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Wczesne stadia rozwoju embrionalnego ryjkowca *Polydrosus pterygomalis* Boh. (*Coleoptera, Curculionidae*)

Early stages of embryonic development in the weevil *Polydrosus pterygomalis* Boh. (*Coleoptera, Curculionidae*)

napisała

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Introduction

Polydrosus pterygomalis Boh. belongs to the weevil family — *Curculionidae* — a family most numerous in species among the *Coleoptera*. Up to the present the knowledge of the embryology of the weevils has been inadequate and the data in the literature concerning this family are collected in the paper of Krzysztofowicz [8] upon the embryonic development of another representative of the genus *Polydrosus* Germ. — *P. sericeus* Schall.

In researches hitherto conducted upon the embryology of the insects a comparison of the development in closely related species has only occasionally been attempted. To fill up the gaps joint researches upon the different species of the genus *Polydrosus* Germ. have been undertaken in the Department of Zoology of the Jagiellonian University, and my work forms a part of these.

Material and methods

Polydrosus pterygomalis Boh. occurs in some places in the neighbourhood of Kraków. The specimens for my work were taken from Radziszów, where the species was found in masses feeding exclusively on oaks. The collected specimens were put into glass pots covered with gauze or a piece of thin linen. The

food, consisting of oak twigs and water, was changed every day or every second day.

The period of oviposition in *P. pterygomalis* Boh. occurs in the second half of May and in June. I do not know the manner of oviposition in natural conditions. In the culture the eggs could be found in the corner of a rolled-up leaf, between leaves touching each other or where a leaf was in contact with the wall of the vessel. Eggs were also laid on the gauze which covered the glass pot, in the folds of the linen which fixed the twigs in a small vessel, or on the pieces of linen or of tissue paper placed in the bottom of such a vessel.

During oviposition the female places herself parallel to the line of the folded edges of the linen and pushes her ovipositor between them. The time of laying a clutch of eggs lasts approximately 20 minutes. The bed contains on the average 50-70 eggs, arranged usually in the shape of a segment of a circle. In the clutch the eggs lie close to one another united by their envelopes; on the periphery the eggs are fastened to the substrate with a sticky secretion from special glands of the female. This secretion also covers all the eggs.

I fixed the eggs every six hours from the moment of oviposition till the stage of the maximal elongation of the germ band.

For fixing the eggs I used exclusively Bouin's fluid, in which the eggs remained for three days. Before putting them into the fixative I punctured the chorion with a fine pin. In addition, I fixed a part of the eggs with warm Bouin's fluid (at a temp. of + 80° for 1 minute). The method of „warm fixing" gave better results, especially in the earlier stages. At the same time I observed the development of the eggs *in vivo* in Ringer's fluid. Subsequently I embedded the eggs in the usual manner in paraffin and cut them into sections 9μ thick. The sections were stained with haematoxylin and eosin, and the whole eggs with boric carmine.

Structure of the egg

The eggs is oval in shape, its length measures up to 0.55 mm on the average, the width up to 0.28 mm; sometimes one of the poles is a little sharper. The egg has a smooth, somewhat shining

surface; immediately following oviposition it is creamy — whitish, and as the embryo develops it darkens, even to brown.

The egg is covered with two membranes: a strong, elastic external membrane, the chorion, and a delicate internal yolk membrane, the membrana vitellina, which always sticks closely to the plasmatic layer. Inkmann [6] distinguished two layers in the chorion in the eggs of *Calandra granaria* L.: the external one is supposed to be quite impermeable. I failed to observe in the chorion of the eggs of *Polydrosus pterygomalis* Boh. any difference between the external and the more deeply placed parts. The chorion appears as a uniform membrane somewhat detached from the yolk membrane.

On the periphery of the egg there is a very thin layer of superficial protoplasm, uniformly developed throughout the whole length, excepting the neighbourhood of the posterior pole and the place where the polar bodies are extruded, where it forms larger swellings. The superficial protoplasm shows a fine net-like structure, denser in the peripheral part than on the internal side. Very often some of its sectors stain rather more strongly, giving the impression of a granulated protoplasmatic layer. Sometimes there is a marked difference in the staining of the separate layers. Under the immersion objective one can clearly distinguish a narrow, superficial, lightly stained zone and a darker internal stripe. A similar appearance was observed by Butt in *Otiorrhynchus ligustici* L.

The layer of superficial plasma passes in the central part into many protrusions which join up into an irregular network spread within the egg.

This thickening of the protoplasm occurs on the posterior pole. The thickening is hardly visible and it either covers the pole like a hood or spreads as an irregular protoplasmatic projection deep into the egg (fig. 1). Butt (1936) observed a similar protoplasmatic swelling in *Otiorrhynchus ligustici* L., and called it the oösome or the germinal cytoplasm. According to Butt the oösome is connected with the differentiation of the primordial germ cells.

The above-mentioned protoplasmatic thickening on the po-

sterior pole stains somewhat more strongly than the remaining part of the superficial protoplasm.

The interior of the egg is occupied by the yolk, held in the meshes of the protoplasmatic network. The yolk globules are smaller on the periphery of the egg, increasing in size rather rapidly as they proceed towards the centre.

In the eggs of the species in question I never found any micropyle, though this was observed both by Krzysztofowicz [8] in *Polydrosus sericeus* Schall. and by Smreczyński [12] in *Phyllobius glaucus* Scop. Inkmann [6] suspected its presence in *Calandra granaria* L. but could not identify it for certain.

