

On the Development of Araneina.

by

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With Plates XI—XVI.

The following observations on the development of Araneina were made in the Zoological Laboratory of the Imperial University during the academic session of 1888–9. Some of the results I have arrived at seem to be not without interest. Before going further I wish to express my thanks to my teachers, Dr. K. Mitsukuri and Dr. I. Ijima for their kind and valuable advice during my work.

The materials used for the investigation were all collected by myself during the summer of 1888 in the grounds of the university. The genera that have been most carefully studied are *Lycosa* and *Agalena*, while *Theridion*, *Epeira*, *Dolomedes*, *Pholcus* were more or less examined for comparison. A species of *Lycosa* which is very abundant among grasses breeds constantly from the end of March to the latter part of September, and carries about the cocoon so that we are able to obtain its eggs in various later stages with great ease. It, however, failed to breed in captivity, and for this reason, in the study of earliest stages recourse was had to the eggs of a species of *Agalena* which breeds very freely in captivity. The statements made in the following pages refer to all the species examined unless otherwise specified.

A few words about the methods of investigation may be of use. Eggs of later stages were killed by heating in water to 70–80°C., while segmenting eggs were plunged directly in hot water. Heating was stopped when the eggs became somewhat opaque and white. They were then allowed to cool and transferred to 70% alcohol. After 24 hours, they were examined one by one under a dissecting microscope and those with unburst egg-membranes were perforated with the point of a needle to facilitate the penetration of reagents. They were then hardened in ascending grades of alcohol. I have always found this method to be excellent for all spider eggs.

Staining was done with alcoholic cochineal, picrocarmine, alcoholic carmine, or hæmatoxylin. Alcoholic cochineal and picrocarmine have given best results. It is a remarkable fact that paraffin penetrates into eggs stained with picro-carmine more easily than into those stained with any other reagent. Alcoholic cochineal proved to be especially good for staining sections on the object glass. Imbedding for section-cutting was done in paraffin.

Composition of the Freshly Laid Egg.

The egg has two investing membranes, the inner of which is the vitelline membrane, and the outer the chorion. The external surface of the latter is covered with a crust of minute spherical granules, insoluble in alcohol. In a species of *Epeira*, these granules are comparatively large and closely encrust the surface of the eggs, in some places in two or three layers, making the examination of the inside almost impossible. They were easily removed by gentle rubbing with the fingers. In species of other genera examined, the granules were tolerably crowded in one layer, but being smaller than those of *Epeira* did not seriously obstruct the view of the inside.

The composition of a freshly laid egg has been tolerably accurately described by previous writers, their opinions differing only in some points of details. It may be conceived of as a scanty network of protoplasm in the wide meshes of which yolk granules are imbedded. There is always more or less concentration of protoplasm toward the centre which may be called the *centroplasm*. An extremely thin layer of protoplasm is found on the external surface of the egg, directly inside the vitelline membrane and may be distinguished as the *periplasm*. The centroplasm and periplasm are no doubt connected with each other by a scanty protoplasmic network, although not always apparent in sections. The space between the centroplasm and periplasm is almost entirely taken up by large yolk granules which are arranged in characteristic radiate columns. In each column the yolk granules are in several rows, one placed outside another, and in each row there are generally two granules abreast. The granules near the centroplasm are much smaller than those placed more to the outside. In a freshly laid egg I was unable to detect the germinal vesicle in any part. The first segmentation nucleus appears in the centroplasm a few hours later. In *Lycosa*, the so-called yolk-nucleus of the usual appearance was distinctly seen in the centroplasm. In *Agalena*, I could not find it.

The periplasm when seen from the surface presents the appearance of being divided into irregular polygonal areas (Pl. XI, fig. 1). The cause of this appearance has been a point of dispute, Ludwig* even maintaining that there is no such. That the periplasm is marked out into irregular polygonal areas, there can be no doubt. I agree with Locy** in assigning the cause of this marking to a pressure which is exerted on the periplasm and presses it against

* Ludwig—Ueber die Bildung des Blastoderms bei den Spinnen, Zeit. für wiss. Zool. XXVI.

** Locy—Observations on the Development of *Agalena naevia*, Bull. Mus. Comp. Zool. XII.

the peripheral end of the underlying yolk columns, thus causing the former to receive the impression of the latter. The fact that in freshly laid eggs the polygonal areas correspond with the underlying groups of yolk granules favours this view. I must, however, differ from Loey as to the cause of this pressure brought to bear on the periplasm. Loey ascribes it to the contraction of the egg. This can hardly be, for I could find in no case any trace of contraction, the eggs being always very closely covered by the two membranes. I think it much more probable that the polygonal markings are the effect of the pressure to which the eggs are subjected as they pass through the narrow oviduct. Loey states moreover that at an early stage a number of faintly marked areas made their appearance at the animal pole, while they could not be detected upon the opposite hemisphere. I can not corroborate this statement, for I found the polygonal marking covering the whole surface of the eggs from the earliest period after being laid. It should be stated that after a while when segmentation begins, the yolk granules more or less shift their places; hence we no longer find the coincidence of polygonal areas with groups of yolk granules. The polygonal areas do not seem to change their positions nor do they vary in number after they are once formed.

From the Segmentation of the Ovum to the Formation of the Germinal Layers.

According to Ludwig*, who gives a detailed description of the segmentation of the ovum in *Philodromus*, the nucleus and the yolk divide simultaneously first into two, then into four, eight, sixteen, and so on. Morin** who studied *Theridion*, *Pholcus*, *Drassus* and

* Ludwig—loc. cit.

** Morin—Zur Entwicklungsgeschichte der Spinnen, *Biolog. Centralbl.* VI.

Lycosa, states that there is no division of the yolk before there are formed eight nuclei. In the species studied by myself, the yolk columns are grouped into as many masses (yolk-pyramids or rosettes) as there are nuclei, from the time when there are only two of the latter.

In Pl. XII, fig. 8, I have represented a section of an egg in which there are two nuclei. It will be seen that the yolk is already evidently divided into two masses or segments. In the lower segment, the nucleus is distinctly seen. In the upper, the nucleus does not happen to be in the section, but there is seen the yolk-nucleus (*y. n.*). The latter does not divide and was often found even in eggs of the 4 cell stage, always by the side of one of the segmentation nuclei. The segmentation cavity (*seg. cav*) is already present. The yolk granules immediately adjoining the perinuclear protoplasm are split up into small particles at whose expense the protoplasm evidently seems to increase in bulk (Pl. XII, figs. 8, 9, 10). This process of assimilation is no doubt continued during the whole process of segmentation.

From this stage on, as the nuclei divide, the yolk masses also divide, assuming characteristic rosette or pyramidal shape (Pl. XI, fig. 2). Strictly speaking, the segmentation is not total but syncytial, as the periplasm remains undivided. Nor is it entirely regular, as stages with 3, 11, 22, 34, 85 &c. nuclei were found. Nevertheless the nuclei, after repeated division, are distributed fairly uniformly in the egg.

As the process of segmentation goes on, the segmentation cavity which was already present in the 2-cell stage gradually enlarges so that in stages represented in figs. 9 and 10 the centre of the egg is occupied by a large cavity.

Side by side with their increase by division the nuclei together

with their surrounding protoplasm gradually travel toward the periphery of the egg through the yolk pyramids (Pl. XII, figs. 8, 9, 10). When about 30 in number, they all reach the surface. When they are almost at the surface, the continuity of the perinuclear protoplasm with the periplasm by means of pseudopodia-like processes can be demonstrated on surface views. Figs. 3, 4, Pl. XI. are two figures giving such views in which the radially arranged processes of the perinuclear protoplasm (represented in the figures as dark lines) become lost in the periplasm whose polygonal markings are still visible. Soon after such a stage the perinuclear protoplasm and the periplasm are entirely mixed together forming a nucleated layer at the surface. So far as my observations go, the nuclei emerge simultaneously all over the surface of the egg—not, as Locy states, earlier at the animal pole than at the opposite pole. When there are formed about a hundred nuclei, this nucleated layer separates itself from the underlying yolk, and then by the continual division of the nuclei the one-cell layered blastoderm is established (Pl. XIII, fig. 15). Coincidentally the polygonal markings disappear and the egg recedes from the investing membranes. Probably this is due to the swelling of the membranes and not to the contraction of the egg.

