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ON THE STRUCTURE OF THE BRAIN OF THE SESSILE-EYED CRUSTACEA.

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READ AT WASHINGTON, APRIL 14, 1884.

By A. S. Packard.

The following descriptions and notes have grown out of an attempt to compare the nervous system, particularly the brain and other ganglia of the head, of the eyeless species of cave-inhabiting Arthropods with their out-of-door allies. We have begun with the structure and morphology of the brain of *Asellus communis* Say as a standard of comparison with that of the blind Asellid, *Cecidotæa stygia* Pack., which is so common in the brooks of Mammoth and other caves and in the wells of Southern Indiana and Illinois. Studies of this nature are, it seems to us, well calculated to throw light on the origin of the cave forms, and to show what great modifications have been produced in these organisms by a radical change in their surroundings; consisting, as it does, mainly in the absence of light, and perhaps of the usual food, or at least the usual amount of food.

It is plain enough that the species of Cecidotæa are simply eyeless, slender, depauperated Aselli, which have originated from some one of our out-of-door species within a comparatively recent time, at least since the river-terrace epoch of the Quaternary Period. The facts bearing upon the general relations of the blind to the eyed Asellidæ, and a discussion of the change in form of the body and its appendages, and of the causes of the transformation of the species and genus, are reserved for another occasion.

My present purpose is simply to describe and depict the brain and other nerve-centers of the head of *Asellus communis* Say and *Cecidotæa stygia* Pack.

I. The brain of Asellus communis.

The nervous system of the European *Asellus aquaticus* Linn. has been referred to by Leydig and also by Sars, who published a figure of the nervous system as a whole. Leydig's "*Vom Bau des thierischen Körpers*" gives a careful and comprehensive general account of the nervous system of Arthropods, the most complete and authoritative, up to 1864, we possess, supplemented as it is by his excellent *Tafeln von vergleichenden Anatomie*, published in the same year (1864). According to Leydig, in the Isopoda (Oniscus, Porcellio) the optic lobes are very large and overlie the cerebral lobes.

In *Asellus aquaticus* the abundant fat body around the ventral cord belongs to the blood sinus which envelops the nervous cord. Of this form Leydig has little to say, remarking that he did not examine the entire ventral cord, but only sections, which agree in appearance with those of the land wood-lice.

Sar's figure of the brain of *Asellus aquaticus* is drawn on a small scale, is rather indifferent, and does not show more than the cerebral lobes and optic nerves. He evidently did not perceive the other ganglia.

Leydig's valuable figures of the brain of *Oniscus murarius* show that he did not study the nervous centers of the head by means of longitudinal sections, and that he simply dissected the brain from above, a dorsal view showing the large optic lobes to be mostly above and in front of the smaller cerebral lobes, while the ganglion, *e*, in his figure 8 (Taf. VI), which he denominates *nebenlappen*, is probably one of the antennal ganglia. The other ganglia of the head he does not represent, nor speak of in his Vergleichende Anatomie.

The other sketches of Isopod brains by Brandt and Ratzeburg, Rathke, Lereboullet, and Milne-Edwards, as well as those in our "Zoology,"* are drawn on a small scale, are in some cases rather indifferently drawn, and only represent a dorsal view, the antennal and those ganglia posterior to it being concealed from view in dissecting from above downward.†

The observations I have made are based on vertical, longitudinal sections kindly made for me by Mrs. C. O. Whitman, under the direction of Dr. C. O. Whitman. The sections were thin, clear, well-mounted in Canada balsam, in consecutive order, and made from alcoholic specimens, which had, however, been kept for several years, though the nervous system had been well preserved.

THE HISTOLOGICAL ELEMENTS OF THE GANGLIA.

Unlike the central nervous system of Vertebrates, in which there are but two kinds of nerve tissue, viz, ganglion cells and fibers, there are in the Asellidæ, as in insects and Decapods, three kinds of elements in the brain and other ganglia, viz: (1) ganglion cells; (2) nerve fibers; and (3) Leydig's *puntzsubstanz* (*marksubstanz* of Leydig and Rabl-Rückhard, and especially Dietl), which might be called the *myeloid* tissue or substance.

(1) *Ganglion cells.*—These have not, as in the brain of the lobster, a simple nucleus and nucleolus, but they usually have numerous, from 10 to 20, nuclei, the nucleolus of each nucleus readily receiving a stain and forming a distinct dark mass. They resemble those of the locust.‡ They are, as a rule, much smaller, however, than in the locust. As seen in most of the sections they appear to be spherical, being cut through transversely by the microtome, but as shown by Fig. 3*a* they are of the usual pyriform shape. In size they are very much smaller than those of the lobster and much more uniform in size, very few of the cells being twice as large as those of the average size; as already remarked, the nucleus in the ganglion cells of the American lobster are almost uniformly simple and homogeneous, with a single nucleolus. The largest ganglion cell of the lobster's brain which we have found is six times as large as the largest ganglion cell ot Asellus.

The ganglion cells appear to be entirely unipolar; no bipolar or multipolar cells were observed, though special search was made for them. Nothing noticeable was observed in respect to the nerve-fibers. The *punktsubstanz*, *marksubstanz* or myeloid substance, as we may designate it, differs in its topographical relations from that of the brain of Decapoda. This myeloid substance, which seems to be peculiar to the worms, mollusks, and especially the crustacea and insects, has been most thoroughly studied by Leydig. This is the central finely-granular part of the brain, in which granules have short irregular fibers passing through them. In his *Vom Bau des thierischen Körpers*, p. 89, Leydig thus refers to it:

> In the brain and ventral ganglia of the leech, of insects, and in the brain of the Gastropods (Schnecken) I observe that the stalks (stiele) of the ganglion-cells in nowise immediately arise as nerve-fibers, but are planted in a molecular mass or *punktsubstanz* situated in the center of the ganglion, and merged with this substance. It follows, from what I have seen, that there is no doubt *that the origin of the nerve-fibers first takes place from this central punktsubstanz.*
>
> This relation is the rule. But there also occur in the nerve-centers of the invertebrates single definitely situated ganglion cells, whose continuations become nerve-fibers without the intervention of a superadded punktsubstanz.