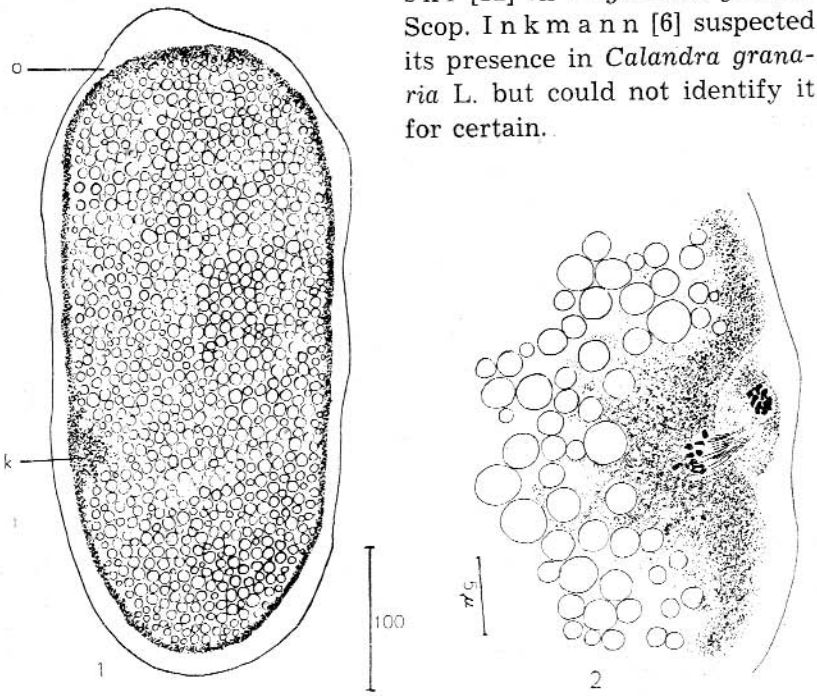

Fig. 1. Longitudinal section through the egg.
o — oösome, k — protoplasmatic thickening in the place where the polar bodies are extruded.
Fig. 2. Maturation of the egg — telophase of the first division.

Maturation of the egg

The earliest stage in my material was the telophase of the first maturation division (fig. 2). The axis of the karyokinetic spindle is perpendicular to the surface of the egg. The spindle

lies in the protoplasmatic swelling which has the shape of an open cone. (The swelling can be seen on 3-4 successive sections 9μ thick).

The chromosomes of the first polar body in the shape of short rods are placed in a small plasmatic protrusion which rises out of a small depression in the superficial protoplasm. The protoplasm of the first polar body stains somewhat less intensively than the surrounding peripheral plasma.

The expulsion of the polar body occurs at about 1/3 of the length of the egg from the anterior pole, sometimes nearer to the equator of the egg. The first maturation division of the egg

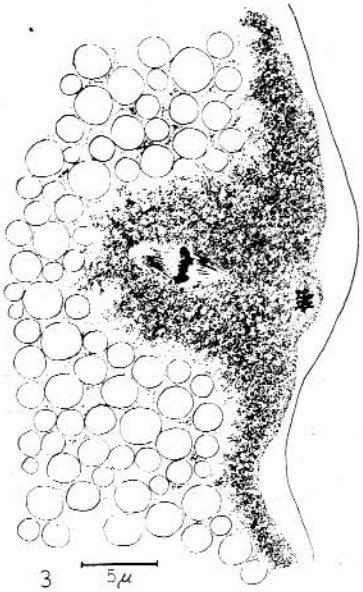

Fig. 3. Maturation of the egg — second division.

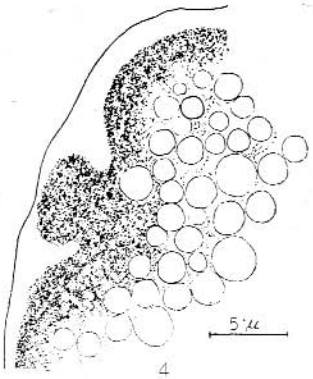

Fig. 4. Pseudo-body.

is the reduction division, as in *Polydrosus sericeus* Schall. According to Inkmann [6], in *Calandra granaria* L. reduction of the chromosomes occurs only during the second division.

Shortly after the first division the nucleus undergoes the second karyokinesis. It is very likely to be preceded by a transient resting stage, resembling the stage observed by Krzysztofowicz [8] in *Polydrosus sericeus* Schall. The axis of the second division lies under the first polar body. (fig. 3)

The result of the second mitosis is the formation of the second polar body, which, unlike the first, changes into the resting nucleus and lies in the immediate neighbourhood of the base of the first; it is never extruded beyond the superficial plasma.

After the second division the nucleus recedes deeply back towards the axis of the egg. Shortly after the formation of the second polar body the chromosomes of the first divide into two groups, which corresponds to its abortive division.

In the second polar body the nuclear membrane soon disappears in consequence of which the chromosomes lie loosely in the plasma. Simultaneously the chromosomes of the first polar body begin to shift towards its base, come into the neighbourhood of the chromosomes of the second polar body, and form with them an irregular group of strongly stained rods or crooked structures which slowly degenerate. The plasmatic protrusion of the first polar body is drawn back into the superficial plasma.