Whether the yolk still contains nuclei or is entirely free from nuclei when the blastoderm is established has been a matter of dispute. In my own sections, I could not at this stage detect any nucleus at all in the yolk, thus confirming the views of Morin in opposition to Balfour's.* Yolk granules are, however, still aggregated into masses.

The change that comes next is of great importance. The cells of the blastoderm when it is at first established are of uniform spherical shape throughout its extent. While these cells gradually assume a

* Balfour—Notes on the Development of the Araneina, Quart. Journ. Micr. Sci. XX.

flattened shape over the greatest part of the blastoderm, there is one spot where the nuclei become conspicuously spherical and multiply rapidly. The spot may be distinguished by reflected light as a round whitish area (Pl. XI, fig. 5, *prim. th.*). It is often a little depressed at first; but it soon becomes flat and eventually a little elevated. Sections through this spot show a large accumulation of blastodermic cells about seven cells deep (Pl. XII, fig. 11). I shall call this thickening the *primary* thickening.

Shortly after this another thickening appears, close to the primary thickening, on the future median line (Pl. XI, fig. 6, Pl. XII, fig. 12, *sec. th.*). This is also slightly elevated above the general surface of the blastoderm (Pl. XII, fig. 13). I shall call it the *secondary* thickening. The primary thickening now gradually extends itself in all directions and forms a whitish disc-like area of the blastoderm, the centre of which is thicker than the periphery (Pl. XI, fig. 7). This white area is the first trace of the ventral plate. The primary thickening as it spreads out surrounds and pushes away the secondary thickening, so that the latter now lies at the margin of the white area but is further from the centre of the primary thickening than before (Pl. XI, fig. 7).

There has been much confusion in regard to the nomenclature of these two thickenings of the blastoderm. The secondary thickening corresponds to the primitive cumulus as described by Claparède.* This appears at least very probable when we compare my fig. 7, Pl. XI, with figs. 3 and 4, Planche I, of this author. Balfour was of the opinion that the primitive cumulus becomes lost in the caudal thickening. What is called the primitive cumulus by Locy is undoubtedly the primary thickening above described, while his "caudal thickening" is the secondary thickening. Morin admitted

* Claparède—Recherches sur l'Évolution des Araignées, Naturk. Verhandl. I.

the existence of a blastodermic thickening giving rise to germinal layers, but denied the identity of it with the primitive cumulus. He says that the primitive cumulus is formed after the formation of the germinal layers and is composed of mesoderm cells. My observations on *Lycosa* show that the secondary thickening, or the primitive cumulus of Claparède, is formed after the formation of the primary thickening and that both are formed before the distinction of germinal layers is possible. Both are accumulations of indifferent cells, not yet referable to any germinal layer (Pl. XII, figs. 11-14). I can not tell whether the position of the secondary thickening corresponds to the anterior or to the posterior of the future ventral plate. This much is certain, that it entirely disappears at the time when the germinal layers are established.

These two thickenings, the primary and secondary, are of a great significance, as the germinal layers are established from them, the primary thickening contributing the largest part in their formation. In a longitudinal section, these two thickenings are as in figs. 12 and 14, while in a cross section they appear as in fig. 11. From these figures it is evident that they together form along the median ventral line of the future embryo a ridge-like thickening which sticks out into the cavity of the yolk. Cells from the top of this ridge (the lowest part of the ridge in the figures) proliferate into the yolk and become scattered without any definite arrangement through the entire yolk. These are the endoderm cells. They become large by taking nourishment from the yolk as they pass through it. The cell-layer of the ridge nearest the external face of the egg becomes established as the definite ectoderm. The cells of the ridge which are left close under the ectoderm form the mesoderm (Pl. XIII, fig. 17). They soon spread horizontally below the ectoderm. The mesoderm is at first in a single median mass on the

ventral face and does not extend to the dorsum of the embryo which is composed of the ectoderm only.

As to the nature of these two thickenings, the primary and secondary, it is difficult to state anything definite. The stage in which the one-cell layered blastoderm is established on the surface of the egg is to be looked upon as the blastosphere stage. When the ridge appears in this blastosphere along the line which becomes the median ventral line of the future embryo and sends off cells into the yolk cavity, the whole process must be regarded as a modified form of invagination and the ridge is to be looked upon as the blastopore. Why there should arise two thickenings instead of one remains inexplicable to me. The primary thickening is without doubt the remnant of the blastopore. Whether the secondary is to be looked upon as a part of the same, I cannot decide.

From the Formation of the Germinal Layers to the Reversion of the Embryo.

After the establishment of the ventral plate, its anterior part becomes marked off as the cephalic, and its posterior part as the caudal lobe, and the middle region between the two lobes is divided by transverse ridges into segments. The least number of segments observed between the cephalic and caudal lobes was five. The foremost of these corresponds to the segment which bears the pedipalpi and the four following are the thoracic segments, each of which subsequently produces a pair of ambulatory appendages. The segment which is to bear the chelicerae is soon after cut off from the cephalic lobe and the abdominal segments are gradually cut off from the caudal lobe, the process proceeding posteriorly, until there are formed eight abdominal segments (*Lycosa*).

In this process of segmenting the mesoderm of the ventral plate shares (Pl. XIII, fig. 16), and is divided into as many parts as there are segments in the body of the embryo. Moreover it divides itself into two longitudinal bands at the median line except at the cephalic and caudal lobes. Thus there is formed in each segment a pair of mesodermic plates. After a while, each of these paired mesodermic plates produces a cavity—the cœlom—apparently by its splitting into two layers (Pl. XIII, fig. 18). The outer of the two layers is the somatopleure, and the inner the splanchnopleure. The cœlom therefore consists at this time of a number of paired cavities (Pl. XIV, fig. 22), which are separated from one another. Cœlomic cavities in the cephalic and caudal lobes appear only later on.

Shortly after the formation of the cœlom, a pair of protuberances appear on each segment. They are the first traces of the appendages (Pl. XIV, fig. 23, *th. app*). The order of their appearance corresponds to the order of appearance of the segments to which they belong. The appendages are formed on segments of the chelicerae and pedipalpi in all the thoracic and the second, third, fourth, and fifth abdominal segments (Pl. XIII, fig. 20, Pl. XIV, fig. 22). The cephalothoracic appendages are formed at the lateral ends of the segments, while the abdominal appendages are formed nearer the median line (Pl. XIII, fig. 20). The abdominal appendages are little round protuberances, and do not elongate as rapidly as other appendages. The first abdominal segment bears no appendages, as Schimkewitch* has correctly observed. This segment is gradually aborted, and is not distinctly visible at the time of the reversion of the embryo. The cœlomic cavities of each segment extend into the appendages.

The foundations of the nervous system are laid soon after the

* Schimkewitch—Étude sur le Développement des Araignées, Arch. de Biolog. VI.

establishment of the ventral plate during this period. The ectoderm of the cephalic lobe is very much thickened as shewn in figs. 22 and 23. This process of thickening proceeds backwards as two longitudinal bands, one on each side of the body, along the inner side of the attachment of the appendages in the thoracic and abdominal segments, finally meeting each other in the caudal lobe. These two bands are the first rudiments of the ventral nerve chain. Thus it is continuous from the first with the cephalic thickening above mentioned which becomes the brain, as in the case of scorpions observed by Kowalevsky and Schulgin.* This is not in accordance with the view of some authors who maintain that the brain and the ventral nerve cords are formed independently of each other. The cells composing the ventral cords aggregate in each segment and give rise to the ganglia.

The cephalic thickening of the ectoderm is now divided into two semicircular lobes (Pl. XIII, figs. 20, 21). Near the front edge of these lobes, there is formed on each side a semicircular groove (*sem. gr.*). This paired groove which is cut off from the ectoderm is the chief origin of the brain. Bruce** compares it with the amniotic fold of insects; but the comparison is certainly not justifiable. Kowalevsky and Schulgin found that in Scorpions the ectodermic invagination comparable to the amniotic fold of insects is distinct from and formed earlier than the semicircular groove, which is no doubt homologous with the similar groove of the spider, as it also gives rise to the brain. Sections of the semicircular groove are represented in fig. 23, Pl. XIV.