Leydig subsequently (p. 91) further describes this myeloid substance, stating that the granules composing it form a reticulated mass of fibrillæ, or, in other words, a tangled web of very fine fibers.

> We at present consider that by the passage of the continuation of the ganglion cells into the *punktsubstanz* this continuation becomes lost in the fine threads, and on the other side of the *punktsubstanz* the similar fibrillar substance forms the origin of the axis-cylinders arranged parallel to one another; so it is as good as certain *that the single axis-cylinder derives its fibrillar substance as a mixture from the most diverse ganglion cells.*

The myeloid substance in the brain of Asellus is not however differentiated into distinct spherical masses, the *punktsubstanzballen* of Krieger (*Balken* of Dietl) or whitish ball-like masses

* Fig. 255, *Idotæa inorata*, and Fig. 256, Serolis, drawn by J. S. Kingsley.

† Since this essay has been prepared I have obtained Dr. Bellonci's excellent memoir on the nervous system of Sphæroma, in which he figures and describes the brain and nervous system in general of that Isopod.

‡ Second Report United States Entomological Commission, ch. xi. The Brain of the Locust, 1880 (Pl. xi, Fig. 3b–3e).

which are so characteristic of the brain of the Decapod Crustacea and the insects; and in this respect there is probably a wide difference between the brain of Decapoda and Edriophthalmata.

HISTOLOGICAL TOPOGRAPHY OF THE NERVE-TISSUES.

(1) *The ganglion cells.*—These cells form a cortical layer enveloping on all or nearly all sides the central myeloid mass. The cells being distinct and more or less loosely arranged readily take a deep carmine stain, while the much more dense myeloid mass remains white and unstained.

The ganglion cells are collected into more or less definite masses, enveloped by connective tissue, the latter as it were forming a mesh, inclosing spherical masses of ganglion cells. In a vertical section, such as that represented by Figs. 2 and 3, passing through the anterior and middle part of the brain and in the horizontal section (Fig. —), while the ganglion cells are seen to be packed more or less solidly around the central myeloid portion, they are also seen to be disposed in more or less distinct lobular masses, which are inclosed by connective tissue. Seven or more distinct lobes or subspherical masses of these ganglion cells may be distinguished on each side of the brain.

As seen in Figs. 2 and 3, the uppermost or dorso-frontal lobes are the double sets filling the upper or dorsal fissure between the right and left lobes of the brain and marked *a* and *b*; *b* is divided into two sublobes, the upper (b^1) being small, flattened, and lying on the dorsal and inner edge of the central lobe. The third set is a double lobe, $c\ c^1$; these may be called the dorso-lateral set; they are more or less connected with the lateral lobes $d\ d^1$, and the latter with the externo-commissural set of lobes ($e\ e^1$). On the dorsal side of the brain near the base of the optic ganglia are two sets, one above and one below (*g*) the base of the optic ganglion; the exact relation of these to the others is not very plain from our sections, but they are in front of and external to the outer edge of the lobes of the brain.

The optic ganglion is enveloped by a lobulated mass of ganglion cells exactly like those of the brain proper, and these lobes (*h i k*, Fig. 27) which envelop the myeloid mass can be distinguished from the outer one at the beginning of the outer division of the nerve fibers sent to the eye from the ganglion cells.

(2) *The nerve fibers.*—The fibers arising from the ganglion cells form the commissures which unite the brain with the subœsophageal and succeeding ganglia; and also the commissures between the two cerebral lobes.

One set of fibres arise in the dorso-frontal group of ganglion cells (Fig. 3, *f b*), to become lost in the myeloid substance. The fibers are seen to pass down, and to form a part of the subœsophageal commissure, although we did not trace them to the last abdominal ganglion. Judging from Michel's observations on the commissural fibers of *Oryctes nasicornis*,* there is little doubt but that in all Arthropoda certain nerve-fibers arising in the pro-cerebral lobes pass uninterruptedly to the last ventral ganglion.

It will be further seen by reference to Figs. 2, 3 (Asellus), and especially Fig. 27 (Cecidotæa), that the fibers arising from certain of the ganglion cells in lobes *c* and c^1 pass into the cerebral lobe in two directions, some connecting the two lobes, forming the transverse commissure, while others pass down and run parallel with the fibers from the dorso-frontal lobes and aid in building up the subœsophageal commissures. The latter commissure is also re-enforced by fibers from the lateral lobes $d\ d^1$, $e\ e^1$.

From what we have seen in the sections represented by the camera sketches referred to (Figs. 2, 3, and 27), and from what is known of the cells and fibers of other Arthropods, there is no doubt but that all the ganglion cells give rise to fibers, some of which at least pass directly through or above or around the myeloid substance of the cerebral lobes and form the commissures. This independence of the myeloid substance appears to be more general in the Asellidæ, at least this we would infer from Leydig's statements previously quoted. When we look at Fig. 1, which is a composition (drawn, however, with the camera) from the sections represented by Figs. 5 and 8 we see that the two main longitudinal commissures pass above the seven post-cephalic ganglia represented in the figure. Those ganglia are masses of myeloid substance, with a cortical layer of gan-

* Michels. Beschreibung des Nervensystems von *Oryctes nasicornis* in Larven, Puppens und Käferzustand. Zeits. f. wissens. Zoologie., xxxiv, 641–702. 1880.

glion cells, from which fibers arise after passing through the myeloid substance; there becoming broken up into a tangled mass of fibrillæ, which unite finally to form the fibers constituting the nerves of the appendages. Without doubt also a few commissural fibers from the procerebral lobes pass into each post-cerebral ganglion so as to afford the means to the cerebral lobes (*primi inter pares*, as happily styled by Leydig) of coördinating the nervous power of the other ganglia, their histological and morphological equivalents. It should be said that although Leydig's view as to the relations of the nerve-fibers to the myeloid substance may be the correct one, yet though it may apply to the Annelids, it may not be so general an occurrence in the Arthropods. It seems to us, though we are still open to conviction, that the transverse and longitudinal commissural fibers, which undoubtedly arise from the cortical ganglion cells, have little or nothing to do with the myeloid substance. This latter substance does not exist in the nervous system of the vertebrates, and just what its nature and function clearly are in the invertebrates has yet to be worked out. In the hands of a skillful and expert histologist, much light will yet be thrown upon this difficult subject; certainly the present writer has not the qualifications for the task. His own opinion from what little he has seen is, that the myeloid substance is the result of the splitting up into a tangled mass of very fine fibrillæ of certain of the fibers thrown off from the mono-polar ganglion cells, *i.e.*, such fibers as do not go to form the main longitudinal commissures. It should also be borne in mind that in the embryo the ganglia are composed of ganglion cells alone, with few if any primitive fibers.