At the time when the polar bodies were extruded I observed in some eggs the appearance of small protoplasmatic protrusions at different points on the periphery of the egg, for instance in the neighbourhood of the poles; by their appearance and structure the protrusions very much resembled the polar bodies. These pseudo-bodies were deprived of chromatin and were sometimes a little larger than the normal polar bodies (fig. 4.). Their significance has not yet been explained. I did not find any mention of them in the literature, but they have also been observed in *Polydrosus sericeus* Schall. (K r z y s z t o f o w i c z) and in *Agelastica alni* L. (W ę g l a r s k a).

Fertilisation

When maturation ist completed the nucleus of the egg surrounded by the plasmatic islet places itself more or less on the axis of the egg in the neighbourhood of the anterior pole. The spermatozoa of *Polydrosus pterygomalis* Boh. have a very thin, thread-like head which makes their observation in the egg very difficult. The head of the spermatozoon swells as it approaches the nucleus of the egg and between it and the super-

ficial plasma on the anterior pole there is visible a thin plasmatic stripe meandering between the yolk globules and intensivelv stained with basic stains. Immediately before copulation, the nuclei of the egg and of the spermatozoon are spherical and of the same size.

In one case I observed very distinctly two spermatozoa close to the nucleus oft the egg.

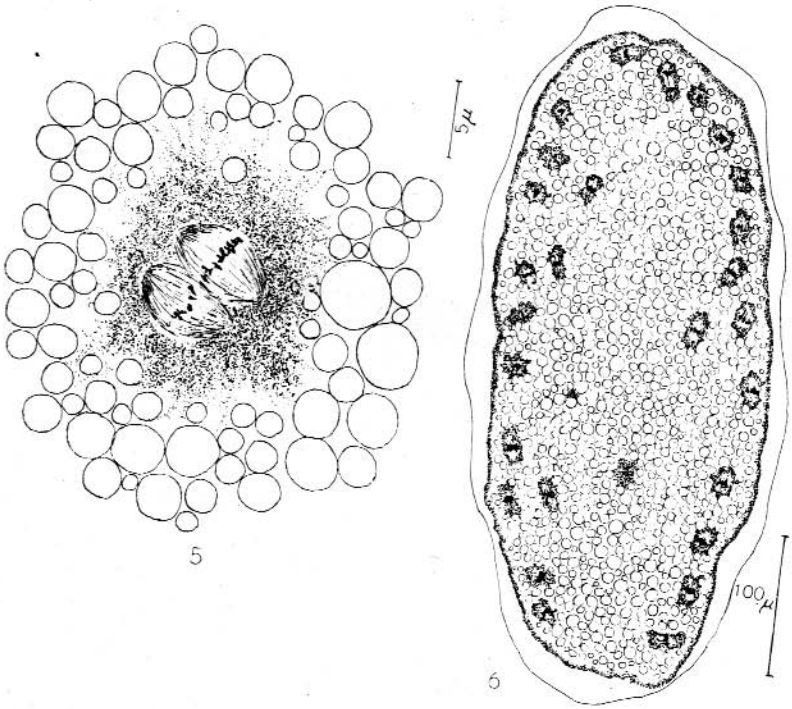

Fig. 5. First division after copulation — preserved individuality of the male and female nuclei.

Fig. 6. Karyokinetic division of the blastomeres before emergence on the surface.

Cleavage and formation of the blastoderm

After the copulation of the nuclei, the first division occurs 3-4 hours after the moment of oviposition, at a temperature of +18° to +22° C (fig. 5).

Often the karyokinetic spindle places itself more or less parallel to the longer axis of the egg. Sometimes during the first division after copulation the two spindles are distinctly seen lying close to each other, emphasizing the still preserved individuality of the male and female nuclei (fig. 6). At about the 6th hour after oviposition (at a temperature of +18° to +22° C) the blastomeres are four in number. By successive divisions the number of blastomeres increases and afterwards

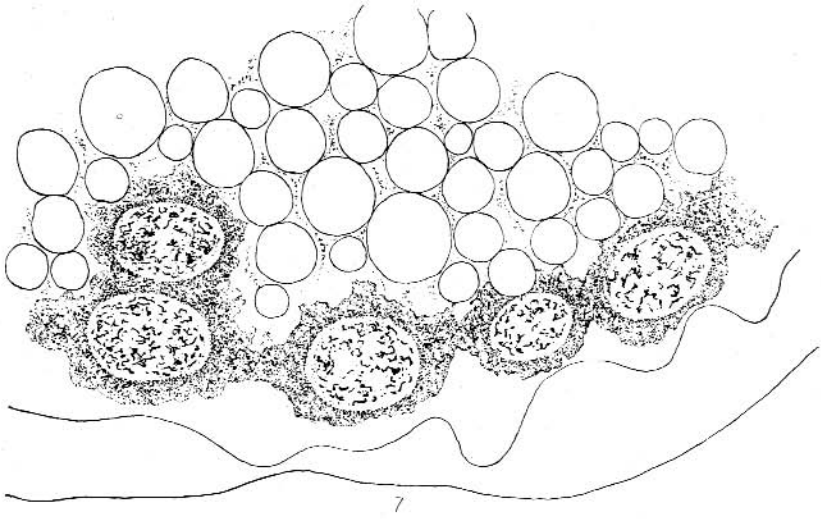

Fig. 7. Blastomeres on the surface.

begins their migration towards the surface of the egg. Therefore cleavage in *Polydrosus pterygomalis* Boh. resembles the conditions described in *Hydrophilus*, but takes a different course from that in the type of *Platycnemis* [11].