Besides the semicircular grooves, there is a pair of small ectodermic invaginations in the posterior part of the head near the outer border (Pl. XIII, fig. 20, Pl. XIV, fig. 23, *lat. v.*). So far as I

* Kowalevsky and Schulgin—Zur Entwicklungsgeschichte des Scorpions, *Biolog. Centralbl.* VI.

** Bruce—On Insects and Arachnids.

know these invaginations have been till now entirely overlooked. In fig. 19, Pl. XXI, of Balfour's work, I find one of these invaginations represented; but he gives no information about it. It is globular in form; henceforward I shall call it the *lateral vesicle*. The lateral vesicles, which are also gradually constricted off from the ectoderm, go to form a part of the brain (Pl. XV, figs. 44-46).

The stomodæum is formed as an ectodermic invagination at the anterior margin of the cephalic region (Pl. XIII, fig. 20, Pl. XIV, figs. 24, 25). At this stage it is easy to see that all the appendages are postoral in origin.

Late in this stage a number of large cells appear at the dorsal part of the embryo. They are never found in the ventral plate. They are very easily recognised by their large size and the peripherally situated nuclei, their central portion being filled with fat (Pl. XV, figs. 40, 41, *f. c*). Undoubtedly they are nourishing cells, wandering everywhere, and some of them are changed into blood corpuscles. They were called by Balfour the secondary mesoderm, by Schimkewitch the secondary endoderm, and by Locy the endoderm cells. These three authors ascribed the origin of these fat cells to the cells in the yolk, whereas according to Morin they are formed in *Pholcus* from dispersed mesoderm cells originally composing the so-called primitive cumulus,* and in *Theridion* which wants the cumulus probably from cells of the mesodermal somites. Schimkewitch, Locy, and Morin observed that these cells become blood corpuscles. For my own part, I am inclined to agree with Balfour, Schimkewitch, and Locy and to derive them from the endoderm. For in the first place, they are found immediately above the yolk, and in some cases between yolk granules presenting the appearance as

* Morin states, what I have before referred to, that the primitive cumulus is formed after the formation of germinal layers, and consists of mesoderm cells.

if they have just emerged from the yolk. In the second place, their nuclei agree in their large size with those found in the yolk.

At the end of this stage the mesoderm in the caudal lobe is faintly divided into two layers, between which an unpaired cavity makes its appearance (Pl. XIV, fig. 24). In the cephalic lobe also the mesoderm is faintly divided into two layers on each side (Pl. XIV, fig. 23), enclosing the rudiments of the cœlomic cavities. It is still undivided in the median line. The cœlomic cavities in the thorax secondarily fuse together into a single cavity. They remain, however, quite distinct in the abdominal region.

The Period of the Reversion of the Embryo.

The stage in which the reversion of the embryo occurs is as difficult to study as it is important, since many organs arise at the same time. At the end of the last stage, the ventral plate had reached the maximum limit of dorsal flexure, the cephalic and the anal lobes almost touching each other (Pl. XIV, figs. 24, 25). As Balfour states, the reversion of the embryo is due to the expansion of the dorsum; and the expansion of the dorsum is due to the horizontal increase of cells which compose that part. The head and the tail are pushed away from one another further and further. As the dorsum is very rapidly expanding and the cells are pressed for room, a groove is produced immediately behind the tail lobe to increase the surface of the dorsum, and the tail lobe then stands out as a conical process (Pl. XIV, figs. 26-29). The cœlomic cavities belonging to the segment in front of the tail lobe being pressed from the dorsal side by the increase of cells in the dorsum are compressed horizontally and pushed into the conical tail process, enveloping the unpaired cœlomic cavity of that process from the dorsal side. The caudal lobe stands

out gradually more and more prominent, until the stage represented in fig. 27 (surface view, fig. 21) is reached. After this, the tail process gradually shortens (figs. 28, 29) until after a while there is no tail projecting from the general body surface (fig. 32).

At about the same time with the increase of cells of the dorsum, the two nerve cords begin to diverge from each other. They are most widely separated from each other at the anterior part of the abdomen and gradually approach each other anteriorly and posteriorly until they meet in the cephalic and tail lobes (fig. 21). Their divergence together with the expansion of the dorsum makes the embryo assume the ventral flexure.

The cœlomic cavity of the caudal lobe now becomes gradually conspicuous. This unpaired cavity is transformed into the so-called stercoral pocket (Rectalblase, Kloake) of the adult spider. Hence the stercoral pocket does not arise from the swelling of the internal end of the proctodæum, as has been supposed by other authors. This organ is purely mesodermic in origin and nothing more than a remnant of cœlomic cavities. This may be understood by examining figs. 24-32, Pl. XIV. From these figures it will be seen that the proctodæum is formed in the caudal lobe later than the stercoral pocket.

The fact that any part of the adult alimentary canal should be derived from the cœlom seemed to me so remarkable that I have repeatedly examined my series of sections and am convinced of the correctness of the observation. I do not know how to interpret this fact unless it be that the stercoral pocket is a part of the primitive excretory system—a supposition which is strengthened by its peculiar relation to the remaining part of the digestive tube (Pl. XVI, fig. 55) and by the fact that the Malpighian tubes open into it.

At this period the mesodermic somites and the ganglia of the

anal lobe and of the four appendage-bearing abdominal segments have attained their utmost development. The first abdominal segment and those between the fifth and the last abdominal segments are aborted.

The mesodermic somites which are produced at first in the ventral plate now grow on dorsalwards and meet at the dorsal median line (Pl. XV, figs. 40-43). They first meet at their dorsal part, enclosing some of the large fat cells and their derivatives between them. The ventral part fuses later. Thus the dorsal circulatory tube is formed, the wall of which is produced from the mesoderm, while the blood corpuscles are produced from large fat cells (endodermic in origin). I am inclined to believe that both the aorta and the so-called heart are formed as stated above and not separately as many authors believe. The fusion of the mesodermic somites to form the dorsal vessel does not take place throughout the entire length, as there are left paired lateral slits between each two consecutive somites. The blood aerated at the lung-book returns to the heart through these lateral slits. These slits shut and open as the heart beats. They are found in the abdomen only.

In the basal part of the first abdominal appendage of each side, there arises an ectodermic invagination whose opening faces away from the median line. It is neither deep nor spacious but is a little pocket-like invagination. This is the beginning of the lung-book. The development of this organ, briefly stated, is as follows: Of the wall of the invaginated pocket, that which faces the distal end of the appendage is much thicker than the opposite wall, filling the interior of the appendage. The cells composing it become after a while arranged in parallel rows (figs. 34 and 47). Each two of these parallel rows adhering together produce the lamellæ of the lung-book. The external epithelium of the appendage which cover these

lamellæ becomes the operculum of the lung-book after it is depressed in height. Judging from figures (figs. LXXIX and LXXIX') given in "On Insects and Arachnids," Bruce seems to have mistaken the caudal prominence of the early period of this stage (see my figs. 24-28) as the operculum of the lung-book. According to him the abdominal appendage is invaginated to form the lung-book, but as we have seen, it is not so. Locy has correctly described the formation of the lung-book lamellæ. He says that the lungs arise from infoldings; but he is silent about the place where these infoldings arise.

In the basal part of the second abdominal appendage on the interior side, another ectodermic invagination is produced. It assumes the shape of a deeply invaginated tube and remains in this condition till after the time of hatching. The appendage itself is not invaginated and becomes from this time gradually shorter.

It is very probable that the lung-books were derived from the gills of some aquatic arthropodous animals such as *Limulus*; for the lung-books are nothing more than the lamellar branchiæ of *Limulus* sunk beneath the body surface. The tubular trachea may afterwards have been derived from the lung-books. The branchial lamellæ of *Limulus* are formed as outgrowths of the ectoderm at the lower (posterior) surface of abdominal appendages, and those of spiders are also produced really in the lower surface of the first abdominal appendage (in the dipneumonous spider). Hence I think that the spider with two pairs of lung-books is the most primitive one, and the one with one pair of lung-books and the other pair transformed into the tubular tracheæ is more primitive than the spider with only one pair of lung-books. I cannot agree with the view of some authors who maintain that the lung-book is derived from a cluster of tracheæ.