MORPHOLOGY OF THE BRAIN.

The brain of the Isopods and Amphipods is a *syncerebrum*, though far less complicated than in the Decapoda. It will be remembered that Professor Lankester in his memoir on Apus designates the simple brain of that crustacean as an *archicerebrum*, while the composite brain of "all crustacea, excepting Apus, and possibly some other Phyllopods," he denominates a *syncerebrum*. In our Monograph of N. A. Phyllopoda, p. 403, we adopted the view that the brains of all Crustacea except the Phyllopoda and Merostomata were syncerebra, and we divided the syncerebrum into three types; adding that the syncerebrum of sessile eyed crustacea (Edriophthalma) was built on a different plan from that of the Decapoda.

Fig. 1 has been drawn to give a general view of the nervous centers of the head, including the first thoracic segment and its ganglion. It has been drawn with the camera from a number of sections, especially those represented by Figs. 5–8, so that it is believed to be approximately correct and not merely a schematic plan. The section passes through the head on one side of the œsophagus, which of course is not represented in the sketch; being so near the median line it does not involve the optic lobes and eyes, which, especially the latter, are on the extreme side of the body, so that these organs could not well be shown in the drawing. The general relation of the nervous system to the body walls, to the stomach and the appendages are made obvious in the sketch, and their description need not detain us. It should be borne in mind that the mouth and œsophagus open between the mandibles. They are shown in Fig. 5. The end of one of the ovarian tubes is seen to overlie the pyloric end of the stomach; it does not pass into the head. The drawing of the heart is somewhat diagrammatic, as it was not well shown in the sections, but its position is believed to be approximately correct. The sympathetic nerve was not discovered.

As seen in Fig. 1, the brain or supraœsophageal ganglion is a composite mass or group of four pairs of ganglia, *i. e.*, (1) the brain proper or procerebral lobes, (2) the optic ganglia, (3) the first antennal, and (4) the second antennal lobes. These lobes are quite separate from each other in the Isopoda and Amphipoda as compared with the Decapoda.

THE PROCEREBRUM OR PROCEREBRAL LOBES.

These constitute the brain proper, and have been usually called the "cerebrum" or "cerebral lobes." As, however, they are not the homologues of the lobes of that name in Vertebrates, either structurally or functionally, we would suggest that the ganglion be termed the *procerebrum* and the individual lobes the *procerebral lobes*, not only in allusion to its position in advance of all the other ganglia, but since it stands as the co-ordinating, regulating ganglion, the first in importance of all the ganglia.

As regards size, the procerebral lobes are more than double that of the other ganglia; they bulge out dorsally and backward, so as to conceal from above the antennal and mandibular ganglia. Plate 1, Fig. 2, represents a section through the lobes in front of the commissure, showing at *a, b*, the dorso-frontal group of ganglion cells, those nearest the myeloid substance sending fibers downward (*fb*) to form a part of the œsophageal commissure. At Fig. 3, a section farther back and passing through the commissure, the fibers are seen to pass directly through the myeloid substance along the inner side of the commissure. Fig. 4 represents a still more posterior section; this shows distinctly the origin of the fibers of the transverse commissure (*tr. c*) from the ganglion cells of the upper and outermost portion of the lobes. The commissure is seen to be composed of three bundles of fibers—an upper, middle, and lower or ventral; the space between the upper and middle bundles being filled with myeloid substance.

Vertical sections of the procerebral lobes are seen in Figs. 5 to 8. Fig. 5, which passes through the median line of the head, through the mouth, œsophagus, and the median line of the stomach, shows the procerebral lobe on one side of the commissure; and, below, the second maxillary and maxillipedal ganglia. Fig. 7, passing through one side of the first antennal ganglion, shows the procerebral lobe nearly separate from the antennal lobe. Fig. 8 represents a section passing through the main commissure and a portion of the procerebral lobe.

Horizontal sections from the top of the head downwards are seen in Figs. 9 to 18. Fig. 9 represents a section through the upper part of the procerebral lobes; Fig. 10, through the lobes above the transverse commissure; Fig. 11, through the entire procerebrum, near the origin of the optic ganglia and optic nerves.

THE OPTIC GANGLIA AND OPTIC NERVES.

The eyes being smaller in Asellus than in most other genera of Isopods, particularly Oniscus and Porcellio, the forms figured and described by Leydig; the optic ganglion and nerve are also much smaller, while the eyes being set farther back on the sides of the head, the ganglion and nerve are directed obliquely backward, so that a series of vertico-frontal sections pass through the brain before reaching the optic nerve. Pl. IV, Figs. 19–21, represent these organs. Fig. 19 shows the procerebral lobes, and on the left the optic ganglion and the optic nerve leading to the eye. Fig. 20 represents a section just behind the procerebral lobes, passing through the hinder edge of the cortical layer of ganglion cells. Fig. 21 is an enlarged view of the sam e. The optic lobe is divided into two parts, the inner connected with the procerebral lobe, with an abundant supply of ganglion cells, while from the smaller, outer division arise the fibers which unite to form the optic nerve, which divides at or just beyond the middle into several branches sent to the eyes. These branches are seen to end in slightly bulbous expansions among the small retina cells, forming the deep-brown pigment-mass in which the lenses are imbedded.

