

On the structure and physiology of the retina / by Max Schultze.

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TRANSLATION.

On the STRUCTURE and PHYSIOLOGY of the RETINA.
By Professor MAX SCHULTZE.

THE paper of which we here give an abstract has just appeared in the last number of the author's 'Archiv f. Mikroskop. Anatomie,' in which it occupies more than 100 pages, and is illustrated with eight quarto plates. It is undoubtedly one of the most interesting and important contributions to our knowledge of the very difficult structure of which it treats that has ever appeared, and it may be taken as giving an almost exhaustive account of all that is known on the subject, together with much, more especially in the physiological part of the subject, altogether new; and we deeply regret that our space prevents our giving a more lengthy notice of its contents, or, what would have been very desirable, a complete translation of it.

Bd II

In his general account of the structure of the retina we do not perceive that Professor Schultze differs very materially from most later writers on the subject. What he says respecting it may, however, be very briefly stated as follows:

The retina in man is composed of a fibrous or trabecular framework, composed of connective tissue, and which serves as a support to the nervous or sentient elements. The fibrous framework consists of an *outer* and an *inner membrana limitans*, connected together by a network of fibres, the principal of which, passing from one limiting membrane to the other, constitute the "radial fibres of Müller." These are connected by irregular lateral fibres, so that the whole constitutes, speaking generally, a sort of wide trabecular network; but at two special levels in the retina the fibrous tissue forms a very close, almost membraniform plexus, the

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outer and thinner of which corresponds with the so-termed "intergranular layer," and the inner in the same manner corresponds with the "molecular layer" or outer part of the "layer of grey substance." The *membrana limitans externa* in the fully developed organ does not constitute a continuous expansion, but is perforated with numerous closely placed openings, like the shelf of a bottle-rack. The *membrana limitans interna*, properly speaking, is also not a continuous membrane, but a reticulated tissue composed of the expanded ends of the radial trabeculæ or "fibres of Müller." This fibrous framework supports the nervous part of the retina, which may be subdivided into six, or more properly, perhaps, seven distinct layers. These layers, proceeding from without inwards, are—1. The bacillary layer, composed of "rods" and "cones," placed vertically on the periphery, and each lodged by its inner extremity in one of the openings in the outer limitary membrane. 2. The "outer granule-layer," composed for the most part of granular nucleated cells, connected with either the "rods" or "cones," and traversed by the filaments proceeding from those bodies. 3. The "intergranular layer," which is constituted, as before remarked, in part of a fine, fibrous, trabecular network, intermixed with which is a still finer plexus of very delicate nerve-fibres, for the most part, as it would seem, continuous with the terminal fibrillæ of the cone-filaments, and perhaps also in part with the terminations of the rod-filaments, although this has not been as yet clearly made out. 4. The inner granule-layer, containing for the most part bipolar ganglion-cells and abundance of fine nerve-filaments. 5. The "molecular layer," which is of considerable thickness, and, like the "intergranular layer," apparently composed of an intricate interlacement of very delicate nerve-filaments and the fine trabecular network before mentioned. 6. The "ganglionic layer," constituted chiefly of large multipolar nerve-cells, each of which on its inner aspect appears to be connected with a fibrilla of the optic nerve, and on its outer to give off several processes which break up into the delicate fibrils contained in the molecular layer. 7. The layer of "optic nerve-fibres," which in most animals appear to have no sheath, but to represent axial filaments.

The author's researches have been directed more especially to the distinction between the "rods" and "cones." But his attention has been turned, not so much to their morphological characters, with respect to which little now remains to be said, as to their relations to the other retinal elements, so that he might be able, if possible, to obtain some insight into their physiological differences. That such differences must

exist cannot be doubted by any one who regards the unequal distribution of the two elements in different parts of the human retina, and remembers that in the most sensitive part of it, as is well known, "cones" only exist, whilst in every other part the "rods" far exceed the "cones" in number. But these conditions have hitherto remained unexplained, as has also the remarkable fact that in the retina of many animals the "rods" alone are found, and in others only "cones." In the prosecution of his object, therefore, M. Schultze has found it necessary to examine, not only the human retina in its various regions, and particularly in the *macula lutea* and *fovea centralis*, but also to investigate all the varieties of structure exhibited in other animals. And in order to leave no means untried for arriving at a satisfactory elucidation of the subject, he has further closely studied the development of the retina, and particularly that of the bacillary layer.

The first section of the paper is devoted to the consideration mainly of the bacillary layer in the human subject, whose general structure is described much in the usual terms. The observations were made upon the recent human retina prepared with dilute osmic acid, and the beautiful illustrative figures are stated to have been taken from nature. They are excellently done, and doubtless accurately represent the structure as thus prepared. Retinas hardened by immersion in solutions of osmic acid containing $\frac{1}{5}$ — $\frac{1}{10}$ per cent. are readily split up by means of needles into their laminæ parallel with the radial fibres; and these products of natural fissure are clearly, the author thinks, preferable to thin sections. The principal points to which we shall refer, contained in this section, are:—(1) The fine longitudinal striation observable in the "cones" and "cone-filaments." (2) That the space between the "cone-filaments," as they cross the outer granule-layer, is entirely occupied by small, closely crowded cells, all of which are connected by finer or coarser filaments with the "rods." These cells may be regarded, with H. Müller, as bipolar ganglion-cells. (3) The distinctive characteristics of "cone-filaments," which are much thicker than those of the "rods," are then detailed, and the differences between them and the fibrous radial trabeculæ pointed out.

The relations of the "rods" and "cones," and the disposition of their filaments in the neighbourhood of and in the *macula lutea*, are next described, and particular pains are taken to render the structure of the retina in the *macula* and *fovea centralis* clear and intelligible, and, as it appears to us, with complete success.

The structure of the retina in mammals and other vertebrates is then compared with that of the human eye regarded as a typical form.

Apes, as is well known, possess a *macula lutea*, and in other respects their retina seems to agree very closely with that of man, even in the comparatively great thickness of the "cone-fibres."

Among the other mammalia a very remarkable and, as it would seem, hitherto unnoticed diversity, with respect to the distribution of "rods" and "cones," exists. Whilst most of our larger domestic animals, especially the sheep, ox, pig, horse, and dog, present an arrangement of those elements resembling that which is observed in the human subject and in apes, except, of course, in the absence of the *macula lutea*, the cones, according to the author's observations, are entirely wanting in bats, the hedgehog, mole, mouse, and guinea-pig. A sort of intermediate condition is met with in the cat, rabbit, and rat, in which animals are found either very slender true "cones," as in the cat, or merely indications of them, as in the rabbit. But in any case the "rods" preponderate so much that the "cones" among them may readily be overlooked. According to Ritter, the "cones" are also wanting in *Balæna mysticetus*.

In the rat the "rods" are the longest and slenderest yet met with by the author. In the other vertebrate classes the proportion of "rods" and "cones" to each other approaches nearest to that observed in the mammalian retina in the osseous fishes. In the ray and shark "rods" only exist. In *Petromyzon* elements of one kind only occur in the bacillary layer; but whether these be "cones" or "rods" is undetermined, nor is it determined whether, as supposed by some, both elements may not really be present. The osseous fishes afford excellent materials for the study of the "cone"-fibres; which at one time M. Schultze regarded as belonging to the connective-tissue framework of the retina, and to represent in the outer granule-layer the "radial fibres of Müller" in the other layers of the retina; but of their nervous nature, as of the corresponding fibres in the human retina, he is now thoroughly convinced.

The structure of the retina in birds, reptiles, and amphibia, differs in a very peculiar manner from that of mammals and fish. In the bird's retina the proportion of "cones" to "rods" is in the reverse proportion to that in the mammalia. In other words, the retina of the bird, as regards the distribution of "rods" and "cones," approaches that which is observed in the human *macula lutea*, inasmuch as the "cones" pre-

ponderate greatly over the "rods." The same disposition is found in the retina of reptiles. In the turtle the arrangement is precisely the same as in birds, whilst in the lizards the "rods" are wholly wanting, as they would appear to be also in snakes. An exception, however, to this rule, as regards birds, is afforded in the owl, in several species of which (*S. aluco*, *noctua*, and *flammea*) the preponderance in number would seem to be in favour of the "rods;" and from this circumstance, as well as owing to the enormous length of the "rods" in proportion to the "cones," the mosaic aspect of the outer surface of the retina in these birds bears a striking resemblance to that of the bat. And owing to the same condition also, the owl's retina is almost everywhere destitute of the colours so characteristic of the membrane in other birds. And another remarkable circumstance with respect to the retina in owls is the total absence in it of red pigment-globules; and even the few yellow cones become paler and paler towards the *ora serrata*, until at length they are entirely colourless. These facts would seem to point out that, as the retina of nocturnal mammalia is distinguished by the total absence of "cones," so in the case of the owl the comparative paucity of the same elements, together with the pale colour of the few pigment-globules, may also be connected with its nocturnal habits and avoidance of light. It would, therefore, M. Schultze remarks, be very interesting to examine the retina of other nocturnal birds, as of the Caprimulgidæ, &c.

Another and most characteristic peculiarity of the retina of birds, some reptiles and amphibia, but more especially of the first, is the presence in most of the "cones" of a spherical globule of red or yellow colour, but chiefly yellow, and which is situated at the junction of the inner and outer segments, that is to say, at the internal end of the latter, whose whole diameter is occupied by it, and consequently all the light reaching the outer segment of the cone must pass through this coloured medium. The author's observations would seem to show that the yellow colour predominates in the more sensitive parts of the retina. At least, this presumption arises from the circumstance that in such birds as the pigeon, crow, and hawk (although swift-flying birds), which present a *fovea centralis* (in the hawk two), the elements in that part all contain yellow spherules.