The third and fourth pairs of the abdominal appendage are modified into spinning mammillæ (Pl. XV, fig. 34). At the distal end of each of these appendages a solid proliferation (*sp. gl*) of ectodermic cells is formed. This becomes the spinning gland. Spiders have generally three pairs of spinning mammillæ; two of which are modified abdominal appendages, while the remaining one is added very late, after the hatching of the embryo. The primitive spider must have had only two pairs of spinning mammillæ. Some tetrapneumonous spiders have only two pairs.

The two semicircular halves of the cephalic lobe, between which there is at first a deep median notch (Pl. XIII, fig. 20), now fuse with each other at the median line above the stomodæum, so that the notch becomes much shallower (fig. 21). The grooves formed along their anterior margin during the preceding stage separate from the ectoderm beginning from their external end and sink down beneath the body surface. They are cut off from the ectoderm latest at the hindermost parts of their inner limbs (Pl. XVI, fig. 48). The lumina in the two separated semicircular grooves come to communicate with each other at the anterior median part (Pl. XV, fig. 45).

At the last point of separation there is left a shallow invagination or rather sac on the surface. The invagination is paired. The openings of these sacs are directed towards the mouth of the embryo, and the invaginations are directed anteriorly. They are the first traces of the *posterior* median eyes (see below) or the 'Hauptaugen' of Bertkau* (Pl. XV, figs. 44-46, 48, *P. M. E.*). The *anterior* wall of the sac is thicker than the posterior, the former being two to several cells deep, the latter only one cell deep. The formation of

* Bertkau—Beiträge zur Kenntniss der Sinnesorgane der Spinnen, Arch. f. Mik. Anat. XXVII.

the posterior median eyes in connection with the brain in spiders is quite analogous to the similar process in scorpions as observed by Kowalevsky and Schulgin. This interesting relation was not observed by Locy who studied the spider, or by Parker* who studied the scorpion.

Hitherto these eyes were called the anterior median eyes; but morphologically speaking, this nomenclature is not correct. For all the eyes of spiders are formed in reality in the ventral plate, never in the dorsum, and gain their apparently dorsal position in later stages only by the bending upward of the ventral plate. Hence, in this last position the eyes that composed the posterior row in the ventral position come to occupy the anterior position, while those that formed the anterior row in the ventral position are thrust further backward by the curving upward of the ventral plate and thus become the apparent posterior row. Hence those I called the posterior median eyes are in the apparent anterior row of the adult.

The three remaining pairs of eyes are formed later than the posterior median pair and in a different manner. Their first traces are the local thickenings of the ectoderm of the cephalic region. Anterior lateral eyes (*A. L. E.*) appear above the lateral vesicle (Pl. XV, fig. 46).

At this time the lateral vesicles are completely cut off from the general ectoderm (Pl. XV, figs. 44, 46). Their walls are thick and their lumen is conspicuous. In development and position they very much resemble the eyes of *Peripatus*.

The chelicerae are now two-segmented. They have shifted their position a little anteriorly and have approached toward the median line (Pl. XIII, fig. 21). Their ganglia are placed at the sides of the stomodæum and form the commissural part between the supra-

* Parker—The Eyes in Scorpions, Bull. Mus. Comp. Zool. XIII.

and infra-oesophageal ganglia. They are in contact with each other at the anterior part. The basal joint of the pedipalpi is very broad, the maxillary part being easily distinguished. The ganglia of the pedipalpi and of the succeeding four thoracic segments are well developed and are in close contact with each other, thus forming the large sub-oesophageal ganglion. The ganglia belonging to the abdominal segments are also well developed.

The stomodæum elongates itself obliquely upwards and is surrounded externally by the well developed upper and lower lips (Pl. XIII, figs. 19-21; Pl. XIV, figs. 24-26). The ectoderm forming the wall of the stomodæal invagination is thick.

The ectoderm of the ventral part of the anal lobe is conspicuously thicker than that of the dorsal part, being continuous with the two ventral bands. At the beginning of the reversion, it is uniformly two or three cells deep (Pl. XIV, fig. 27); but when the reversion is fairly advanced, so that the elongated anal lobe begins to become short again, the cells in the middle part of it are elongated and there they are only one cell deep (fig. 28). At this part an invagination takes place (fig. 29). From this stage the ectoderm of the ventrum of the anal lobe, placed anterior to the invagination becomes two or three times thicker than the posterior part, and is differentiated to form the anal ganglia (figs. 29-32, *G*). The invagination is the protodæum. It is very shallow and small, and its bottom is in direct contact with the wall of the stercoral pocket. The wall of the proctodæum is thinner than that of the stomodæum. It is remarkable that the proctodæum is not formed at the extreme hind end of the ventral plate but somewhat in front of it directly behind the anal ganglia, and that both the stomodæum and the proctodæum are produced at the two extremities of the nervous system simultaneously with the development of the latter near them. The portion

of the ventrum, posterior to the proctodæum, gradually thins off, and after the process of reversion is completed it can not be distinguished from the dorsum (Pl. XIV, figs. 31, 31).

The posterior part of the mesenteron is formed by an accumulation of endoderm cells at the anterior ventral part of the stercoral pocket. It is a wide open funnel-shaped tube, resting above the mesoderm (fig. 32, *Post. mesent.*).

The stercoral pocket produces paired diverticula from its lateral sides (fig. 33). At first, I was inclined to think that these diverticula become the Malpighian tubes, as these tubes were formerly thought to arise as a pair of outgrowths from the stercoral pocket. But I found that these diverticula give rise to no definite structure in the adult, and that the Malpighian tubes arise in a different way, as will be explained further on.

At this stage a very important organ is produced, which has been almost entirely neglected by embryologists. I mean the *coxal gland*, which is formed from an ectodermic invagination at the internal posterior base of the coxal joint of the first ambulatory appendage (Pl. XV, fig. 38, *Co. gl.*). The invagination opens into the cœlomic cavity (figs. 35, 36). Its development is traced further in the next stage.

After the formation of the circulatory system the cœlomic cavities atrophy, except the one of the anal lobe forming the stercoral pocket, and some part of the thoracic ones in connection with the coxal gland. The so-called body cavity of the adult is not the remnant of the cœlomic cavity; but it is a secondarily produced blood-space. The mesodermic cells which formed the wall of these cavities form the covering of the nervous system, the alimentary canal and other organs.

Some mesodermic cells at the base of the cephalothoracic appen-

dages become rounded in outline (Pl. XV, figs. 35, 36). They are easily distinguished from the fat cells by their centrally located nuclei, and from other cells by their well-defined spherical form and slightly stainable protoplasm. They appear first in the chelicerae, then in the pedipalpi, and so on gradually backwards. These cells have no relation whatever with the coxal gland nor with the poison gland. Their function is unknown. It seems to me that Locy has mistaken these cells at the base of the chelicerae for the first rudiments of the poison gland. He says that these cells are probably derived from an infolding of the ectoderm.

From the End of the Reversion to the Hatching of the Embryo.

This stage is characterized by the appearance of a constriction separating the cephalothorax from the abdomen. The yolk in the ventral part of the abdomen is absorbed, so that the abdominal appendages of both sides approach each other at the median line.

The semicircular grooves of the cephalic lobes formed in the preceding stage are no longer grooves, nor semicircular in form. Now they are completely constricted off from the general ectoderm, and are consequently tubes. Their inner limbs approach each other in the median line and they form as a whole a T-shaped body (Pl. XV, fig. 45). The lumina of the two tubes communicate with one another at the anterior median part. They as well as the lumen of the lateral vesicle begin to atrophy by the thickening of their walls and finally disappear. At the same time the transverse bar of the T-shaped mass becomes curved on each side to a peculiar shape shewn in profile in fig. 45a. This and the disappearance of the lumen change the brain into a compactly packed mass, instead of having its various

parts standing apart as heretofore. The transverse bar (fig. 44, *a*) of the T-shaped brain is separated from the median stem just behind the point where the lumina of the two sides communicate with each other, while the median stem is in its turn transversely divided into two segments (Fig. 44, *b, c*). Thus the spider's brain consists of three segments, as Patten* claims. These three segments may be called the transverse dorsal (Fig. 44, *a*), the anterior vertical (Fig. 44, *b*), and the posterior ventral section (Fig. 44, *c*). The lateral vesicles are in the level of the third segment. From his description, Patten seems to mean that in scorpions and spiders the three segments of the brain are formed from three separate invaginations; but I cannot corroborate this statement. Moreover he says that the anterior median eyes (my posterior median eyes) belong to the second segment, while the three remaining pairs belong to the third segment. Supposing that his second segment is anterior to the third segment, I cannot corroborate this statement either, as according to my own observations all the eyes belong to the third segment. It seems to me impossible that the posterior eyes should arise in a segment anterior to that in which the anterior eyes are produced.