The first antennal ganglia (Figs. 1, 7, and 12).—The relations from a side view to the other parts of the brain are seen in Figs. 1, 7, and 7*a*. It will be seen that the ganglion is much freer from the procerebral lobes than in the Decapoda. It may be seen from above, when looking down upon the brain, projecting somewhat in advance of the procerebral lobes, the first antennal nerve arising from the upper and anterior side, ascending a little at its origin, and passing horizontally into the base of the antenna. Fig. 12 represents a horizontal section through the lobes, showing the ganglion cells, the myeloid substance, and the origin of the antennal nerves.

The second antennal lobes (Figs. 1, 7, 7*a*, 14 to 16).—The second antennal ganglion lies directly beneath the upper or first antennal lobes, and appears to be slightly larger than the latter, the nerves being larger, corresponding to the much larger size of the second antenna. It will be seen by reference to Figs. 14 to 16 that the œsophagus passes between the lower part of the lobes, which are almost wholly separate. (Figs. 17 and 18, which represent sections just below that represented by Fig. 16, are introduced to show the œsophageal commissures and their ganglion cells on each side of the œsophagus.)

The first subœsophageal or mandibular ganglion (Figs. 1, 6, 7, 22, 23, *md. g.*).—This is rather larger than either of the antennal ganglia, as its relations to the brain are well seen in the sections represented by Fig. 6. By reference to the sections represented by Figs. 5 and 6, it is clearly seen to lie directly under the antennal ganglia, and to be separated from the brain proper by the short œsophageal commissures. It is therefore the first subœsophageal ganglion, giving off but a single pair of nerves, those supplying the large tripartite mandibles.

The ganglion lies in front of the main longitudinal commissure, and in position in front of the lower side of the stomach, being situated in an inclined plane, nearer vertical than horizontal The sections represented by Figs. 22 and 23 pass through a portion of it, and in them is well seen. the mode of origin of the large mandibular nerves.

The first and second maxillary ganglia.—These are situated widely apart, neither coalescing with the other ganglia in front or behind. The first maxillary ganglion (Figs. 1, 8, 22, 23, *mx. g.*) is situated nearer the mandibular than the second maxillary ganglion, as seen in Figs. 1, 22, and 23. It lies in an inclined plane, and is much smaller than any of the other postœsophageal ganglia, as it innervates smaller appendages.

The second maxillary ganglion (Figs. 1, 8, 22, 23, mx^2 *g.*) is situated next to the maxillipedal ganglion, and like that lies in a horizontal position. It is of nearly the same size but a little smaller than the ganglion next behind it, and the commissures connecting it with the maxillipedal ganglion are very short.

The maxillipedal ganglion (Figs. 1, 8, 22, 23 *mx p. g.*) is a little larger than its near neighbor, the second maxillary ganglion, inasmuch as it innervates the large maxillipedes.

At some distance behind this ganglion and situated in the first thoracic segment is the first thoracic ganglion supplying the nerves to the first pair of feet. It is a little larger than the maxillipedal ganglion.

The main longitudinal commissures (Figs. 1, 22, 23) pass over the ganglia, and are united in the head, except at two points indicated by the clear spaces in the figure, behind which point we have not traced it. Sars, however, represents the main longitudinal commissure behind the head as double.

In the section represented by Figs. 22 and 23 the limits of the mandibular and first maxillary ganglia are not definite, and they are seen to be connected by a bridge or tract of myeloid substance. Towards the second maxillary ganglion the fibers in the section are fewer and lower together, and are seen in some cases to enter the myeloid substance, but in others to pass over it. The ganglion cells of the maxillipedal ganglion are more numerous than those about the myeloid mass of the second maxillary ganglion

From the foregoing facts it will be seen that the brain of the *Asellidæ* is composed of four preœsophageal pairs of ganglia, situated at greater or less distance apart from each other, being a very loosely constructed syncerebrum compared with that of such Decapods as have been thus far examined. The mouth-parts in the *Asellidæ*, if not all Isopoda, are not innervated from a single subœsophageal ganglion, but each appendage, beginning with the mandibles, is supplied by a nerve arising from a separate ganglion. Thus there are eight ganglia of the first order in the head of these Isopods, our observations not referring to any secondary ganglia, which may or may not exist in connection with the brain or sympathetic nervous system. It will be remembered that in the Decapods, the lobster for example, the brain innervates the eyes and antennæ, while the only other ganglion in the head is the subœsophageal, from which the mouth appendages are all innervated; thus there are but two nerve-centers in the head of adult Decapods; the subœsophageal ganglia being concentrated probably during embryonic or larval life.

II. The brain of the eyeless form Cæcidotæa.

It is a matter of great interest to know just what, if any, changes take place in the brain or nerve-centers of the head of the eyeless forms related to Asellus; whether the modification is confined to the external parts of the eye, or to the optic lobes and nerves alone.

It is well known that a blind Asellus-like form is abundant in the brooks and pools of Mammoth and other caves in Kentucky and Indiana, as well as in the wells of the cavernous and adjacent regions. The foregoing observations on the brain and eyes of the common Asellus of our brooks and ponds were made to afford a basis of comparison with the similar parts in the eyeless form.

Cæcidotæa in its external shape is seen to be a depauperate Asellus, with the body, however, much longer and slenderer than in the eyed form, and with slenderer appendages. It is not usually totally eyeless. In a number of specimens from a well at Normal, Ill., kindly sent us by Mr. S. A. Forbes, a minute black speck is seen on each side of the head in the positions of the eyes of Asellus, just above the posterior end of the base of the mandibles. In some specimens these black dots are not to be seen; in others they are visible, but fainter than in others. In twelve specimens which I collected in Shaler's Brook in Mammoth Cave I could detect no traces of eyes, and infer that most, if not all, the Mammoth Cave specimens are totally eyeless. It thus appears that different individuals have eyes either quite obsolete, if living in caves in total darkness, or, if living in wells, with eyes in different degrees of development up to a certain stage—that represented by black dots—which, however, are so easily overlooked, that we confess, after handling dozens of specimens, we did not suspect that the rudimentary eyes existed, until our attention was called to them by Dr. C. O. Whitman when he sent the slides. The European *Cæcidotæa forelii* is also said to be blind. The specimens we received through the kindness of Professor Forel, which were, unfortunately, dried and spoiled, seemed to be entirely eyeless, though special search was not made for the eye-specks.