The retina of reptiles closely resembles that of birds. In lizards, according to Leydig, two kinds of elements are distinguishable—one of a slender form, and furnished with a deep yellow spherule; and others of a broader conical shape,

whose apex is coloured with a diffuse yellow pigment. Both these elements, however, it would seem, according to Schultze, should be regarded as "cones." According to H. Müller, the retina of the chameleon contains only elements of one kind, which must also be regarded as cones. In the cones of *Anguis fragilis*, which have been subjected to osmic acid, and, apparently, according to Müller, in the chameleon, a peculiar differentiation of the contents of the inner segment of the cones is observable, in the appearance of a conical, strongly refractive body, the base of which is directed outwards, whilst the pointed proximal extremity looks towards the *membrana limitans externa*, though it does not actually reach it.* These bodies were supposed by Müller to represent cell-nuclei, but M. Schultze suggests that they are refracting lenses.

Throughout the amphibia a great uniformity exists in the retinal elements. Amongst numerous colossal "rods" are lodged a few very minute "cones," each of which contains a minute-coloured or colourless spherule.

M. Schultze confirms Henle's discovery of the presence of one or more *transverse lines* in the outer granules, or rather on those of the outer granules which are connected with the "rods," as they are not found on those belonging to the "cones." These markings appear to be absent in all other vertebrates.

A very full account of the structure and relations of the black pigmentary layer is given, and reasons shown for its being regarded as an element, not of the choroid, but of the retina itself. It consists essentially of a layer of cells containing black pigment, and which send down fine filamentary processes, like the pile of velvet, to fill up the spaces between the outer segments of the "rods" and "cones."

The paper then proceeds to give an account of the arrangement, &c., of the "cones," which alone constitute the percipient stratum in the *macula lutea*. It is shown that as the border of this spot is approached the number of "rods," in proportion to that of the "cones," gradually and regularly diminishes, until at last the former cease altogether, whilst at the same time the "cones" themselves become longer and slenderer up to the centre of the *macula*; the direction, also, of the cone-fibres becoming more and more oblique as they radiate, as it were, from the centre of the *macula*. As is now well known, the layer of "cones" is continuous over the so-

* This is probably the "albuminous substance which, in chromic-acid preparations, retires as an opaque granular mass towards the outer end of the body of the cones," noticed by Mr. Hulke ('Proc. Roy. Soc.,' xiii, p. 109).

termed *fovea centralis*. Some very interesting observations are given on the subject of the relation of the diameter of the "rods" and "cones" to the acuteness of vision, &c.; and the probability is shown that at the point of junction of the outer and inner segments of the "rods" and "cones," which differ so much in their refractive properties, and between which, as pointed out by Krause, even in the perfectly fresh state so sharp a line of demarcation exists, the light passing through the retina to the "rods" suffers reflexion upon the end of the inner segment, or upon true percipient nervous point, as it may be termed.

The third section treats of the development of the retina, and especially of the "rods" and "cones," and it contains many extremely interesting original observations. The author's study seems to have been principally directed to the development of the eye in the chick. He shows that the pigment-layer of the retina, or the inner layer of the choroid, as some deem it, is formed in the outer coat of the primitive eye-bulb-sac, and that the outer and at first perfectly even surface of the inner coat of the bulb is in close contact with the outer. The surface of the inner fold of the primitive bulb-sac is formed by, or rather represents, the future *membrana limitans externa*. The first indication of the formation of the "rods" and "cones" is visible on the previously perfectly even surface of this membrane in the appearance, about the tenth day of incubation, upon it of minute hemispherical elevations, which are, in fact, the rudiments of those elements into which the elevations gradually grow.

In mammalia the necessary continuous observation is not so readily made, but sufficient has been ascertained to show that the development of the retina in them proceeds in the same way as in the fowl. In fresh embryo calves, in specimens from fifteen to twenty-five centimeters in length, the *membrana limitans externa* was in close contact with the pigment-layer, and no trace of either "rods" or "cones" was visible. In specimens fifteen to twenty centimeters long, hardened by immersion in "Müller's fluid," or in a weak solution of nitric acid, although the nerve-fibre-layer of the retina was distinct enough, none of the other layers were as yet differentiated from the general substance composed of spindle-shaped cells having elongated nuclei and processes passing to the outer and inner *membrana limitans*.

In embryo sheep, at the time of birth or very nearly so, "rods" and "cones" were present, but not at an earlier period. They were, however, shorter, and, above all, much more delicate, than in the full-grown animal.

It would appear that in the sheep and other mammals the "rods" are not developed until the differentiation of the other parts of the retina has advanced some way, nor before the end of embryonal life; but in some instances, as in the rabbit and cat, this is seen in a far more striking manner. Neither of these animals at birth present any trace of "rods" and "cones." The blindness, therefore, of the new-born rabbit and kitten does not depend solely upon the closure of the lids, but is also associated with an undeveloped state of the retina itself. The "rods" and "cones" do not appear to be fully developed before the thirteenth day, when they are in the same condition as in the calf or lamb at birth.

The development of the "rods" and "cones" in man appears to follow the same course as in the ruminants above named.

The fourth section relates to the differences between the "rods" and "cones," with respect more especially to their functions. And in it is given a recapitulation of the principal anatomical facts upon which the physiological conclusions or suppositions are based, in the following words:

"With the enlargement of our knowledge of the structure and disposition of the two elements composing the percipient layer of the retina—the 'rods' and 'cones'—arises the question whether we are thus in a condition to attempt the problem of the hitherto unknown physiological distinction between them. We hear that, at any rate, the direction in which the solution of this question is to be sought may now be indicated with some degree of certainty, and I will endeavour briefly to state my views, as follows:

"The anatomical facts upon which we have to rely, shortly recapitulated, are these:

"1. The difference in size and form. This is manifested more particularly in the so-termed inner segment, which in the 'rods' is always sharply defined from the outer segment, but which may also be distinguished as a separate element also in the 'cones.' The inner segments in both the 'rods' and 'cones,' in the perfectly fresh condition, consist of an apparently almost structureless substance, but which very rapidly, after death and in all preservative media, coagulates into a more or less distinctly granular matter. This substance, to judge from micro-chemical reactions, most nearly resembles albuminous matter, as, for instance, the protoplasm of young cells. An essential distinction between the substance of the inner segment of the 'rods' and of the 'cones' is manifest in the circumstance that solutions of osmic acid of a certain strength produce in that of the cones a very distinct parallel striation, which, under similar conditions, I am unable to perceive in the inner segments of the 'rods.' No universal distinction exists in the absolute diameter of the inner segments, as, for instance, in the human retina; for although the cones throughout by far the greater part of the retina are fully twice as thick as the rods, their inner segments in the *fovea centralis* are quite as slender as those of the 'rods.' The outer segments or shafts consist of a more highly refracting substance, which after death coagulates in

a different manner from that composing the bodies. This substance does not become granular, like protoplasm, but either hardens into a homogeneous mass or shrinks and curls up in a peculiar manner, at the same time cracking, generally transversely, but sometimes also longitudinally. That an external tunic and contents—a cortex and central filament—can be distinguished in them I hold to be highly improbable. The outer segments of the ‘rods’ are cylindrical, though a very slight attenuation towards the choroid may occur (frog); on the other hand, the outer segments of the ‘cones’ are of a decidedly conical form, the apex pointing outwards, and usually terminating below the summits of the rods.

“2. A very remarkable difference between the ‘rods’ and ‘cones’ is presented in the filaments proceeding from them to the external granule-layer. The filaments belonging to the ‘cones’ are of considerable thickness, which sometimes is as much as 2–5 micro-millimeters; they exhibit here and there a delicate longitudinal striation, as if they were composed of parallel fibrils; and they always break up on the upper surface of the intergranular layer into an indeterminate number of extremely delicate fibrils, which are lost in that layer.* The fibres proceeding from the rods, on the contrary, have a scarcely measurable thickness, and they can only be traced to the surface of the intergranular layer, where they apparently terminate in a minute enlargement whose nature is at present obscure. Each filament, whether belonging to a ‘cone’ or ‘rod,’ is in some part of its course connected with a cell—an outer granule—so that the outer granules may be divided into ‘rod’ and ‘cone-granules,’ of which the latter, at any rate in the mammalia, are the larger. Both kinds of filaments present all the characters of nerve-fibres, and much resemble those of the optic nerve-layer, and, on the other hand, they are manifestly distinguishable from those of the trabecular framework.

“3. At the yellow spot of the human and simian retina ‘cones’ only exist. Close to its periphery, however, ‘rods’ become interposed between them, and at a few millimeters from the middle of the spot they are present in the number of two to three between each two ‘cones,’ a proportion which is continued uninterruptedly up to the *ora serrata*. In proportion as they become crowded together at the *macula lutea*, their fibres, as well as those of the ‘rods’ interspersed among them, assume an oblique direction, radiating, as it were,

* In a valuable communication to the Royal Society, read in June, 1866, on the “Chameleon’s Retina,” Mr. Hulke states “that from the inner ends of the cones fine fibres proceed obliquely from the outer to the inner surface of the retina in a radial direction from the centre of the *fovea* to the periphery of the retina.” These fibres connect the cones with the cells of the outer granule-layer; they next form a thick plexus at the inner surface of this layer, which he terms the “cone-fibre-plexus;” then traverse the inner granule-layer, in which they connect themselves with round and roundly oval cells, and are continued through the medium of the ganglion-cell-like cells of this layer into the granular (molecular layer, Schultze), where they join the processes directed outwards from the cells of the ganglionic layer. “Thus,” he says, “they constitute an anatomical path between the cones and optic nerve-fibres.”