The opening of the sacs of the posterior median eyes becomes gradually smaller and is finally closed (Pl. XVI, fig. 49). The anterior wall of the sac becomes enormously thick and obliterates its lumen. The ectodermic cells which lie upon the sac elongate and form the vitreous body (figs. 49, 54, *vit*). The anterior wall of the sac forms the retinal part (fig. 49, *R*). The retinal cells elongate *anteriorly*. The anterior surface of the anterior wall of the posterior median eyes, is morphologically the inner side of the ectoderm though it faces externally. The lens is formed by a local thickening of the cuticula, which is secreted from the epithelium at this stage

* Patten—Segmental Sense-organs of Arthropods, Journ. of Morph. II.

(Pl. XVI, fig. 49, *L*). The nerve does not enter the posterior median eyes even a few days after the hatching of the embryo. Probably the nerve is sent out from the retina from the anterior (morphologically inner) surface of it, as this is the case in the adult. The development of the posterior median eyes is comparatively slow. They are homologous with the median eyes of scorpions, as the development is quite the same.

The three remaining pairs of the eyes or 'Nebenaugen' of Bertkau* are formed later than the posterior median eyes; but their development is completed earlier. They arise from ring-like depressions of the ectoderm (fig. 50). The walls surrounding these depressions grow over them and finally meet (fig. 51). The spot where the walls meet is one-cell layered. This spot gradually extends to a certain extent and forms the vitreous body which is characterized by elongated cells (figs. 51, 54, *vit*). The growth of the walls of the depressions is not uniform in every direction and therefore the point of closure may not correspond with the centre of depression. Thus the 'Nebenaugen' are also formed from ectodermic sacs; but these sacs are different from the sacs of the posterior median eyes. While it is the *anterior* wall of the sac that becomes the retina in the posterior median eyes, it is in the case of the 'Nebenaugen' the *posterior* wall of the sac, which, forming a central elevated portion thicker than the anterior wall and surrounded by a ring-like depression, gives rise to the retina (figs. 50-54, *R*). Also retinal cells elongate *posteriorly* instead of *anteriorly*, as in the posterior median eyes, and form nerve fibres (figs. 50, 51, *N*). These nerve fibres are subsequently connected with the fibrous portion of the brain. The retinal portion is cut off from the general ectoderm at about the time

* Bertkau, loc. cit.

of hatching, and at the same time becomes concave (fig. 54), instead of being convex as heretofore (fig. 51).

In the 'Nebenaugen'—but not in the posterior median eyes—there are formed transverse bars and a circumferential ring (figs. 51-54, *tap*) of chitinous nature, posterior to the retinal cells and secreted by these cells. These chitinous bodies (the tapetum) are transparent and lightly yellowish by transmitted light and silvery glittering by reflected light. The lens is formed in a similar manner as in the case of the posterior median eyes. The tapetum and the lens are equally secretion products of the ectoderm and both of them are chitinous in nature, but they are not homologous. The former is produced at the proximal end of the ectoderm cells, while the latter is formed at the distal end.

I know of only two authors who have studied the development of the spider's eyes by recent modes of investigation. They are Locy and Schimkewitch. The results obtained by these authors are not entirely satisfactory. Locy could not find the difference in the mode of development between the two different types of eye. He says that the 'Nebenaugen' originate in substantially the same way as the anterior median eyes (my posterior median eyes). Moreover he states that the development of the eyes begins by a local thickening of the hypodermis and a backward directed infolding which inverts the thickened region. Schimkewitch says only that the retinal part of the eyes originate from a pyriform enlargement from the brain, upon which the ectoderm invaginates in the form of a ring.

Patten recently gave a short account of the spider's eyes in an article entitled the "Segmental Sense-organ of Arthropods" in the *Journal of Morphology*, Vol. II.; but his account differs from mine in many points, as I have already mentioned. He says that there are segmental sense-organs, homologous with the eyes, at the base

of the legs. Unfortunately I could not find any trace of such an organ, though I carefully searched after it.

The development of the pigment begins from the cephalic region backwards, after the differentiation of the vitreous body (fig. 51). In the case of the 'Nebenaugen' the pigment is first produced in those cells which form a kind of a cup around the retinal portion (figs. 51-53), and it seems to me most probable that these cells wander in to the retinal portion, first among the nerve fibres beneath the tapetum (fig. 53), then among those above the tapetum (fig. 54). In the case of the posterior median eyes, however, the pigment is produced from the beginning in retinal cells, below the vitreous body.

As we have already seen, all the eyes of the spider are formed in the ventral plate and near its anterior margin.

The concentration of the nervous system towards the cephalothorax goes on further in this stage than in the previous stage. In the thoracic region the two lateral ganglionic chains are united into one and form the subœsophageal ganglion. The inner portion of the ganglion becomes finely fibrous. The abdominal ganglia gradually atrophy and attach themselves to the posterior end of the subœsophageal ganglion. At this stage the whole nervous system is completely cut off from the ectoderm.

The stomodæum has developed very much. After elongating itself obliquely upwards, it takes the horizontal backward direction and reaches to about the segment of the fourth ambulatory appendage. It is lined with a cuticular covering which is continuous with the cuticula of the general body surface. In the pharynx, the cuticular lining is thick and transversely ridged. The ridges run parallel with each other and appear in the sagittal section like teeth, the pointed edge turning dorsalwards. The wall of the stomodæum is very thick. The stomodæum gives rise to the pharynx, the œsophagus, and the stomach.

Early in this stage some endoderm cells accumulate at the posterior end of the stomach and form the anterior part of the mesenteron. These cells are arranged as a funnel-shaped tube wide open posteriorly. The posterior funnel has united with the wall of the stercoral pocket at its hind end (fig. 55). The anterior and the posterior funnels of the mesenteron do not at this stage unite with each other.

Locy says that on each side of the stomach are given off cæca, which extend into the bases of the limbs. He adds that the cellular elements composing the walls of these tubes are flattened; but he gives no account concerning the time of their appearance. Though I have carefully examined embryos of all the stages, I could not find such tubes.

The proctodæum is lined with a cuticular covering as the stomodæum; but the stercoral pocket has no such covering. This fact confirms my observation that the stercoral pocket is not a portion of the proctodæum. The communication between them is formed at this stage. The communicating canal is very narrow. In the last stage, the stercoral pocket was somewhat globular in shape (Pl. XIV, fig. 32), now it is elongated anteriorly and is oblong (Pl. XVI, fig. 55). Its lateral diverticula have disappeared.

I could not make out the development of the Malpighian tubes satisfactorily; but I am certain that they do not originate from the ectoderm. Also it is certain that they are not outgrowths from the stercoral pocket. It seems to me probable that they originate from mesodermic cells belonging to the abdominal somites in front of the anal lobe. At this stage they are solid paired cords of cells (fig. 55, *Malp. t*) extending from the anterior end of the second abdominal segment to the sides of the confluent point of the posterior mesenteron with the stercoral pocket.

The mesodermic cells of the coxal gland, which was formed in the preceding stage, are very much differentiated from the ectodermic cells of it. They are the glandular cells, their size becoming large and their protoplasm granular and unstainable (Pl. XV, fig. 37). The ectodermic cells form the duct.

At the distal end of the chelicerae a solid growth inward of ectodermic cells takes place. These cells are surrounded by mesodermic cells. The distal half of the former becomes the glandular portion, and its proximal half the duct, of the poison gland, while the mesodermic cells form the muscular wall of the gland (fig. 39).

In this stage four paired transverse septa are formed between the four appendage-bearing segments of the abdomen by the sinking of the mesoderm into the yolk. A median unpaired septum, similarly formed, also stretches forward from the posterior end. These septa are formed after the disappearance of the coelomic cavities in the abdomen. In fig. 34, Pl. XV., two anterior septa are represented. The first pair of septa probably give rise to the generative organ, and all or some of the others to the so-called liver.