It will be seen that the eyeless Cæcidotæa differs from Asellus as regards its brain and organs of sight, in the complete loss of the optic ganglion, the optic nerve, and the almost and sometimes quite total loss of the pigment-cells and lenses.

After a pretty careful study of numerous vertical sections of the brain of *Cæcidotæa stygia* as compared with that of *Asellus communis* we do not see that there are any essential differences, except in the absence of the optic ganglia and nerves. The proportions of the procerebral lobes, of the ganglion cells, their number and distribution, the size of the transverse and longitudinal commissures are the same. The head and brain as represented is smaller than in Asellus, the form itself being considerably smaller.

Fig. 25 represents a section through the middle of the procerebral lobes, which may be compared with that of Asellus, Fig. 4. Another section a little posterior is represented by Fig. 26. Fig. 27 is an enlarged view of a section still further back, which shows that there is little, if any, difference between the brain at this point and that of Asellus represented by Fig. 3. In this section it is easy to see that the ganglion cells on each side of the procerebral lobes send fibers directly through the myeloid mass to form the transverse commissures. The section at this point does not show the fibers arising from the fronto-dorsal group of ganglion cells; but traces of them are seen in Fig. 28, which represents a section corresponding to that indicated by Fig. 3.

Careful examination of the sections passing behind the procerebral lobes and œsophageal commissures failed to show any traces of the optic ganglion of either division, or of the ganglion cells and myeloid substance composing it. Every part connected with the optic ganglia seems to be totally abolished. The same may be said of the optic nerve throughout its length. The amount of time spent in examining the numerous well cut, thin, and beautifully mounted sections made by Dr. Whitman, or under his direction, enables us to affirm positively that the entire nervous portion of the optical organs are wanting. And we are glad to add that Dr. Whitman also observed to us the absence of the optic nerves.

With the eye itself it is different. The modification resulting from a life in total darkness has left traces of the eye, telling the story of degeneration and loss of the organs of sight, until but the merest rudiments of the eye remain as land marks pointing to the downward path in degradation and ruin taken by the organs of vision as the result of a transfer to a life in total or partial darkness, as the case may have been, in the well-inhabiting or cave-dwelling individuals.

Fig. 29 represents a section through the head of *Cæcidotæa stygia* behind the procerebral lobes and œsophageal commissures, showing the absence of any traces of the optic ganglia or optic nerves, but indicating the rudiments of the eye, showing that the pigment mass of the retina and the lenses exist in a very rudimentary condition, while the optic nerve and ganglion are entirely aborted.

Figs. 30 and 31 represent enlarged views of the rudimentary eye of two different specimens of *C. stygia* from Mammoth Cave. In the sections represented by Fig 30 *a b* we see that the number of facets has been reduced apparently to two (*b*), the rudimentary lenses being enveloped by a black pigment mass. This section, examined by Tolles' $\frac{1}{5}$ A, is magnified and drawn to exactly the same scale as that of the eye of Asellus represented by Fig. 21. In that figure may be seen the normal size of the lenses and of the retina cells. It will be seen that in Cæcidotæa the retina cells are broken down and have disappeared as such, and that the rudimentary lens (or the hyaline portion we suppose to be such) which the retinal pigment incloses is many times smaller than in the normal eye of Asellus.

On comparing the eyes of the two specimens as shown in Figs. 31*a* and 32*a*, it will be seen that the eyes in one are considerably larger than in the other specimen. Fig. 32*b* shows that in the eye of this individual there were at least four lenses, if not more, not included in the section. At the point indicated by 32*d* on the edge of the eye one lens is indicated (though the divisions are wanting), not wholly concealed by the pigment of the retina; a more magnified view is seen at Fig. 32*e*. The four sections *a–d* passed through the eye, the section in front and behind not touching the eye itself.

It thus appears from the observations here presented that the syncerebrum of the blind Cæcidotæa differs from that of the normal Asellus in the absence of the optic ganglia (both divisions) and the optic nerves, while the eyes are exceedingly rudimentary, the retinal cells being wanting; the black pigment mass inclosing very rudimentary minute lens-cells, which have lost their transverse zonular constriction or division; the entire eye of Cæcidotæa finally being sometimes wanting, but usually microscopic in size, and about one-fifth as large as that of the normal Asellus.

The steps taken in the degeneration or degradation of the eye, the result of the life in darkness, seems to be these: (1) the total and nearly or quite simultaneous loss by disuse of the optic ganglia and nerves; (2) the breaking down of the retinal cells; (3) the last step being, as seen in the totally eyeless form, the loss of the lens and pigment.

That these modifications in the eye of the Cæcidotæa are the result of disuse from the absence of light seems well proved; and this, with many parallel facts in the structure of other cave Crustacea, as well as insects, arachnids, and worms, seems to us to be due to the action of two factors: (a) change in the environment; (b) heredity. Thus we are led by a study of these instances, in a sphere where there is little, if any, occasion for struggling for existence between these organisms, to a modified modern form of Lamarckianism to account for the origination of these forms, rather than to the theory of natural selection, or pure Darwinism as such.

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EXPLANATION OF PLATES.

PLATE I.—ASELLUS COMMUNIS.

Fig. 1. Longitudinal section through the head on one side of mouth and œsophagus, showing the brain or procerebrum (*p c m*), first and second antennal ganglia; mandibular, first and second maxillary, the maxillipedal ganglia and nerves passing to the antennæ and mouth-parts × 1½ inch A.

Fig. 2. Section through the procerebral lobes in front of the optic nerves × ½ A.

PLATE II.—ASELLUS COMMUNIS.

Fig. 4. Section of the procerebrum posterior to Fig. 3, × ½ A.

Fig. 3. Section through procerebrum and main commissure × ½ A, 3*a*, ganglia cells from lobe *b*. × ⅛ C.

Fig. 5. Section through the median line of the head, involving the œsophagus and one of the procerebral lobes.

Fig. 6. Section through the head. × ½ A.