This, if confirmed by future observation, is a most important fact, and one of great import with relation to the apparently more direct and immediate communication between the “cones” and optic nerve-fibres than would seem to obtain with respect to the “rods.”

from the centre of the *macula* in a meridional and forward direction, in order, after a longer or shorter course, to reach the outer granular layer.

"4. In most mammalia the relative number of 'rods' and 'cones' is exactly the same as in man, with the exception, of course, of the *macula lutea*. But in many the cones are altogether absent. This is the case in animals which prefer darkness to light, such as the bat, hedgehog, mole, mouse, and probably a great many others. In the rabbit, which, as is well known, in the wild state inhabits subterranean passages, there are, it is true, indications of cones, though these appear to be in quite a rudimentary state.* The cat has distinct though slender cones, which are placed wide apart, so that room is left between them for twice or thrice the number of 'rods' than in the human retina.

"5. Birds have many more 'cones' than 'rods,' the former, in fact, standing to the latter in the inverse proportion to that in which they occur in the human subject. In both the *foveæ centrales* of the falcon 'cones' only exist [as well as in the single *fovea centralis* in some other birds]. But the owls almost resemble the bat, their retina containing but very few cones and an enormous proportionate number of rods. In their retina scattered 'cones' only occur at wide intervals, and these are so overcrowded by the very long outer segments of the 'rods' as to be seen with great difficulty.

"6. The 'cones' in birds are distinguished by a very remarkable character. The greater number of them are furnished, at the end of the inner segment and immediately in front of the point of attachment of the outer segment, with a highly refractive globule, for the most part of a deep yellow or red colour, anything analogous to which, so far as is at present known, is wanting in all mammals. The yellow globules are more numerous than the red. The coloured globules have a diameter precisely corresponding with that of the base of the outer segment, so that no light can reach that part without passing through the globule. The few 'cones' which have no coloured globule contain at the corresponding point a strongly refractive colourless body, apparently of the same kind. The few 'cones' existing in the owl's retina are furnished with pale yellow or colourless globules. Red globules are entirely wanting in the retina of those birds (*Strix aluco*, *noctua*, and *flammea*).

"7. Among reptiles, in some, as the turtle, the retina appears to present the same structure as that of birds. Lizards and snakes have only cones, and in some instances these contain pigment-globules in the same situation as in birds (*Lacerta*, sp. *Anguis fragilis*), whilst others are without these coloured elements (chameleon and snakes).

"8. The amphibia (frog, toad, triton, and salamander) have very thick rods and very minute cones, but in each of the latter is a bright yellow or colourless globule situated between the outer and inner segment.

"9. The osseous fishes, so far as researches have hitherto gone, appear to possess rods and cones like the mammalia; and the latter are without coloured globules. Cartilaginous fish, on the other hand, as the ray and dog-fish, are wholly without 'cones,' like the bat among mammalia.

"10. The difference which in mammals and fish is so apparent

* It would be very interesting to examine the hare's retina, which, though so closely allied to the rabbit, differs so much from it in its habits.

in the relative thickness of the 'rod-' and 'cone-' filaments, is not apparent in birds or amphibia. How the case may be in those reptiles which possess both elements has not yet been ascertained."

The author then enters upon the question of the physiological relations of the "rods" and "cones;" and the following may be taken as a very brief summary of his highly interesting observations on this point.

The organization of the "yellow spot," and of the *fovea centralis*, in the human retina, clearly proves that the cones alone are not only sufficient for vision, but also that they possess certain physiological advantages over the "rods." But it is, at the same time, obvious that the "rods" alone suffice for the purpose of vision, since the bat and other mammals are wholly unprovided with "cones." But these mammals without cones in the retina prefer the dusk or night to daylight. The question, consequently, arises, what impression communicated through the retina in the dusk is useless?—by the solution of which we may be guided to some conclusion with regard to the peculiar function of the "cones."

The visual sense comprises three fundamental impressions, which have been termed by Aubert "Lichtsinn," "Farbensinn," and "Raumsinn;" that is to say, "light-sense," "colour-sense," and "space-sense." It is at once obvious that the light-sense, or the power simply of perceiving luminosity, including [perhaps] *quantitative* differences in the degree of light, is a fundamental requirement in any, even the simplest, visual organ. For this purpose, it is clear that a single termination of a nerve, or, in other words, in the case of the retina of the higher animals, a single rod or cone, would suffice. And it may also be admitted that a number of such visual points, associated so as to form a single percipient organ, would, in addition to the simple perception of light, also give the power of estimating space, and consequently of conveying ideas of form. These two faculties of the perception of light and of space as conveyed by light are inherent in the eyes of all vertebrates. The "coneless" retina of the bat, hedgehog, and mole, does not, in this respect, differ from the "rodless" retina of snakes and lizards, seeing that the "cones" are, at any rate, quite as fully percipient of light as the "rods," inasmuch as they equally represent the termination of sentient nerves. It may be assumed that the mere sense of luminosity is more strongly developed in nocturnal animals, as the bat, than it is in the sunshine-loving snake; so that the former would find a sufficiency of light when the latter was in darkness. This would seem to indicate that the "rods" were

more adapted for the simple perception of light than the "cones."

We have next to consider the *colour-sense*; that is to say, the sense by which *qualitative* differences in light are perceived. To judge from our own experience, which in such a question can be the only guide, the simplest trials will show that, as dusk and darkness approach, the power of perceiving colours ceases at a comparatively early stage. In the evening, though we may *see* objects well enough, we are quite uncertain as to their absolute or relative colour. We may suppose, therefore, that an animal which pursues its prey only at night, and which habitually frequents dark or obscure places, has no sense of colour, or, at any rate, only needs to distinguish different degrees of brightness in the different colours, as is the case with ourselves in the dusk [or even, in the case of colour-blindness, sometimes even in the daytime]. If we assume, as from the theory of Young and Helmholtz we are compelled to do, that the sense of colour resides in a determinate anatomical substratum, we are justified in concluding that that particular substratum is wanting in the retina of nocturnal animals. The conclusion naturally follows, that the "*cones*" *may*, in all probability, *be the terminal nerve-organs of the colour-sense*.

It should be borne in mind, however, that the "cones" cannot be regarded as *exclusively* confined to the perception of colour. The colour-sense necessarily includes the light-sense, or is, as it were, superadded to it; and thus we may conclude that, where the colour-percipient cones are sufficiently closely aggregated, they may also suffice for the *sense of space*, and thus fulfil all the functions of a retina by themselves alone. The only question, therefore, as M. Schultze remarks, that can arise, is as to whether it is probable that the "cones," together with the power of conveying impressions of luminosity and space, have not in addition that of conveying impressions of colour, and whether we have any reason, in like manner, to suppose that the "rods" have no such power.

The author then proceeds to show, in reference to the experiments of Purkinje, Hueck, Helmholtz, Aubert, and Schelske, that, although the sense of colour exists throughout the human retina, it is most acute in proportion to the preponderance or number of the "cones" over the "rods," and that the latter alone are unable to convey impressions of colour. He also points out that the probabilities that this function resides in the "cones" is strengthened by the fibrillated structure of the "cones" and their filaments, which is in accordance with the well-known theory of colour-

perception, propounded by Young and Helmholtz, that at least three different kinds of fibre must be required for this perception. Each "cone," therefore, in the mammalia and fishes, having this compound structure and all being alike, it would appear to follow that all are equally capable of perceiving every variety of colour. And his argument is still further strengthened by the consideration that, inasmuch as all or nearly all the "cones" in a bird's retina are furnished with a coloured spherule, through which all the light reaching the percipient part must pass, it would be absurd to suppose that they were incapable of receiving impressions of colour, for which, so far as shown by that circumstance, they alone would seem to be fitted. Furthermore, it is to be borne in mind that all the "cones" in a bird's eye do not contain spherules of the same colour, and that some are without any, whence we may conclude that in all probability the differently coloured "cones" are adapted for the perception of monochromatic light corresponding to that of the spherule contained in them, and that each is not, as in the mammal, capable of conveying equally impressions of all colours. And this view is curiously in accordance with the circumstance that the "cone"-filaments in the bird are scarcely thicker than those of the "rods." Whether this be the case with the filaments proceeding from the colourless "cones," has not been made out. But it may be that these "cones" are adapted for the reception only of the violet rays, which would, of course, be absorbed in their passage through the coloured "cones."

The structure of the owl's retina, in contrast with that of diurnal birds, may be cited in support of the same argument. And the author refers to a suggestion of his own, made in a former paper on the *macula lutea*,* that the intervention of the yellow spherule in birds, and of the yellow colour in the human *macula*, may serve for the interruption of the more powerful photo-chemical rays in their passage to the delicate percipient tissue.†

This part of the paper concludes with a highly interesting disquisition respecting several other points connected with the simple visual sense and the estimation of sizes and forms, &c., for which the reader must consult the original.

* 'Ueber den gelben Fleck der Retina,' &c. Bonn, 1866.

† Should M. Schultze's ingenious speculation respecting the use of the yellow and red spherules in the retina of birds and some sun-loving reptiles be entertained, it would seem to suggest the propriety of using yellow glasses to protect the eyes in strong daylight, as on snow or at sea in the tropics, for instance, instead of blue or violet ones, which transmit only the very rays which nature seems to be so solicitous to intercept.

In his researches on the retina M. Schultze has found the greatest advantage in the use of a solution containing 1 to $\frac{1}{10}$ th of osmic acid (OsO_4); and he recommends that a solution of that substance containing 1 per cent. should be kept at hand, which can be diluted at pleasure. Microscopic preparations made with it he prefers to keep simply in water.