After undergoing one or two moults, the embryo hatches. The body of the embryo is covered with cuticular hairs. At the end of the pedipalpi and the four ambulatory appendages, the claws are produced, and at the end of the chelicerae the poison fangs, by thickenings of the cuticula.

Summary.

(1) The polygonal areas are on the periplasm, and are probably formed when the eggs pass through the oviduct.

(2) In the process of segmentation the yolk and the nucleus are divided at the same time. The segmentation is syncytial.

(3) The yolk nucleus is found in segmenting eggs on to the four-cell stage.

(4) After the segmentation all the nuclei are found only at the surface of the egg, and none of them remain in the yolk.

(5) The primary blastodermic thickening may be considered as a modified gastrea mouth, the formation of which was obstructed by the abundance of yolk.

(6) The secondary blastodermic thickening or 'primitive cumulus' of Claparède plays a secondary part in the formation of the germinal layers.

(7) The brain and the ventral nerve cords are formed as a continuous ectodermic thickening.

(8) All the appendages are postoral in origin.

(9) The first abdominal segment bears no appendages.

(10) The large fat cells are derived from the endoderm. They form blood corpuscles.

(11) An invagination at the posterior base of the first abdominal appendage gives rise to the lung-book. A similar invagination at the base of the second gives rise to a tube—abortive trachea.

(12) The unpaired cœlomic cavity, belonging to the anal lobe, changes to the so-called stercoral pocket. Probably it is excretory in function, not a part of the alimentary canal.

(13) The dorsal circulatory vessel is formed by the fusion of the mesoblastic somites at the dorsal median line.

(14) The so-called body cavity of the adult animal is not the descendant of the cœlomic cavity, but it is a secondarily formed space.

(15) The brain is composed of the semicircular grooves and the lateral vesicles cut off from the ectoderm. Later it is divided into three segments.

(16) The development of the posterior median eyes is connected with that of the brain. Their development is quite different from that of the other eyes ; but all the eyes are dermal in origin, not neural. And the nerves of the eyes enter always from the inner ends of the ectoderm cells.

(17) A pair of coxal glands opens at the base of the third appendage. The glandular portion of it is formed from a portion of the cœlom, while its duct is formed from an ectodermic invagination.

(18) The alimentary canal of the spider is formed from the ectoderm and the endoderm. The pharynx, the œsophagus, the stomach, and the anus are produced from the former, and the intestine from the latter.

(19) The Malpighian tubes are produced neither from the ectoderm nor from the stercoral pocket. They are mesodermic in origin.



Explanation of Plates.

The figures are all exact representations of preparations, the outlines, the nuclei, and other details being drawn faithfully by myself with the use of the camera lucida, and they are not diagrammatic, except in the case of a few figures expressly so stated.

List of References.

- | | |
|---|---|
| <i>a</i> , first segment of brain. | <i>Malp. t.</i> , Malpighian tube. |
| <i>abd. app.</i> , abdominal appendage. | <i>mes.</i> , mesoderm. |
| <i>a. l.</i> , anal lobe. | <i>N</i> , nerve. |
| <i>A. L. E.</i> , anterior lateral eye. | <i>pedip.</i> , pedipalpi. |
| <i>ant. mesent.</i> , anterior portion of mesenteron. | <i>P. M. E.</i> , posterior median eye. |
| <i>b</i> , second segment of brain. | <i>post. mesent.</i> , posterior portion of mesenteron. |
| <i>c</i> , third " " " | <i>prim. th.</i> , primary thickening. |
| <i>ceph. l.</i> , cephalic lobe. | <i>proct.</i> , proctodæum. |
| <i>ch.</i> , chelicerae. | <i>R</i> , retina. |
| <i>ch. g.</i> , cheliceral ganglion. | <i>sec. th.</i> , secondary thickening. |
| <i>co. gl.</i> , coxal gland. | <i>seg. cav.</i> , segmentation cavity. |
| <i>cut.</i> , cuticula. | <i>sem. gr.</i> , semicircular groove. |
| <i>d</i> , dorsal side. | <i>sp. gl.</i> , spinning gland. |
| <i>dor.</i> , dorsum. | <i>sterc. p.</i> , stercoral pocket. |
| <i>ect.</i> , ectoderm. | <i>stom.</i> , stomodæum. |
| <i>end.</i> , endoderm. | <i>tap.</i> , tapetum. |
| <i>f. c.</i> , fat cell. | <i>th. app.</i> , thoracic appendage. |
| <i>G</i> , ganglion. | <i>v</i> , ventral side. |
| <i>inv.</i> , invagination of lung-book. | <i>vit.</i> , vitreous body. |
| <i>L</i> , lens. | <i>y. n.</i> , yolk nucleus. |
| <i>lat. v.</i> , lateral vesicle. | |

Explanation of Figures.

Fig. 1. An unsegmented egg, showing the polygonal areas above yolk granules. (*Lycosa*). 2 B (*Zeiss*).

Fig. 2. A segmentation egg of the four-cell stage, showing the rosette-like yolk pyramids. (*Lycosa*). 2 B.

Fig. 3. A segmentation egg, shewing the union of the polygonal areas with the segmentation nuclei. (*Lycosa*). 2 B.

Fig. 4. The same as above, but of a little later stage. This shows that the yolk pyramids become very small and that the polygonal areas do not correspond in position with the yolk granules. (*Lycosa*). 2 B.

Fig. 5. An egg shewing the primary thickening of the blastoderm. (*Lycosa*). 2 A.

Fig. 6. An egg having the secondary thickening of the blastoderm, produced at the margin of the primary thickening. (*Lycosa*). 2 A.

Fig. 7. An egg in which the primary thickening has extended enormously, and the secondary thickening is at the margin of the primary one as before. (*Lycosa*). 2 A.

Fig. 8. A section of an egg of the two-cell stage, shewing the division of the yolk, and also yolk columns, the segmentation cavity, and the yolk nucleus. (*Lycosa*). 2 C.

Fig. 9. A section of an egg of the sixteen cell stage. (*Lycosa*). 2 C.

Fig. 10. A section of a segmentation egg in the stage of Fig. 3, containing twenty two nuclei. (*Lycosa*). 2 C.

Fig. 11. A portion of a section of an egg in the stage of Fig. 5. (*Lycosa*). 2 C.

Fig. 12. A portion of a section of an egg in the stage of Fig. 6. (*Lycosa*). 2 C.

Fig. 13. A section of the secondary thickening. (*Lycosa*). 2 D.

Fig. 14. A portion of an section of an egg, a little more advanced than the egg in the stage of Fig. 12. (*Lycosa*). 2 C.

Fig. 15. A section of an egg after segmentation showing the absence of the nucleus in the yolk and a number of small yolk balls. (*Lycosa*). 2 B.

Fig. 16. A longitudinal section of an egg of the protozonite stage. (*Agalena*). 2 B.

Fig. 17. A portion of a cross section of an egg of the protozonite stage. (*Agalena*). 2 D.

Fig. 18. A cross section of an egg showing the separation of the mesoderm into two lateral halves, the formation of the cœlomic cavity, and the appearance of the appendage, in the thoracic region. The mesoderm of the cephalic region is not yet divided. (*Agalena*). 2 B.

Fig. 19. The median longitudinal section of the embryo in the reversion stage. (*Agalena*). 2 B.

Fig. 20. A diagram of the ventral plate (imagined as unrolled) of an embryo in the stage of the maximum dorsal flexure.

Fig. 21. A diagram of the ventral plate (imagined as unrolled) of an embryo in the stage of reversion.

Fig. 22. A longitudinal section of an egg in the stage of Fig. 20, showing the appendages and cœlomic cavities. (*Agalena*). 2 B.

Fig. 23. A cross section of an egg in the same stage as of the previous figure, showing the semicircular groove, the lateral vesicle, the continuous mesoderm of the head, and the cœlomic cavities and thoracic ganglia. (*Agalena*). 2 B.

Figs. 24, 25. Portions of median longitudinal sections, showing

closeness of the cephalic and anal lobes, and the formation of the stomodæum (*Agalena*). 2 B.

Fig. 26. A portion of the median longitudinal section of an egg in the reversion stage, showing the expansion of the dorsum. (*Agalena*). 2 B.

Figs. 27-32. Longitudinal sections of the anal lobe in successive stages, showing the formation of the proctodæum and the change of the cœlomic cavity of the anal lobe to the stercoral pocket. (*Agalena*). 2 D.