As is known, in the latter type the blastomeres migrate towards the surface immediately after the first divisions. The cleavage in *Polydrosus pterygomalis* Boh. takes a similar course to that in *P. sericeus* Schall., *Phyllobius glaucus*. Scop., *Calandra granaria* L., and *Otiorrhynchus ligustici* L.

The blastomeres begin their migration simultaneously, and divide several times during its course. Fig. 7 shows the last mitosis before emergence on the surface. The karyokinetic

spindles are placed parallel to the surface of the egg. Only in the places where the polar bodies were extruded, in which the protoplasmatic swelling still remains, do the blastomeres reach

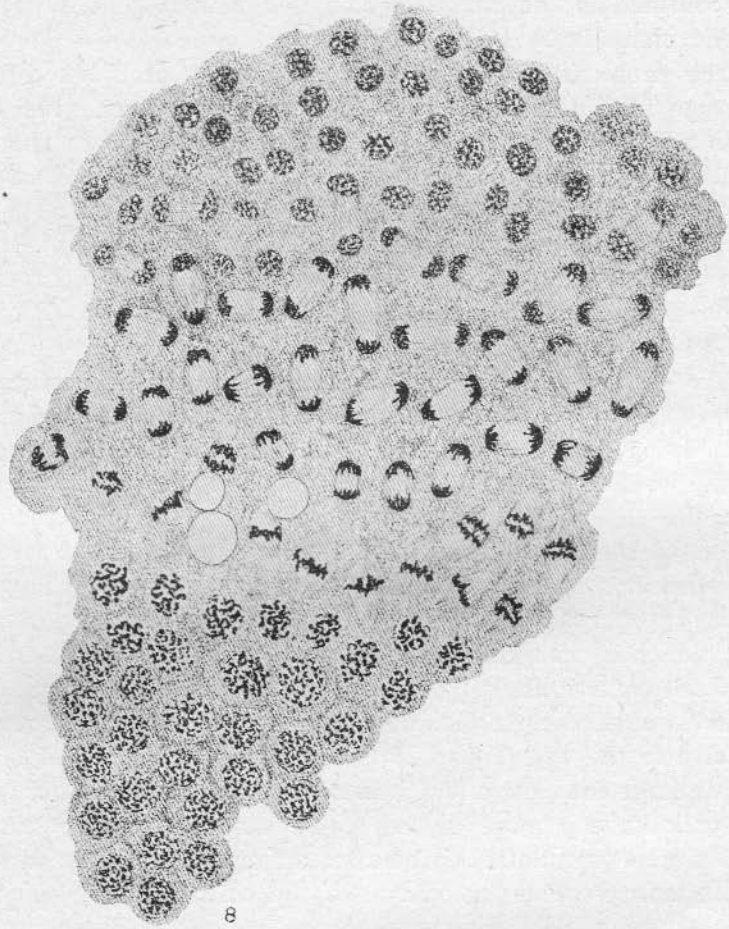

Fig. 8. Undifferentiated blastoderm — karyokinetic divisions.

the surface later. Butt has observed in *Otiorrhynchus ligustici* L. that in the place where the polar bodies degenerate a few blastomeres appear, and that the formation of the walls which surround them occurs after some delay.

All the blastomeres are identical; no difference is seen between them either in their appearance or in their reaction towards the stains. Generally their divisions are synchronous. The deviations from the general rhythm are insignificant, and are confined to the single blastomeres which are one karyokinetic phase late.

The problem of the synchronism of the divisions during cleavage in the insects has been given very much attention. Strict synchronism was observed in the representatives of some families, for instance in *Hydrophilus* Geer (H e i d e r), *Musca* L. (B l o c h m a n n), *Ephestia* Gn. (S e h l), *Platycnemis* (S e i d e l). Nevertheless the latest papers dealing with the embryology of the insects express the opinion that the synchronism of the divisions is not quite strict. (S m r e c z y ń s k i, K r z y s z t o f o w i c z, W ę g l a r s k a).

The blastomeres emerge simultaneously on the surface of the egg (fig. 9). At first they are shaped like flat irregular islets, lying at some distance from one another. The protoplasmatic islets of the blastomeres become completely united with the superficial plasma. The following karyokinetic divisions of the blastomeres increase their number and actuate their denser arrangement. Lastly the syncytial layer is formed, uniformly surrounding the whole yolk except for the posterior pole, which is occupied by the primordial germ cells, described in detail in a folloving chapter. In this layer the boundary lines between the neighbouring blastomeres appear arranged radially to the egg (about 27 hours after oviposition, fig. 10). In this stage the cells of the blastoderm not yet separated from the yolk have a more or less cubic shape and large nuclei, with finely granulated chromatin, arranged near the surface of the embryo. The protoplasm of the cells is finely alveolar (fig. 11). Now the karyokinetic divisions follow. These do not take place synchronically but with distinct fluctuations (fig. 8). The divisions begin on the posterior pole and spread towards the anterior pole.

The formation of the tangent walls separating the blastoderm and the yolk occurs later. Simultaneously the blastodermal cells lengthen and assume a cubic shape (fig. 12).

