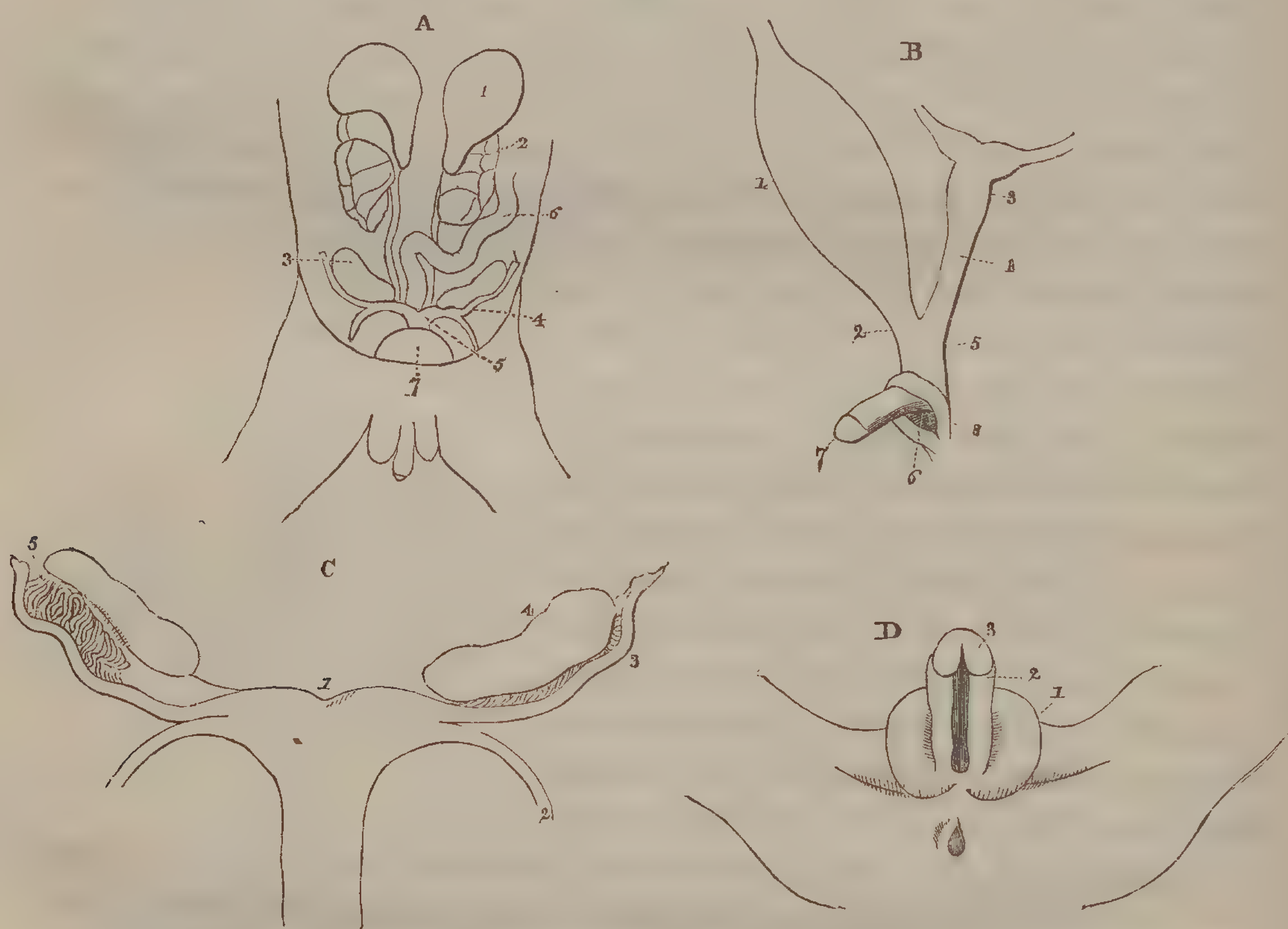


* The right ovary and oviduct become atrophied in most birds with the exception of the predaceous birds.

* [Fig. 248.—A. Human embryo measuring eight lines in length. B. Magnified representation of the urinary and generative organs of the same embryo: 1. the supra-renal capsule of the right side, totally concealing the corresponding kidney which lies behind it; 2. the kidney and ureter of the left side exposed by the removal of the suprarenal capsule; 3. the testis or ovary of the right side; 4. the Wolffian body; 5. the Fallopian tuba or vas deferens. After Müller.

into strongly marked convolutions along the outer border of the Corpus Wolffianum contributes to the formation of the epidydimis, and from the point where the convolutions cease, a band or ligament, the gubernaculum testis Hunteri, which was developed before those convolutions of the tube were visible, passes off to the inguinal canal. In the female the tube remains free from convolutions, but from the same point as in the male a ligament, afterwards the ligamentum uteri teres, extends to the inguinal ring. The part of the tube which lies below the point of attachment of this ligament becomes the cornu uteri. In those animals in which a middle portion or body of the uterus exists, this part is formed by the coalescence of the two cornua. In the human uterus the two cornua gradually become shorter and shorter, and are lost in the body or fundus of the uterus which is at the same time developed. (See fig. 249, A, C.) In the human subject the Wolffian bodies can be detected only

Fig. 249.*



* [Fig. 249. Urinary and generative organs of a human embryo measuring 3½ inches in length. A. General view of these parts: 1. suprarenal capsules; 2. kidneys; 3. ovary; 4. Fallopian tuba; 5. uterus; 6. intestine; 7. the bladder. B. Bladder and generative organs of the same embryo viewed from the side: 1. the urinary bladder; 2. urethra; 3. uterus (with two cornua); 4. vagina; 5. part as yet common to the vagina and urethra; 6. common orifice of the urinary and generative organs; 7. the clitoris. C. Internal generative organs of the same embryo: 1. the uterus; 2. the round ligaments; 3. the Fallopian tubes; 4. the ovaries; 5. the remains of the Wolffian bodies. D. External generative organs of the same embryo: 1. the labia majora; 2. the nymphæ; 3. the clitoris. After Müller.]

in the earliest period of development, their disappearance taking place here much sooner than in quadrupeds. Traces of these organs, however, can be discovered by means of the microscope in the fold of the peritoneum which connects the ovary and Fallopian tuba as late as the middle of utero-gestation, or even later. (See fig. 249, c.) It might be supposed that in ruminants and hogs the Wolffian bodies and their secreting tubuli are converted into the Malpighian canals observed by Malpighi and Gartner, lying at the sides of the uterus and opening into the vagina; but it is by no means proved that such is the case.

The ovarium of mammiferous animals, according to the observations of Valentin,* is originally composed of tubes in which the Graafian follicles are developed.

A sinus urogenitalis has been referred to as existing in the embryos of mammals and man. This is a cavity or canal opening externally, in which the excretory ducts of the Wolffian bodies, the ureters, and the efferent parts of the generative apparatus terminate internally. This canal is also prolonged into the urachus. Subsequently it becomes divided by a process of division extending from before backwards, or from above downwards, into a "pars urinaria" and a "pars genitalis." The former, extending towards the urachus, is converted into the urinary bladder, whilst from the latter are formed the vesiculæ seminales in the male and the middle portion of the uterus in the female. (See fig. 249, B.) The external parts of generation are at first the same in both sexes. Tiedemann perceived about the fifth or sixth week the opening of a cloaca where he had observed no opening previously. At the tenth or eleventh week the anal aperture and the orifice of the sinus urogenitalis become separated by a transverse band. The opening of the genito-urinary apparatus has the same characters in both sexes. Soon it is seen to be bounded by two folds of the skin, whilst in front of it there is formed a penis-like body surmounted by a gland, and cleft or furrowed along its under surface. The borders of the furrow diverge posteriorly, running at the sides of the genito-urinary orifice internally to the cutaneous folds just mentioned. (See fig. 249, B, D.) In the female this body becoming retracted forms the clitoris, and the margins of the furrow on its under surface are converted into the nymphæ, or labia minora, the labia majora pudendæ being constituted by the great cutaneous folds. In the male fœtus the margins of the furrow at the under surface of the penis unite (about the fourteenth week), and form that part of the urethra which is included in the penis. The large cutaneous folds at a later period, namely, in the eighth month of development, receive the testicles, which descend into them from the abdominal cavity. Sometimes the urethra is not closed, and the deformity called hypospadia then results. The appearance of hermaphroditism may in these cases be increased by the testes

* Müller's Archiv. 1838, p. 530.

being retained within the abdomen. This condition is merely the result of an arrest of development of the male sexual organs, and may be attended with all the feelings of the male sex and other signs of virility. There are indeed hypospadiacs in whom the defect of development is so great that even in all other respects the character of the male sex is not maintained. But these imperfect male individuals are still by no means true hermaphrodites. Hermaphroditism consists in the coincidence of male and female organs in the same individual—for example, in the presence of all the male sexual organs together with a uterus and Fallopian tubes, though without an ovary. It is not certain that a case of perfect hermaphroditism, with both the male and the female productive organs, (the testis and ovary,) has ever yet been observed in the human species. Amongst insects hermaphrodites, with male organs on one side and female organs on the other, are not rare.

As long as the testes remain in the abdominal cavity they are held fixed by a covering of peritoneum, the reflected parts of which form for each a suspensory band or mesorchium. They at this time have no tunica vaginalis. In their descent through the inguinal canal they follow the "gubernaculum testis;" but in front of them there passes through the inguinal canal into the scrotum, though independently of their descent, a purse-shaped prolongation of the peritoneum, the processus vaginalis peritonei. The testis on each side sinks, together with its mesorchial fold of peritoneum, into this bag or purse-like prolongation of that membrane, and since the neck of the bag closes above the testis generally before birth, this organ lies in a distinct serous cavity, the tunica vaginalis testis, which does not communicate with the abdomen. Sometimes this neck of the tunica vaginalis remains open after birth, and gives rise to the hernia inguinalis congenita.

In the kidneys of the fœtus the pyramidal bodies are separate from each other, each covered with a layer of the cortical substance; but subsequently they coalesce. The suprarenal capsules are not proportionally of large size in the fœtus of mammiferous animals; but in the human fœtus they are of very great relative size, so as at first even entirely to conceal the kidneys.*

* Concerning the development of the Wolffian bodies, the generative and the urinary organs, consult J. Ch. Müller, De genitalium evolutione; Halæ, 1815. Rathke, Beiträge zur Geschichte der Thierwelt 3, and Abhandl. zur Bildungs- und Entwickelungs-geschichte. J. Müller in Meckel's Archiv. 1829, and Bildungs-geschichte der Genitalien, Düsseldorf, 1830. Jacobson, Ueber die Primordialnieren, Copenhagen, 1838. Valentin, Entwickelungs-geschichte; Tiedemann, Anatomie der kopflosen Missgeburten. Landshut, 1813, p. 84; Seiler, De testiculorum descensu, Lips. 1817.

CHAPTER II.

Development of the animal tissues.

In several parts of this work mention has already been made of the recent observations respecting the organic cells, their development, and the phenomena which they present. A connected account of these observations must now be given. Modern vegetable Physiologists had already arrived at the result that the different tissues of plants, such as cellular tissue, woody fibre, ducts and spiral vessels are all originally developed from cells. The mode of formation of these cells has been explained by Schleiden.* He has shown that they are produced from the "nuclei" of Robert Brown, and hence he calls these bodies "cytoblasts" [κύτος a cell, βλαστὸς a germen]. The cytoblast is generally of a yellowish colour, and internally of a granular structure. In its interior Schleiden has detected a second nucleus (nucleolus) called by him the nucleus corpuscule, which sometimes resembles a mere spot, at other times a hollow globule. The cytoblasts are developed in a mass of mucous granules contained within previously existing cells. As soon as they have attained their full size, a delicate transparent vesicle rises upon the surface of each. This is the young cell, which at first bears the same relation to the flat nucleus as the watch-glass bears to a watch. When the cell has increased in size the cytoblast appears merely as a solid body included in the wall of the cell. The layer which now covers the cytoblast on the side towards the interior of the cell is extremely delicate,—indeed, seldom to be recognised by the eye,—and it soon becomes wholly absorbed, while the cytoblast itself disappears at the same time. The newly developed cells lie free in the cavity of the parent cell, and, as they grow and exert reciprocal pressure against each other, assume the polyhedral form.

The following are the more important observations of Schwann† respecting the cells of animals and the agreement of animals and plants in their ultimate structure.

In the chorda dorsalis, the cellular structure of which I had myself pointed out long since, Schwann first discovered the nuclei or cytoblasts. Each cell of the chorda dorsalis of Pelobates fuscus has its disk-like cytoblast lying at the inner surface of the wall of the cell; and in this nucleus there is seen one, rarely two or three, clearly

* Müller's Archiv. 1838, p. 137.

† Froriep's Notizen, 1838, No. 91, 102, 112. Schwann, Mikroscopische Untersuchungen über die Ueber-einstimmung in der Structur und dem Wachsthum der Thiere und Pflanzen, Berlin, 1838. [A review of this work with a copious abstract of its contents is contained in the 9th volume of the British and Foreign Medical Review.]

defined spots. In the cavity of the cells young cells are developed, as in plants.

Cartilages also are, according to Schwann's observations, composed entirely of cells, when first formed. The cartilaginous branchial rays of fishes at their apex are composed of small polyhedral cells, lying in close contact with each other, and having very thin walls. These cells have rounded granular nuclei. Towards the middle of the branchial ray the septa between the cavities of the different cells formed by their walls, gradually become thicker. Nearer to the root or base of the branchial ray the walls of the contiguous cells can no longer be distinguished from each other, and the mass appears to be formed of a homogeneous substance containing small cavities; but around some of the cavities a circular line can be distinguished which indicates the boundary of the wall of the cell, and proves that the whole mass is not formed by the thickened walls of the cells, but that a real intercellular substance also exists. Even while the walls of the cells are still in contact with each other, this intercellular substance is present, at that time appearing here and there like a triangular space between three contiguous cells. (See fig. 250.) In this form of

Fig. 250.*

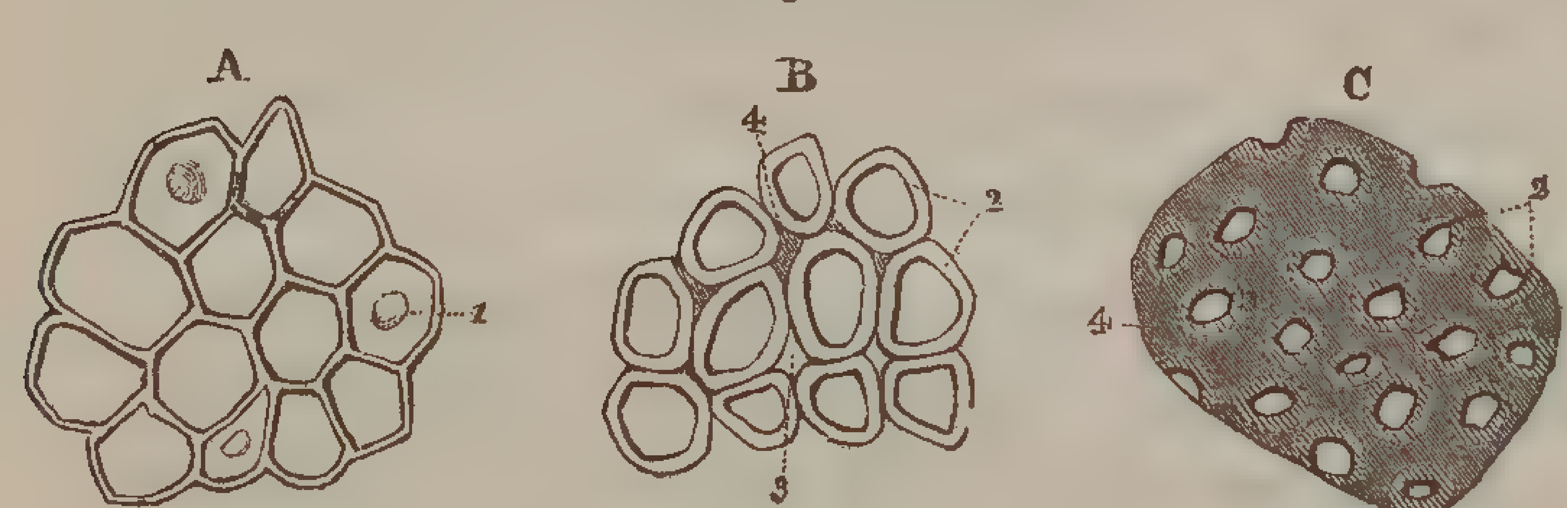
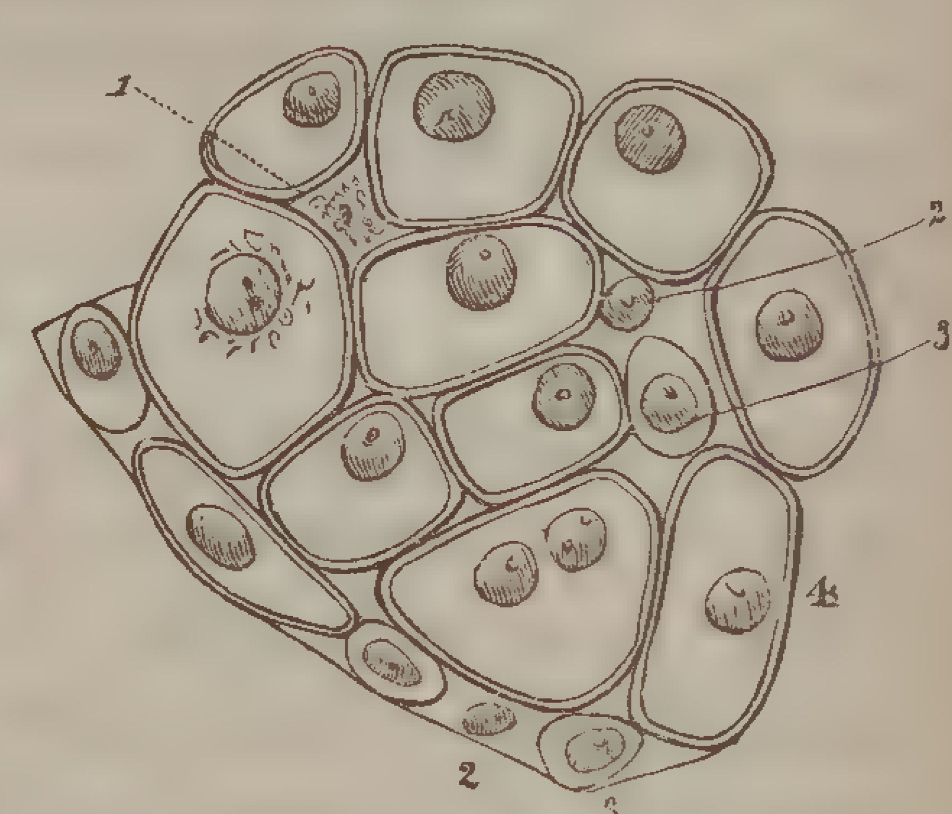


Fig. 251.†



cartilage the process of development consists partly in the thickening of the walls of the cells and partly in the production of an intercellular substance. In higher vertebrate animals the thickening of the walls of the cells is not observed, and the principal mass of the future cartilage appears to be formed by the intercellular substance in which the cells with the younger cells within them are included. The development of cells in the manner of the cells of plants has been observ-

* [Cartilage of the branchial ray of Cyprinus erythrophthalmus. A, from the extremity of the ray; B, from the middle of the ray; and C, from its root. 1, Nucleus of a cell. 2, walls of the cells. 3 and 4, intercellular substance. In one cell two nuclei are seen. Magnified about 450 times.]

† [Cartilage from the extremity of a branchial cartilage from a tadpole. The lower margin of the figure represents the natural margin of the cartilage. Magnified about 450 times.]

ed by Schwann in the branchial cartilages of Pelobates fuscus, in which some cells contain mere nuclei; others, nuclei with small cells developed upon them and scarcely larger than themselves; others, again larger fully formed cells. So that here all the stages of the development of a cell are present. (See fig. 251.) The process of the development of cartilage seems to be independent of blood-vessels and to be wholly analogous to the process of growth in vegetable tissues. How the canals radiating from the corpuscules of ossified bone are developed is not known. Two hypotheses are proposed by Schwann. If the osseous corpuscules are the cavities of cells the thickened walls of which have coalesced with each other and with the intercellular substance so as to form the mass of the cartilage of the bone, then the radiating canaliculi must be regarded as canals extending from the cavities of the cells through their thickened walls, and would be analogous to the pore-like canals of some vegetable cells. But if the osseous corpuscules are the cells themselves and not merely their cavities, the whole substance between the corpuscules being intercellular substance; in this case the canaliculi will probably be radiating prolongations of the cells extending into the intercellular substance. According to the latter view, which Schwann regards as the more probable, the canaliculi would correspond to the processes given off from some cells of plants.