The black colour which is assumed by the preparation, even within a few minutes of its immersion, is at first uniform throughout. But subsequently the different parts of the retina exhibit slight differences, the optic nerve-fibres and the molecular and intergranular layers exhibiting the deepest tint. In frogs and fishes the deepest colour is seen in the outer segments of the "rods." In this way may be obtained preparations in which the outer segment is of a deep black colour, whilst the inner is almost uncoloured, the line of demarcation between the two being very abruptly defined. A similar difference is observable also in mammals, but not so constantly, and under circumstances which cannot at present be explained. But the demarcation between the segments is always well defined, and the author can recommend no better medium for the examination of the "rods" and "cones" than osmic acid. A special advantage of the osmic-acid solution is that it hardens the elements of the connective-tissue framework more slowly than the nervous; and another is that, except in very strong solutions, it does not produce granular coagulation either within or without the elementary parts of the retina.

The observer is cautioned against the injurious effects of osmic acid upon himself, unless great care be taken.

Another medium greatly employed by him is what he terms "Iod-serum," or iodized serum, which is used for the immersion of fresh dissections of the eye and other parts—the most delicate tissues, such as the retina, remaining for a long time unaltered in it. It is prepared from the amniotic fluid of the calf, to which a sufficient quantity of tincture of iodine is added to give it a faint yellow colour. And he has found that an albuminous fluid of this kind may be kept unaltered for any length of time if a very minute quantity of bromine be added to it. But as bromine acts very powerfully in causing cells, &c., to contract, the quantity added to the iodized serum must be less than will remove the whole of the yellow tint.

[It is not improbable that a few drops of carbolic acid would answer the same purpose as the bromine, and perhaps the iodine also.]

REVIEW.

Histoire Naturelle des Annelés marins et d'eau douce. Annélides et Gephyriens. By ARMAND DE QUATREFAGES.

THE worms of our seas and fresh waters—variously classified and arranged by those who have studied them—have commanded till quite recently but a very poor share of the attention of the working naturalist. The probable reasons of this circumstance are to be found in the retiring nature of these animals, and the comparative obscurity of the characters which separate them specifically and generically, as well as the difficulty of tracing their life-histories and anatomical development. We believe that we are not exaggerating the true state of the case when we say that there is not a single work extant, such as is available for other groups of animals, by which species of Annelida may be satisfactorily identified—even those occurring in such limited areas as our own and neighbouring seas. The few systematic works which are to be had, of which the British Museum Catalogue published in 1865 may be taken as a specimen, are simply useless for the purposes of the present day, owing to insufficiency in details in both descriptions and figures. On the other hand, the work of M. Malmgren on the Annelids of the North Sea, and such descriptions of species and ample drawings as those of Kinberg* and Ehlers,† are examples of the manner in which the Annelida should be treated; and until we get such works from many different localities the synonymy must remain in its present shocking condition, very many species which bear the same name in France, England, Germany, and Scandinavia, being quite distinct, and those bearing different names being often identical.

* Eugenie's Resa, &c., Zoologi, 1857.

† 'Die Borstenwürmer,' 1864.

The unfortunate worms have also been greatly ignored by the anatomist, the labours of Cuvier, Audouin and Edwards, Claparède and De Quatrefages, leaving large gaps to be filled up; while, as regards external morphology, Professor Huxley* alone has made the attempt to advance upon Grube's useful though by no means perfect nomenclature.

Matters being thus, the announcement of a work on the annuloid animals of the sea and fresh waters by one who has laboured so successfully during the last twenty years at their anatomy as M. de Quatrefages, was a subject for great rejoicing to those interested in the group, and high expectations were raised. The work has at length appeared, in two volumes, with twenty illustrative plates. It does not treat of the whole sub-kingdom Annuloida (Annelés), nor of all worms which are sometimes classed as Annelida, but only of the *Polychæta appendiculata* and *Gymnocopa* of Grube, to which M. de Quatrefages restricts the class Annelida, and the *Gephyrea*, once regarded as Echinoderms; the other classes, embracing the earthworms, leeches, &c., are, we believe, to be discussed in other volumes by other authors.

We propose in the few following pages briefly to notice the various chapters of M. de Quatrefages' work, which we may at once state contains a vast amount of information, and numberless valuable facts, never before placed so readily to the hand of the naturalist. Much, indeed, of the matter is quite new, and the plates are for the most part very good, though sometimes over-coloured. While fully acknowledging the value of the work, we cannot but express some disappointment at the absence of any general views and philosophical exposition of the facts treated of in the first few chapters. The author appears as a most diligent observer, but fails to go beyond this. In the systematic portion of the work he has done great service in characterising all the known genera and most of the species of Annelida and Gephyrea; he has not, however, attempted to reduce the confusion in synonymy directly, and indirectly has added a little to it by not fully figuring and describing his new species.

In the Introduction the author defends his views on the classification of the Annuloida, or worms, which he divides primarily into two parallel series—the monœcious and diœcious—which contain groups presenting *analogies* to each other (the monœcious to the diœcious groups), but not *affinities* strictly so-called. In the following tables we give

* Lectures in 'Med. Times and Gaz.,' 1856.

M. de Quatrefages' classification, and that in Carus's 'Handbuch,' representing the last German view of these animals:

VERS.		VERMES.
DIOÏQUES.	MONOÏQUES.	Annulata.
<i>Annelides.</i>	<i>Erythrèmes (Oligochaeta).</i>	Gephyrea.
Rotateurs.		Chætognatha (Sagitta).
Géphyriens.		
<i>Malacobdelles.</i>	<i>Bdelles (Hirudinea).</i>	Nematelminthes.
Miocælés.	Turbellariés.	Platyelminthes.
Nematoïdes.		
	Cestoïdes.	

Those groups printed in italics in the left-hand table form the Annulata of Carus's arrangement.

It is an unfortunate thing for M. de Quatrefages' high estimate of the value of the unison or conjunction of the sexes as separating characters that Professor Huxley, some years since, described a small tubicolate Annelid which had the sexes united. M. de Quatrefages, while admitting this as rather an awkward hitch in his arrangement, contends that such an Annelid was only an accidental exception—one of those curious exceptions which prove the rule. This, we think, can hardly be maintained in the present very limited state of our knowledge of the reproductive organs of Annelida, and prefer such an arrangement as that of Carus, which should, however, include the Rotifera.

After thus clearing the way, the author proceeds to deal with the class Annelida as limited above.

His first chapter is devoted to "external organization," the remarks on the general form of the body and its division into regions being well worth perusal. The division into a fore part, a hind part, and a middle part—a head, a tail, and a thorax—exists in Annelids as in all animals of any complexity of organization; it is but faintly indicated in the errant Annelids whose thorax is not marked off from the tail, but in the sedentary forms is most obvious. M. de Quatrefages gives numerous details of the modifications of these parts, but hardly seems to recognise the fact that they are built up by the modification of homologous somites. In his review of the nomenclature of these various parts, and in particular those of the cephalic region, it is unfortunate that he has not noticed in any way the brief but most clear and philosophical view of the structure of Annelida given by Professor Huxley in the lectures already referred to. In all probability, M. de Quatrefages has never seen these lectures, which have been allowed to remain in comparative obscurity for more than ten years.

We have not space here to do more than glance at the morphology of the "cephalic region," as expounded by our author, which is the name he gives to the *kopflappen* and *mundsegment* of Grube taken together. All Annelids possess this "head," though in some of the sedentary forms it can only be distinguished by its appendages, while in the Errantia it is highly developed. The two parts of the head already distinguished by Grube and others he re-names, the first as "lobe cérébral," "tête," or "caput," the second as "anneau buccal" or "annulus buccalis." The names given by Professor Huxley to the same parts are respectively "prostomium" and "peristomium," names which we cannot but hope will be in the end generally adopted, as they have been already to some extent in Germany, since they express in the neatest form the most important relations of these two parts of the worm. The nomenclature of the appendages of the head is, M. de Quatrefages says, unsatisfactory, since appendages receive the same name in different Annelids which receive totally different nerves, and *vice versâ*. He considers that the distribution of the nerves should be made the criterion of homology in these parts in different genera, and we believe that he has here found the only test, save that of embryological relationship, which can be applied to such parts. The theory of the Annelid's head is in many ways analogous to that of the vertebrate skull.

The term "antennæ" is limited by our author to the appendages which are placed *on* the head properly so-called (*kopflappen*, prostomium); it is not always easy to ascertain what appendages are "placed on" the head, but we have a more tangible definition in this—"the antennæ receive their nerves directly from the brain itself (præ-oral or supra-œsophageal ganglia)."

The name "tentacula" is reserved for those appendages which proceed from the buccal ring; these receive their nerves from the ganglia of the "connective" or "accessory connective" (pharyngeal commissures).

The term "cirrhi tentaculares" is used to designate the appendages of the first feet when they assume the characters of the more strictly cephalic segments; these receive their nerves from the ventral chain of ganglia.

While these considerations are of value in recognising equivalent appendages in different genera and families, we cannot think M. de Quatrefages' choice of terms at all happy, since it rather tends to create confusion. Let us compare the corresponding titles used by different authors.

<i>Audouin and Edwards.</i>		<i>De Quatrefages.</i>	
1. Antenne impaire ou médiane.		1. Antenne médiane.	
2. Antennes mitoyennes.		2. Antennes latérales.	
3. „ externes.		3. Tentacules inférieurs.	
4. Cirrhes tentaculaires.		4. „ supérieurs.	
5. „ „		5. Cirrhes tentaculaires.	

<i>Grube.</i>	<i>Kinberg.</i>	<i>Huxley.</i>
1. Tentaculum impar.	1. Tentaculum.	1. Tentaculum prostomiale.
2. Tentacula media.	2. Antennæ.	2. Cirrhi prostomiales superiores.
3. Tentacula lateralìa.	3. Palpi.	3. Cirrhi prostomiales inferiores.
4. Cirrhi tentaculares.	4. Cirrhi tentaculares.	4. Cirrhi peristomiales.
5.	5. Cirrhi buccales.	