The nuclei retain their former appearance, but their excentric position is more emphasized on account of the elongation of the cells. In their basal parts I, like Krzysztofowicz [8] in *Polydrosus sericeus* Schall., have never seen any of the small yolk globules whose presence Smreczyński [12]

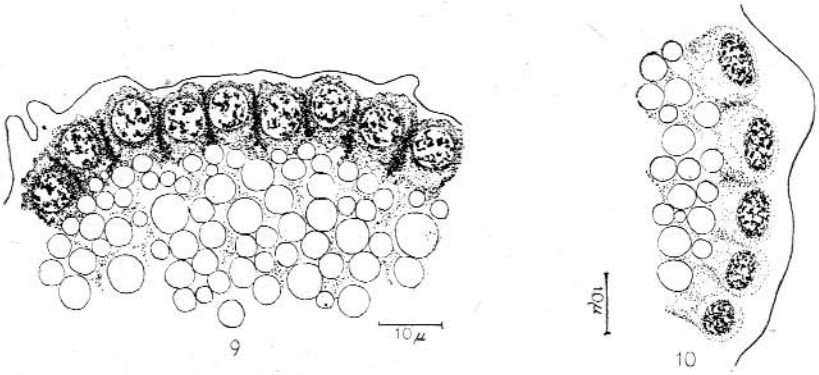

Fig. 9. Formation of the radial walls in the blastodermal syncytium.
Fig. 10. Blastoderm after the formation of the radial walls.

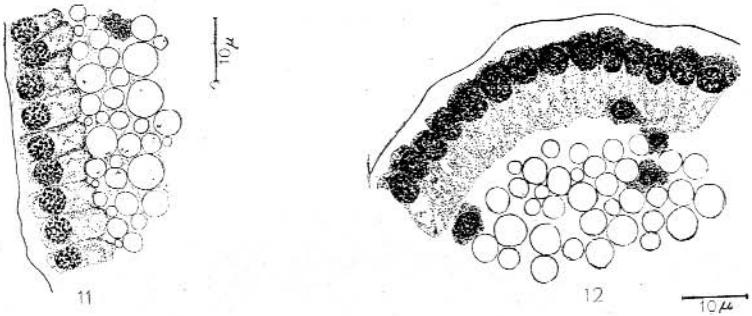

Fig. 11. Blastoderm — later stage.
Fig. 12. Migration of the blastodermal cells into the yolk

has observed in a part of the blastoderm in *Phyllobius glaucus* Scop.

The blastoderm, composed of the cells described, surrounds the whole yolk quite uniformly with the exception of the posterior pole.

Vitellophags

A number of the blastomeres do not take any part in the formation of the blastoderm. They remain in the yolk and at first do not differ in appearance from the blastomeres migrating towards the surface. These are the yolk nuclei or the vitellophags, which continue to multiply karyokinetically. The rhythm of their divisions is not synchronised with the divisions in the blastoderm and takes place differently in the separate vitellophags.

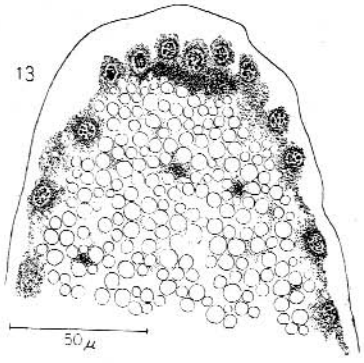

Fig. 13. Primordial germ cells at the moment when the blastomeres emerge on the surface.

At the moment when the blastoderm differentiates, the vitellophags begin to gather together into strings or lumps, (5-8 in number), as in other insects. In the later stages, even after the differentiation of the blastoderm, the migration of

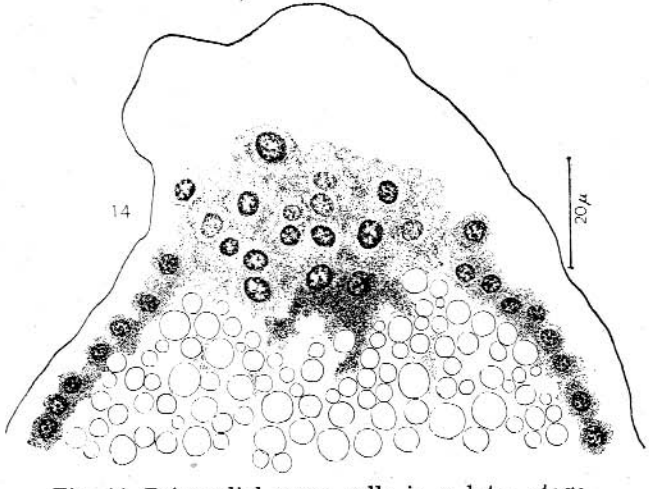

Fig. 14. Primordial germ cells in a later stage.

separate cells from the blastoderm to the yolk can be observed here and there (fig. 13).

According to Johannsen and Butt those cells which Heymons [4] called parycytes are not to be confused with the vitellophags. The described migration of the cells from the blastoderm takes place only in that part which in the following development forms the germ band. The presence of paracytes was observed by Butt in *Otiorrhynchus ligustici* L. The vitellophags take part in the assimilation of the yolk, but the role of the paracytes has not yet been explained.

Primordial germ cells

On the posterior pole there is in the early stages a swelling of the superficial protoplasm, which takes the basic stains more strongly than the rest of the protoplasm. Some of the blastomeres, not differing in any way from the rest, get into the swelling. These blastomeres push out over the surface of the egg and form the polar cells or the primordial germ cells, well-known in the development of other insects (fig. 14).