Fig. 7. Section of the head passing through one side of the first antennal ganglion and showing the origin of the first antennal nerve; also the second antennal ganglion, and mandibular ganglion (*md.g*) × ½ A.

Fig. 7*a*. Section passing near 7 and through the main commissure.

PLATE III.—ASELLUS COMMUNIS.

Fig. 8. Section passing through the main commissure from the procerebral to the 1st pedal ganglion.

Fig. 9–18. Horizontal sections from the top of the head downwards × ½ A.

PLATE IV.—ASELLUS COMMUNIS.

Fig. 19. Transverse section of the head through the procerebral lobes and through the eyes and optic nerves and commissures $\times \frac{1}{6}$ A.

Fig. 20. A section back of the procerebrum passing through the optic ganglion, optic nerve and eye.

Fig. 21. Same section as in Fig. 20, enlarged $\times \frac{1}{6}$ A, *rc*, retinal cells; *op*, *n*, optic nerve; *h*, *i*, *k*, masses of ganglion cells.

Fig. 22. Horizontal section through the main commissures and the first and second maxillary ganglia, and maxillipedal ganglia, and showing the origin of the mandibular nerves. $\times \frac{1}{2}$ A.

Fig. 23. The same section as in Fig. 22, enlarged. $\times \frac{1}{6}$ A.

PLATE V.—CÆCIDOTÆA STYGIUS.

Fig. 25. Transverse section through the procerebrum and commissures. $\times \frac{1}{2}$ A.

Fig. 26. Section a little posterior to that of Fig. 25. $\times \frac{1}{2}$ A.

Fig. 27. Enlarged sketch of section still farther back. $\times \frac{1}{6}$ A.

Fig. 28. Enlarged sketch of section still farther back. $\times \frac{1}{6}$ A.

Fig. 29. Section behind procerebrum and showing the rudimentary eye, but entire absence of the optic ganglion and optic nerve.

Fig. 30. Section through the eye. $\times \frac{1}{6}$ A.

Fig. 31. Section through the eye of another individual. $\times \frac{1}{6}$ A. *c*, lens. $\times \frac{1}{6}$ *c*.

Fig. 32. Section through a ventral ganglion.

Fig. 33. Section through a ventral ganglion.

Fig. 34. Section through a ventral ganglion under the stomach.

Fig. 35. Section through a ventral ganglion under the stomach.

NOTE.—All the figures drawn by the author with the camera lucida.

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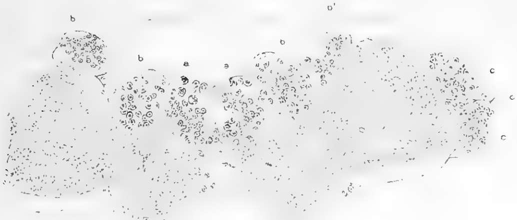