Of these it will be seen that the terminology of M. de Quatrefages is only a modification of that of Audouin and Edwards. It is an important modification, however, since he couples the third pair of appendages with the fourth, whilst the other authors, with the exception of Kinberg, couple them with the second. Kinberg's names are extremely short and useful, but do not express any of the relations of the parts. Professor Huxley's names are valuable, since they serve to enforce the idea that each of these pairs of appendages correspond to the appendages—the cirrhi—of a somite. If we are to have a simple nomenclature, short, for use, we prefer Kinberg's; but if by the names given it is desirable to express the homologies of the parts, those of Professor Huxley are the best. M. de Quatrefages does not discuss in any way the structure of the prostomium and peristomium as consisting of modified somites; and hence, though on account of the origin of their nerves he associates with the appendages of the peristomium, in name, what all other authors appear to have regarded as one pair of the appendages of the prostomium, we are at a loss to know whether he really considers the third pair of appendages, the “palpi” of Kinberg, as belonging morphologically to that portion of the head in front of the mouth or to that portion around it. The omission of any attempt to discuss this question of the structure of the cephalic region is very much to be regretted.

Applying his principle of “antenna” and “tentaculum” to the sedentary forms, the author shows that in *Terebella* the prehensile cirrhi are modified “antennæ,” as also are the respiratory fans of *Sabella* and *Serpula*, whilst the opercula of *Hermella*, &c., arising from the peristomium—the buccal ring—are the homologues* of the tentacula or peristomial cirrhi.

* M. de Quatrefages says “les analogues;” but here, as elsewhere, we observe that the terms “homologue” and “analogue” have not with him

The modifications of the appendages of the feet in the thoracic and abdominal regions of the body are more carefully discussed. The elytra of Aphroditaceæ are considered as respiratory organs—certainly not homologous with the notopodial cirrhi, since in some genera they exist on the same somite with the notopodial cirrhi, as shown by Audouin and Edwards. There can, however, be little doubt that there is a very intimate relation between elytra and cirrhi, both in structure and function, the absence of cirrhi on those somites provided with elytra in most Polynoïna sufficiently proving this. The elytra are described by M. de Quatrefages as composed of two lamellæ, in the space between which the fluids from the general cavity of the body circulate, passing in by a fine aperture in the pedicle of the scale. The cirrhi are described as more or less cylindrical and tapering appendages, whose function is that of an obscure sense of touch, similar to that of the “whiskers” of certain mammals. Now, though this description of elytra and cirrhi is true for general purposes, it does not state the whole case. In many Polynoïna the two lamellæ of the elytra are rendered entirely continuous by a tough, fibrous, intermediate structure, similar to that which in most cases forms the central portion of a cirrhus; no passage is thus left for the circulation of fluids, and a hard leather-like plate is formed, on the surface of which are papillæ, having, to all appearance, a sensory function. On the other hand, the cirrhi in some Polynoïna (*Antinoë nobilis*, from the Channel Islands, and the *Gastrolepidia* of Schmarda) are excavated, and form delicate bladder-like sacs, communicating with the general cavity of the body, whilst the foliaceous form and respiratory function of the cirrhi in Phyllodoce are well known.

The chapter on external form concludes with a minute description of the various forms of setæ and hooklets met with in the Annelida.

The second chapter, devoted to anatomy and physiology, is, perhaps, the most valuable in the work, since in it a *résumé* is given of those numerous and excellent essays of the author on various genera of Annelida already published, whilst there is much additional matter. It would have made the work more valuable had not the author dwelt so entirely on his own observations, and noticed more fully those of other writers. A large portion of this chapter is, we regret to see, necessarily taken up in controverting the claims and opinions

the same definite sense of structural and functional equivalent which they have gained in England.

of our late unfortunate countryman, Dr. Williams, of Swansea, who M. de Quatrefages seems to think is regarded by other observers as a credible and sound investigator. This we can assure him is not the case in England. There is, however, one great merit due to Dr. Williams which ought to be universally acknowledged, as it is by M. de Quatrefages; it is that of having first discovered and appreciated those excretory ducts to which he applied the name "segmental organ." When we have given credit for this to Dr. Williams, it is all we can do for him; for the "segmental organ" appears really to have worked upon his brain in a most serious way, and rendered him truly monomaniacal. All the lower animals, he attempted to show, possessed this "segmental organ;" it was from this that the generative glands were developed, &c., and in order to support these statements he published most extraordinary drawings of dissections (which happily very few people believe in now), and treated the most distinguished writers, whose views differed from his, with contempt or abuse. M. de Quatrefages undoubtedly drew attention to the nature and functions of the general cavity of the bodies of Invertebrata before Dr. Williams, and throughout the researches of the former on the circulation and respiration of Annelida have precedence over those of the latter.

The various organs of the Annelida are treated in this chapter of 100 pages under the following heads:—1. *Teguments and general muscular system.* 2. *General cavity of the body.* 3. *Organs and functions of digestion.*—The description of the exsertile pharynx and its teeth and denticles in various genera is a specimen of the author's great attention to details, and his minute acquaintance with these structures from personal observation. We cannot, however, agree to the statement that the pharynx is ever entirely everted in life by the Polynoina, which is, indeed, put forward somewhat doubtfully; it seems to be merely owing to a strong convulsive action of the muscles that this takes place, generally resulting from such an irritation as causes death; and we doubt if the pharynx is ever withdrawn again, since the worm dies almost directly after its protrusion. 4. *Organs and functions of absorption.*—Under this heading the author states "there are no special organs of absorption." He assigns this function to the vessels of the red fluid which are intimately connected with the intestine. 5. *Organs and functions of circulation.* 6. *Organs and functions of respiration.*—Treated separately as the respiration of the blood (red vascular fluid), and respiration of the liquid of the general cavity. These two

subjects of circulation and respiration are discussed very fully. The researches of Milne-Edwards were the first in elucidating this portion of the anatomy of the Annelida; and it almost seems to have become specially appropriated to the investigation of French naturalists. 7. *Organs and functions of secretion*.—Under this head the abundant secretion of viscid material from the skin, such as is observed in *Lumbrinereis*, *Cirrhatus*, *Chaetopterus*, and all tube-building forms, is briefly discussed. 8. *Organs and functions of innervation*.—The nervous system is described as consisting of a general and a visceral system, the first comprising the "brain," or large bifid supra-œsophageal mass and the ventral chain of ganglia; the second of a chain or series of stomato-gastric ganglia, variously modified in the different genera. 9. *Organs of the senses*.—The sense of touch is very briefly passed over, very little being said as to the sensitive papillæ and hair-like appendages of some Annelids. The author inclines to the belief that the Nereides possess the sense of taste, from the structure of the pharynx, but no evidence is adduced from other Annelids. The organ of hearing, first recognised by Grube and Siebold in *Arenicola*, is considered by M. de Quatrefages the only well-attested example of such a structure in Annelida. Carus, however, in his 'Handbuch' (1864) regards all Annelids as possessing such organs. M. de Quatrefages says he has twice observed some such organ in *Eunice sanguinea*, but he does not feel sufficiently certain of its nature. The eye is well developed in many Annelids, as the researches of Muller, Wagner, Rathke, Siebold, and chiefly M. de Quatrefages himself, attest. The curious genera *Amphicorine* and *Polyophthalmus*, the one with eyes at the tail, the other with an eye to each ring of the body, are refigured and described. 9. *Organs and functions of locomotion*.—The explanation offered of the mode of action of the feet in those Annelids in which they are developed as locomotory organs is worth notice. A very large share of importance is ascribed to the fluid of the general cavity, in relation to locomotion. It acts by distending the erectile tissue of the feet, and also stiffens each part of the body successively in a similar manner, thus giving a *point d'appui* to the muscles which are attached to those parts. 11. *Organs and functions of generation*.—The different subjects coming under this head—ovaries, spermatozoa, accessory organs, &c.—are treated at some length. The modifications which the embryo undergoes, and the subsequent phenomena of alternating generation, or geneagenesis, as M. de Quatrefages calls it, are discussed as far as the facts at

hand will allow. The embryogeny of the Annelida is, indeed, a field of study which has been but little entered on, and which is most urgently in need of workers. M. de Quatrefages himself has traced the development of *Hermella*, and gives a *résumé* of his work in this chapter. We may here call to mind Busch and Müller's arrangement of the different larval stages of Annelida into Telotrocha, Mesotrocha, Polytrocha, and Atrocha, according to the varying development of the ciliated rings which characterise these larvæ. Claparède has lately attempted a more complete classification, dividing the larvæ into two large primary groups—Matachætæ and Perennichætæ, the first of which is subdivided into the three groups Gasterotrochæ, Nototrochæ, Amphitrochæ; the second into Cephalotrochæ, Polytrochæ, Atrochæ.

M. de Quatrefages does not at all like this classification of Claparède's, since, a Polytrocha becoming an Atrocha in the course of development, and other similar changes occurring, his nomenclature will only give rise to confusion. He further observes very truly that we know very few facts relating to this subject, the larvæ of scarcely thirty species having been examined. He gives a list of these species, and references to the papers in which they are described. This list is really so valuable to any one who wishes to carry on investigations in this branch of inquiry, that we copy it here in full.

APHRODITEA.—*Polynoë cirrata*.—Sars, 'Wiegman. Archiv,' 1845, i, p. 11.

Polynoë cirrata.—Max Müller, 'Müller's Archiv,' 1851, p. 23. Désor, 'Boston Journ. Nat. Hist.,' vol. vi, p. 12.