The protoplasm of the blastomeres pushing out over the surface stains less strongly than the protoplasmatic gathering at their base and the difference also remains in the later stages (fig. 15). Contrary to the blastomeres in the other parts of the egg, which later from a syncytium, the primordial germ cells

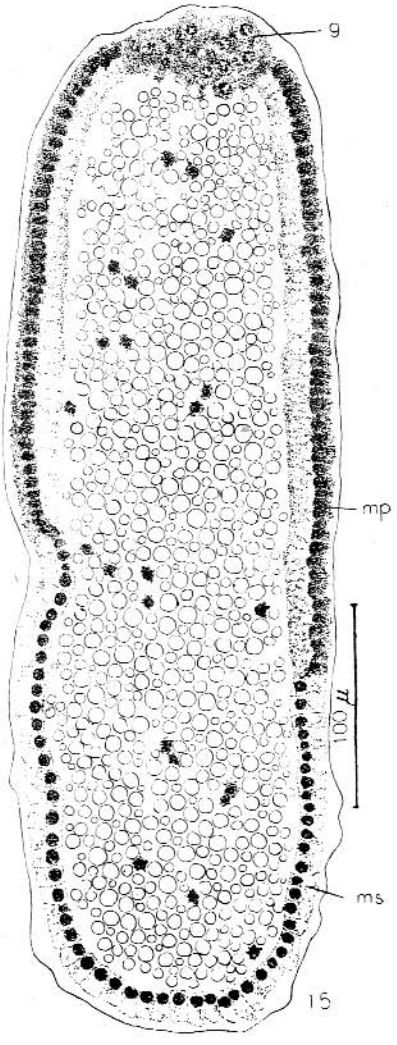

Fig. 15 Differentiation of the blastoderm.
mp — material for the germ band and for the amnion, *ms* — material for the serosa, *g* — primordial germ cells.

surround themselves very early with walls, which later remain permanently. The divisions occurring in the blastomeres cause distinct differences in the size of the separate cellular elements. Sometimes the primordial germ cells do not lie on the pole but are somewhat shifted towards the ventral side.

In the stage of the differentiation of the blastoderm the primordial germ cells are surrounded by the cells of the future germ band as if included within them, so that they are a great deal more difficult to observe. They then become similar to the cells of the germ band in their mode of staining, showing a less vacuolised protoplasm and nuclei of a different size, with the chromatin gathered chiefly under the nuclear membrane. Inkmann [6] supposed that the primordial germ cells develop in *Calandra granaria* L. from one blastomere, which notwithstanding the lack of morphological differences, has been physiologically differentiated earlier. His opinion, however was called in question by Scheinert [9], who investigated the same species.

Differentiation of the blastoderm

The stage in which the blastoderm (fig. 12) uniformly covers the whole yolk, with the exception of the posterior

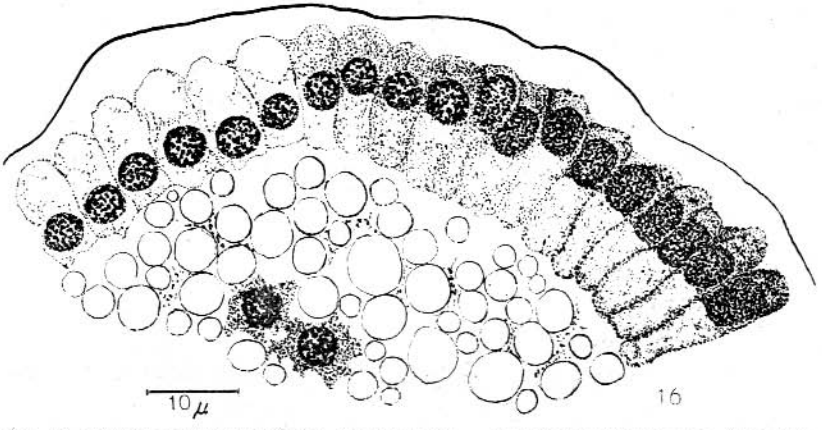

Fig. 16. Differentiation of the blastoderm — border between the two territories.

pole, does not last long. Embryos 3 hours older present already

a different appearance. The changes occurring in the blastoderm take place so quickly that I failed to observe their course. The result of the changes is the differentiation of the blastoderm into territories sharply separated from each other and differing distinctly in the appearance of their cells (fig. 16).

The posterior part of the yolk, even beyond the equator of the egg, is occupied by deep cells, whose oval nuclei are placed near the top of the cells. Their finely granulated chromatin is uniformly displaced. The protoplasm in the upper parts of the cells is dense, in the basal parts strongly vacuolised and weakly stained.

The anterior, distinctly smaller part of the egg is occupied by somewhat smaller and wider cells. Their spherical nuclei, with the chromatin arranged as in the previously mentioned cells, are smaller and placed at the base of the cells; their plasma is so strongly vacuolised that in preparations the cells seem empty. The latter cells are the material for the serosa, while the former give later the germ band and the amnion (fig 17). In *Polydrosus sericeus* Schall. the differentiation of the blastoderm takes place similarly, but the cells of the germ band shift on the dorsal side beyond the equator of the egg, and in *Phyllobius glaucus* Scop. the cells of the germ band form a regular bowl covering the posterior half of the egg. In *Calandra granaria* L. the cells of the germ band appear only on the ventral side and form as a whole a small oval disc reaching from the posterior pole to about