Besides the formation of young cells in the cavities of previously existing cells, Schwann has observed their development in the exterior of other cells in a structureless substance, the cytoblastema. In this case also the nucleus generally appears to be first formed and the cell to be afterwards developed around it. In many animal tissues the new cells are formed on the exterior of the earlier cells. In the one case the cytoblastema exists in the interior of the cells already existing; in the other it is external to them.

Schwann arranges the tissues of the animal organism, according to the mode of their development, in five classes:

I. Isolated independent cells which either float free in a fluid, or if deposited in contact with each other are still unconnected and movable.

II. Independent cells arranged so as to form a continuous membrane.

III. Tissues formed of cells, the walls of which have coalesced, while their cavities remain distinct.

IV. Fibre-cells,— cells which have become elongated in different directions and resolved into bundles of fibres.

V. Cells, both the walls and the cavities of which have coalesced, so as to form tubes.

To the *first class* belong the corpuscules of the blood. The vesicular nature of these bodies was observed by C. H. Schultz. Their nucleus, as Schwann remarks, remains attached to the inner surface of their membranous parietes when they are rendered turgid by the action of water. The red colouring matter of the corpuscules is to be regarded as the contents of the cells. The lymph corpuscules, the globules of mucus and those of pus belong to the same class. They are all nucleated cells.

To the *second class* belong the horny tissues, the pigment membranes, and the tissue of the crystalline lens.

1. *Epithelium.* — Generally composed of round cells, to the inner surface of whose parietes a nucleus containing one or two nucleoli is attached. When united into a membrane they are polyhedral. In the epithelium of the skin of a frog Schwann saw two nuclei in one cell, and also a nucleated epithelium cell within another larger cell, a fact which Henle has not observed in Mammalia. The epithelium cells, at first globular, undergo modifications of form in one or two directions. Either they acquire the form of perpendicular cylinders, as in the epithelium of the intestinal mucous membrane, described by Henle; or they become flattened into laminæ, which have the nucleus in the middle of one surface and which sometimes are elongated or riband-shaped, as in the epithelium of blood vessels according to Henle. In the latter case it is observed that the young cells are found beneath the older ones, and are at first globular, but become more and more flattened as they approach the free surface of the epithelium.

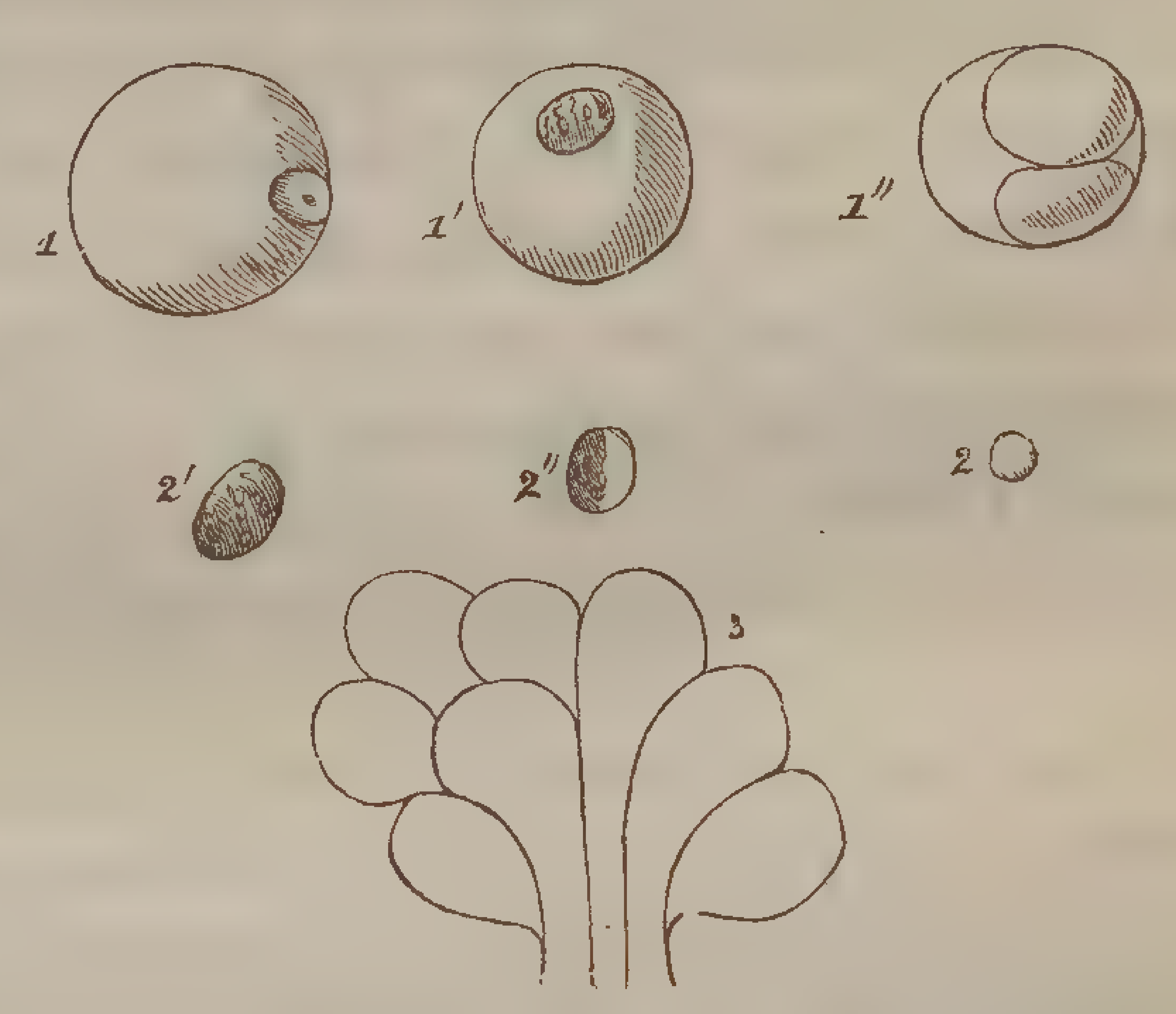
2. *Pigment cells.*—These have a nucleus at one part of their parietes, which produces the well known white spot in the middle of some pigment cells. The nucleus has usually one or two nucleoli. Many pigment cells in the process of their growth send out hollow fibre-like processes in different directions, so as to become stellate cells.

3. *Nails.* — The nail of a fully developed human fœtus consists of laminæ lying horizontally one upon the other. These laminæ become less and less distinct at the inferior surface of the nail, in proportion as the part examined is nearer to the root of the nail which is inserted into the fold of the skin of the finger; and the posterior half of this portion of the nail presents nothing of a laminated structure, but consists merely of polyhedral cells with distinct nuclei. Laminæ of the nail treated with acetic acid separate into scales in which an indistinct nucleus can in very rare cases be observed. The polyhedral cells of the root of the nail must become flattened into these scales, and the nail ought consequently to become thinner towards its free margin. This is probably prevented by the formation of laminæ of epithelium at the under surface of the nail. The horny tissue of the hoofs of animals also consists in the fœtus entirely of cells.

4. *Feathers.* — The medullary substance of feathers is composed of polyhedral cells. In the young feather a nucleus is visible in the wall of each of these cells. The cells are developed around small nuclei which lie in great number in a finely granular matter. This formation of new cells takes place not in old parent cells but near the surface of the vascular matrix of the feather, which affords the cytoblastema. Some of the nuclei contain nucleoli. The fibres of the cortical part of the shaft of the feather are produced from large band-like epithelium cells which contain nuclei and nucleoli. These cells become resolved into several fibres while all trace of the cell disappears. The barbs of the feather are themselves miniature feathers; the secondary shafts have the same structure as the main shaft, while the secondary barbs or barbules in their turn consist at first of nucleated cells applied to each other by their edges.

5. *The crystalline lens.*—The fibres of the crystalline lens are developed from the cells first observed by Werneck. In the lens of a chick after eight days' incubation there are as yet no fibres, but merely pale round cells, some of which contain a nucleus. In lenses further developed some of the larger cells contain one or two smaller cells in their interior. In embryo pigs, measuring $3\frac{1}{2}$ inches in length, the greater part of the fibres of the lens is already perfect; but a part is still not completely formed; and there are besides many round cells which are about to undergo their metamorphosis. The perfect fibres compose a nucleus in the centre of the lens. The next fibres are seen to be tubular prolongations of globular cells. (See fig. 252.) The dentated borders of these cells, like those of some vegetable cells, are formed subsequently.

Fig. 252.*



Class III.

1. *Cartilages.*—Their structure and mode of development has already been described.

2. *The teeth.*—The enamel of a tooth not yet fully formed retains the same form and structure after it has been treated with dilute acid. The inner surface of the enamel membrane which envelopes the crown of the tooth is formed of short hexagonal fibres, placed perpendicularly, so that

* [Fig. 252. Cells of the crystalline lens of a fœtal pig ; 1 and 1′ cells with nuclei ; 1″, a cell with two young cells enclosed ; 2, nuclei ; 2′, an isolated nucleus with two nucleoli ; 2″, a nucleus with a young cell developing upon it ; 3, cells elongating themselves into fibres. After Schwann.]

each fibre of the enamel membrane corresponds to a fibre of the enamel. These fibres of the enamel membrane appear to be elongated cells. In the fresh state they contain a nucleus with nucleoli. Beneath these prismatic fibres of the enamel membrane is a layer of round cells which probably represent the primary condition of those fibres. The true enamel fibres probably separate from the enamel membrane, coalesce with the enamel already formed, and at the same time become impregnated with calcareous salts. The substantia propria or ivory of the tooth is formed of fibres, between which the dental tubuli run. The pulp of the tooth at its surface consists of cylindrical cells which contain nuclei with nucleoli. The interior of the pulp is composed of round nucleated cells. Schwann conjectures that the fibres at the surface of the pulp are in successive layers added to and converted into the growing dental substance.*

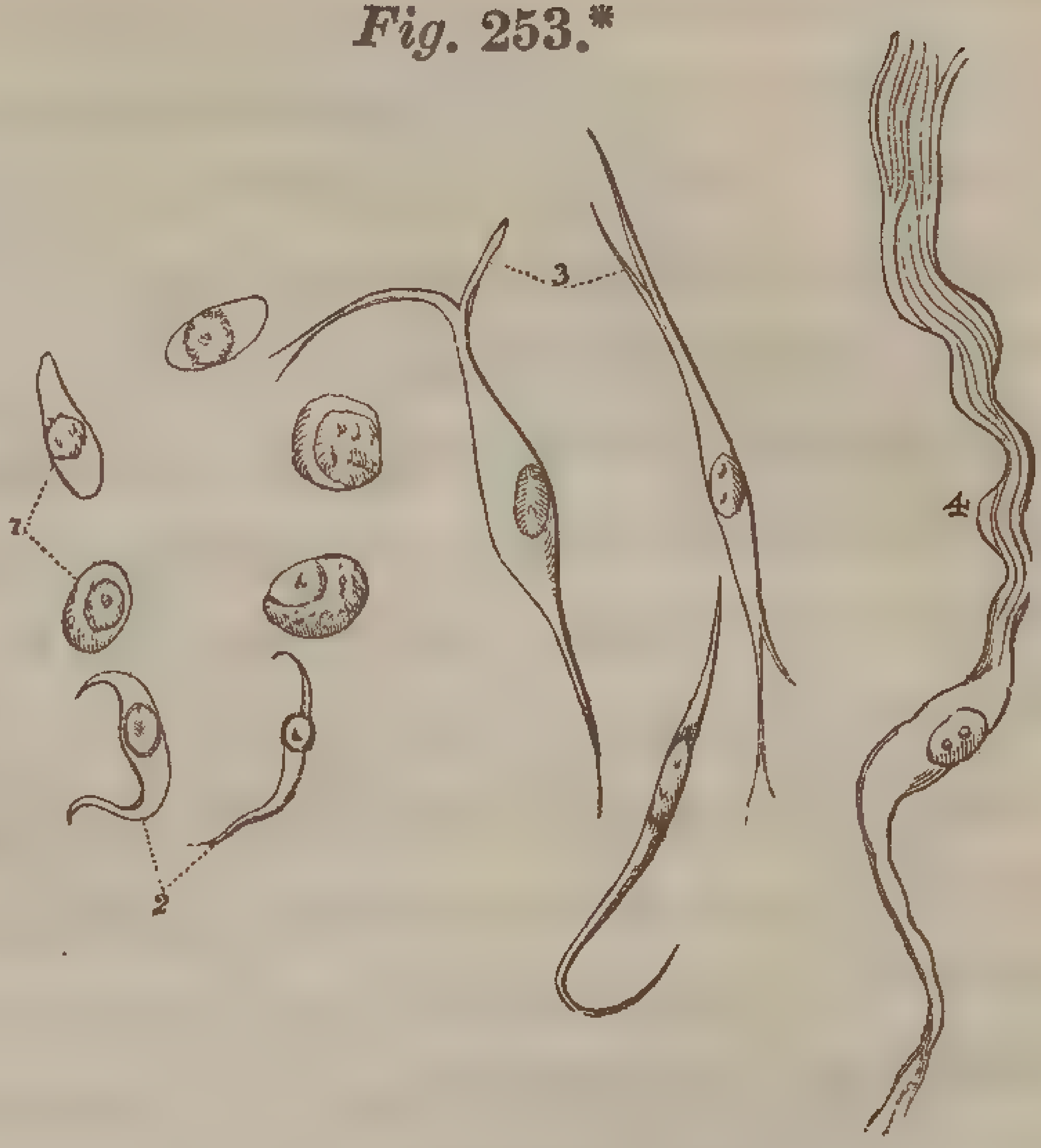
Class IV.

1. *Cellular tissue.*—In the development of cellular tissue there first appears a structureless cytoblastema, in which round nucleated cells are subsequently formed. These cells become transformed into spindle-shaped bodies, which have in their interior, but attached to their wall, a round or oval nucleus, while this nucleus in its turn includes one or two dark points (nucleoli). These elongated cells become more and more drawn out at their extremities, and give off fibres, which are sometimes branched; and at length become resolved at each end into a fasciculus of extremely delicate fibrils. The division of the fibre-like prolongations of the cells into more minute fibrils gradually extends towards the centre of the cell, so that at a later period the fasciculus of fibrils proceeds immediately from the body of the cell. Lastly, the division into fibrils takes place even in the situation of the nucleus of the cell, and then the cell becomes wholly resolved into a fasciculus of fibres, upon which the nucleus lies. (See fig. 253.) The fibres are probably tubular.

The cells of adipose tissue which are found even in the cellular tissue

* In the first volume of this work the author described the growth of the teeth as taking place by a process of apposition in successive layers, and merely remarked that in the genera Myliobatis and Rhinoptera amongst the Plagiostomatous fishes there was an exception to the general rule, since in these instances, according to my observations, the plate-like teeth attained their full size before the calcareous salts were deposited in them. Schwann supposes that in the higher animals the fibre-like cells on the surface of the pulp are in succession converted into the ivory of the tooth, the pulp being as it were converted into cartilage, and then ossified. If this be the case, the processes of chondrosis and ossification must advance by successive strata. The researches of Mr. Owen (Ann. des Sc. Nat. 1839, Oct. Odontography, pt. i.) [and those of Mr. Nasmyth (Three Memoirs on the Development and Structure of the Teeth and Epithelium. London, 1841)] confirm this view.

Fig. 253.*



of the fœtus present at first a distinct nucleus attached to their membranous wall. When the wall of the cell is thin, the nucleus forms a prominence above the surface of the fat globule contained in the cell. When the wall of the cell is thick, the nucleus is entirely included in its thickness. The nucleus contains one or two nucleoli. The fat cells in the cranium of a young fish (Plötze) sometimes have each two nuclei which bear the same relation to the membranous wall of the cell. In the cellular tissue of the fœtus a third kind of cells is met with. These are round and pale; each has a nucleus with one or two nucleoli attached to their wall; they do not become elongated into fibres, contain no fat, but are filled with granules; and this deposit of granules is first formed about the nucleus.

The cellular tissue of the fœtus, when submitted to boiling, yields no gelatine; but in its place a substance which resembles pyine, except in the particular that the turbidity produced in the solution by hydrochloric acid is removed by the addition of an excess of the acid.

2. *Tendinous tissue.*—The fibres of tendinous tissue are formed from cells, in the same way as those of cellular tissue.

3. *Elastic tissue.*—The middle coat of the arteries in embryo pigs, six inches in length, contains numerous isolated cells, some of which are globular, and some have an oblong form, while others give out two or more branching processes of various length. At the inner surface of the wall of each of these cells lies the usual nucleus with one or two nucleoli. In addition to the cells thus variously modified, fully developed elastic tissue is also present. The branching fibres of elastic tissue, which, according to Purkinje, are hollow tubes, appear to be formed from the cells just described.

Class V.

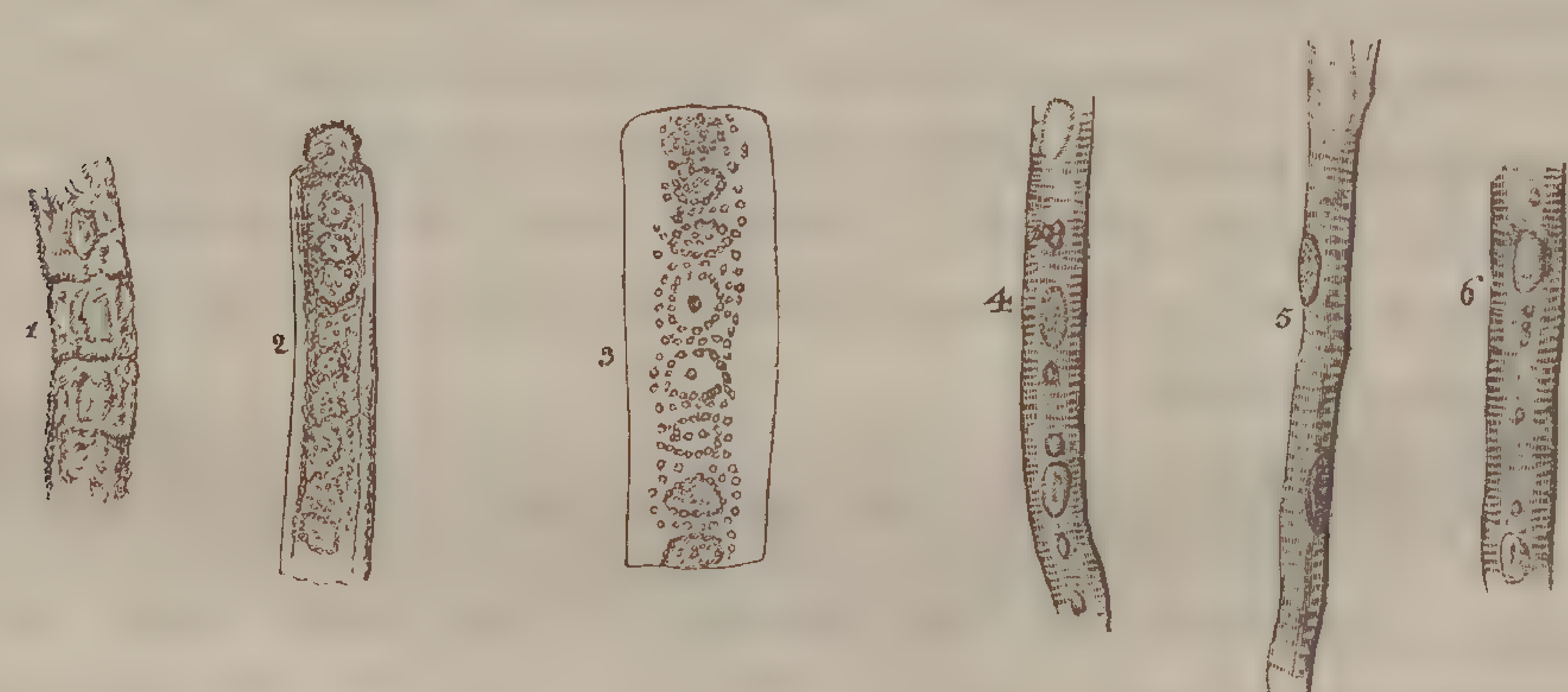
In the development of the tissues of this class there are first formed independent cells, which either are round or cylindrical, or have a stellate form. In the former case the primary cells arrange themselves in longitudinal series, their walls coalesce at the points of

* [Primary cells in different stages of development into fibres of cellular tissue taken from beneath the cutaneous muscle of the neck of a fœtal pig, which measured seven inches in length. After Schwann. Magnifying power about 450 times.

contact, and the septa thus formed between the cavities of the different cells are subsequently absorbed, so that in place of several primary cells one secondary cell is produced. This secondary cell now continues to grow as the simple cells grow. In this way the fibres of muscles and nerves appear to be developed. In the case of the stellate primary cells the radiating processes of contiguous cells unite, and their walls becoming absorbed at the points of union, a network of communicating canals is formed. This seems to be the process by which capillaries are developed.