Polynoë.—Claparède, 'Beobacht. über Anat. und Entwick. Wirbell. Th.,' p. 80, pl. 8, figs. 7—11.

EUNICEA.—*Eunice sanguinea*.—Koch, "Ein Worte zur Entwick. von Eunice" ('N. Deutschr. der Schweiz. Gesch.,' vol. vii).

LYCORIDEA.—*Nereis diversicolor*.—Max Schultze, 'Abhandl. der naturforsch. Gesellsch. zu Halle,' vol. v, p. 213.

Nereis.—Milne-Edwards, 'Ann. des Sci. Nat.,' 3rd ser., vol. iii.

PHYLLODOCEA.—*Phyllodoce*.—Max Müller, 'Müller's Archiv,' 1855, p. 17.

SYLLIDEA.—*Syllis pulligera*.—Krohn, 'Wiegman. Archiv,' 1852, p. 251.

Autolytus prolifer.—Krohn, 'Wiegman. Archiv,' 1852, p. 66. 'Müller's Archiv,' 1855, p. 489.

Autolytus cornutus.—A. Agassiz, 'Journ. of Boston Soc.,' vol. vii, 1862, p. 392.

Sacconereis helgolandica.—J. Müller, 'Müller's Archiv,' 1855, p. 13. Mac Schultze, loc. cit., fig. 10.

Sacconereis Schultzii.—J. Müller, loc. cit., p. 7.

Cystonereis Edwardsii.—Köl liker (Koch, loc. cit.).

Exogone naïdina.—Ørsted, 'Wieg. Archiv,' 1845, p. 20.

Odontosyllis.—Claparède, loc. cit., p. 81.

ARICIEA. — *Nerine longirostris*. — Leuckart, 'Wieg. Archiv,' 1855, i, pp. 63 and 77. Busch, 'Beobacht. über Anat. und Entwick. ein Wirb. Th.,' pl. 8.

Leucodore ciliata.—Ørsted, 'Ann. Dan. Conspectus,' p. 39, pl. 6. Claparède, loc. cit., p. 69, pls. 7, 8. "Annélides voisines de la précédente," Claparède, ibid.

Magelona papillicornis.—Claparède, loc. cit., p. 74.

TELETHUSA. — *Arenicola piscatorum*.—Max Schultze, 'Abhandl. naturforsk. Gesellsch. zu Halle,' vol. v, p. 213.

TEREBELLACEA. — *Terebella nebulosa*.—Milne-Edwards, 'Ann. des Sc. Nat.,' 3rd ser., vol. iii, p. 145 (1845).

Terebella conchilega.—Claparède, loc. cit., p. 63.

HERMELLACEA. — *Hermella alveolata*.—Quatrefages, 'Ann. des Sc. Nat.,' 3rd ser., vol. x, 1848, p. 153.

SERPULACEA. — *Protula*.—Milne-Edwards, loc. cit., p. 161.

Fabricia.—O. Schmidt, 'N. Beiträge zur Naturg.,' p. 27.

Spirorbis spirillum.—Pagenstecher, 'Zeitschr. für wiss. Zool.,' 1862, vol. xii, p. 486.

CHÆTOPTEREA. — *Chaetopterus*. — J. Müller, 'Müller's Archiv,' 1846, p. 101. Busch, 'Müller's Archiv,' 1847, p. 187; and 'Beobacht.,' 1851, p. 59. Max Müller, 'Obs. Anat. de Verm. quib. mar.,' p. 25, pl. 3; and 'Müller's Archiv,' 1855, p. 1.

We must pass over the pages on the fissiparous reproduction of Annelida, and their growth and death, in which, as elsewhere, the author dwells chiefly on his own researches published from time to time in the 'Annales des Sciences Naturelles;' and, indeed, the whole chapter on anatomy and physiology is little more than a *résumé* of those researches, which, though valuable and good, still are not the whole of what has been done. The four plates illustrative of this part of the work are very good for small plates, but are not quite so numerous as might be wished, nor do they equal the drawings of Ehlers in execution.

The third chapter is entitled "Natural History," and deals with the habits of Annelida in freedom and captivity. There are many interesting observations in this short chapter.

The fourth chapter is devoted to geographical distribution. The author observes that but little is known of the distribution in the world of Annelids; but that from the researches

of Schmarda and Kinberg, it appears that many genera are cosmopolitan. He dwells upon his notion that the Oligochaeta represent what he calls the true Annelida—the Polychæta; the former being fresh-water and terrestrial forms, the latter always marine. Holding this view, he is led to doubt the occurrence of Nais on the sea-shore, such as the *Pachydrilus* and *Clitellio arenarius* described by Claparède. He suggests that a spring running down to the sea might account for their appearance, but cannot believe that they are marine. We ourselves, last summer, met with *Clitellio arenarius* at low-water mark in the Isle of Man, and the circumstances attending its occurrence were precisely those suggested by M. de Quatrefages. A small fresh-water spring ran into the sea at the point where *Clitellio* occurred, and spread itself over the sands.

In the fifth chapter, on the “History and Zoological Relations” of the group, the literature of the Annelida, and the various arrangements of the class which have from time to time been offered, are discussed from their earliest day. We cannot here pass in review the systems of all those who have attempted to arrange Annelids into natural groups, but we may compare the divisions of Cuvier, Grube, and M. de Quatrefages. The latter states that he has chiefly occupied himself in limiting the families or small assemblages of genera, which he considers of fundamental importance, representing, as they do, the Linnean genera. While Grube, with Cuvier, embraces in his class Annelida the leeches and earth-worms, as well as the marine setigerous forms, M. de Quatrefages, it will be remembered, only allows the latter to come under this class, separating the other groups as distinct classes. Other writers, again, have gone so far in the other direction as to include nearly all worms—the Turbellaria, Gephyrea, &c.—under this class Annelida. Cuvier took for the basis of his subdivisions the absence or the presence of respiratory organs. Savigny neglected this character, and founded his classification, in the first place, on the absence or presence of setæ, on the structure of these parts, on the presence or absence of a distinct head, antennæ, pharynx, and jaws. Blainville took above all things the general form of the body, the similarity or dissimilarity of the rings, the greater or less complication of their appendages. Audouin and Edwards applied themselves chiefly to the modifications of the soft appendages, and regarded considerations drawn from the respiratory organs as of secondary importance. Grube occupied himself chiefly with the nature and development of the hard parts which arm the feet. M. de Quatre-

fages states that, in arranging his limited groups of Annelids, he has endeavoured to take all characters into consideration, and not to be exclusively guided by any one special set of *differentia*.

Cuvier.—ANNÉLIDDES. Tubicoles. Dorsibranches. Abranches.
(Limivora of (Rapacia of (Oligochæta and
Grube.) Grube.) Discophora of
Grube.)

Grube.—

Class ANNELIDA.

Ord. Appendiculata Polychæta. Gymnocopa. Onychophora. Oligochæta. Discophora.
(All the marine setigerous (Tomopteris (Peripatus (Earthworms.) (Leeches.)
worms.) only.) only.)

Grube divides his Polychæta thus:

RAPACIA, with the families *Aphroditea*, *Amphinomea*, *Nephtydea*, *Glycera*, *Phyllodocea*, *Lycoridea*, *Amytidea*, *Eunicea*, *Aricea*, *Syllidea*.

LIMIVORA, with the families *Chætopτερα*, *Pherusea*, *Maldania*, *Opheliacea*, *Telethusa*, *Terebellacea*, *Hermellacea*, *Serpulacea*.

M. de Quatrefages' class Annelida, the relations of which to the other groups of his Annelés (Annuloida) may be seen by the table at the beginning of this article, is thus divided:

Order 1. ERRATICÆ.

Order 2. SEDENTARIÆ.

Sub-Order 1.		Sub-Order 2.		Sub-Order 3.		Sub-Order 4.	
Erraticæ aberrantes.		Erraticæ propriæ.		Sedentariæ aberrantes.		Sedentariæ propriæ.	
Fam.		Fam.		Fam.		Fam.	
1.	<i>Aphroditea</i> .	1.	<i>Eunicea</i> .	1.	<i>Chætopτερα</i> .	1.	<i>Tomopteridea</i> .
2.	<i>Palmyrea</i> .	2.	<i>Lumbrinerea</i> .			2.	<i>Clymenea</i> .
		3.	<i>Amphinomea</i> .			3.	<i>Arenicolea</i> .
		4.	<i>Nephtydea</i> .			4.	<i>Ophelea</i> .
		5.	<i>Nerinea</i> .			5.	<i>Aricea</i> .
		6.	<i>Cirrhaturea</i> .			6.	<i>Leucodorea</i> .
		7.	<i>Chloremea</i> .			7.	<i>Hermellea</i> .
		8.	<i>Nereidea</i> .			8.	<i>Pectinairea</i> .
		9.	<i>Syllidea</i> .			9.	<i>Terebellea</i> .
		10.	<i>Hesionea</i> .			10.	<i>Serpulea</i> .
		11.	<i>Phyllodocea</i> .				
		12.	<i>Glycera</i> .				
		13.	<i>Polyophthalmea</i> .				