Fig. 33. A cross section of the anal lobe, showing its unpaired cœlomic cavity and ganglion, and its two lateral diverticula. (*Agalena*). 2 D.

Fig. 34. A sagittal section of the abdomen of an embryo after the reversion stage. Two anterior abdominal septa are represented. (*Agalena*). 2 C.

Figs. 35, 36. Sagittal sections of the coxal joint of the first thoracic appendage, showing the communication of the cœlomic cavity with the exterior by an ectodermic invagination. (*Agalena*). 2 D.

Fig. 37. The glandular portion and the outlet of the coxal gland. (*Agalena*). 2 D.

Fig. 38. A cross section of the cephalothorax, showing the position of the coxal gland. (*Agalena*). 2 B.

Fig. 39. A cross section of the poison gland of an embryo, a little before hatching. (*Agalena*). 2 D.

Figs. 40-43. Portions of cross sections of the abdomen, showing the formation of the dorsal circulatory organ. (*Agalena*). 2 D.

Fig. 44. A portion of a frontal section of an embryo in the reversion stage, showing the three segments of the brain. (*Agalena*). 2 B.

Fig. 45. A diagram of the brain and the cheliceral ganglia.

Fig. 45a. A diagram of the profile view of the brain and the cheliceral ganglia of an embryo in the reversion stage.

Fig. 45. A frontal section of the brain of an embryo in the reversion stage, showing the formation of the eye. (*Agalena*). 2 C.

Fig. 47. A portion of a cross section of the abdomen in the reversion stage, showing the formation of the lung-book lamellæ. (*Agalena*). 2 F.

Fig. 48. A sagittal section of the brain of an embryo in the reversion stage, showing the formation of the posterior median eye. (*Agalena*). 2 D.

Fig. 49. A sagittal section of the posterior median eye of a hatched embryo. (*Agalena*). 2 D.

Figs. 50, 51. Portions of frontal sections of the cephalothorax in different stages of growth after the reversion of the embryo, showing the development of the anterior eyes and the formation of nerve fibres, the tapetum, and the vitreous body. (*Lycosa*). Fig. 50. 2 F. Fig. 51. 2 D.

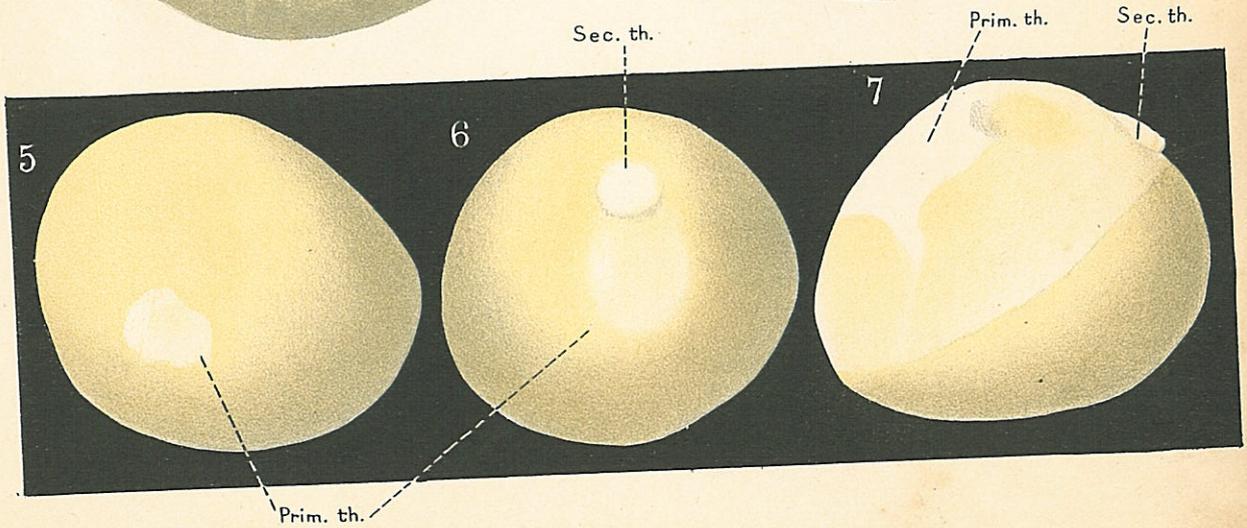
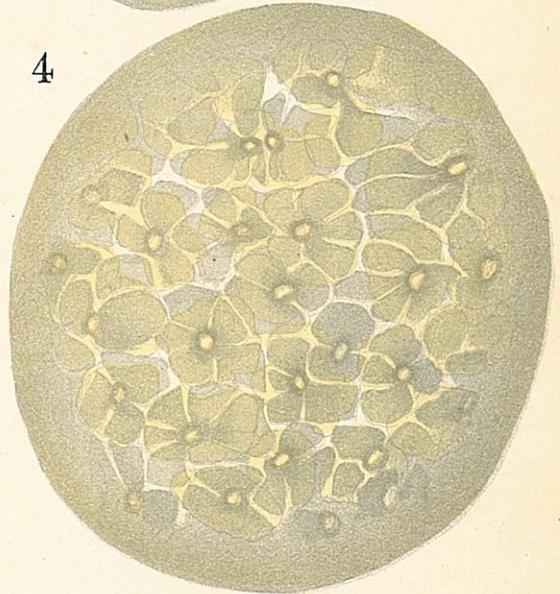
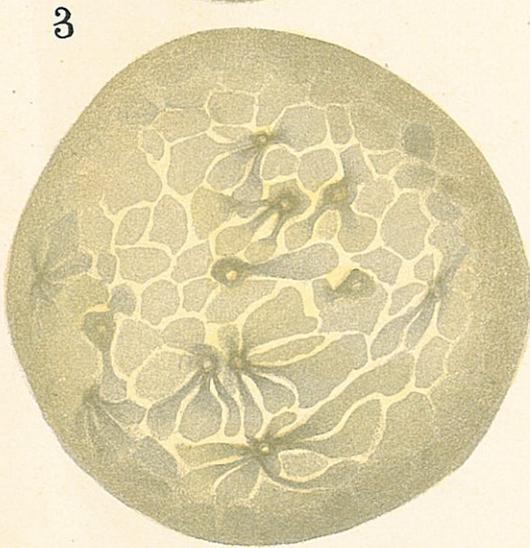
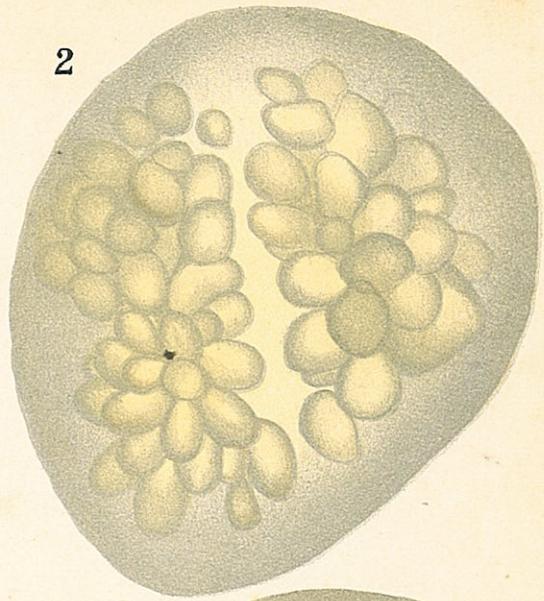
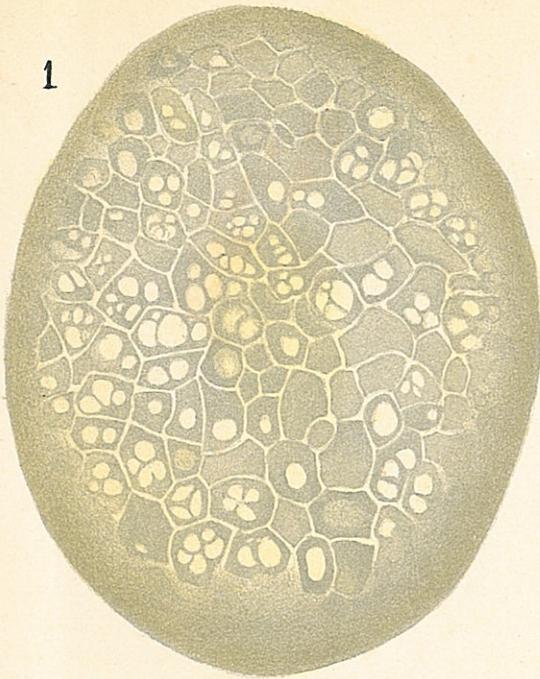
Fig. 52. An oblique frontal section of the anterior lateral eye of an embryo about the time of hatching. (*Lycosa*). 2 F.