1. *Muscles.*—Valentin had observed that the primitive fasciculi (fibres) of muscles are formed by granules arranging themselves in a linear manner and coalescing; but that the primitive fibres (fibrillæ) are produced by the subsequent division of the primitive bundle. Schwann has remarked that the primitive fasciculi in the muscles of a fœtal pig, measuring 3½ inches in length, present a dark border—and a middle, more transparent part, probably a cavity. In this more transparent part he perceived besides some small granules a series of larger oval flat bodies, which appeared to be the nuclei of cells, and frequently contained one or two smaller corpuscules,—their nucleoli. These nuclei lay at pretty regular distances from each, in the thickness of the cylinder, but external to its axis. In muscles more advanced in development, the primitive fasciculi present no indication of a cavity; but the nuclei remain visible for a long period, frequently producing slight prominences on the surface of the cylinders. (See fig. 254.) According to recent observations of Rosenthal the nuclei are still present in the muscular fibre of adult animals.) The proper substance of the muscular fibres is produced by a deposit taking place within the tube. (The

Fig. 254.*



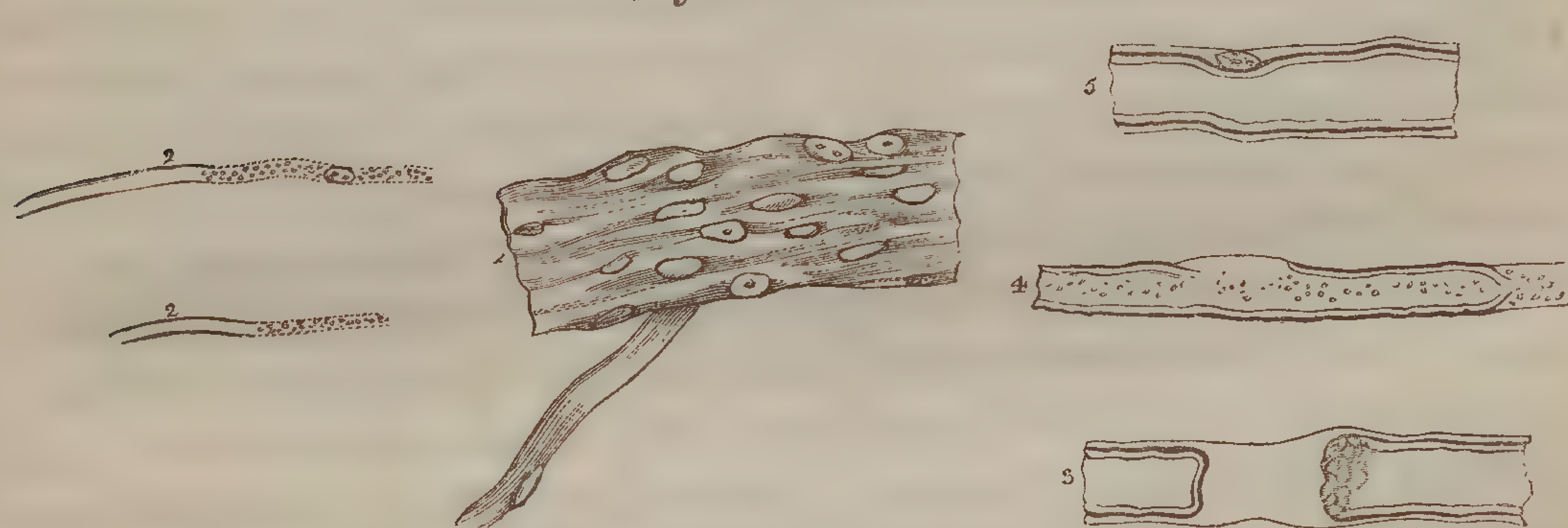
* [Development of muscular fibre after Schwann. 1, 2, 3, are fibres from the dorsal muscles of a fœtal pig, 3½ inches in length. 3, represents the fibre (2) after the action of acetic acid. 4, 5, 6, are fibres from the muscles about the humerus of a fœtal pig, which measured 5 inches in length. 5, shows the fact of the nuclei being attached to the wall of the tube; in 4 and 6, is also seen the gradual deposition of the substance from which the fibrillæ are formed on the inner surface of the tubular fibre. Magnifying power about 450 times.]

structureless sheath of the primitive muscular fasciculus, which I observed long since in insects, appears to be the remains of the tube formed by the united walls of the primitive cells.)

[According to the late observations of Valentin* there are first visible in the blastema of muscle nuclei with nucleoli, which soon become surrounded by extremely delicate cells. These cells assume an oblong figure and arrange themselves in linear forms like filaments of confervæ. On the inner surface of the membranous walls of the tubes or secondary cells formed by the coalescence of the primary cells, longitudinal striæ or fibres are deposited, while the septa dividing the tube into compartments are absorbed. The muscular fasciculus then has the form of a tube, with proportionally thick walls which are composed of perfectly transparent longitudinal fibrils. The nuclei of the primary cells are contained in the cavity of the tube.]

2. *Nerves.*—Each entire nervous fibre is to be regarded as a secondary cell, formed by the coalescence of a series of primary nucleated cells. Schwann is of opinion that the white substance of the nervous fibre, which forms a tube around Remak's band-like axis of the fibre, or the cylindrical axis of Purkinje, is a secondary deposit on the inner surface of the membranous wall of the secondary cell. He finds that the white substance of each nervous fibre is invested externally by a peculiar structureless sheath like that of the primitive muscular fasciculi. This membranous sheath can be distinguished as a transparent border external to the opaque white substance of the fibre. (See fig. 255.) Its defined outline is opposed, Schwann remarks, to the view of its being composed of cellular tissue. In perfectly formed nervous fibres Schwann some-

Fig. 255.†



* Müller's Archiv. 1840, p. 197.

† [Development of the nervous fibres after Schwann. 1. Portion of nerve from a fœtal pig four inches in length. 2. Nervous fibres from a fœtal pig six and a half inches in length. 3 and 4. Fibres from the nervous vagus of a calf, in which the nervous matter has been displaced at one point while the transparent tube remains. 5. Nervous fibre from the same nerve, displaying a nucleus apparently contained in the membranous tube of the nerve. Magnifying power about 450 times.]

times perceived here and there at the side of the fibre a nucleus which lay included in the transparent border formed by the membranous sheath. In the grey nervous fibres no white substance is formed.

[In the substance of the brain of young embryos Valentin observed cells on the outer surface of which a granular mass was gradually deposited. These cells subsequently became nuclei; and their former nuclei became nucleoli; while the granular matter deposited around them formed the mass of the ganglionic globules which were thus developed. Valentin has also observed that after the development of nervous fibres, nuclei, elongated fibre-cells, and fully developed fibres of cellular tissue are formed around them.*]

Schwann's discoveries are to be ranked amongst the most important steps by which the science of physiology has ever been advanced. They afford the basis for a general theory of vegetation and organization which it had hitherto been impossible to frame. Valuable observations had been made in all parts of physiology, and some branches of the science had been brought to a high state of perfection. But as regards the fundamental principles on which all should rest, these it must be confessed were either very unstable or entirely wanting, and hence the slight connection which seemed to subsist between different important observations in parts of the science which were far advanced. These fundamental principles are now attained. Schwann himself has pointed out with equal lucidity and acuteness the general conclusions which are to be deduced from the observations of Schleiden and himself, and has framed from them a theory of the organization and vegetation of organized beings. It is not possible to give in this work more than the principal features of his theory.

There is one common mode of development observed in the formation of the most different elementary tissues of plants and animals, and that is the development from cells. In a pre-existing structureless substance, which may be situated either within or on the exterior of cells already formed, new cells are developed in a manner regulated by determinate laws, and these new cells undergo various modifications and transformations by which they are converted into the elementary organic tissues. In every tissue the new cells are formed only in those parts to which new nutritive matter has direct access. On this alone depends the difference subsisting between the vascular and non-vascular tissues. In the former, the nutritive fluid, the liquor sanguinis, is distributed through every part of the tissues, and hence new cells are formed through its substance. In the non-vascular tissues, on the contrary, the nutritive fluid has access

* Compare Valentin's observations on the development of tissues in Wagner's Physiologie, p. 132. [Willis's translation, p. 214.] Henle's observations on the Structure of the tissues in his Symbolæ ad Anatomiam cet. Berol, 1837. Müller's Archiv. 1838, p. 102. Froriep's Not. n. 294.

to one surface only, as in the case of the epidermis. Hence in cartilages, also, when they are destitute of vessels the new cells are formed only at their surface, or to a slight depth, namely, as far as the liquor sanguinis, their cytoblastema, penetrates. The expression, growth by appositio, is correct, when understood to signify the development of new cells, and not the growth of those already existing; for in the epidermis new cells are formed only at the inferior surface of the membrane, whilst in the vascular tissues the new cells are developed in the whole substance of the tissue. In both cases, however, the cells themselves grow by intus-susception. Cartilage is at first destitute of vessels, and the new cells consequently are formed only in the vicinity of the external surface. But after vessels have extended into the medullary canals, the formation of new cytoblastema and new cells can proceed not only on the surface of the bone but also around each of these canals. This explains the structure of the cartilage of bone, the lamellæ of which are concentric, partly around the whole bone, and partly around the medullary canals. The process by which the primary cells are formed is the following. The cytoblastema, which is at first structureless or only finely granular, presents after a time round corpuscules. These corpuscules are in their earliest recognisable condition the nuclei of cells, around which cells are subsequently to be developed. The nucleus is granular, and may be either solid or hollow. The part of the nucleus first formed is the nucleolus. Around this there is deposited a layer of fine granules. The nucleus thus formed increases in size, and then the cell is developed around it by the deposition of a layer of substance different from that of the surrounding cytoblastema. This layer has at first no defined outline; but when it has become consolidated into a membrane, it expands by the continued addition of new molecules in the interstices of the old ones. It thus becomes removed from the surface of the nucleus, which remains attached to one point of the wall of the cell. This formation of the cell around the nucleus is only a repetition on a larger scale of the process by which the nucleus was formed around the nucleolus. The membranous wall of the cell differs in its chemical properties in different kinds of cells, and even in the same cells it varies in chemical composition at different periods of its growth. Thus the walls of vegetable cells, when first formed, are, according to Schleiden, soluble in water, which is not the case with the cells which are perfectly developed. The matter contained in the cells varies in a still greater degree; for example, it is in one case fat, in another pigment. In a cell which is at first perfectly transparent a granular deposit may gradually appear, its formation commencing around the nucleus; or, on the other hand, a granular deposit contained in a cell may be gradually dissolved.

SECTION III.

Of birth and the changes of development which take place after birth.

CHAPTER I.

OF BIRTH.

a. The process of birth.

In nine solar or ten lunar months the development of the human embryo is completed. During this period the uterus serves as the medium of communication between the maternal system and the fœtus, and itself undergoes an increase of substance, by the constant development of new muscular fibres [of organic life]. These muscular fibres are developed by the same process as that by which muscles are originally formed in the embryo; hence at this period all the stages in the development of this tissue may be observed simultaneously in the uterus.* The muscular power of the uterus, however, remains in a latent state. When the process of development is complete, the child becomes independent of the maternal system, and is as it were a foreign body in the uterus, which reacts against it by muscular contractions. These contractions of the uterus are the cause of birth. Similar contractions of the uterus, however, occur even when the fœtus is not contained in its cavity, (in graviditas extra-uterina,) at the time of the interruption of the physiological connexion between the mother and the child. The contractions of the uterus being attended with the violent compression of living structures, are generally productive of pain, and hence are called "pains." They recur at regular periods, but even in the intervals of the "pains" the uterus is not relaxed but continues to embrace its contents. After birth the contractions of the uterus are still repeated for a certain length of time, and are then called "after-pains." In women who have died before giving birth to their child, contractions of the uterus have frequently taken place after death, and have caused the expulsion of the fœtus when the mother has been no longer living. The uterine contractions appear to commence at the os uteri, to be propagated towards the fundus, and again to return thence towards the mouth of the uterus. By this succession of muscular contractions the fœtus is first raised and then propelled downwards towards the os uteri, when the lips or sphincter of the latter part become thinned and dilated. These movements, like those for the expulsion of the urine or fæces, when energetic, are aided by the muscles of the abdominal parietes and the diaphragm, which diminish the cavity of the abdominal capacity from above, from the front, and

* [Not less remarkable is the development which the nerves of the uterus undergo during pregnancy. These nerves have been dissected with great labour both in the impregnated and in the unimpregnated uterus by Dr. R. Lee, and will be described by him in the forthcoming volume of the Philosophical Transactions.]

from the sides. The action of these voluntary muscles under these circumstances is involuntary and regulated by the law of the consentaneous movements as well as by that of the reflected movements; for the uterus is the seat both of violent movements and of intense impressions on sensitive [or centripetal] nerves. At the same time many of the muscles of the trunk exhibit a tendency to consentaneous effort; the extremities seek points of resistance; the breath is held; and the arms seize anything which is capable of giving support during the contraction of the abdominal cavity. In the last month of pregnancy the uterus sinks lower in the pelvis. Towards the termination of the period of utero-gestation, also, the position of the fœtus is such that its long axis corresponds to the long axis of the uterus, and that some part, generally the head, applies itself to the os uteri or "presents" itself. The knees of the child are drawn up, the arms folded across the breast, and the head pressed down towards the sternum. In the process of birth the parts of the child, passing through the pelvis, adapt their longest diameter to the longest diameter of each region of that cavity, and hence they make a spiral turn. In the most frequent cases, those in which the head presents, the process is generally as follows. The antero-posterior diameter of the inlet of the pelvis will not allow the passage either of the greatest (antero-posterior) diameter of the head or of the breadth of the hips of the child, but the head of the child can pass with its long diameter either in the transverse or in the diagonal or oblique diameter of the pelvis. Birth begins by the long diameter of the head of the child being placed in the oblique diameter of the inlet of the pelvis. As the successive pains cause the head to descend lower, its long diameter comes to correspond with the antero-posterior diameter of the cavity of the pelvis, so that in the most common variety of head presentations the vertex and occiput are now placed under the pubes, while the face looks towards the hollow of the sacrum. In consequence of the curvature of the canal of the pelvis, the part of the child which descends along the anterior wall of the cavity travels through a very small space, while the part descending along the posterior wall describes a large arc of a circle.

The process of birth is usually divided into several stages. The first comprehends the period extending from the commencement of the "pains" to the opening of the os uteri; the second reaches to the rupture of the membranes of the ovum. This takes place when, the os uteri having opened, a part of the membranes containing the liquor amnii are protruded through it in the form of a pouch; this pouch bursts and the "waters" escape. The third stage extends from the rupture of the membranes to the presentation of the head at the outlet of the pelvis. During this stage the head descends through the dilated os uteri into the vagina. In the fourth stage the occiput escapes from the external parts of generation, whereupon the other parts of the child follow, the shoulders entering the pelvis in the oblique diameter of its inlet, and leaving it in the antero-posterior diameter of its cavity. During the last stage of birth, the "after-birth," consisting of the placenta and the membranes of the ovum, is expelled. For after the birth of the child the contractions of the uterus continue; and in consequence of the part to which the placenta was attached becoming very much contracted, that organ is separated, an effusion of blood taking place from the torn vessels. The separation and expulsion of the placenta occur in from half an hour to an hour after the birth of the child; so that all the stages of delivery are completed in the space of six or twelve hours. When the after-birth is expelled, the uterus contracts still more closely.*

In animals the process of birth is in general attended with less difficulty than in the human species, both on account of the wedge-like form of the head of the fœtus, which is preceded in its passage through the pelvis by the fore-feet, and on account of the greater mobility of the os coccygis.† In the vampires the birth of the young is facilitated by the pubic bones not being united in the middle line in these animals, and in Cavia aperea and other animals by the symphysis pubis being capable of dilatation.

b. The mother and child after birth.

The child breathes immediately, and cries as soon as its respiratory organs are relieved from the pressure to which they were subjected during birth. The umbilical cord is tied and divided by the persons assisting at the labour. In brutes the umbilical cord generally becomes ruptured spontaneously during birth at a soft spot not far distant from the navel; in some cases it is bitten asunder by the mother. The umbilical vessels soon contract, so that their cavity is quite obliterated. During the first two or three weeks after birth, also, the foramen ovale in the septum auriculorum, and the ductus arteriosus Botalli become closed; and hence from this period all the blood sent to the body must pass through the lungs, and *vice versâ;* the pulmonary circulation now becoming a part of the general circuit which the whole mass of blood performs, whilst before merely a fraction of the blood in the general circulation traversed the lungs.

The newborn mammiferous animals instinctively seek the teats of the mother, and the newborn child also exhibits a constant impulse to suck every object which is offered to it.

* See F. C. Naegele, Ueber den Mechanismus der Geburt, in Meckel's Archiv. t. v. 1819, p. 483. Hueter, im Encyclopæd. Wörterb. d. Med. Wiss. xiv. p. 44. Those readers who desire more full information respecting the process of birth and its variations, should consult the above treatises and special works on midwifery,—such as those of Carus, Stein, Busch, Kilian, Ritgen, and H. F. Naegele.

† See Stein, Unterschied zwischen Mensch und Thier im Gebären. Bonn, 1820.

In the maternal organism, during the first days of the puerperal state, the secretion of milk, which had shown itself in a slight degree during pregnancy, becomes suddenly increased, and the organic activity which was previously expended in the uterus is now transferred to the breasts; while all the maternal feelings at first expressed in the mother's joy at the birth of her living but helpless offspring, are concentrated in the fond office of nourishing and protecting the child. A bloody discharge in moderate quantity, the "lochia," flows from the female organs during some days after birth, and then is succeeded by a serous discharge which gradually, as the inner surface of the uterus regains its state of integrity, becomes a mere mucous secretion. The secretion of milk is excited in increased quantity by the mechanical irritation of the nipples during the act of sucking, and by all ideas of the mother relating to the nourishing and presence of the child. When once in existence, this secretion may often be maintained for a very long and indefinite period, as is observed in brutes, and sometimes also in the human female. Usually, however, it diminishes in quantity when the menstrual flux reappears about the ninth month. In women who do not suckle their children, the menstrual flux is generally restored at an earlier period, about the sixth week after birth.

The milk of pregnant women, and of puerperal women, immediately after birth, is called the "colostrum." According to the observations of M. Donné, it contains, besides the ordinary milk or fat globules, peculiar granulated corpuscules which may be detected in it until about the twentieth day after birth. The proper milk globules which give the milk its white colour consist principally of fatty matter; but they seem to be invested by a layer of some other substance, since they are not very readily dissolved by alcohol and ether. When milk is left at rest, the fat globules collect, for the most part, at the surface of the fluid and form the cream, which consists of the fat of milk or butter. When milk is subjected to continued agitation, the fat globules coalesce and form butter; and when this is removed, merely the fluid part of the milk remains. This fluid holds in solution the other components of milk,—namely the caseine, the sugar of milk, and the salts. The fatty matter of milk is one of those fats which are destitute of nitrogen, and convertible into soap.