Fig 2

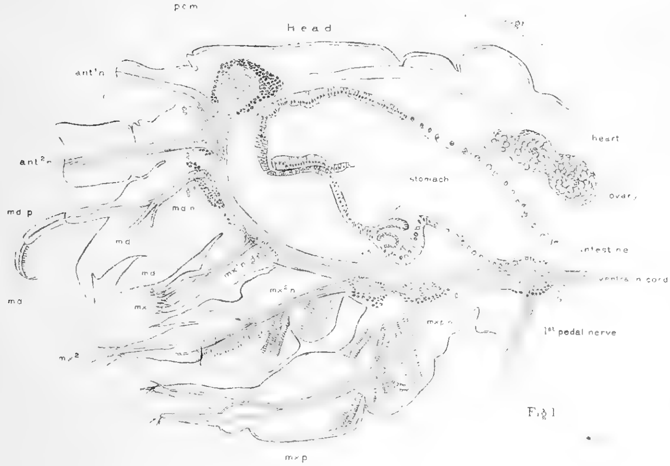

Fig 1

Fig 4

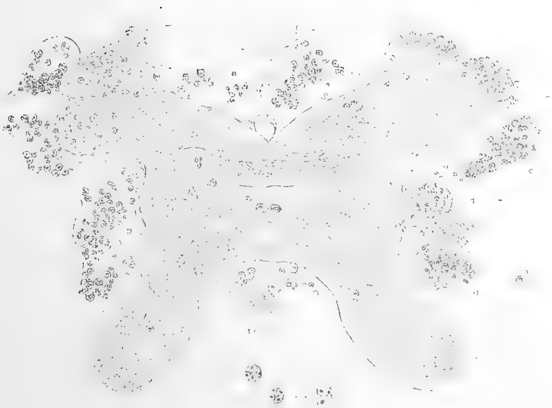

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Plate II

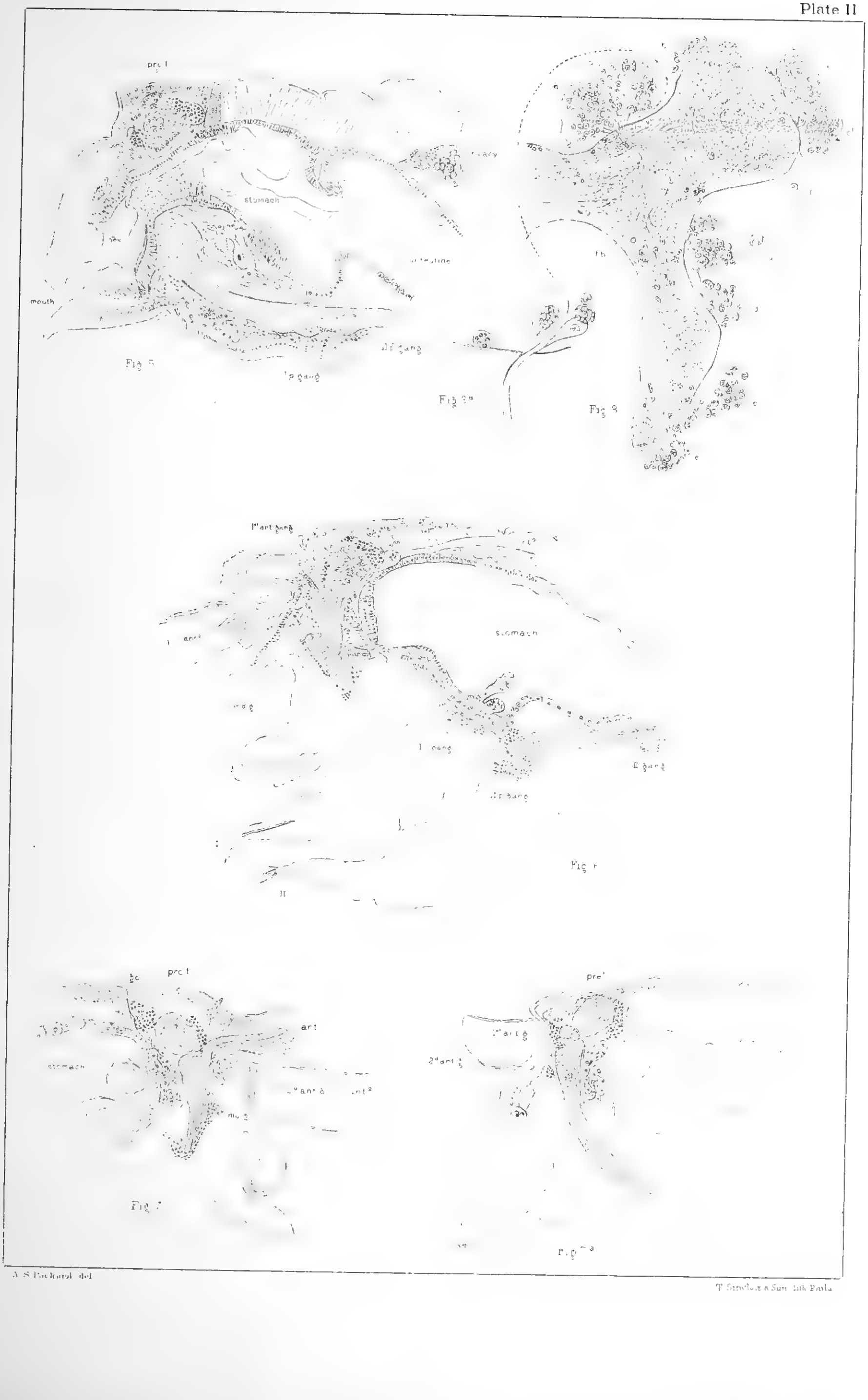

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Plate III.

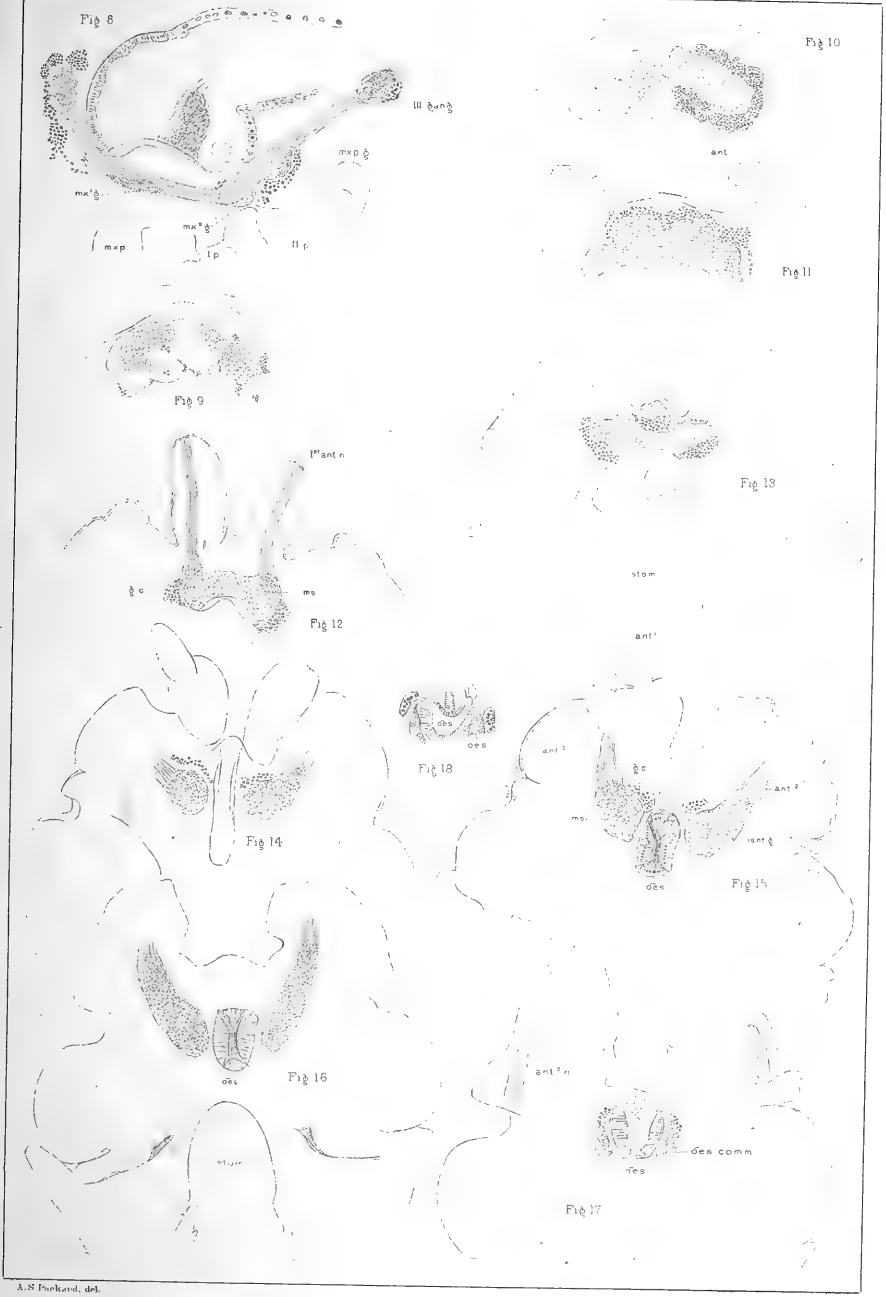

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Plate IV.