This arrangement of the families has much to recommend it, although there may be grounds for objection here and there. It is infinitely better, in a systematic work, that small and numerous groups should be made, than that large and roughly defined assemblages of genera should be treated as families. M. de Quatrefages has shown great conscientious-

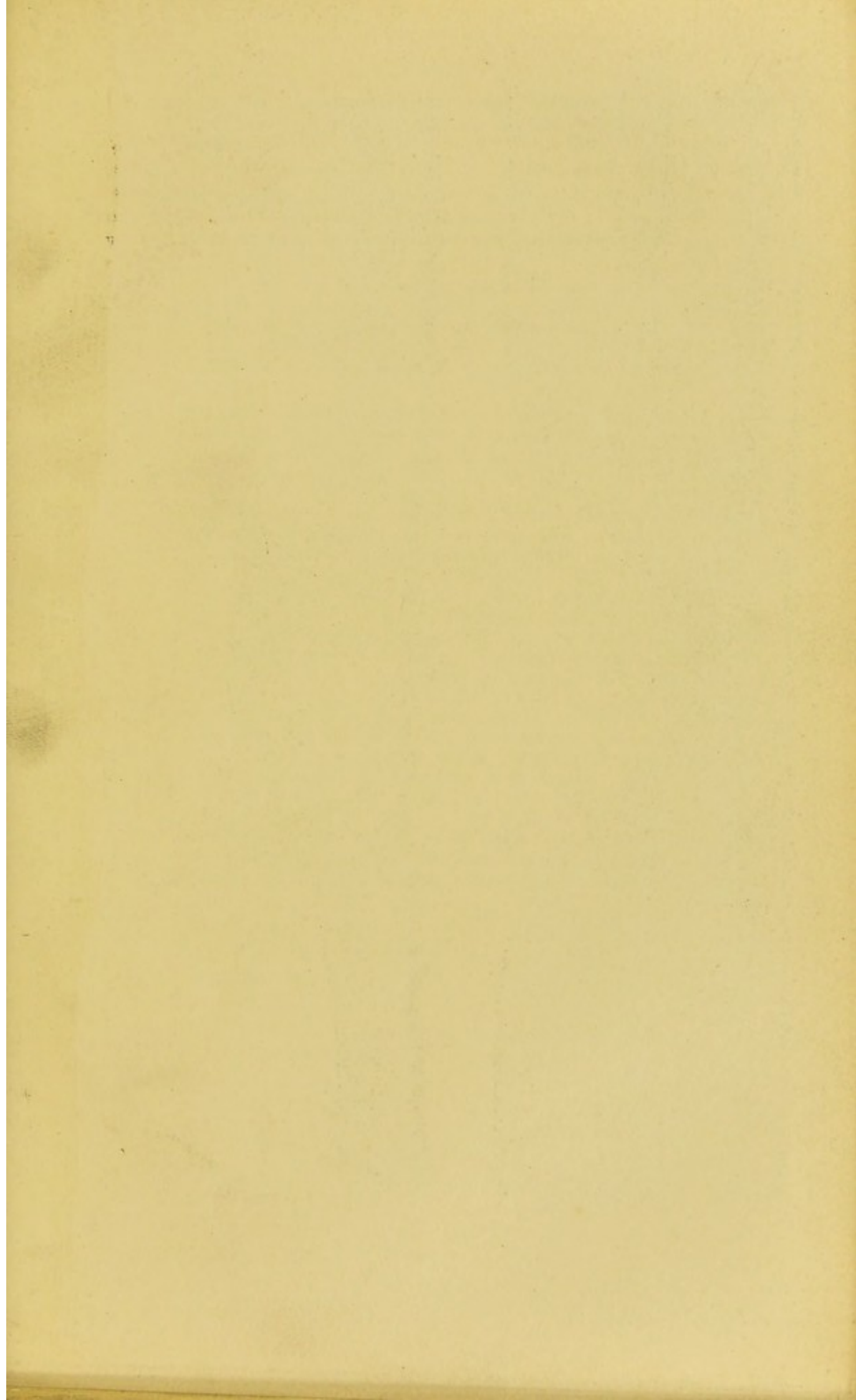
ness in leaving many genera as "*incertæ sedis*," rather than force them into a position which he did not feel sure naturally was theirs.

We now come to the chief part of the work, the systematic description of the families, genera, and species. There are many new genera introduced, and new arrangements of species advocated, which we cannot here examine; and, indeed, they will be best appreciated by a study of the work itself. M. Claparède has already criticised some points in the arrangement of genera very fully, which has given rise to a rather sharp contest in the 'Comptes Rendus' of the French Academy. The family of Syllidea appear to be the great cause of discussion, which present great difficulties to the naturalist by their metamorphoses and alternation of generations, the same species appearing under very different phases. Many new species are described and figured in the work from the collection of the museum; and here we must object to the frequent insufficiency of descriptions and figures. In several cases—*e. g.* *Polynoë setosissima* and *Aphrodita talpa*—the most characteristic parts of the worm are not figured, but merely a general view of the animal is given; and, moreover, in a large number of cases no figure at all is given of the worm described. This cannot but cause difficulty to other zoologists, and is much to be regretted. The figures of species, we notice, moreover, are not infrequently over-coloured—*e. g.* *Hermione hystrix* and *Chætopterus Valencinii*. With regard to the *Chætopterus* of our coasts, M. de Quatrefages re-names it without any compunction, though it has been described and figured most fully in the 'Linnean Transactions' by Dr. Baird as *Chætopterus insignis*. The author was, however, most probably, not aware of this, since these descriptions of species have been in hand for some years. At the same time, there is no evidence in the book of any careful bibliographical research, with a view to reducing the confusion of names at present existing, or even avoiding its increase.

The class Gephyrea, which owes its establishment to the labours of M. de Quatrefages, is treated of in the last 114 pages of the second volume, and in proportion to the size of the group this part of the work will, perhaps, be more valuable to the naturalist than that on the Annelida. This class of Vermes, at present so little known, is discussed in much the same manner as the Annelida, through which we have just passed, and is illustrated in the same way.

Before taking leave of this book we wish again to express our conviction that it will be found of great value to the zoologist and anatomist, since it contains nearly all the

author's original observations rewritten, descriptions of many new species, and many beautiful figures. At the same time, we feel that there is ample scope for a more detailed systematic work, and that the introductory portion is by no means fully up to the time as a special treatise on the anatomy of Annelida.



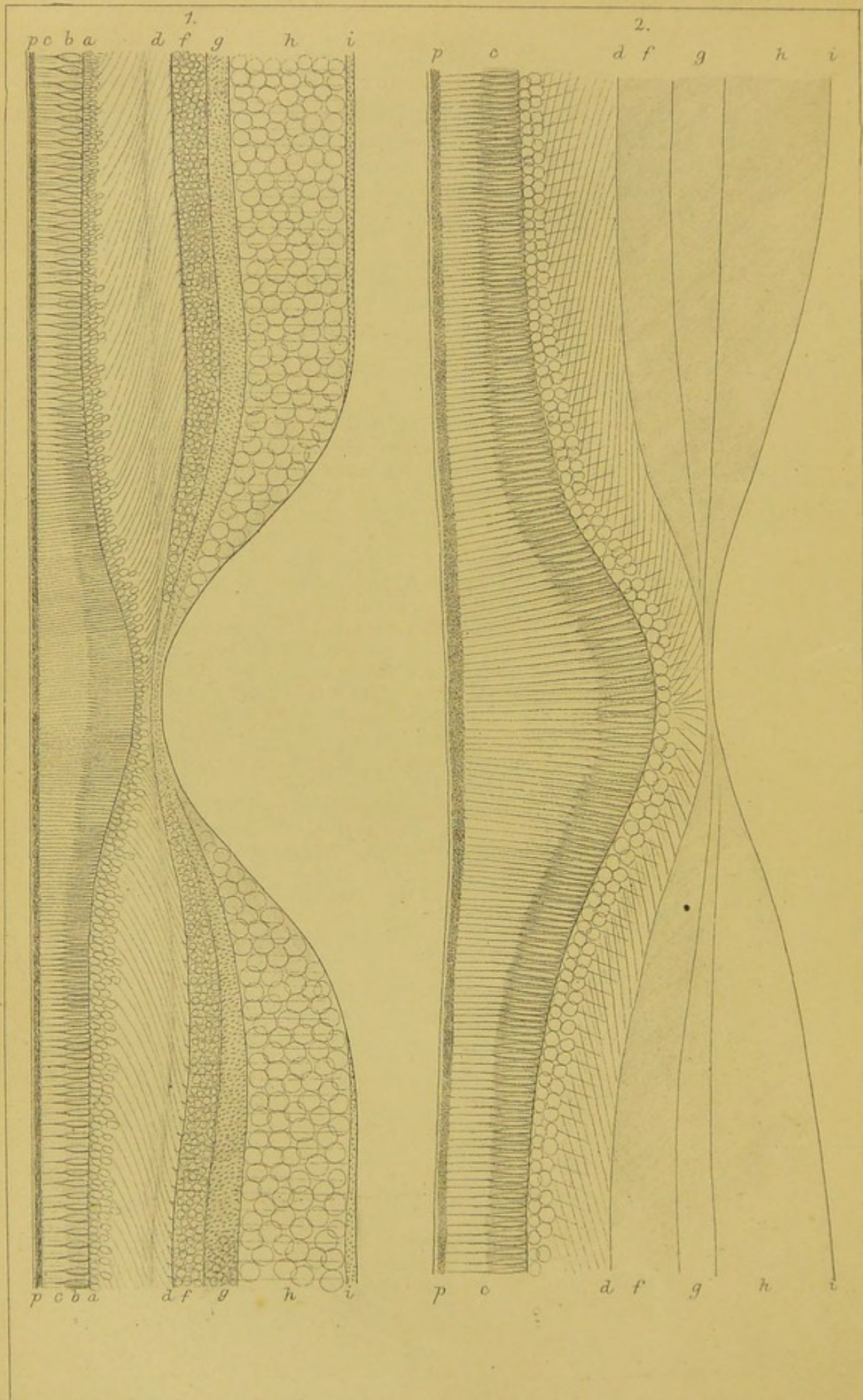


PLATE IV.

Diagrammatic representations of the two kinds of tissue of which the retina of mammals, and especially that of man, is composed. $\times$ about 500 diam.

Fig.