The caseine is soluble both in warm and in cold water, and is not coagulated by boiling. It is precipitated by alcohol, corrosive sublimate, alum, and acetate of lead; the precipitate in every case being redissolved by water after the reagent has been removed by washing. Acids in small quantities precipitate the caseine; but when added in excess, they redissolve the precipitate. Pepsine and the rennet containing it exert a peculiar action on caseine; they precipitate it and at the same time render it insoluble in water. The ferro-cyanuret of potassium renders the solution of caseine in acids turbid, or precipitates the caseine. In respect of its elementary composition, caseine, and consequently milk, are to be ranked amongst the nutritive substances which abound in nitrogen. According to Mulder's analysis, it contains, in addition to a small proportion of sulphur (namely 0·41)—

Carbon	55·10
Hydrogen	6·97
Nitrogen	15·95
Oxygen	21·62

Both the other principal ingredients of milk, the fatty matter, and the sugar of milk, are destitute of nitrogen. After the separation of the butter and the caseine from milk, the sugar remains in solution. The sugar of milk crystallizes readily: when pure it is not susceptible of fermentation; but, under the influence of the azotised caseine, it appears to become changed into sugar of mucus. The composition of the sugar of milk, according to the analyses of Gay-Lussac, Thenard, Prout, and Berzelius, is as follows:—

Carbon	40·46
Hydrogen	6·60
Oxygen	52·93

Fresh milk of the human female is slightly alkaline; cow's milk, even when fresh, is sometimes feebly acid; but, when allowed to stand for some time, and especially when the atmosphere is in a state of electric tension, all milk becomes acid owing to the transformation of some of its components, probably of the sugar. The acid of sour milk is lactic acid.

The milk of different animals is not identical in all respects. Simon found that the caseine of the milk of the human female was not precipitated by acids. This was probably owing to the small quantity of the caseine contained in the milk, and the large quantity of acid added. For a diluted solution of caseine is not precipitated except by the smallest quantity of acid. A slight excess of acid redissolves the caseine.

The milk of the human female is, according to Payen, of the following composition:—

Butter	5·18	5·16	or 5·20
Caseine	0·24	0·18	or 0·25
Solid residue of the evaporated fluid of the milk	7·86	7·62	or 7·93
Water	85·80	86·00	or 85·50

Cow's milk, from which the cream had been removed, was found by Berzelius to contain:—

Of caseine, with a portion of the fatty matter	2·600
Sugar of milk	3·500
Alcoholic extract, lactic acid and its salts	0·600
Chloride of potassium	0·170

Alkaline phosphate	0·025
Phosphate of lime, free lime combined with caseine, magnesia, and traces of oxyde of iron	0·230
Water	92·875

The specific weight of human milk is from 1·020 to 1·025; that of cow's milk 1·03.*

CHAPTER II.

OF THE DIFFERENT AGES OR PERIODS OF LIFE.

Processes of development continue to be in operation after birth through a great part of life, although they are of a less important nature than those perfected in the fœtal state. It is only in a few classes and orders of animals which undergo metamorphoses, (as the Insecta, some Crustacea, the Cirrhopoda, the Hydrachinda amongst spiders, and the Amphibia amongst Vertebrate classes), that fundamental changes of form, and the new development of organs and groups of organs, are observed after the termination of embryonic life. The changes of development which occur in the higher animals and man after birth are limited to certain modifications of form, &c., which mark the different ages or periods of life. Adopting that division of the life of a human being which is defined by the most remarkable processes of development or by their completion, we may distinguish the following ages or periods of life.

1. *The period of embryonic life.*—During this period the processes of formation and growth are in their greatest activity. The organs which are being formed present none of their functional phenomena, or only the gradual commencement of them. In the Amphibia there is no distinction of sex during embryonic life; in fact, the organs of generation are not formed. These organs are developed in the larva a considerable time after its escape from the ovum. In the rest of the Vertebrata, however, the distinguishing marks of the sexes become manifest during embryonic life. The causes which determine the sex of the embryo are unknown, although it appears that the relative age of the parents has some influence over the sex of the offspring.† In animals which bring forth many young at a birth, one act of coitus produces both males and females, and in those animals in which the

* See Donné, Du lait et en particulier de celui des Nourrices. Paris, 1837. Müller's Archiv. 1839, p. 182. Henle, Froriep's Notiz. 1839, p. 223. Simon, die Frauenmilch. Berl. 1838. Marchand im Encyclop. Wörterb. d. Med. Wissensch. 23 Bd. p. 309.

† See Girou de Bouzareingues, Ann. d. Sc. Nat. t. xi. pp. 115, 314; t. xiii. p. 134. Hofacker, De qualitat. parent. in sobol. transeunt. Diss. præs. Tubing, 1827; and Heusinger, Zeitschrift für org. Physiol. t. ii. p. 446.

impregnation of the ova is effected out of the body, the same seminal fluid fecundates ova which yield young of both sexes. But how different soever the proportion of the sexes in different families, in larger numbers they always bear an equal proportion. The law which effects this equalization of the numbers of the sexes is in operation in each individual of the species. The equalization of particular deviations from the general proportion is the result of an original provision, just as is the balance of the gain and loss, or of the "even" and "odd" in lotteries or any game of chance which is governed by a general law.

2. *The period of immaturity.* — This period extends from birth to puberty. It is marked by growth, by the development of the forms of the different parts of the body, and by the gradual perception and analysis, by the mind, of the different phenomena of the senses. Several local phases of development occur in this period; for example, in the human subject the first irruption of the teeth, beginning about the middle of the first year after birth, and the displacement of the temporary teeth by the permanent set, which commences in the sixth year. The changes of development afford a basis for the establishment of a period of childhood, extending to the sixth year; and a period of boyhood, reaching to the fourteenth or fifteenth year. In the former of these periods the necessity for nourishment is greatest, the changes of material which the organs suffer is more rapid and greater in degree, and the quality of the food is consequently now of the greatest importance. Hence, in childhood, the organs frequently become affected with various defects of material composition, or defects which are maintained by improper food being given. Such are the diseases called mollities ossium, scrofula. When the period of boyhood commences, the mind has acquired the capacity and strength required for the accumulation of knowledge and for its own cultivation; the process of growth now progresses less rapidly; and the organs of the body receive their permanent material composition. This is the age occupied by education and mental culture, when the foundation is laid in which all the future operations of the mind have their root.

3. *The period of maturity* begins at puberty and ends at the period when the generative power is lost, which in woman occurs about the forty-fifth or fiftieth year. The period of maturity may be subdivided into the ages of youth, and manhood or womanhood. While the changes of development more especially characterising puberty, and already described, take place, the organs of respiration and voice (as has been mentioned in the section on the voice) undergo a further development, and the external form of the different parts of the body is perfected; the features at this period frequently undergoing a very rapid change and taking that character which they afterwards retain throughout life. The previously boyish countenance now serves to express more vio-

lent passions; the leading influence of others ceases and is no longer tolerated; the tricks of the child are cast off, and the errors of the youth who has become independent, who trusts to his own experience and feels himself free, begin to manifest themselves. The corresponding changes take place earlier and more rapidly in the female organism, and hence the girl deserts the games still followed by boys of equal age upon whom she looks down with contempt, though when they also have passed the period of puberty she is timid and bashful in their presence. In both sexes the imagination is now most active; this is the period when the mind is most under the influence of a poetical fancy, when it is devoid of envy, avarice, and jealousy, and is filled with open disinterested friendship. A boundless field of action and meditation is in prospect. The limits to his capabilities of which the serious, cold man becomes conscious, are yet unknown. Love is the centre of the most noble feelings. The vegetative development as far as it regards the individual is now complete, and the increase of the organic force is applied to the new products of the generative function. Those individuals in whom the formative and equalizing power was at first unstable and the material composition of the organism defective, already manifest an inability to resist the action of external stimuli, particularly when these are applied to such important organs as the lungs; for the lungs at this period, on account of the increased development which they are undergoing, possess an extraordinary degree of irritability. Hence when the system has undergone the changes of puberty there frequently appears a predisposition to pulmonary disease which had previously remained latent during the active growth and development of the different parts of the body, just as hectic frequently ceases during pregnancy.

While the body continues to grow, the epiphyses of the bones remain separated from the diaphyses by sutures; the elongation of the bones taking place at these points. When the individual has attained his full stature, the epiphyses become united to the diaphyses by ossification.

In the age of manhood the slim forms of youth frequently give place to greater bulkiness and obesity of figure, which manifests a failing influence of the formative power over the masses of the body. At this period of life also the mind has attained its maturity, has laid aside the exuberance of the feelings, and is conscious of efforts made, of endeavours miscarried, of the limits of its faculties and of the feeling of possession; life has become more tranquil; the views of the individual are more clear and more serious; he still has his passions, but they are active in another direction, in the acquisition of possessions and in self-defence.

Within the age of manhood there is no predominant disposition to diseases of particular organs. Yet in advanced manhood the morbid changes by degrees manifest a preference for those organs which are chiefly engaged in impressing chemical changes on the matters submitted to their influence, for example in the large glandular viscera; and the weakened vegetative power is the less able to resist obnoxious agencies the more frequently they are excited. It is not the lungs which now suffer; after the excitement which they experience in youth those organs gradually regain a state of repose. The organs of the abdomen are now especially subject to the abnormal changes; whilst the effects of foregone disturbances of the nervous system are more perceptible and more enduring than in youth when the foundation for them possibly was laid. The age of manhood is moreover particularly prone to mental diseases owing to the intensity of the shocks to which the mind at this period of life is subject.

4. The last great period of life may be designated the *period of sterility.* It extends from the cessation of the fruitful exercise of the generative function to extreme old age. The form of the body now loses its plumpness and "turgor." The growth of the hair which began on the head, and, subsequently, in the periods of youth and manhood, extended to the face, ceases also first on the head and continues to extreme age only in the beard. In old age also there is manifested a tendency to the deposition of calcareous salts in the cartilages and coats of the blood-vessels. The teeth or their remains lose their firm attachment to the jaw-bones, and after they have fallen out, the alveoli disappear. Hence the jaw-bones in old age become shortened. In this period of life, when all the development is at an end, there is a more or less uniform diminution in the energy of the different vital functions, while the intensity of the propensities, inclinations, and sympathies, the acuteness of the senses, the liveliness of the fancy, and the spirit of self-defence and resistance fail. Very few individuals reach an age in which this diminution of the faculties leads imperceptibly to the close of natural life. In most persons the foundation of premature decay is laid in local causes. But even independently of this circumstance the organism in old age after all the processes of development are completed bears a stronger resemblance to a piece of artificial mechanism than does the primary form of being which generates the mechanism of the body out of its own mass, and therefore can make good the lesions which it may suffer. In old age a slight disturbance produced by an external cause is capable of arresting the whole mechanism.*

* The subject of the different ages of man's life is treated of very fully in the third volume of Burdach's Physiologie.

CONCLUDING REMARKS ON THE VARIETIES OF MEN AND ANIMALS.

From this review of the process of development of the individual animal organism, we are brought back again to the contemplation of the general forms to which the individuals belong as examples of species or genera; and thus the conclusion of the "Special Physiology" connects itself with those considerations which were discussed in the "Prolegomena on General Physiology." The races of animals and plants suffer modifications under the various conditions to which they are exposed in their distribution over the surface of the globe. These modifications do not exceed the limits marked out by species and genera, but they are perpetuated as types of "varieties" of the species through successive generations. It is to these phenomena that our attention must now be directed.

It is important in this inquiry to attach definite ideas to the terms "species" and "variety." The species is a living form represented by individual beings, which reappears in the product of generation with certain invariable characters and is constantly reproduced by the generative act of similar individuals. The latter character distinguishes the species from hybrid forms. It is not an exclusive character of the living form, which we denominate species, that one form produced by generation is capable of productive union with another individual: this character is inadequate to mark the two individuals thus propagating as belonging to one species. For individuals belonging to two different species of one genus are likewise in some instances capable of propagating with each other, as in the cases of the dog and wolf, and the horse and ass, where mules or hybrids are produced. The type of the genus, represented by different species and individuals, is alone incapable of fruitful union with individuals of species belonging to another genus. But hybrids, the production of which is rendered infrequent by the natural repugnance of the individuals of different species to generative union, cannot propagate their distinguishing characters by generation. The sexual union of hybrids is generally unfruitful; and when fruitful, as in the case of the union of a hybrid with an individual of one of the species which had co-operated to form the hybrid, the product relapses into the type of one of the original species. The constant reproduction of the same form by the sexual union of similar individuals is therefore an invariable and essential characteristic of the species.*

* Consult on this subject Rudolphi, Beiträge zur Anthropologie und allgemeinen Natur-geschichte. Berlin, 1812. Prichard, Naturgeschichte des Menschen-geschlechts. Leipz. 1840, p. 174. [Physical History of Man, London,] translated into German by Rudolph Wagner; and also the notes of Wagner in the same work, p. 439.

"Varieties" are forms represented by individuals but included within the definition of the species. The individuals constituting one variety are capable of fruitful union not only with each other but also with individuals belonging to other "varieties" of the same species. Individuals belonging to different genera are not capable of fruitful union; and individuals of different species can propagate with each other, but their products cannot reproduce their peculiar form by generation; varieties have both these faculties. The mixed race produced by the union of two races is capable of propagation by union with similar individuals; but the union of the mixed race with the original race which had concurred in its production yields an offspring which in successive generations approaches more and more nearly to the type of the unmixed races. These characters sufficiently distinguish the "variety" of a species, which, when permanent, is a "race." The variety may however be otherwise defined and distinguished from the species. The different species always remain distinct. The races composing them present no stages of transition of one species into another. Where different forms of animals exhibit this gradual transition of the one into the other, they cannot be regarded by the zoologist as distinct species. With the "variety" the case is otherwise. There is a remote possibility that the similar productive individuals of one variety of a species, or a race, inasmuch as they contain within themselves the essential properties of the species, might produce all the other varieties of the species, provided the internal and external conditions necessary thereto were in action during a long series of generations. But there is no remote possibility of one species being produced from another. All the phenomena at present observed in the animal kingdom seem to prove that the species were originally created distinct and independent of each other. While the different varieties of each species may be accounted for by supposing the original existence of a pair of individuals of opposite sexes belonging to the same species, and the constant action of different external modifying agencies, such as that of climate, upon several or many successive generations.

The causes which give rise to the varieties of species are partly seated in the organisms of the animals themselves, and partly external conditions, — such as the food, the elevation above the sea, and the climate. Each species of plants and animals possesses within itself a power of variation within a certain limit, quite independently of any external influences. To this cause are to be referred the varieties of form which may present themselves in the offspring of one act of generation. In each individual of a species there is an innate capability of producing such varieties as these, since each individual of a species does not produce by generation the mere repetition of itself, but generates the new beings in accordance with laws which regulate the whole species. Thus from the same parents there may be produced individuals with fair and others with dark hair; some of spare and slender figure, and others of plump and stout robust form; individuals of different temperaments, and with different features, eyes, mouth, and nose, with hair in some instances curly, and in others straight. The most common varieties arising in this way from internal causes, are the fair and the dark haired. Fair persons are occasionally met with amongst races for the most part characterised by black hair, — for example, amongst the Mongolians; and Dr. Prichard adduces several examples of fair-complexioned negroes who were not albinos.

It is true that these varieties are chiefly due to the parents being individuals of different complexions, and to the characteristics sometimes of one and sometimes of the other being predominant in the offspring. But even when the parents have the same complexion, a certain variety of forms and internal properties may present itself in the offspring. In consequence of the mingling of these different varieties in marriage, their peculiarities are not preserved, and are not propagated as constant fixed types. It is easy to conceive the conditions which must be combined in order, independently of climate, food, and locality, to convert these accidental varieties into persistent types. The longer individuals of the same stock continue to unite in marriage, without foreign admixture, the longer will the type to which they belong be preserved. In this way, and independently of all external influences, a race will be formed. Sometimes when the type has become fixed through a series of generations in the members of a family, even the admixture of a foreign type is not sufficient to efface the fixed characters of the family, and the foreign element becomes lost in the older fixed type. Hence we see in many royal families that in spite of their union by marriage with other houses, the type of the family features is in a remarkable way preserved and transmitted from generation to generation, — as, for example, in the Bourbon family, and equally in many princely houses in Germany. It was previously shown how one family, being isolated by the intermarrying of its members exclusively with each other, might produce a nation or tribe with general distinguishing characters. History teaches us how the national type once formed is preserved in spite of individual variations through thousands of years, and that, except when modified by admixture with other types, it is maintained unchanged, as in the case of the Jews, even in the most varied climates which produce their peculiar modifications of form and complexion.

The propagation of like with like is, however, capable of perpetuating, not merely a physical type forming one of the varieties of a species, but also the faculty which individuals acquire by education. The peculiar properties of the hound, the shepherd's dog, and the watch-dog, for example, are all comprehended in the general notion of the species; and it is probable that in the brood of a single wild dog, or in the generations descended from this brood, through the inherent tendency of the species to the production of varieties, individuals occur which, when tamed, discover very different talents,—the one being more adapted for the chase, another for tending of sheep, and a third for keeping watch or guarding property. But the education and rearing of the dogs with the requisite endowments for the purposes mentioned, cause the faculties thus improved or acquired to be transmitted to succeeding generations, when this object is provided for by the pairing of males and females with similar endowments.

Varieties of species are also produced by external influences; and the longer the action of these causes is continued, the more constant does the particular variety become, and the more does it acquire the character of a type. To these external causes belong the climates or zones in which the animals live. The warmth or coldness of the climate has an especial influence on the fur or hairy coat of animals. Most animals, as is well known, have two kinds of hair in their coat, — namely, long and stiff hairs, and between these a shorter, curly, woolly hair. Now, the further a sheep is carried towards the north, the more equal does the proportion of the two kinds of hair in the coat become; while in sheep living in southern countries the woolly hair increases in quantity at the expense of the stiffer, longer hair. This is exemplified in the merino sheep inhabiting the mountains of Spain. Climate modifies also the "habitus" and size of animals. Cattle transported from the temperate zones of Europe, — for example, from Holland or England to the East Indies, — are said to become considerable smaller in their succeeding generations.* On the other hand, the skin of the cattle carried to South America has in a series of generations gradually become so much changed in its properties, that the Brazilian hides now supply the best leather. The guinea-pig, Cavia aperea, which in its native country is of a grey colour, since its introduction into Europe has become changed into a variety marked with brown, black, and white spots. The elevation of the locality above the sea also, independently of the degree of latitude, has an influence over the forms of animals. According to Sturm, the hog in low countries or districts, — as in East Friesland, — attains the greatest size of trunk, with long and deep flanks, but with short legs. While in proportion as the country the hog inhabits is elevated above the level of the sea, the smaller and more compressed becomes its body, the less tapering and shorter its head; the shorter and thicker its neck, and the more rounded its hind quarters. But the food

* See Sturm, Über Racen, Kreuzung, und Veredlung der landwirthschaftlichen Hausthiere. Elberfeld, 1825, p. 54.

also modifies the form and nutrition of animals; hence in the low countries of Holland, East Friesland, and Holstein, the cattle are remarkable for their large size, and for the abundant supply of milk which they yield, while they are defective in both these qualities in barren Iceland.

The concurrence of different conditions of internal as well as external nature, which cannot be severally defined, has produced the existing races or fixed varieties of the different species of animals; the most remarkable of which varieties are to be met with in those species which are susceptible of the most extended distribution over the surface of the earth.

The principal modifications, in addition to those of external form, are to be found in the skin, in the coat, the horns, and the adipose deposits. Sometimes the ears are lengthened and become pendulous, — as in the Kirghisic sheep, and some varieties of the dog; sometimes the horns are wanting, — as in the English sheep, or are spirally twisted, — as in the Hungarian sheep; sometimes the adipose tissue is accumulated in the form of a hump on the back, — as in the little zeburind, or in the tail, — as in the sheep of Thibet and the bucharei; sometimes the hair of the coat is curled, as in the poodle-dog, or forms a very thick wool, as in the merino sheep. In the human species also prolongations of the skin, varieties in its appendages, and local accumulations of fat occur in different races; for example, the elongation of the nymphæ and their commissures in the Hottentot females and the females of the Bosjesman or Bushman race; the straight hair which may be abundant or scanty, the curly hair and the woolly crisp hair, and the accumulation of fat about the buttocks and sacrum of the Hottentot and Bosjesman females.

The modifications in the form of the species produced by the influence of climate are seldom so deeply rooted, that they are not gradually lost when the climate is changed, and then they may be replaced by the peculiarities produced by the new climate. Thus the wool of merino sheep, imported by Englishmen into some of the South Sea Islands, has soon become changed into straight hair. The wool of the same variety of sheep, when they are transported to Peru and Chili, very soon gives place to straight stiff hair.* A German gardener repeatedly imported the seeds of the white cabbage from Germany into Naples in order to rear heads of cabbage which at the latter place were still unknown; but he always failed, for he could raise only leafy cabbage, or the cauliflower variety. According to Sturm also, the Siberian naked barley, Hordeum cæleste, when grown on the Rhine frequently degenerates into common barley.

* Sturm, op. cit. p. 42 and 50.

There are, however, examples of typical varieties produced by influences connected with climate, which have not lost their peculiarities in successive generations when transplanted to a different climate, provided the preservation of the type has been favoured by the individuals of the variety constantly propagating with each other. The different races of mankind afford the most striking examples of this fact.