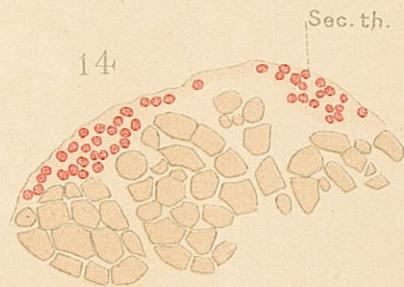
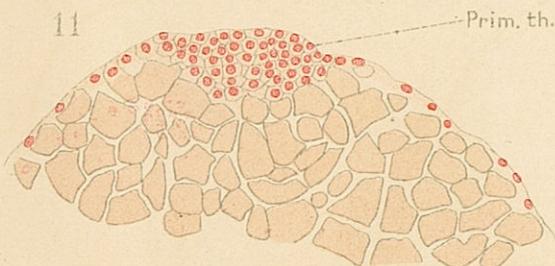
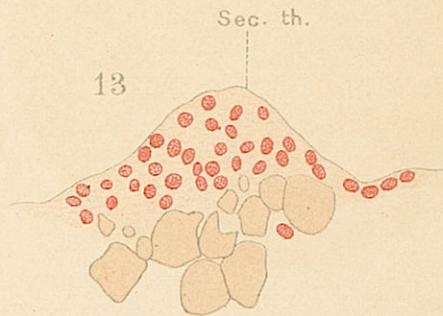
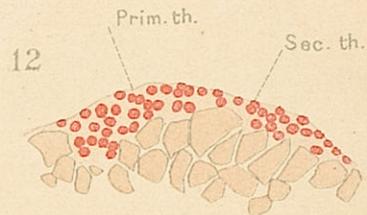
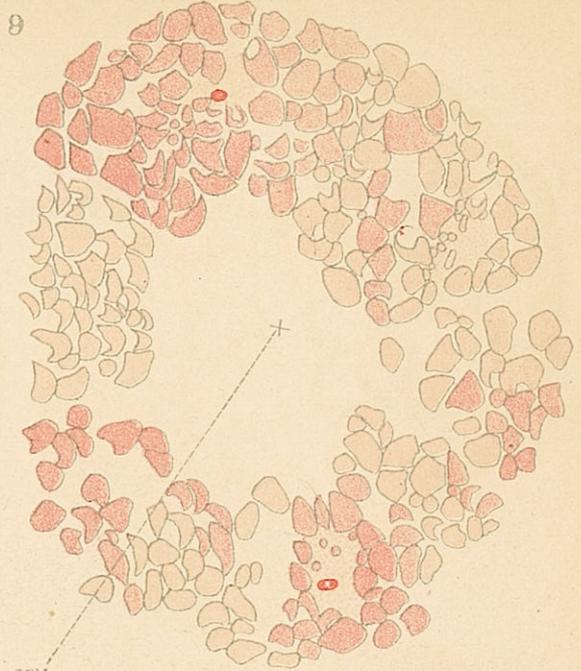
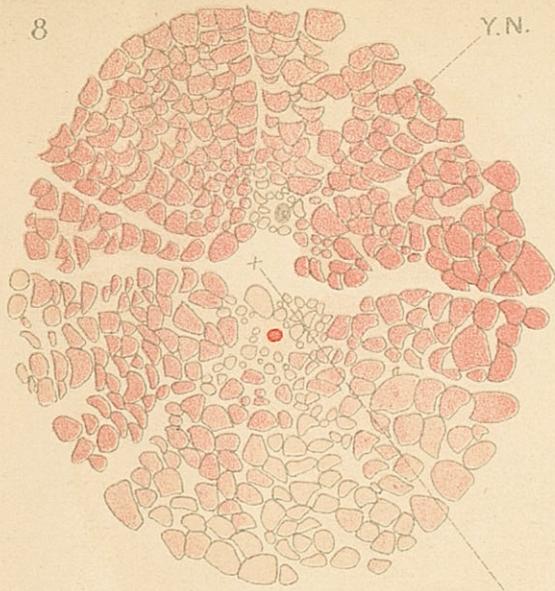
Fig. 53. A longitudinal section of the anterior median eye about the time of hatching. (*Lycosa*). 2 F.

Fig. 54. A frontal section of the anterior median eyes of a hatched embryo. (*Lycosa*). 2 D.

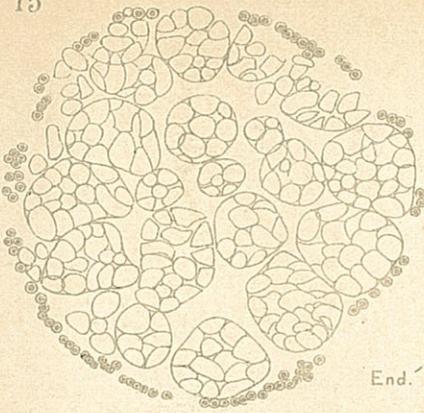
Fig. 55. A sagittal section of the abdomen about the time of hatching. (*Lycosa*). 2 B.



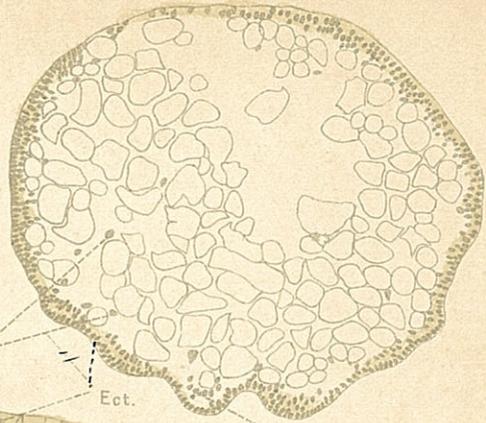




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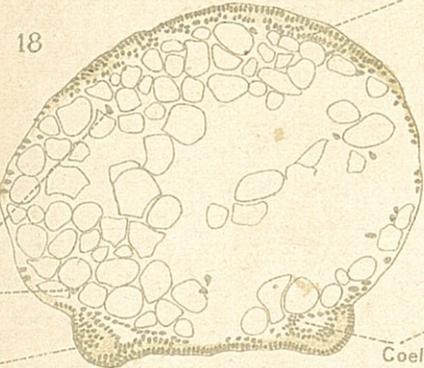
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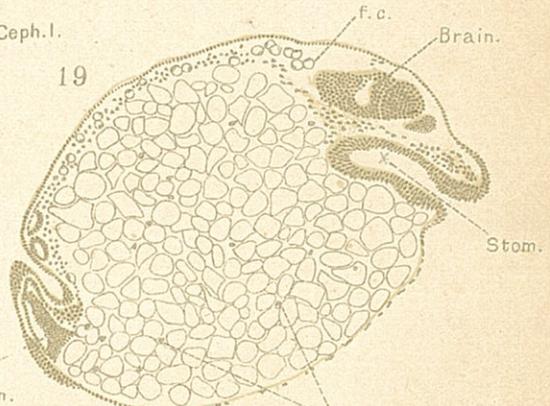
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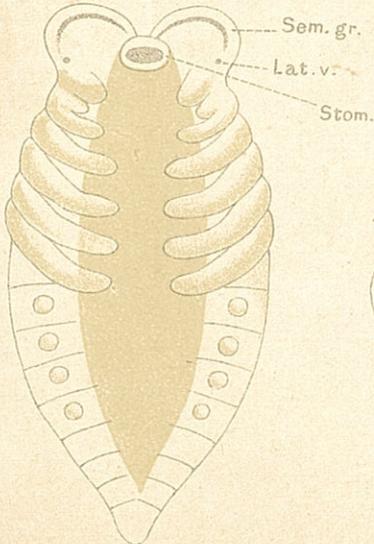
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