Fig 19

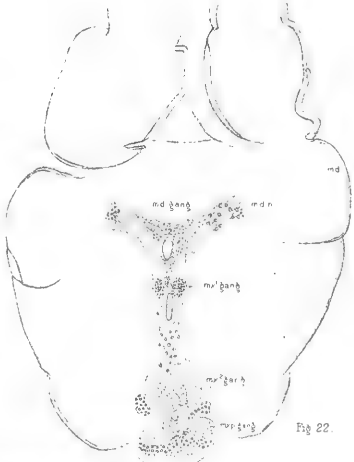

Fig 22.

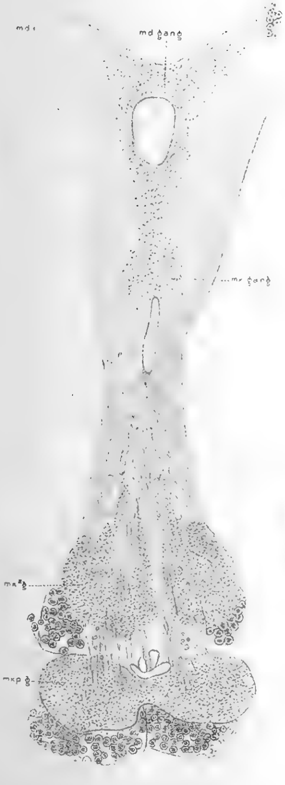

Fig 23

Fig 20

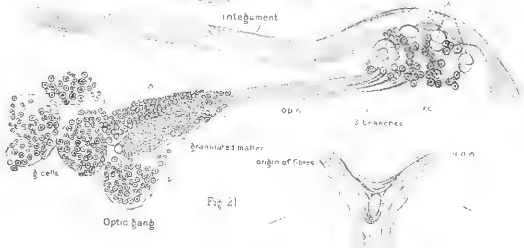

Fig 21

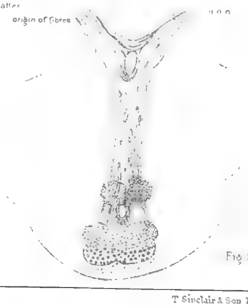

Fig 24

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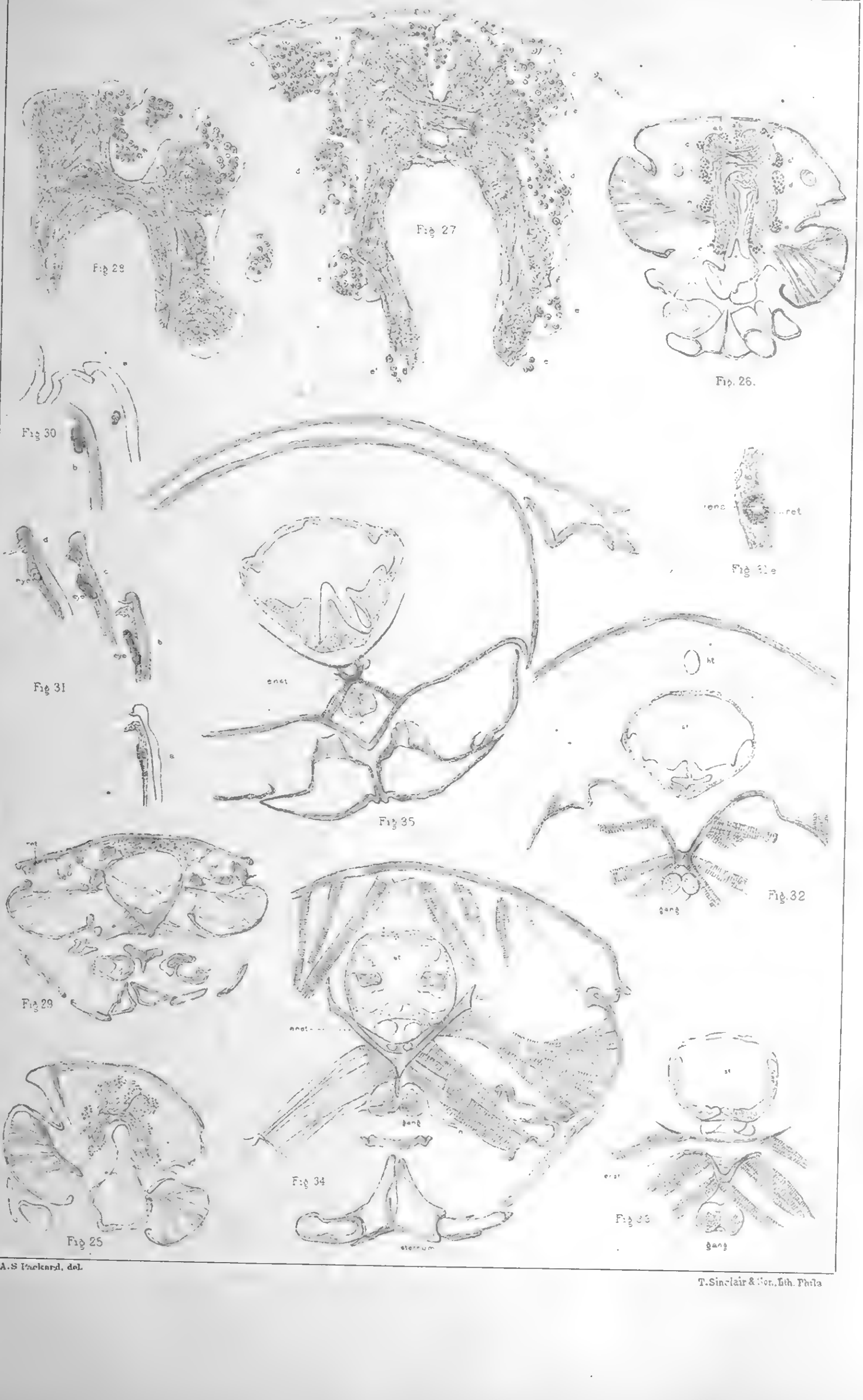

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