The races of the human species answer to the general notion of a "race;" they are different forms of one species which are capable of fruitful union, and are propagated by generation: they are not different species of one genus; for were that the case their hybrids would be unfruitful. Here, as in the case of other animals, all the varieties are to be regarded as aberrations from one type, caused partly by differences in the progeny of the same parents maintained by repeated propagation of similar forms with one another, and partly by the external influences connected with climate. Whether the first individuals of the species were originally placed in different parts of the globe at the same time, or whether they existed originally in one spot, and have spread themselves thence over other parts, is a question not affecting this statement. Some of the extreme forms of the races of mankind are certainly varieties which are no longer produced anew with all their distinguishing peculiarities, either by internal causes, or by the influences of climate, and which lose their characters in no climate, but propagate them in all their purity when foreign admixture is avoided. For negroes in the temperate and colder climates remain black, and retain all the characters of negroes, and also by generative union with each other produce only negroes; whilst Europeans in hot climates, except that the colour of their skin becomes somewhat darker, retain the characters of the European race. Under the same degrees of latitude negroes, Europeans, and the copper-coloured American Indians retain their respective forms and colours; and on many of the Australian islands there are found natives with all the characters of the Malay race, and with them black men of the negro variety. Yet even these races are not so absolutely distinct that the innate tendency to variation does not determine in one race individual cases of approximation to another, and that the same does not happen from the influences of climate. Individuals of the European race sometimes have hair nearly as crisp and woolly as that of negroes. The negro form of the face and head likewise occurs in individual cases amongst the Europeans. Weber states, that besides the ordinary oval form of the skull, there may be found amongst Europeans skulls of the elongated and quadrangular forms which are to be regarded as instances of sporadic approximation to the negro and mongolian types. The differences in the form of the pelvis in different races have been much elucidated by Vrolik. The form of the pelvis is sometimes very different from the ordinary European type, and particularly in the negroes and

Bosjesmans, in whom the vertical position of the iliac and other characters indicate an approach to the form of this part of the skeleton in brutes. But in the form of the pelvis also the different races present aberrations from their proper type. According to Weber's researches there are in every race examples of pelves with the inlet of the oval, the round, the quadrilateral, and the wedge-like form. In the negro race there are many aberrations from the general type, such as the brown-black colour of the Hottentots and Bosjesmans, the only half-woolly hair of the Papuan negroes of Australia, the coalescence of the ossa nasi into one bone, which sometimes occurs among the Hottentots and Bosjesmans, and the elongated nymphæ of those tribes. Moreover, although the action of light and the temperature of different climates on the skin is extremely various in different races and nations, yet their influence is to a certain extent evident in all races; in all the skin is more or less darkened by residence in hot climates. This susceptibility to the action of light and heat is greatest in the negroes; so that the child, which during its embryonic existence was white, becomes coloured by exposure to the light after birth. In Europeans of fair complexion the skin does not become darkened from exposure to the light, which it does in Europeans with dark hair.

The question whether the different races of mankind all derive their origin from one parent stock or from several stocks, can never be determined by practical observation. But this question is not so important in reference to the theoretical explanation of the races, as some physiologists have supposed. For whether many or a few individuals of an animal or plant were created at the same time, still the conditions which give rise to the varieties would exert their influence on individuals. The history of the races of animals and plants conducts us inevitably to the conclusion that all the true varieties of one species may be produced by the action of internal and external causes through a sufficiently long period of time on individuals of the species.

It is impossible to make a strict division and classification of the races of mankind. For the various forms do not possess equally marked peculiarities, and there is no such sure, scientific, intrinsic principle to guide us in defining their limits, as there is in the case of the species. The object of a physical history of man is to describe all the peculiarities of the nations which maintain themselves distinct by the successive generations of each not mingling with those of the others; but the contemplation of mankind in this extended manner does not come within the scope of this work. All that is here practicable is to enumerate the most conspicuous of the races of mankind according to the arrangement proposed by Blumenbach, which is still preferable to all others, because it is the most convenient.

The races distinguished by Blumenbach are:—

1. The *Caucasian race.*—In this race the colour of the skin is more or less white, passing into flesh colour; more rarely it is of a light brownish colour. The hair is more or less wavy, and of a light or dark tint. The forehead is high and arched; the face oval; the facial angle* large, namely, from 80° to 85°. The nose is slender, more or less arched or prominent; the teeth perpendicular; the lips of moderate thickness; the chin prominent; the beard abundant; and no scantiness of the growth of the hair of the surface generally. To this race Blumenbach assigns the Europeans (with the exception of the Laplanders and Finns) the inhabitants of Western Asia, as far as the Obe, the Ganges, and the Caspian Sea, and also the North Africans.

2. The *Mongolian race.*—The characteristics of the Mongolian variety are a yellow complexion; black, straight, scanty hair; a broad, flat face, which is widest where the cheek-bones project; a flat and broad glabella (the space between the eyebrows); a short, broad, and flattened nose; narrow and oblique openings of the eyelids and eyes, placed wide apart.

To this race Blumenbach refers all the Asiatics not belonging to the Caucasian variety, except the Malays; the Laplanders and Finns in Europe; the inhabitants of the most northern parts of America, the Esquimaux and Greenlanders.

3. The *American race* has a brownish copper-coloured skin; black, straight, scanty hair; a beard more or less feebly developed; a nose more or less prominent. All the other characters assigned to this race are neither constant nor striking.

This race comprehends all the Americans not included in the preceding variety.

4. *The Ethiopian race.*—The characters are a black or a brownish black complexion; black, generally coarse, short, woolly, and frizzly

* By the facial angle is understood the angle included between the facial line and a horizontal line drawn from the base of the cranium. The former of these lines touches the glabella or space between the eye-brows and the most prominent part of the superior maxilla beneath the nose; the latter line is the middle line of a plane passing through the anterior nasal spine of the superior maxilla and the meatus auditorius externus. This angle is always larger in children than in adults. In the same way it is proportionally large in young apes as in the young ourang, while in full grown apes it is much smaller, and the face has consequently a more brutish character. The size of the facial angle is determined by the proportion borne by the cranial portion of the head to the parts occupied by the senses and those engaged in mastication and the taking of food. In the antique sculptures this angle is enlarged to the extent of a right angle, and still further, in order to give a more noble expression to the head, and hence in this point the form of the child is transferred to the adult. According to the researches of Tiedemann the capacity of the cerebral cavity of the cranium is the same in different races of men, how different soever the external forms of the skulls may be. See Tiedemann, Das Hirn des Negers mit dem des Europäers und Orang-utans vergleichen. Heidelberg, 1837, p. 4.

hair; a narrow and long skull; a retiring forehead; a prominent upper jaw with a retiring chin, and teeth projecting obliquely; a small, turned-up nose, compressed above; thick lips; and a facial angle of only 70 to 75°.

All the inhabitants of Africa, except those belonging to the Caucasian variety, namely, the African negroes, and the negroes of New Holland and the Indian Archipelago, or the Papuas, constitute this race.

5. *The Malay race.*—The skin is black; the hair black, soft, curling and abundant; the cranium moderately narrow; the forehead arched; the upper jaw moderately prominent; the nose short and broad; the lips thick, and the mouth wide.

To the Malay race belong the brown islanders of the South Sea; the inhabitants of the Sunda Isles, the Moluccas, the Philippine and Marianne Isles and the true Malays of Malacca.

It would, doubtless, be more consonant with nature to regard these races as constant and extreme forms of the varieties of mankind than to endeavour to make them include all the nations of the earth, a task which is impracticable and which science does not require to be performed. The attempt to effect such an arrangement of all the varieties of mankind under one or other of these classes inevitably leads to an arbitrary classification. The position of the Tartar and Finnish tribes in relation to the Mongolian and Caucasian races is quite uncertain, and they cannot be referred to either exclusively except by a mere arbitrary decision. The same remark applies to the Papuas and Alfouros in regard to their classification with the Malays or with the negroes. Amongst the islanders of the Pacific both black and brown and even white men may be distinguished; at all events, in the Society Isles there are white natives as well as those of a yellowish brown complexion. In this case the whites cannot be referred to the Caucasian race, any more than the idea can be entertained of classing the Guyacas of America with the Caucasian race on account of their light complexion. On the contrary these varieties seem to have arisen among those nations in the same way as the fair and dark complexioned varieties have been produced among Europeans. But it further admits of inquiry whether the Papuas and Alfouros should not be regarded as distinct from the African negroes in their origin, and whether these black races of the Indian Archipelago are not, on the contrary, much more nearly related to the brown Malay race, in which case these blacks and the brown Malays might be supposed to stand in the same relation to each other as the true negroes and the dark brown inhabitants of Southern Africa. No necessity exists for deriving all the black people on the globe or all the brown or all the white races from the same root; on the contrary, since we have seen that varieties may arise among the progeny of one stock, it is easy to conceive how it is possible for nature to produce similar forms in nations which are far removed from each other and according to the records of history have never mingled.

Similarity or difference of language may sometimes aid us in determining the relation borne by a particular people to the principal races of mankind, but even this criterion is not always trustworthy. For not unfrequently languages sprung from very different roots are met with amongst the people of one race. Languages, like races of men, perish and are displaced by others.

With respect to the original roots of languages there may be distinguished upon the great continent of Europe and Asia:

1. The nations whose languages are derived from the Indo-European root; these languages are the Sanscrit, the Persic, the Greek, the Latin, the German Celtic, and the Sclavonic Celtic.

2. The nations speaking the Semitic tongues, namely, the Aramæic, Phœnician, Hebrew, Arabic, to which must be added the Aethiopic or Geezic in the Northern and North Eastern parts of Africa.

These are the nations of which the most perfect history has been preserved, and who have in the greatest degree been susceptible of civilization. The same nations are comprehended under the name of the Caucasian race.

3. The nations using the Tschudic tongues, to which are referred the languages of the Hungarians, Finns, Laplanders, Samoyedes, Esthonians, Livonians, Permiens, Wogules, Ostiakes, Cheremisses, Mordwines, Koriakes, Tchuktches, and Kuriles, and, by some writers, the languages of the nations of the Caucasus, as the Georgians and the Circassians.

4. The nations speaking the Tartar or Mongolian tongues, as the Mantchoo in China, the Turkish, and the dialects of the Uzbecks, Bucharians, Bashkires, Yakutes, Kirghises, Calmucks, Tungooses, &c.

5. The nations having monosyllabic tongues, partly languages of symbols, as those of China, Tonkin and Cochin China; partly languages with syllabic alphabets, as those of Thibet, Siam, and Birma. These languages have no inflections and express the relations of words by means of intonation.

Australasia is inhabited partly by brown Malays, partly by the brownish black Papuas and Alfouros. The Alfouros live in the central parts of most of the Moluccas, and Phillippine Isles, of Madagascar and New Guinea, also in the North of New Guinea, of New Britain, New Ireland, Louisiade, Bouka, Santa Cruz, Solomon's Islands, and are scattered through the interior of New Holland. They are regarded as the original inhabitants. M. Lesson describes them as having thin legs, prominent teeth, rough, thick, straight hair, a thick beard, and a dirty brown or black complexion. The Papuas who are a different variety and live on the coasts, call the Alfouros Endamines. The Papuas who live on the coasts of many islands in the Malay Seas, appear to be a mixed variety between the Malays and the Alfouros or true Papuas, and resemble the inhabitants of Madagascar. Their hair is moderately woolly, thick, and long; their nose is flat, the nostrils dilated transversely, the forehead high, the beard thin, and their colour a deep black brown.

The Malays have spread themselves from Sumatra over the Peninsula of Malacca; and here also are found the tribes of both colours in the mountainous districts, namely, besides the true Malays, the Samang tribes, woolly haired Negritos.

Malay dialects nearly allied to each other are spoken in the Philippine and Sunda Isles and in Madagascar. Of similar construction and composed of similar words are the languages spoken in New Zealand, Tahiti, the Sandwich Islands and Tonga.

Africa is inhabited by two races. In the Northern and North Eastern parts dwell the Abyssinians, Nubians, Egyptians and Berbers, nations allied to the Indo-Europeans. All the rest of Africa is occupied by Negroes. The number of languages spoken is immense, and the same is the case in America, all the inhabitants of which continent, except, perhaps, the (Mongolian) tribes of the North Eastern part, appear to be allied to each other, notwithstanding the national distinctions of Peruvians, Guaranians, Araucanians, Pampas, Puris, Botocudos, Moluchas, Patagonians, Fuegians, Mexicans, Caribeans, Canadians, and Californians.*

* The works treating specially of the Natural History of Man, are, Blumenbach, De generis humani varietate nativa, Gott. ed. iii. 1795; Blumenbach, Decades collectionis craniorum, Gott. 1790; P. Camper, Über den natürlichen Unterschied der Gesichtszüge in Menschen verschiedenen Gegenden und verschiedenen Alters, Berlin, 1792; Virey, Hist. Nat. du genre humain, Paris, 1824; Desmoulins, Hist. Nat. des races humaines, Paris, 1826; Bory de St. Vincent, Der Mensch, Weimar, 1837; G. Vrolik, Considérations sur la diversité des bassins de différentes races humaines, Amsterd, 1826; J. M. Weber, Die Lehre von den Ur- und Racenformen der Schädel und Becken des Menschen, Düsseldorf, 1830; R. Wagner, Naturgeschichte des Menschen, Kempten, 1831; Van der Hoeven, in Tijdschrift voor naturlijke geschiedenis, T. i. iv., die Menschenracen in der Deutschen Vierteljahrs-schrift, 1838; Prichard, Naturgeschichte des Menschengeschlechts (Physical History of Man) mit Anmerkungen und Zusaetzen von R. Wagner, Leipz. 1840; Berthold, Menschenracen, im Encyclop. Wörterb. d. Med. Wissensch. B. xxiii. p. 44. [Mr. Lawrence's Lectures on Man; and Morton's, Crania Americana, Philadelphia, 1839.]

INDEX.

The Roman numerals denote the volume of the work. The Arabic figures refer to the pages. The references to the first edition are distinguished by the mark † following the figures. An asterisk * marks the supplementary pages, thus distinguished in the second edition. And the numbers within brackets [ ] refer to the Appendix.

A.

B.

C.

E.

G.

H.

I.

K.

L.

O.

P.

Q.

R.

T.

V.

THE END.

ERRATA.

Page 102, edit. i. or page 116, edit. ii. In the table showing the size of the red particles of the blood in different vertebrate animals, the measurements ascribed to the red particles of the "cat" and those of the "goat" require correction. They should be for the "cat" $\frac{1}{4286}$ of an English inch,

for the "goat" $\frac{1}{6469}$ " " " .

Page 165, line 24, edit. i.; *for* "which is most dense internally," *read* "which is most dense externally."

Page 201, line 17, edit. ii.; *omit* the comma after "lungs" and the words "the experiments on the production of respiration in hydrogen."

Page 374, lines 5 and 6, edit. i.; *for* "That this is not always the result is proved by the following interesting experiment, which Dr. Sharpey has kindly given the translator permission to mention," *read* "The following experiment, which Dr. Sharpey has kindly given the translator permission to mention, is interesting."

Page 490, line 17, edit. i.; *for* "nilghau," *read* "hippopotamus."

Page 882, line 16; *for* "about $\frac{1}{197}$ of an English line, *read* "about $\frac{1}{971}$ of an English line."

LONDON:
PRINTED BY SAMUEL BENTLEY,
Bangor House, Shoe Lane.

APPENDIX,

[CONTAINING some of the additions and corrections made by the author in the third edition of the first part of the original treatise ; the detail of experiments, &c. which appeared too long for insertion except in this form ; and some recently discovered facts having reference to the subjects discussed in the earlier part of the work.]

BOOK THE FIRST.

SECTION II.

Of the circulation.

CHAPTER II.

OF THE GENERAL PHENOMENA OF THE CIRCULATION.

Sounds of the heart, p. 176.

THE facts which the committee of the Medical Section of the British Association * determined by their experiments are the following : — Both sounds of the heart may still be heard (a stethoscope being applied to it) when the sternum and ribs are removed, and the heart is in contact with no part of the thoracic parietes. The two sounds having been heard in this way in a calf, two delicate needles of the proper curvature were thrust one into the aorta, the other into the pulmonary artery below the point of origin of the semilunar valves ; after being carried upwards for about half an inch, they were brought out again through the coats of the respective vessels ; so that between each needle and the parietes of the vessel one of the semilunar valves was included. Afterwards, on applying the stethoscope to the vessels, it was found that the second sound had ceased to be audible. These experiments tend to confirm Dr. Williams's opinion regarding the sounds of the heart. But even admitting that the first sound is due to the contraction of the ventricle,—is a muscular sound,—and the second produced by the reaction of the column of blood in the aorta and pulmonary artery upon the semilunar valves, spreading them out ; yet they must be rendered more perceptible by the heart striking against the thoracic parietes during the systole with its apex,—during the diastole with its anterior surface. [In their second report † the committee state that further observations have verified the above conclusions.]

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* Medical Gazette, Oct. 1836.

† Medical Gazette, Dec. 2, 1837.

CHAPTER IV.

OF THE INDIVIDUAL PARTS OF THE VASCULAR SYSTEM.

Structure of the capillaries, p. 217.

Schwann has recently ascertained, by means of the microscope, not merely that the capillaries have membranous parietes, but that this coat contains distinct circular fibres arranged as in arteries. He discovered them in the capillaries of the mesentery of the frog and brown or fire-toad (rana bombina). It is necessary to employ a high magnifying power and a rather feeble light; but they may be seen in the dead as well as in the living frog. (See also p. 877.)

BOOK THE SECOND.

SECTION I.

Of respiration.

CHAPTER I.

OF RESPIRATION IN GENERAL.

Poisonous gases, p. 293.

Carbonic acid is one of the poisonous gases which can be taken into the lungs, for it does not excite coughing even when inspired in large quantity. It has a narcotic action on the system, producing asphyxia without exciting any symptoms of suffocation. Atmospheric air containing more than 10 per cent. of carbonic acid is quickly fatal.

SECTION II.

Of nutrition, growth, and reproduction.

CHAPTER I.

OF NUTRITION.

Chemical composition of the organised tissues, p. 367.

[Under this head the author in the third edition gives a new classification of the tissues, dividing them into]

1. *Tissues with an albuminous base.*—To which belong the brain and nerves, the muscles, glands, and mucous membranes.

These tissues yield no gelatin by boiling, which moreover produces little change in them; the cellular tissue which enters into their composition can alone be converted into gelatin. The different modifications of albuminous bodies are not at present well understood. We are acquainted with albumen only in the more restricted sense, and with fibrin; and the properties of these substances have been described in the chapter on the chemical analysis of the blood. The ferrocyanide of potassium throws down a precipitate from the acetic acid solution of albuminous bodies, by which character these are distinguished from the following.

2. *Tissues which yield gelatin by boiling.*—To these belong,—1, the cellular tissue; 2, serous membranes; 3, tendinous tissue; 4, skin; 5, one kind of contractile tissue; 6, cartilage; 7, bone; and, 8, elastic tissue [including arterial tissue]. The animal matter which forms their basis either dissolves wholly into gelatin, or they continue to yield this substance for some time when submitted to long boiling. Some tissues, such as cellular and serous membranes, and bone, even after a few hours' boiling, yield a large quantity of gelatin; others, as cartilage and skin, yield but little of this substance even after fifteen or eighteen hours' boiling; while several days are required to extract it in small quantity from other textures, such as elastic tissues. The ferrocyanide of potassium produces no precipitate in the acid solution of these textures which yield gelatin.

The cellular tissue, the contractile tissue of the tunica dartos, the tissue of the serous membranes, the tendinous or fibrous tissue, and the tissue which forms the basis of the skin, yield the common gelatin or glue, *colla*, which is precipitated by tannin, chlorine, corrosive sublimate, and alcohol; but not by alum, acetic acid, acetate of lead, and sulphate of alumen. The precipitate thrown down by alcohol is again soluble in hot water.

The peculiar substance which I have described as the base of the permanent cartilages agrees in many points with the ordinary gelatin, but differs from it in the following particulars. It is precipitated by alum, sulphate of alumen, acetic acid, and acetate of lead. The precipitate produced by alum is redissolved on the addition of an excess of the reagent; that thrown down by acetic acid is not redissolved by the addition of more acid. Casein is likewise precipitated by the same reagents as the gelatin of cartilage or chondrin; but casein does not form a gelatinous mass when its solution cools, and, when thrown down by alum, it cannot be redissolved by an excess of that substance, while the precipitate which acetic acid produces is redissolved on the addition of more acid.