1.—The connective-tissue framework of the retina.

A, A. Membrana limitans externa.

e, e. Radial trabecular fibres, with their nuclei *e', e'*.

l, l. M. limitans interna.

Coarser and finer membranous and fibrous bands connect the radial fibres together, especially in meridional lines, so that the retina may be split into foliaceous sections more readily in a meridional direction than in any other. The closed fibrous plexuses are those corresponding to the intergranular layer *d* and the molecular layer *g*.

2.—The nervous elements of the retina, commencing at the periphery with the rods *b* and the cones *c*, whose outer segments, however, do not appear to be continuous with the inner, but simply in a relation of contiguity. To these succeed the elements of the outer granule-layer, consisting of the rod- and cone-filaments; the latter furnished with nucleated enlargements *b'* and *c'*, corresponding with the granules. In the intergranular layer *d* may be noticed an inextricable plexus of extremely delicate nervous filaments, which are prolonged on the inner aspect into the radial nerve-fibres of the inner granule-layer, which are again furnished with nucleated enlargements, with respect to which it has not yet been determined whether they do not (at any rate, in mammals and man) contribute in one direction or another to the multiplication of the fibres. The straight radial direction of the nerve-fibres is next interrupted by a plexus of extremely delicate fibrillæ, which, together with that formed by the spongeiform connective tissue, constitute the molecular layer of the retina, which may be regarded as resembling the grey substance of the brain, and into which enter, from the inner aspect, the extremely fine ramifications of the processes of the ganglion-cells *h, h*, which, again, are in connection with the fibres of the optic-nerve-layer *i, i*. But, here, the possibility must be regarded, that some of the innumerable and excessively delicate fibrillæ of the optic nerve, which exist together with the coarser ones, in the optic-nerve layer of the retina, may not also enter the molecular layer, without the intervention of ganglion-cells.

DESCRIPTION OF PLATES III & IV,

Illustrating the Notice of Professor Max Schultze's paper on
the Structure and Physiology of the Retina.

PLATE III.

Fig.

1.—Diagrammatic view of a section of the retina through the *macula lutea* and *fovea centralis* magnified about 110 diam.

i. The optic nerve layer.

h. Layer of ganglion-cells.

g. The molecular layer.

f. Inner granule layer.

a—d. Outer granule layer; the outer part of which contains the rod and cone granules, and the inner is almost entirely fibrous.

a. The membrana limitans externa.

b—c. Layer of "rods" and "cones."

p. Pigment.

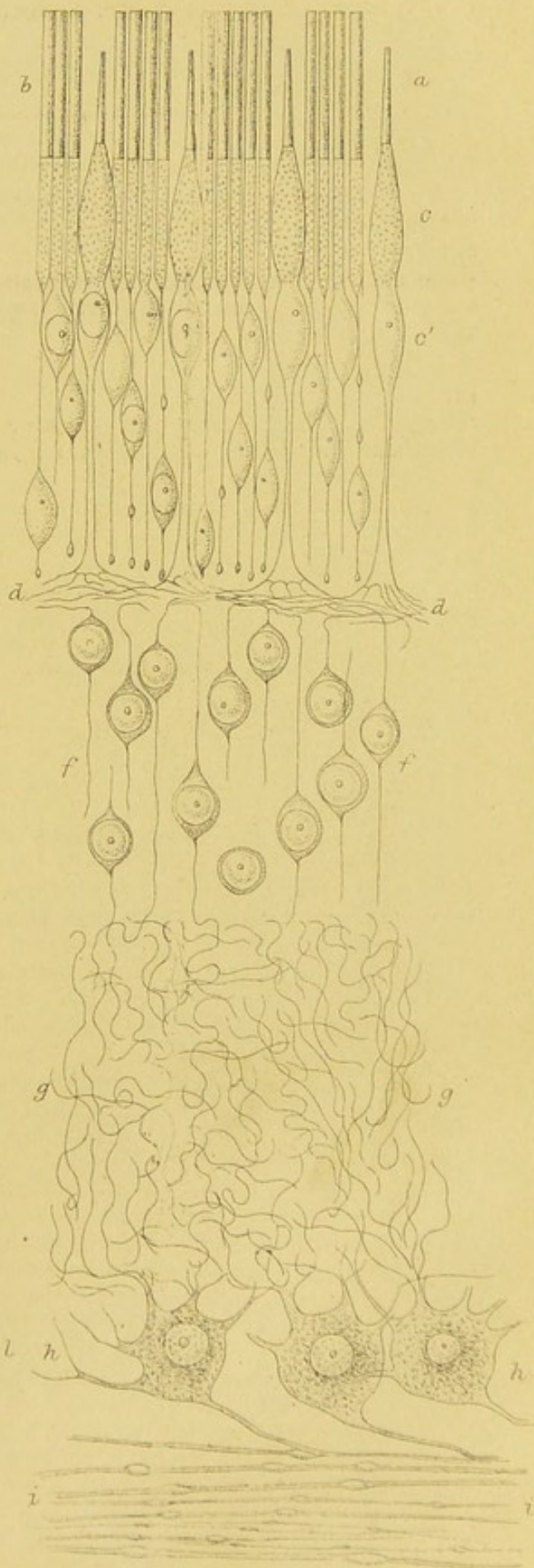
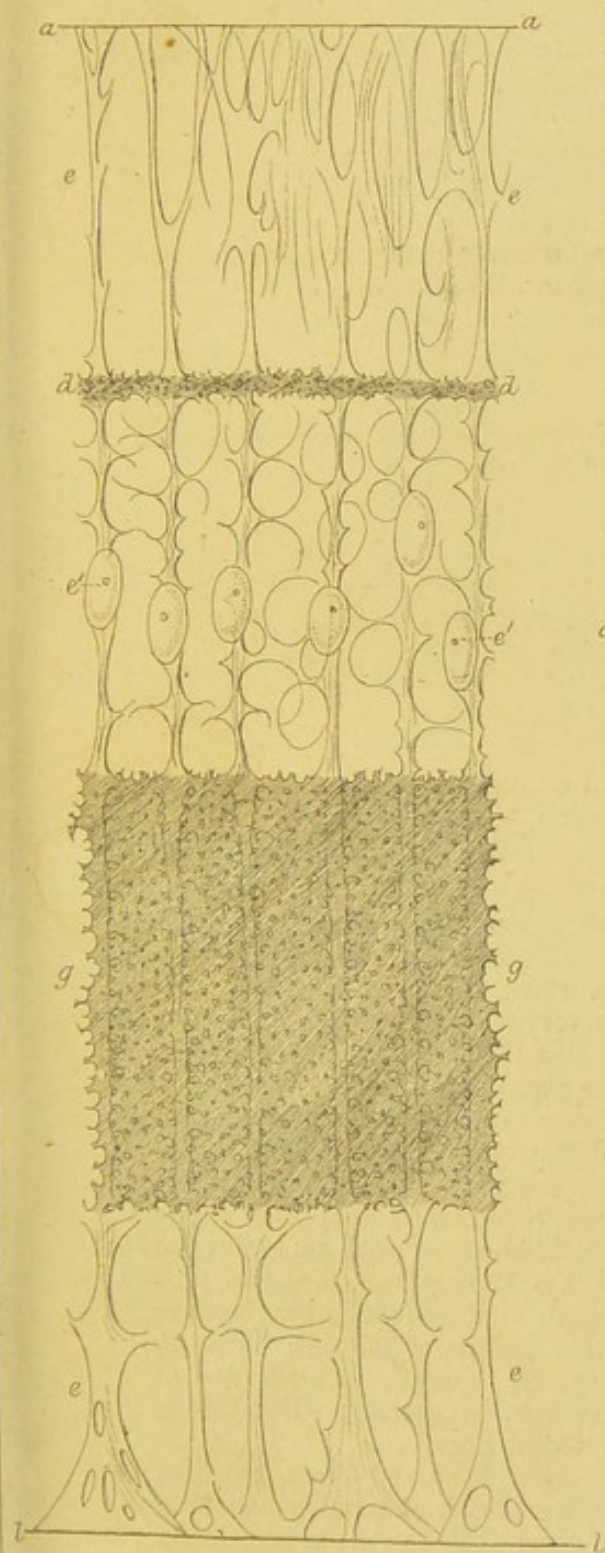
The layers from *a* to *i* are accurately copied from a section through a normal human retina, whose relief, however, towards the vitreous humour was altered in consequence of the commencement of the formation of a *plica centralis*, which, as is well known, makes its appearance at the *macula lutea* very soon after death. But the figure, as it stands, represents the *macula lutea* without the *plica*, and, consequently, in the condition which it would present during life. The bacillary layer was also very well preserved in the same preparation, so that in this respect also the figure very fairly represents the natural condition; but the pigment was no longer attached to the percipient elements, and, consequently, in order to complete the figure, that part has been introduced from other preparations. Under these circumstances, also, the representation of the cones in the *fovea* as it is here given has, of course, been taken from other specimens. Although in the one first mentioned, as well as in several others, in which the central *plica* was already formed, it was possible to determine the increased length of the cones in the *fovea*, as compared with those in the immediate vicinity of it, still, owing to the absence of the pigmentary layer, no criterion was afforded of the absolute length of the cones in the living state. But this is afforded in the preparation represented in Fig. 2.

2.—Represents a section through the *macula lutea* and *fovea centralis*, taken from an eye hardened in Müller's fluid, and which had been extirpated in consequence of staphyloma. $\times 180$ diam. and drawn with the *camera lucida*. Letters as above.

The inner layers of the retina are not represented in detail, as they were in a state of advanced atrophy. The cones were quite perfect, and remained in close connection with the pigmentary layer in which they were ensheathed at the choroidal extremity.

1.

2.



B 35