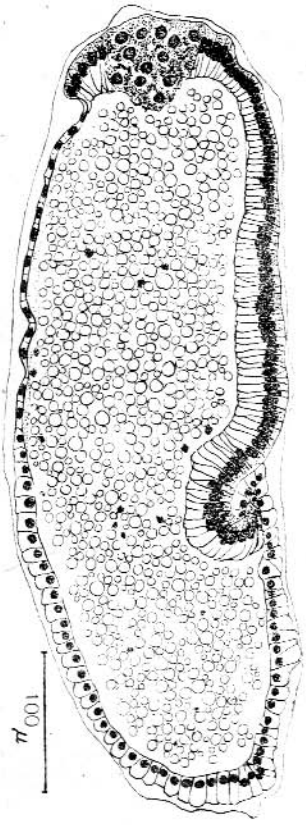

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Fig. 17. Formation of the furrow (rudiment of the amnion cavity) on the ventral side.

1/4 of the length of the egg, while on the dorsal side of the egg the cells become flat and later form the dorsal syncytium in which the serosa arises.

Formation of the germ band and of the embryonic envelopes

In the above-described position of the two parts of the blastoderm far-reaching changes occur in later stages. The epi-

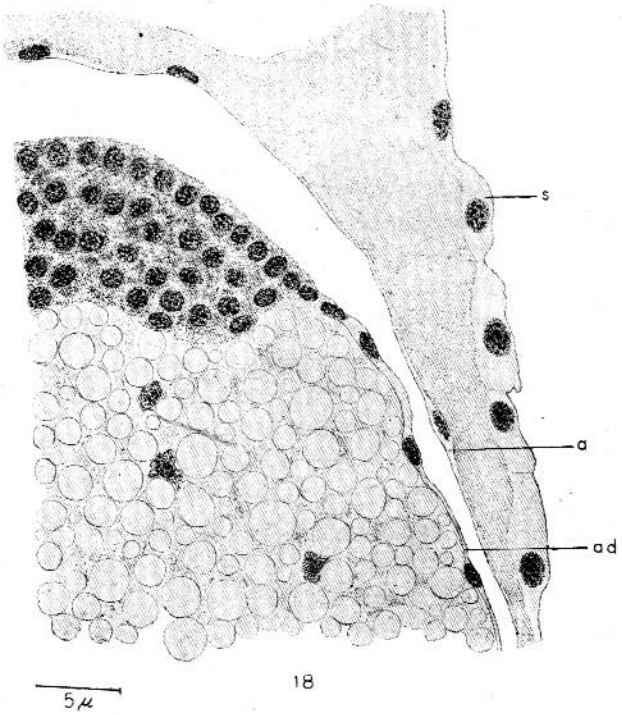


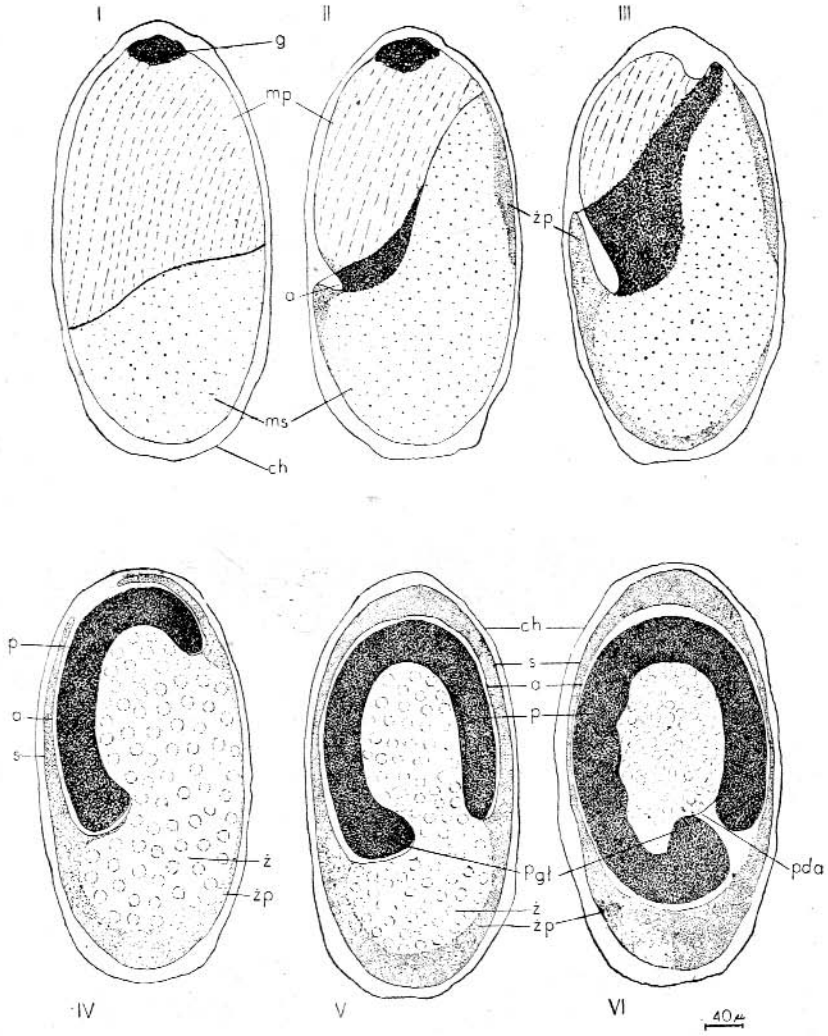
Fig. 18. Embryonic envelopes in the stage of maximal elongation of the germ band.
a — *amnion*, *ad* — membrane over the amnion, *s* — serosa.