The cartilages are divisible into four classes:

a. Cartilages containing peculiar corpuscules.— The greater number of the permanent cartilages, and also the cartilage of bone before ossification, are composed of a semi-transparent, indistinctly fibrous tissue, containing in its substance numerous microscopic corpuscules generally of a flattened form, in the interior of which again there is often a nucleus or several granules. All the cartilages of this kind, namely, the costal cartilages, the majority of the cartilages of the larynx, those of the trachea, of the nose, and of the Eustachian tube, the articular cartilages, and the cartilage of bone before ossification, yield by boiling, according to my observation, the substance which I have named Chondrin, in place of the ordinary gelatin.

b. Chondrinous fibro-cartilage.— The cornea consists of three layers besides the delicate layer of epithelium which invests its free surface. The most superficial layer is rendered by hot water immediately of a snowy-white colour; the most internal lamina is the aqueous membrane, which is attached to the lamina fusca of the sclerotica; the middle layer, which constitutes the chief substance of the cornea, is formed of an interlacement of bundles of bright fibres without any intermixture of corpuscules. This is, according to my observation, reduced wholly to chondrin by boiling.

c. Spongy cartilages; their structure was discovered by Miescher. The cartilages of this kind are the yellowish cartilages of the external ear, the epiglottis, and the cartilagines Santorinii et Wrisbergii of the larynx. They are yellow, and contain none of the corpuscules of Purkinje, but are throughout of a spongy texture, having large cells. After being submitted to boiling during several days, they yield an extract in extremely small quantity, which does not form a jelly, but of which the chemical properties agree with those of chondrin; while the preceding cartilages dissolve within the space of fifteen or twenty hours into a chondrin which gelatinises on cooling.

d. Ligamentous cartilages. — These are interarticular cartilages, the intervertebral cartilages, the cartilages of symphyses. The substance which they yield by boiling is not chondrin, but gelatin entirely similar to that of tendons. They are constituted wholly of fibres, and contain none of the corpuscules of the first kind of cartilages. The tarsal cartilages of the eyelids, which are likewise fibrous, have not at present been examined with reference to their chemical composition.

The animal matter or cartilage of bone is composed of gelatin. It is remarkable that the cartilage of bone before ossification yields only chondrin when boiled, but after ossification affords the ordinary gelatin; such is the result of my observations. And even when the permanent cartilages, those of the larynx, for example, undergo ossification as the result of abnormal action, the ossified portion contains ordinary gelatin in place of chondrin. Bones which are affected with mollities ossium contain, by no means, a larger quantity of gelatin, but an extraordinary quantity of fatty matter.

Elastic tissue is yellow, and preserves its property of elasticity for any length of time in alcohol, and is not deprived of it even by several days' boiling. It yields very little gelatin, and that not until after several days' boiling. The gelatin has peculiar characters; it cannot, therefore, be derived from the cellular membrane which is inclosed in the elastic tissue. It bears a great resemblance to "chondrin," but yet is not identical with it. The solution of the gelatin of elastic tissue is rendered very turbid by acetate of lead and acetic acid, and is precipitated by common alum and by sulphate of alumen; but the sulphate of the peroxide of iron renders it opaline merely, without throwing down any precipitate.

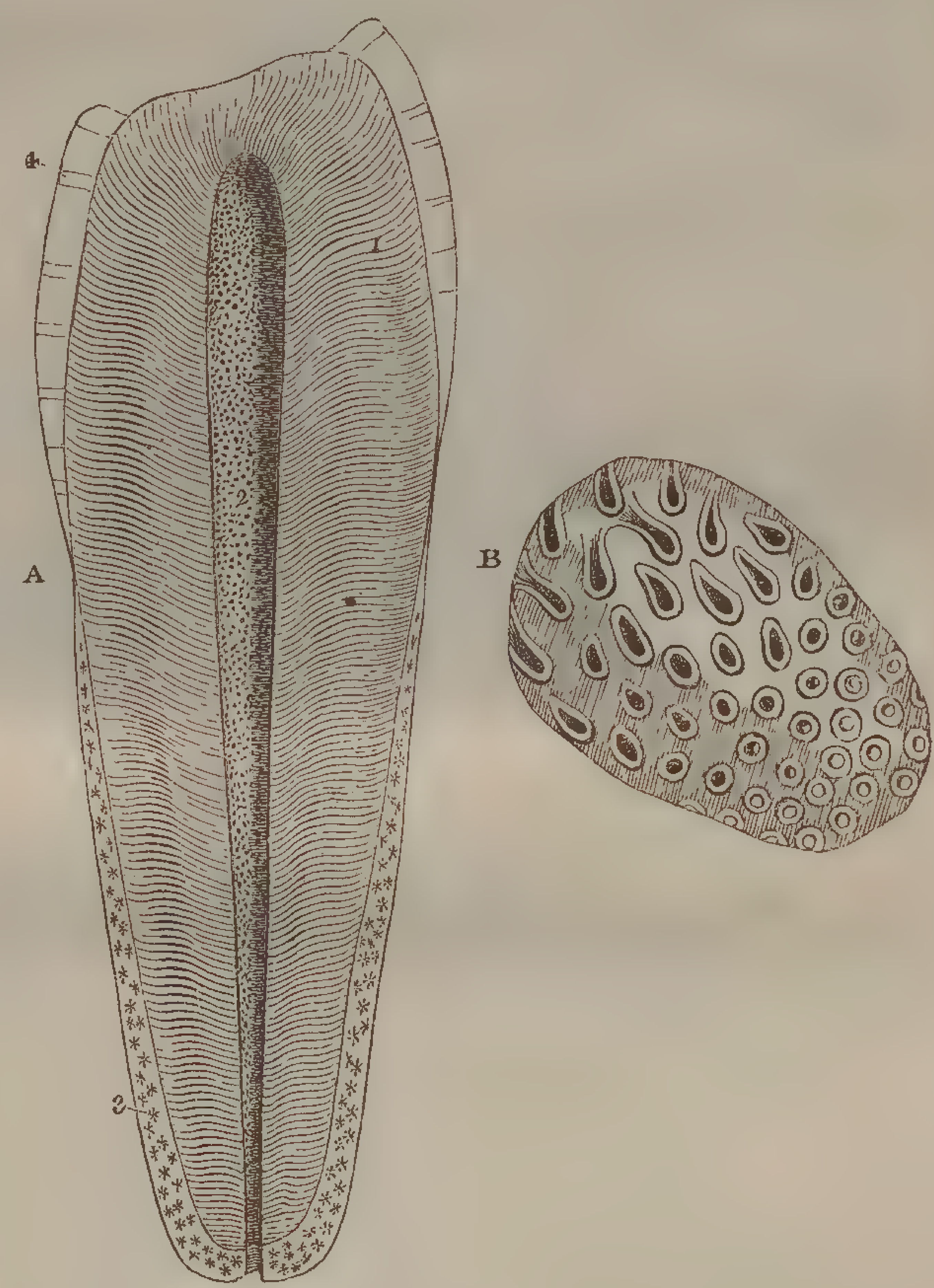
CHAPTER II.

OF GROWTH.

Structure and growth of the teeth, p. 394.

[Important additions have been made to our knowledge of the structure of the teeth by the labours of Professor Retzius of Stockholm.† Retzius discovered, nearly at the same time with Purkinje, that the teeth of man and many animals consist of three distinct substances:— 1, the enamel; 2, a tubular substance (the ivory) composing the greater part of the tooth; and 3, a cortical substance surrounding the fangs, which contains the peculiar osseous corpuscules (fig. I, A). He has, however, since ascertained not merely that the fibres of the ivory are tubular, a fact known, it appears, to Leeuwenhoeck;‡ but also that these tubuli in their course from the cavity of the pulp to the surface of the teeth give off numerous branches, and terminate in fine anastomosing fibres which communicate with minute cells or corpuscules, like those of the cortical layer of the tooth and bone.

*Fig. I.**



The following is the description given by Retzius of the tubes of the ivory in the human tooth. The tubes have a general radiate disposition around the cavity of the pulp, being directed perpendicularly to the surface of the tooth (fig. I, A, 1.) Their

* [Fig. I.— A. Section of a human molaris divided in the direction of the axis of its pulp cavity, magnified four diameters. 1. The ivory, showing the direction and larger curves of the dental tubes. 2. The cavity of the pulp, showing the openings of the dental tubes. 3. The cortical substance, surrounding the fang as high up as the border of the enamel. 4. The enamel. — B. A small portion of a section of a similar tooth made perpendicular to the course of the dental tubes, showing the openings of these tubes and their parietes distinct from the uniting substance. The tubes to the left hand cut obliquely. This, and all the succeeding figures illustrating the structure of the teeth, are copied from Retzius.]

† [Müller's Archiv. 1837, p. 486.]

‡ [Philos. Transact. 1678, and Contin. Epistol. Ludg. Bat. 1780.]

course is for the most part waving, each tube having three curves like the Greek letter (ζ). Besides these primary curves, the tubes, when examined with a higher magnifying power, are seen to present smaller secondary undulations (fig. II, A and B),

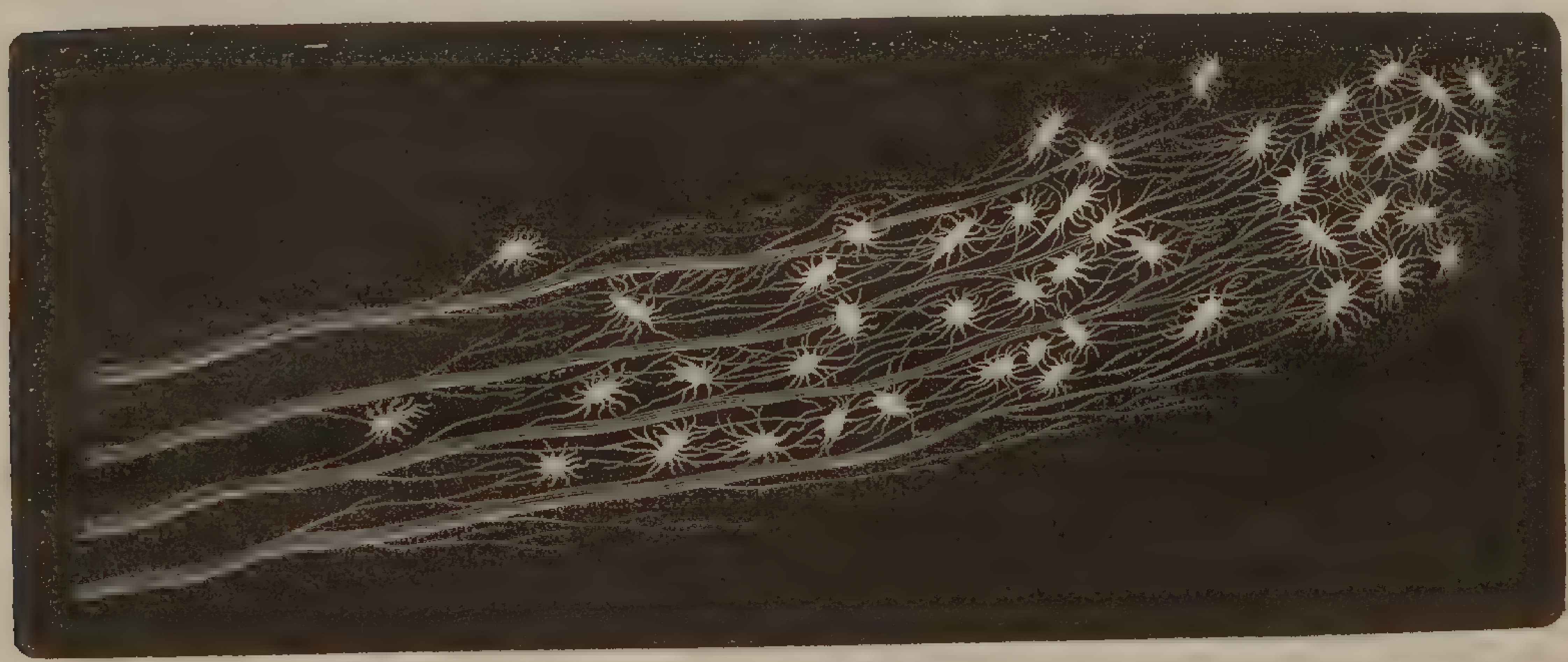
Fig. II.*

which are less perceptible in the deciduous than in the permanent teeth, and less marked at the external extremity of the tubes than in the middle of their course. The undulations are nearly parallel in the different tubes, and thus give rise to the appearance of concentric lines around the cavity of the pulp in a section of the ivory. The diameter of the tubes remains the same (namely, $\frac{1}{417}$ of a French line, or about $\frac{1}{385}$ of an English line,) from their commencement at the cavity of the pulp to the middle of the outer third of their course; it then diminishes rapidly, until the terminal branches cease to be visible, or terminate in small irregularly round cells. With a magnifying power of 300 to 500 diameters, it can be seen that the tubes are not simple, but branch by a dichotomous division (fig. II, A), and in their whole extent give off numerous side twigs, which again subdivide and occupy the spaces between the principal tubes (fig. II, B). These minute lateral branches are seen most readily in the deciduous teeth; those from different tubes appeared to Retzius not to anastomose, except, perhaps, by their finest extremities. The tubes have a more regular arrangement, their lateral branches are smaller, and the cells more minute and difficult to discover, in the human teeth than in those of any other animals. In many mammalia, as the horse, the cells or corpuscules are large and distinct (fig. III). The minute structure of the teeth is examined in sections made by means of the saw, and reduced to the necessary degree of thinness by files. Such laminæ, when as thin as writing paper, are not sufficiently transparent until moistened with water, or impregnated with turpentine, varnish, or oil; but, when completely permeated with these liquids, they become too transparent, and the ramifications of the tubes, particularly the more minute twigs, become invisible; the

* [Fig. II.—A. Innermost portion of the dental tubes from the incisor of a child two years of age, showing their dichotomous division. — B. External portion of the tubes, showing their ramifications.]

branches are seen best when the newly made section is first laid in either of the fluids above mentioned.

Fig. III.



When the wall of the cavity of the pulp of a tooth is regarded with a sufficiently high magnifying power, it is seen to be perforated by numerous small orifices, separated by narrow interspaces (fig. I, A, 1); these are the openings of the dental tubes. In sections also made at right angles to the course of the tubes their lumen can be seen, and they then appear as bright rings surrounding a spot, which according to the variation of the light is dark or light, or in part dark and in part light (fig. I, B). Some of the tubes are seen to be cut obliquely. The rings have a different aspect from the substance in which they are imbedded, and have sometimes a yellowish colour; hence, as well as from the observations of Professor Müller (see page 394), it is evident that the tubes have special parietes, and are not mere excavations in the substance of the ivory. Professor Retzius confirms the observation of Professor Müller, that the tubes contain an inorganic earthy matter in granular masses, which disappears under the action of dilute muriatic acid. The cells, and the small tubes which radiate from them, also contain earthy matter, as in bone (see page 380). They are naturally white and opaque; but, after maceration in dilute muriatic acid, become colourless and transparent.

Examining the ivory in different mammalia, reptiles, and fishes, Retzius met with many varieties of structure, the most important of which are those which show the great resemblance of ivory to bone. The cells or corpuscules are in many mammalia in greatest abundance at the superficies of the ivory; but in others they, together with the fine tubes which issue from them or terminate in them, and which are continuous with the branches of the larger dental tubes, occupy in greater part all the interspaces between the latter. These cells of the ivory contain calcareous matter, and are evidently analogous to the corpuscules discovered by Purkinje in bone, which also have fine anastomosing tubes radiating from them (see plate 1, fig. 13). The part of the ivory formed after the teeth have emerged from the gum, namely, the extremity of the fang, and that part which fills up the cavity of the pulp, has less regularity of structure than the ivory previously formed; the tubes are less parallel, the cells larger, and the anastomoses of the small tubes terminating in these more distinct; all which circumstances give this imperfectly formed ivory a great resemblance to true bone. But the ivory in the teeth of some animals presents characters which assimi-

* [Fig. III.—External portion of the dental tubes from the incisor of a full-grown horse, showing the numerous cells in which the dental tubes terminate.]

late it still more remarkably to the structure of bone. In the teeth of man and most mammalia, the ivory is formed regularly in successive layers on the surfaces of the pulp, which in the body of the tooth undergoes no other change than gradual diminution in size, and periodic movements which give rise to the undulations of the dental tubes. In other animals, however, as the sloth (Bradypus), walrus (Trichechus), pike (Esox), ling (Gadus molva), and wolf-fish (Anarrhichas lupus), the pulp, after forming the most external layer of ivory, consisting of closely set dental tubes perpendicular to the surface, divides into a number of processes, similar to, but more numerous than, those which form the fangs of the human molares ; and around each of these processes or branches of the pulp ivory is formed in layers. In many instances, as in the saw-fish (Pristis), ling, and wolf-fish, the numerous divisions of the pulp anastomose with each other like the medullary canals of bone. This form of ivory presents in many animals, particularly in the walrus, the most striking resemblance to bone; the divisions of the pulp are seen surrounded with concentric laminæ, which, like the layers of bone surrounding the medullary canals, contain rings of cells or corpuscules ; and these laminæ, again, are traversed by fine radiating tubes analogous to the radiating striæ in bone, which were supposed by Deutsch to be tubes (see page 378).

Retzius noticed, that in Gadus molva and Esox lucius there was a gradual transition of the bone, to which the teeth in these as in many other fishes are firmly anchylosed, into the substance of the ivory of the tooth ; and he observed that in the Gadus and Squalus Cornubicus the small remaining pulp cavity of the tooth was continuous with the medullary canals of the bone, while, on the other hand, the trunks of the large dental tubes which issued from the cavity of the pulp contained a red matter similar to the pulp. Mr. Owen,* who has confirmed the researches of Retzius, and has extended his observations particularly among the fossil teeth of different animals, points out in them also the great resemblance of the less perfectly organised ivory of the fish's tooth to bone, the ramification and anastomoses of the divided pulp, the concentric laminæ surrounding the pulp canals, and the smaller radiating tubes traversing these laminæ ; in the tooth of the extinct Acrodus, as well as the existing Lamna, he found that the pulp canals communicate directly with the large cells of the bone with which they are anchylosed.

Retzius shows that, in the sloth and in the pike, the dense layer on the surface of the tooth, which to the naked eye looks like enamel, is really formed of delicate and closely set tubes perpendicular to the surface, while the mass of ivory within this has a coarser structure. Mr. Owen finds the same structure in the teeth of the extinct Megatherium, in which, as in all existing Edentata, the enamel is absent. The external enamel-like layer in the teeth of many existing and extinct fishes also has been detected by Mr. Owen to be a fine layer of ivory, like the analogous part described by Retzius in the teeth of the sloth and pike.

The *cortical substance* or *cement* (fig. I, A, 3), which exists in very various quantity in most mammalia, and some reptiles and fishes, is in all cases characterized by the presence of the osseous cells or corpuscules, and the anastomosing calcigerous tubuli. But in many animals it is traversed by larger canals which communicate with the cavity of the pulp ; to which they probably transmit blood-vessels. It sometimes also contains large canals, which open upon the external surface. Both Retzius and Mr. Owen have seen direct communications between the fine branches of the tubes of the ivory and the tubes and cells of the cortical substance.

The *office of the system of dental tubes and cells* is supposed by Retzius to be the

* [See Report of the eighth meeting of the British Association.—Athenæum, September 1, 1838.]

distribution through the tooth of a nutritive or preservative fluid secreted by the surface of the pulp. The solid material of the tooth undergoes probably no change; but still M. Retzius supposes that the ivory and cortical substance may be the seat of a vital process, consisting in the interchange of material in the fluids of the tooth; this vital process being, he conceives, necessary to maintain in them that property by which they are enabled to suffer constant pressure without injury or wasting. The teeth would, therefore, appear to be not mere extravascular bodies foreign, as it were, to the organism, though formed by it; but structures belonging to the osseous tissue, though characterised by a peculiar arrangement of their parts, and a degree of organisation adapted to the purpose for which they are destined in the œconomy.

Fig. IV.*

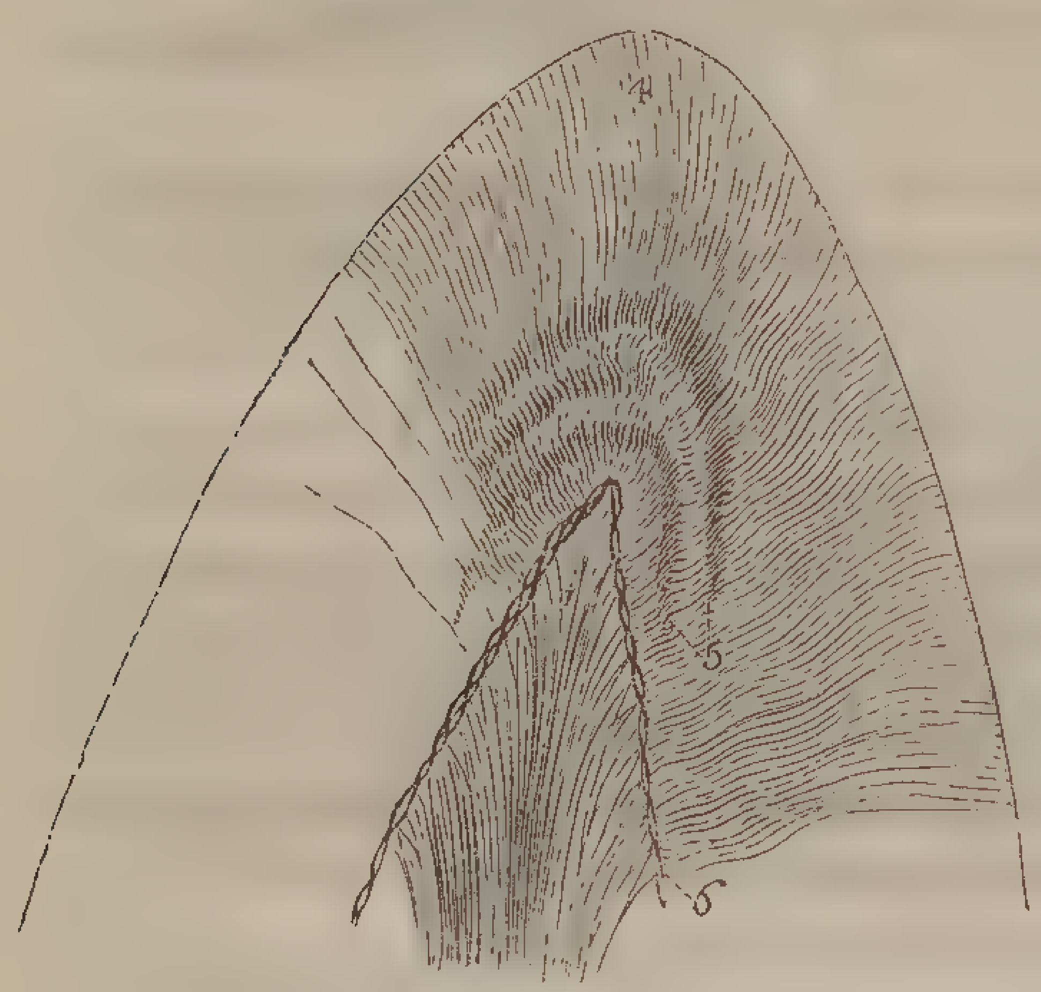
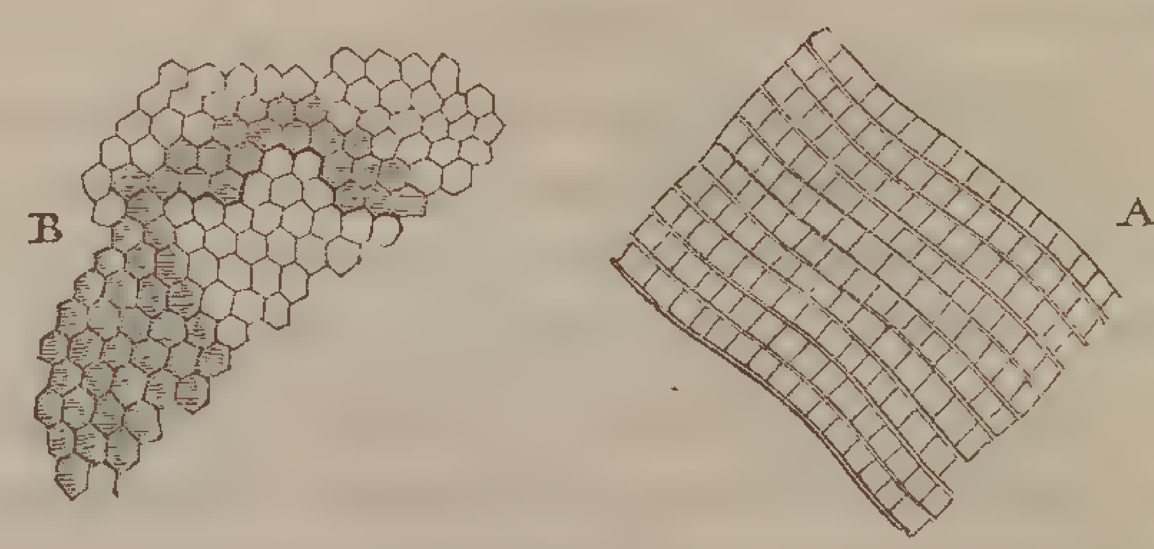


Fig. V.†



The *fibres of the enamel* (fig. IV, 4) are described by Professor Retzius to be six-sided prisms, about $\frac{1}{500}$ of a French line, or $\frac{1}{461}$ of an English line, in diameter. The surface of the fibres is marked with transverse striæ (fig. V, A), which Professor Retzius is inclined to ascribe to a thin organic sheath enclosing the inorganic prismatic fibres. Their hexagonal form is beautifully seen on the surface of the tooth by the aid of a magnifying power of 300 diameters (fig. V, B). In parts where the tooth had not been worn down, the external extremity of each fibre appeared to be rounded. The inner extremity rests on a delicate membrane interposed between the enamel and the ivory. This membrane was known to Berzelius. The surface of the ivory presents a number of small depressions, which receive the ends of the fibres of enamel (fig. IV, 6). In their course from the surface of the ivory to the external surface of the tooth, the fibres of the enamel follow a more direct or oblique line, according as they are nearer to the fang or to the crown of the tooth. In some teeth, and in some parts of the teeth particularly, they are variously curved, sometimes presenting parallel wavings (fig. IV, 5). In the crown of the human teeth, and in some parts of the teeth of mammalia, there are fibres near the superficies of the enamel, which are interposed as wedges between the other fibres, and do not reach the

* [Fig. IV.—Upper portion of a longitudinal section of an incompletely formed incisor taken from the follicle.—1. The ivory and dental tubes. 4. The enamel. 5. Parallel curves of the enamel, giving rise to the appearance of concentric lines when a lower magnifying power is used. 6. Small depressions and points on the surface of the ivory, upon which the fibres of the enamel rest.]

† [Fig. V.—A. Fibres of the enamel seen laterally with a magnifying power of 350 diameters, showing the transverse striæ upon them.—B. A portion of the surface of the enamel, showing the hexagonal ends of the fibres. A fissure is seen following the line of union of the fibres.]

surface of the ivory. The yet soft and pulp-like enamel on the last molar tooth of a calf was found by Professor Müller to consist wholly of acicular fibres acuminated at both extremities.

The *developement of the teeth* has been recently investigated by Mr. Goodsir,* who has succeeded in observing the process at an earlier stage than has hitherto been done, namely, before the formation of the dental sacs. Dentition commences, he says, by the formation of "the primitive dental groove, on the floor of which the rudiments of the pulps of the milk-teeth appear as globular or conical papillæ; septa afterwards pass from the outer to the inner side of the groove, between the papillæ, and thus each of the latter becomes situated in an open-mouthed follicle, which is the primitive condition of the future sac." The rudiments of the ten anterior permanent teeth appear as little depressions in the groove, internal to the mouths of the follicles of the milk-teeth. The papillæ of the milk-teeth now begin to be moulded into the form of pulps, and at the same time the mouths of the follicles become closed "by two or more laminæ, which agree in number, shape, and position with the cutting edges and tubercles of the future teeth." The opposite lips and walls of the groove above the follicles now unite, except in the situations of the ten depressions for the permanent teeth, and for a small extent posteriorly on each side, where a portion of the groove remains in its primitive condition. Here the papilla and follicle of the first large molar tooth appear, and, after the follicle closes over, the lips of the groove above it unite, but not the walls, so that a cavity is left in which the sacs of the two posterior permanent molars are formed. The first large grinder may, therefore, be considered a milk-tooth as to its mode of developement. Mr. Goodsir concludes from his researches that the human teeth originate from mucous membrane, that the permanent teeth have no connection with the deciduous set, and that the sacs and pulps must be referred to the class of organs denominated bulbs.]†

CHAPTER III.

OF REPRODUCTION.

Formation of Callus, p. 414.

THE whole process of the formation of callus has been recently investigated by M. Miescher,‡ and with considerable success. The following are the results at which he arrived.

When a bone is fractured, the surrounding soft parts—the periosteum, cellular tissue, and muscles,—are at first the principal seat of the inflammation; they swell, become thickened and glued together, forming a dense capsule around the fracture. On the inner surface of this capsule a semifluid exudation, which by degrees becomes solid and organised, is formed as the product of the inflammation. A similar substance is effused by the medullary tissue of the broken bones; this unites, and forms one mass with the exudation within the capsule; and the whole constitutes the "substantia intermedia" which envelopes the ends of the bone This "substantia intermedia"

* Report of the eighth meeting of the British Association for the Advancement of Science.—Athenæum, September 15, 1838.

† [Since the above was printed, it has been pointed out to the translator, that Mr. Goodsir has been anticipated in his interesting discovery by Arnold, who, according to Valentin, (Entwickelungs-geschichte des Menschen, p. 482,) has observed that the dental sacculi are formed by diverticula of the mucous membrane of the mouth being received into the groove of the jaws. The reference given for Arnold's observations is: the Salzb. Mediz. Chir. Zeit. 1831. s. 236.]

‡ De inflammatione Ossium eorumque Anatom. generali. Berol. 1836.

acquires a fibrous texture, and fills all the space between the bones; while the muscles, cellular tissue, and periosteum return to their former normal condition. The inflammation does not affect the bone so soon as it does the soft parts; it commences in it at some little distance from the fractured extremities, namely, at the part where the bone is still invested by periosteum, and at the same point in the interior. The bone likewise pours out a gelatinous exudation, in which vessels become developed, and which continues to grow; while, on the side by which it is connected with the bone, it becomes converted into cartilage and bone. This new mass, the proper callus, also occupies to a greater or less extent the medullary cavity. On the exterior its formation is continued towards the fractured extremities, till the exudations of the two portions of bone meet and unite. Thus is formed the primitive callus.

In the mean time the surface of the bone unites with the capsule formed by the soft parts and the primitive callus; the margins of the fracture again unite with the "substantia intermedia." A callus too is formed, and developes itself at the expense of the now ligamentous "substantia intermedia." Periosteum is formed anew on the external uneven surface of the callus.

The first appearance of the primitive callus is at that part of the bone where the periosteum is still in connection with the bone; it is effused as a half-fluid matter between the bone and periosteum; vessels appear in it as early as the fourth day. The callus, therefore, according to Miescher's investigations, always arises from the bone itself. When, in sections of united fractures, nuclei of bone were seen in the callus apparently unconnected with that part of the bone at which the production of callus commences, it was always found, on closer examination, that these nuclei were really connected with that part of the bone.

The further changes which the callus undergoes after the ends of the bone have united, consists in the restoration of the medullary cavity in its substance, and in the change of its form. The texture of the callus undergoes the same changes as the cartilage of bone in ossification. While it is cartilaginous, it contains the peculiar corpuscules of cartilage; when it ossifies, it assumes the cellular texture of bone.

Reproduction of bone subsequent to Necrosis, p. 427.

Miescher has shown Scarpa's opinion, that the old bone undergoes an expansion, to be not exactly correct. The enlargement of the external laminæ of the bone which retain their life in the internal necrosis, is effected by exudation.

BOOK THE FOURTH.

SECTION III.

Of Voice and Speech.

CHAPTER I.

OF THE GENERAL CONDITIONS FOR THE PRODUCTION OF SOUND.

Theory of the sounds produced by tongues.—See page 985.

The observation that sounds can be produced by the mere impulse of fluids upon each other, as exemplified in the Siren, or by a quick succession of impulses of a solid body, as when a piece of wood is struck by the teeth of wheels, has inclined many persons to the belief that sounds produced by vibrating tongues result from the impulses communicated to the air beyond by the current of air interrupted in its passage through the opening of the reed by each vibration of the tongue. This view is apparently confirmed by the circumstance that the sounds produced by striking tongues without the aid of a current of air are very feeble ; but, nevertheless, the theory is by no means proved, and there are several facts directly opposed to it. The elucidation of this question is of great importance with reference to the physiology of voice ; for on it depends whether we should regard the vocal cords or the air as the primary source of the voice.

M. W. Weber * found that a metal plate fixed in its frame might be thrown into strong vibrations by a stroke of a violin bow ; but that a full loud tone, like that produced by a current of air passing through the frame, could not be thus obtained. The tongue of a jew's-harp, however, I find, yields, when held between the teeth, the same sound, whether it be struck or made to vibrate by drawing air into the mouth. [This is most probably owing to the air within the mouth in each case reciprocating the sonorous vibrations of the tongue of the jew's-harp, and thus rendering them louder, on the principle pointed out by Mr. Wheatstone.—(See page 1021, note †)]. The above fact, adduced by M. Weber, does not appear to me to be a decisive proof of the theory in question ; and in the case of the membranous tongues, at all events, the interruption of the current of air, and the impulses thus produced, seem to me to have only a subordinate influence in the production of the sound, rendering it stronger and fuller rather than generating it.

The following are my reasons for thinking it improbable that the sounds of vibrating membranous tongues are produced by the impulses of the air.

1. That explanation of the sounds is unnecessary, since the vibrations of the tongues themselves are alone sufficient to cause those sounds. The difference in strength of the sounds produced by striking membranous tongues, and of those caused by the action of a current of air, is sufficiently explicable on the supposition that the momentary stroke is inadequate to maintain the vibration. There is certainly also a difference in timbre between the two sounds ; but the same is observed in the case of other instruments where the impulse is not continued ; the sound of a stretched string, for example, has a different tone when produced by a stroke of the fingers merely, from that which characterises it when the string is kept in vibration by the continued action of the violin bow. Some membranes, indeed, yield no sound when struck, though they give out loud tones when thrown into vibration by a current of air ; such is the case, namely, with the lips and sphincter ani. But a certain number of vibrations within a given time are necessary for the production of any sound, and the fact just stated merely shows that the regular succession of vibrations can be produced in such lax membranes only when they are at the same time kept somewhat extended by a current of air.

2. The sounds which I have found to be produced by blowing through a small tube upon a delicate metallic, or, still better, a membranous tongue, destitute of frame, cannot be accounted for on the principle of the interruption of the current of air alone ; and, nevertheless, they have exactly the same timbre as those emitted by metallic or membranous tongues fixed in a frame. It might, indeed, be urged, that even here the current of air is in some measure interrupted by the returning vibration of the tongue. But the current of air can in this case scarcely be said to be interrupted, since the air escapes in other directions in proportion as the returning tongue impedes its direct progress. The current of air must rather be regarded as acting, like the violin bow on a string, as a continuous excitant of the vibrations.

3. Moreover, it is not necessary that the opening in the frame should be periodically closed by the vibrating tongue, at least not in the case of the membranous tongues. When the cleft between them is a line in breadth, membranous tongues often yield clear tones of the ordinary timbre.

* Poggendorf's Annal. t. xvi. p. 421.

4. If the sounds of vibrating tongues are really due to the periodic interruption of the current of air, they ought to rise in pitch in direct ratio with the frequency of the interruptions; which is by no means proved. When a tongue is so placed in its frame, that in vibrating it passes quite through the opening, it must interrupt the current of air twice in each vibration, namely, when forced out of the frame and in its return; when, on the contrary, a tongue does not pass entirely through the opening, but only returns to a level with it, and is then forced out again, it only interrupts the current of air once: in the former case, therefore, the sound ought, *cæteris paribus*, to be an octave higher, which is not the case. To this it might be answered, that when the tongue does not pass entirely through the opening, it merely performs half-arcs of vibration, being prevented from completing them either by the frame itself or by the current of air, and that consequently it would vibrate twice as fast as when it traverses the whole arc of vibration, passing and repassing the opening in the frame; but on investigating the mode of action of membranous tongues, difficulties again present themselves. A membranous tongue stretched across the lower extremity of a tube, and having opposed to it a solid plate of pasteboard or wood, yields the same tone whether the solid plate be on the same level with it, or be pressed inwards towards the cavity of the tube. In either case the tongue performs entire arcs of vibration. But if the solid plate be so placed as to lie on a level in front of the tongue, the sound produced by blowing through the tube is, I find, much lower in pitch, namely, as much as the interval from C to the lower F. The arcs of vibration would, nevertheless, here be the same. The difference depends on the different manner in which the current of air acts on the tongue, and on the different degree of resistance which the continuous current of air offers to the return of the vibrating tongue.

These reasons render it probable that the primary source of the sound produced by tongues is not the impulses of the interrupted current of air, but the vibrations of the tongue itself, and that the impulses imparted to the air merely increase the strength of the sound. In studying the vibrations of bodies rendered elastic by tension, the strings of stringed instruments and similar bodies have been kept too exclusively in view; such bodies when much shortened, and at the same time relaxed, lose almost all capability of yielding sonorous vibrations; but other substances, as caoutchouc and elastic animal tissue in the moist state, when much relaxed, have still sufficient elasticity to vibrate with regularity, and yield sounds.

The laws regulating the variation of the notes produced by metallic tongues are generally the same as those for metallic rods, and the membranous tongues in the variation of their notes follow generally the same laws as the stretched strings; but still the metallic and membranous tongues differ in their action from the rods and strings in the circumstance of the pitch of their notes being influenced by the intensity of the action of the cause exciting their vibrations, namely the air (see pages 989 and 991). This difference is not, however, absolute; for a string yields a somewhat lower note when struck with the finger more strongly; and Duhamel * has shown that deeper tones may be obtained by carrying the bow across the string, so as to modify the friction and its rapidity.† This is, however, a contrary effect to that of increased force of the blast on membranous tongues, the notes of which are raised several semitones by blowing with increased force. By blowing with gradually increased force into a small closed pipe two inches in length also, I can produce a gradual sharpening of the sounds from C to F without intervals; a result very different from that of blowing with increased force into longer pipes, where notes with determinate intervals are produced from the developement of nodal points. The various modifications produced in the pitch of the notes yielded by a vibrating tongue by varying its relation to the frame,

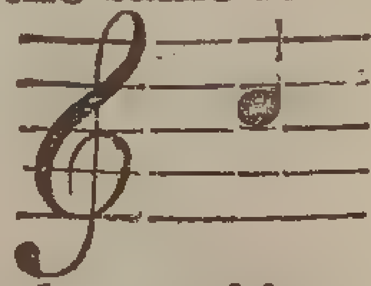
* L'Institut, No. 186. † Compare Pelisow, in Poggendorf's Ann. xix. p. 251.

by directing a current of air upon it when destitute of frame, by altering the form of the mouth in blowing, &c. are, without doubt, owing to the manner in which the air is made to act upon the tongue.

Influence of a pipe conjoined with vibrating membranous tongues on the pitch of the sounds given out by the latter, p. 994.

In my first experiments to ascertain this point, I combined with the pipe of a clarionet reeds constructed with a single tongue of caoutchouc and of various pitch. The result was, that the fundamental note of the tongue was lowered.

I subsequently obtained from an organ-builder five cylindrical pipes of pasteboard one inch in diameter, and of different length, which could be fitted together. The first, with which the reed was connected, served as the "foot" for the others; and it was of such dimensions that the fundamental note of its column of air was C, . A second pipe was of such length that, combined with the first piece or foot, it gave as the fundamental note the lower octave of C, . The third, combined with the foot-piece, gave out the "fifth" of the last C, namely G, . The fourth pipe with the foot-piece had, as fundamental note, the second lower octave of the first C, namely . The fifth was of such length that, with the preceding pipe and the foot-pipe, it yielded the third octave below the first C, namely . These were the notes which the pipes were capable of yielding without the reed. I constructed several reeds of different kinds. Three were of the forms described at page 989: in these the direction of the cleft through which the air passed was perpendicular to the axis of the reed or mouthpiece. In a fourth, two membranous tongues were stretched over a lateral opening in a reed; so that the cleft between them was parallel to the axis of the reed.

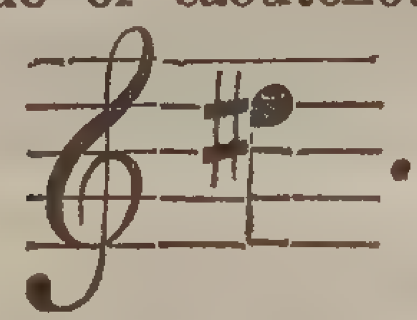
The results of the combination of these reeds with the pipes of different length were very much at variance with each other. Generally the fundamental note of the reed was lowered, sometimes less than a semitone, sometimes from a semitone to an entire tone. No definite law seemed to prevail. When the next pipe to the foot-pipe was added, the note was sometimes lowered one or more semitones, or it was raised to its original pitch; this again seemed to be regulated by no constant law. On account of the difficulty of arriving at a satisfactory result in these experiments, I was careful to adopt as data those sounds only which were produced by the weakest blast. In some instances, even with the addition of the second pipe, by which the fundamental note of the column of air was lowered an octave, the pitch of the sound yielded by the reed was not perceptibly depressed. In this case the addition of the third pipe sometimes lowered the note a semitone or a tone; in other instances, the sound emitted remained at the same pitch even when the second, third, and other pipes were added, as when merely the first pipe was combined with the reed. When the pitch was lowered by the second pipe, it was generally raised, when another pipe was added, to such an extent that the sound produced was identical with or near to the fundamental note of the reed combined with the foot-pipe alone; and then the pitch was not affected by the addition of the other pipes, or was merely lowered to a very slight extent by the last pipe. As the basis of comparison between the sounds of the reed alone, and those which the pipes alone were capable of yielding, a special flute-pipe with the same fundamental note as that of the foot-piece with the next pipe, namely C,  was used. The note yielded by the reed alone, and those produced by the combination of the reed with the different pipes, were always determined by means of a well-tuned pianoforte.

The results of experiments frequently repeated with this apparatus, reeds of various pitch being used, were remarkably at variance with each other. The causes of this discrepancy in the results were the different relation which the fundamental note of the reed bore to that of the pipe, and the different degrees of force with which it was necessary to blow to elicit the notes, and which immediately modified their pitch. Thus much, however, was proved with certainty; that a short tube, of which the fundamental note was much higher than that of the reed separately, when combined with it, the prefixed tube or "portevent" being short, does not raise the note of the reed nearer to its own pitch, but usually lowers it somewhat; and that an increase of the length of the pipe when the note of the reed is already lowered, at length restores it nearly to its original pitch. In these experiments the air was blown upon the membranous tongue from the mouth, in which the mouth-piece was held; the air then necessarily passed through the pipes after acting on the tongue; it is very interesting that when a current of air is directed upon the surface of the membranous tongue from a small tube, so that no current of air traverses the lower pipes, these pipes still had some influence on the note yielded by the tongue.

My experiments thus far afforded me only an imperfect idea of the modification which the sound of a membranous tongue experiences from its combination with a pipe. Pipes of certain dimensions may have little effect on the sounds; while pipes of different proportionate length might have a greater influence. This is indeed a principal reason wherefore, in the experiments to which I have alluded above, the pipes had sometimes only a slight influence on the note given out by the reed; while, when the reed had a different pitch, they produced great changes in it. With the view of attaining to the knowledge of the law regulating these varieties, I have employed tubes one inch in diameter, and so constructed that they could, by the addition of successive small portions, be lengthened from an inconsiderable length to that of four feet; so that the influence of the pipe on the pitch of the reed could be ascertained at all lengths. From the former experiments, in which I used pipes of the same length with tongues of different pitch, it resulted that the influence of the pipe was not uniformly proportionate to its length. The present series of experiments (of which some examples follow) proved still more clearly that the modifications of the sound depend on the relation existing between the fundamental note of the tongue and that of the pipe. [The results are stated more fully at page 992.] The pipes I used being one inch in diameter, their fundamental note would be C , when their length is eleven inches four lines (French measure). The fundamental notes of the pipes of different length in the following experiments may therefore be easily calculated.

Experiment I.—The fundamental note of the reed formed with a one-lipped tongue of caoutchouc (the tube which conveyed the wind to the tongue being three inches in length) was C♯, .

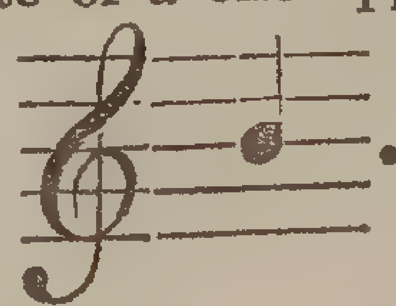
Length of pipe.	*Note produced.*	*Remarks.*
0 inches.	C♯	
6	C	The note becomes lower.
6 " 9 lines.	B	
7 " 6 "	A♯	
9	A	
9 " 6 "	A—C♯	Sudden rise from A to C♯, which is the note produced until the pipe attains nearly the length of 18 inches.
18	C	Flattening of the note.
20	C♯	
22 " 6 "	A—C♯	Sudden rise; C♯ constant until the pipe is nearly 30 inches in length.
30	C	Fall of the note.
31	B—C♯	Sudden rise.
36	C♯	
40	C	Fall of the note.
45	B—C♯	Sudden rise.
48	C♯	

Experiment II.—The fundamental note of the reed constructed with a one-lipped tongue of caoutchouc, sounded directly by the mouth without prefixed tube, was D♯, .

Length of pipe.	*Note produced.*	*Remarks.*
0 inches.	D♯	
3	D	Lower notes are produced.
4 " 6 lines.	C♯	
5	C	
6 " 6 "	B	
7	A♯	
8	A	
9 " 6 "	G♯	
10	G♯—C♯	Sudden rise.
11	C♯	Lower notes produced.
13	C	
17 " 6 "	B	
20 " 6 "	A♯	
22	A	
23 " 6 "	G♯	
26 " 6 "	G♯—B	Successively—the sound rising.
31	A♯	
35	A	The sound falls in pitch.
39	G♯	
41	G♯—B	In succession.
45	A♯	The sound falls in pitch.

Experiment III.—One-lipped tongue without prefixed tube.

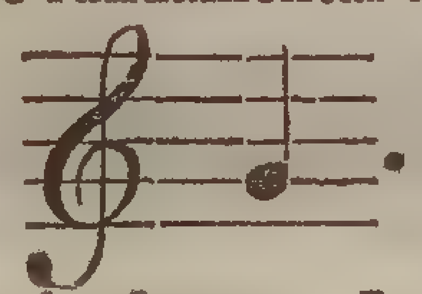
Length of pipe.	*Note produced.*	*Remarks.*
3 inches. 6 lines.	F	The F on the upper line of the treble clef, 
4 ,, ,,	E	The sound falls.
4 ,, 6 ,,	D♯	
5	D	
6	C♯	
6 ,, 8 ,,	C	
7 ,, 6 ,,	B	
8	A♯	
8 ,, 6 ,,	A	
9	G♯	
9 ,, 6 ,,	G	
10	F♯	The F of the lower octave.
11 ,, 3 ,,	F	
12	E	
12 ,, 6 ,,	D♯	
14 ,, ,,	D	
17 ,, 6 ,,	D♯	
19	D♯ & C	In succession.—Rise to the same note as when the length of the pipe was 6 inches 8 lines.
20 ,, 3 ,,	B	The sound falls in pitch.
21	A♯	
22 ,, 6 ,,	A	
24	G♯	
25	G	
29 ,, 9 ,,	F♯	The F of the lower octave.
33	F	
34 ,, 3 ,,	E	
35 ,, 6 ,,	D♯	
38 ,, 6 ,,	D♯ & C	In succession.—Rise.
40	D♯	The sound falls in pitch.
42	D	
42 ,, 9 ,,	C♯	
43 ,, 4 ,,	C	
44 ,, 4 ,,	B	
44 ,, 6 ,,	A♯	
45	A	
46	G♯	

Experiment IV.—Fundamental note of a one-lipped tongue, (sounded directly by the mouth without prefixed tube,) B, 

Length of pipe.	*Note produced.*	*Remarks.*
0 inches.	B	
1 ,, 2 lines.	A♯	Lower notes produced.
2	A	
3	G♯	
7 ,, 6 ,,	G	
9	F♯	
10	F	
13	E	
17	D♯	
22 ,, 4 ,,	A♯+	Sudden rise.
23	G	Lower note again produced.
25 ,, 6 ,,	F♯	
27 ,, 6 ,,	F	
32	E	
39 ,, 6 ,,	D♯	
40	G	Sudden rise.
42 ,, 3 ,,	F♯	Lower notes again produced.
45	F	

Experiment V. — Fundamental note of the one-lipped caoutchouc tongue sounded from the mouth without prefixed tube, E, .

Length of pipe.	*Note produced.*	*Remarks.*
3 inches.	D♯	Lower notes produced.
3 ,, 9 lines.	D	
4 ,, 9 ,,	C♯	
5 ,, 6 ,,	C	
6 ,, 2 ,,	B	
7 ,, 4 ,,	A♯	
10	A	
13 ,, 6 ,,	F	Sudden rise.
15	D	Lower notes again produced.
15 ,, 8 ,,	C♯	
17 ,, 6 ,,	C	
20	B	
24	A	
28	D♯	Sudden rise.
29 ,, 6 ,,	D	Fall of the notes.
30	C	
30 ,, 6 ,,	B	
34	A♯	
35	A	
41 ,, 6 ,,	D♯—F	Sudden rise.
42	C	
43	B	

Experiment VI.—The fundamental note of a one-lipped caoutchouc tongue with a pipe of 5 inches was G, . The border of the tongue rests in some degree on the plate of wood or the frame. Lower notes are produced as the pipe is lengthened until it is 21 inches long, when there is a sudden rise to the original pitch; the pipe being elongated still further, lower notes are again produced until the length of the pipe is 42 inches, when there is again a rise of the notes to the original pitch; after which point elongation of the pipe produces a renewed fall of the notes.

These experiments were frequently repeated, and constantly afforded similar results.

CHAPTER II.

OF THE ORGAN OF VOICE IN MAN AND ANIMALS.

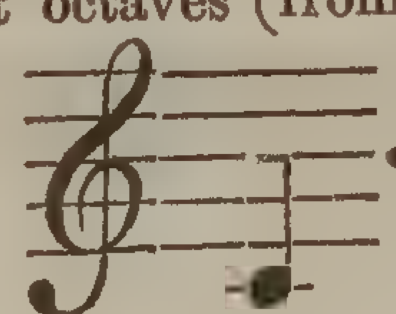
Effect of varying the tension of the vocal cords on the notes they yield, page 1011.

Frequently a larynx is found quite incapable of use in these experiments, on account of its tendency to the production of shrieking harmonic tones by the opposite points of the lips of the glottis coming into contact with each other in their vibration. Generally the male larynx is preferable by reason of the greater length of its vocal cords. The experiments must, however, be frequently repeated before a case will occur where the shrieking harmonic notes can be avoided. I give here the results of several experiments, in which the separated organs of voice acted most favourably.

A difficulty in these experiments lies in the circumstance that the vocal ligaments cannot be extended in the direction of their length by means of determinate weights, without other parts offering some resistance to the extending force. When the extension is exerted from the thyroid cartilage, the elastic tissue between this cartilage and the cricoid will diminish the effect of the tension; this elastic membrane may be divided, and still the articulation between the two cartilages will exert a similar influence; this articulate connection also may be divided, and even then the sounds produced by great degrees of tension will be lower in pitch than they ought to be according to the law of strings and membranous tongues, if the harmonic tones be not produced. In the following experiments the extension was made in somewhat different directions; in some in the exact direction of the vocal cords, in others in a direction a little behind or in front of this line, with the view of ascertaining the extent to which the results might thus be varied. The fundamental note was, of course, somewhat changed according to the direction in which the extending force acted.

Another difficulty arises from the impossibility of always blowing with exactly the same degree of force; the sounds produced being higher in pitch in proportion to the strength of the blast. It is best, however, to take as the basis of comparison such sounds only as are produced by the most feeble blast, or the fundamental notes of the vocal cords. The mode in which the larynx was fixed, and the weights attached to it, is described at page 1008.

	Degree of tension as measured by weights.	4 *Loth.*	16 *Loth.*	64 *Loth.*
Notes produced.	*Experiment* 1	C^1	A^1	$G^2\sharp$
	" 2	$C^1\sharp$	B^1	$A^2\sharp$—A^2
	" 3	$G^1\sharp$	$C^2\sharp$	C^3
	" 4	A^1	D^2	C^3
	" 5	$A\sharp$	$F^1\sharp$	G^2
	" 6	$A\sharp$	$G^1\sharp$	G^2
	" 7	D^1	C^2	A^2
	" 8	$D^1\sharp$	B^1	A^2
	" 9	G	G^1	G^2 (Both octaves imperfect.)

[The notes of the different octaves (from C to C) are distinguished in the above table by cyphers. The C^1 is . The notes of the octave below this C have no cypher.]

The notes were in each experiment ascertained by means of a well-tuned pianoforte.

Compass of the notes produced by various degrees of tension of the vocal cords, p. 1012.

The mode of performing the experiment when the extension is made by depressing the thyroid cartilage in the manner of a lever is as follows:—The arytenoid cartilages being fixed, as before, upon a pin, and bound together, so that the glottis remains open only to the extent of the vocal cords themselves, they are tied to the narrow board to which the larynx is fixed. The board is placed perpendicularly; a thread is attached to the angle of the thyroid cartilage immediately above the anterior extremity of the vocal cords, and is allowed to hang perpendicularly suspending a small scale with weights. As the amount of the weight in the scale is increased, the thyroid cartilage is depressed towards the cricoid, and the space occupied by the crico-thyroid membrane or ligament is narrowed, while the vocal cords are in the same degree stretched. We thus imitate the action of the crico-thyroid muscles. Those notes only were adopted as the basis of comparison which were produced by the most feeble blast. On account of the influence of the force of the blast on the pitch of the notes, it is impossible to determine quite accurately the note produced by a certain extending force; but I feel confident that the errors arising from this source cannot be so much as a semitone, since the lowest note produced by a given tension was always adopted. On the whole, such errors would balance each other; and indeed, the want of purity in the individual notes produced by the given weights did not seem great to the ear of a singer, who determined the pitch of each note by a pianoforte. The extraordinary height to which the notes were raised by tension of the cords, was the more remarkable from the larynx being that of a male subject.

Experiment 1.

Weights in loths.	*Notes produced.*
½	A♯,
1	B
1½	C
2	C♯
2½	D
$2\frac{8}{10}$	D♯
3	E
3½	F
4	F♯
4½	G
5	G♯
5½	A
6	A^1♯
6½	B^1
7	B^1—C^1
7½	C^1
8	C^1♯
8½	D^1
$9\frac{7}{10}$	D^1♯
$10\frac{7}{10}$	E^1
$11\frac{7}{10}$	F^1
13	F^1♯
15	G^1
17	G^1♯
19	A^1
22	A^2♯
25	B^2
28	C^2
31	C^2♯
35	D^2
37	D^2♯

No further note produced.

Experiment 2.

Weights in loths.	*Notes produced.*
½	B,
1	C
1½	C♯
2	D
2½	D♯
3	E
3½	F
4	F♯
4½	G
5	G♯
5½	A
6	A♯
6½	B^1
7½	C^1
$8\frac{3}{10}$	C^1♯
9	D^1
10	D^1♯
11	E^1
12	F^1
13	F^1♯
15	G^1
17½	G^1♯
18	A^1
20	A^1♯
22	B^2
26	C^2
29	C^2♯
32	D^2
37	D^2♯

No further note produced.

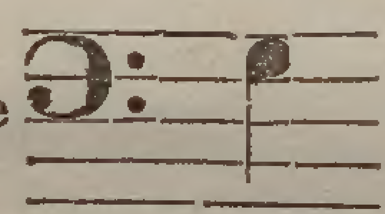
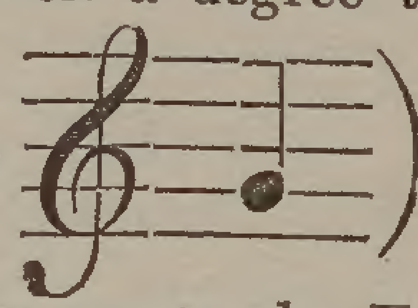
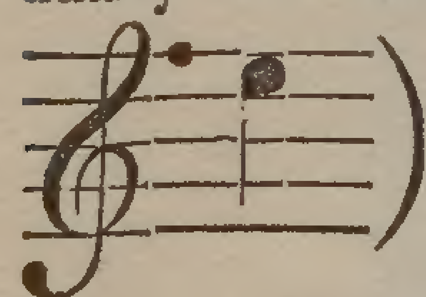
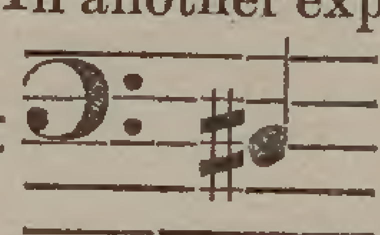
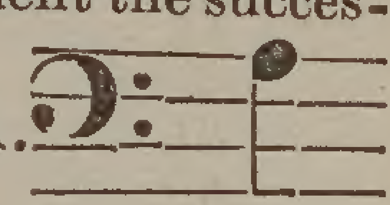
After the completion of the first experiment, the vocal cords had only so far suffered, that with an extending force of half a loth they yielded the note B in place of A♯.

Bass notes produced by pressing the thyroid towards the arytenoid cartilages, page 1012.

For the performance of these experiments, as described at page 1012, the presence of several persons is always necessary: one blows through the tube fixed to the larynx; another puts the weights upon the scale; and a third ascertains the value of the sounds produced by means of a pianoforte. In the experiment which I shall give here as an example, the sound from which we started was D♯, ; the force applied to produce the relaxation of the cords being $\frac{3}{10}$ths of a loth. In proportion as the relaxation of the cords was increased, the sounds fell in pitch as follows:

Notes produced—D♯, D, C♯, C, B, A,♯, A,, E,, and G,♯, E,, D,♯ D,, C,♯, B.
Weight in loths— $\frac{3}{10}$, $\frac{1}{2}$, 1, $1\frac{3}{10}$, $1\frac{4}{10}$, $1\frac{1}{2}$, $1\frac{7}{10}$, $2\frac{2}{10}$, $2\frac{4}{10}$, $2\frac{6}{10}$, $2\frac{8}{10}$, $3\frac{5}{10}$, $3\frac{8}{10}$.

Influence of the force of the blast on the pitch of the sounds; the tension of the vocal cords remaining the same, page 1014.

By blowing with gradually increased force while the weight by which the cords are extended remains the same, the sounds may be raised the extent of a "fifth" or more; the intervening semitones succeeding each other with facility. If, for example, G of the first octave of the bass on the piano forte  was the fundamental note of the vocal cords produced by the feeblest possible blast, by a successive increase of the force of the current of air G, G♯, A, A♯, B, C, C♯, were obtained. If the tension of the vocal cords was now increased to such a degree that with the feeblest blast they yielded the octave of the former G (or ), by blowing with gradually increased force, the successive semitones up to the E above the last G (or ) were produced in considerable purity. In another experiment the successive semitones were produced from D♯  to A. 

This rise in pitch, effected by blowing with increasing force, was observed by Liscovius; Ferrein* also was aware of it, but estimated it too low, namely, at a semitone or tone.

The sounds obtained from dry tongues of caoutchouc also can be raised in pitch, though only the extent of a few semitones, by increasing the force of the blast; while from moist bands of arterial tissue, like the true vocal cords, a succession of semitones to the extent of a "fifth" above the fundamental note can be obtained by blowing with increasing force.

From these experiments it results that one and the same note (x) can be produced in the human larynx in two different ways; 1st, by a gentle current of air, when the vocal cords must have such length and tension (y) that their fundamental note is x;

* Mém. de l'Acad. de Paris, 1741, p. 431.

and, secondly, by a more forcible current, when the length and tension of the cords is such that their fundamental note would belong to the octave below. The two sounds thus produced, though the same in pitch, are very different in quality. The first is much fuller in tone, the latter is harsh and shrieking, and has less fulness of tone, the further distant the fundamental note which the vocal cords would give with a feeble blast is from the note x obtained by blowing thus forcibly. Even when the maximum of tension is attained at which the vocal cords will yield sounds to a feeble blast,—when the highest note which can be produced by mere tension of the cords is attained,—the sounds can still be raised a few tones, though with a shrieking character, by blowing more forcibly. We can experience this, indeed, in our own person; and we thus learn how much experiments on the larynx removed from the dead body tend to elucidate the phenomena of voice during life, and how nearly the latter can thus be imitated.