thelium of the germ band begins to shift on the dorsal side towards the posterior pole and on the flanks towards the ventral side; simultaneously the cells of the neighbouring parts of the material of the serosa become considerably flattened. Diagram I illustrates this process, whose final stage is visible

on the section (fig. 18). Simultaneously with the shifting of the germ band its cells on the ventral side become elongated and slightly flattened; on the border between the germ band and the cells of the future serosa a small furrow appears, which at first deepens perpendicularly to the longer axis of the egg The furrow is the rudiment of the amnion cavity. At a somewhat later stage (Diagram II) the germ band becomes much narrower and loses the bowl-like shape previously covering the whole posterior part of the egg. Now it is a zone which stretches from the posterior part of the egg to $^2/_3$ of its length on the ventral side and on the flanks it reaches to about the half the height of the egg. In this stage the zone has a uniform width. The furrow which is the rudiment of the amnion cavity is placed obliquely to the axis of the egg and is at the same time prolonged on the flanks of the embryo. The furrow which is formed on the back of the band has a different appearance. There it is shallow and relatively wide, and the end of the embryo passes gently into the cells of the amnion. In the posterior part of the band there is no very strong depression into the yolk, which in a similar stage in *Polydrosus sericeus* Schall. is very distinctly marked. While the forepart of the germ band does not change, the following parts become narrower, nad thus the head lobes stand out.

At the moment when the furrow is formed the process of liquefaction of the yolk begins in the anterior part of the embryo. The first traces are found under the furrow and on the ventral side under the flattened cells of the serosa. At first the liquid yolk is shed as a thin layer under the cells of the serosa. In later stages it may be said in general that the liquid yolk always appears in those places where the shifting or depression of the cells occurs. The liquefaction of the yolk does not change its chemical qualities. Its quantity increases gradually and in later stages it approaches more and more towards the serosa so that the yolk not yet liquefied forms a ball immersed in liquid yolk.

The folds of the amnion cover increasingly large parts of the germ band, and simultaneously from the flanks of the germ band at the place where it passes into the amnion a fold



Diagrams I, II, III, IV, V, VI — formation of the germ band and of the embryonic envelopes.

a — amnion, *ch* — chorion, *g* — primordial germ cells, *mp* — material for the band and for the amnion, *ms* — material for the serosa, *p* — germ band, *pda* — membrane over the amnion, *pgł* — head lobes, *s* — serosa, *ż* — yolk, *żp* — liquid yolk.

begins to move forward; it is built of very flat cells and gradually covers the ball of yolk not yet liquefied.

The narrowing of the entrance to the amnion cavity (of the amnioporus) continues and finally it closes in the neighbourhood of the posterior pole. The process of enclosure of the unliquefied yolk also continues, leading consequently to the complete surrounding of the unliquefied yolk on the lateral and dorsal sides by a thin membrane very much resembling the amnion, and to the complete separation of the amnion and the germ band. Therefore in the stage of maximal elongation of the germ band we see the following situation: within the uniform serosa built of somewhat flattened cells there is the liquefied yolk, which stains in the same way as the globules of unliquefied yolk. The liquid yolk surrounds the amnion, which forms a completely closed sac made of very flat cells; the inside of the sac is occupied by globules of unliquefied yolk, and on this is spread the germ band with its well-developed head lobes. The surface of the yolk ball, with the exception of the germ band, is covered by a thin membrane of the same histological structure as the amnion. In this stage the back of the band nearly touches the head lobes; the band has already two layers, because the lower ribbon is well developed throughout its length. As can be seen from this, in the stage of maximal elongation of the germ band the conditions in *Polydrosus pterygomalis* Boh. are identical with those described in *P. sericeus* Schall. and *Phyllobius glaucus* Scop., but the intermediate stages leading to it show distinct differences. In *Polydrosus sericeus* Schall. as well as in *Phyllobius glaucus* Scop. the course of the furrow corresponding to the rudiment of the amnion and also the further shiftings and transformations of the germ band take place differently. This shows that the development in the early stages manifests in every species some characteristics which do not last long and lead the embryos to the common course of the following transformation.

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STRESZCZENIE

Jajo *Polydrosus pterygomalis* Boh., owalne, o średnich wymiarach 0,28-0,55 mm, pokryte jest dwiema błonami: chorionem i błoną żółtkową. Warstwa protoplazmy, cienka na obwodzie, zgrubiała na biegunie tylnym i w miejscu wydzielania ciałek kierunkowych (w 1/3 długości od bieguna przedniego) obejmuje wnętrze wypełnione kulami żółtka. Wydzielanie pierwszego ciałka kierunkowego połączone jest z redukcją chromosomów, drugie ciałko lokuje się u podstawy pierwszego w formie jądra spoczynkowego. W niektórych jajach występują pseudociałka, twory plazmatyczne przypominające ciałka kierunkowe, pozbawione jednakże chromatyny.

Bruzdkowanie i migracja blastomerów na powierzchnię rozpoczyna się w 3-4 godziny po zniesieniu jaja. Na powierzchni jaja blastomery wytwarzają *syncytium*, w którym ściany promieniste powstają wcześniej od ścian stycznych. Od tego momentu podziały kariokinetyczne przebiegają metachronicznie.

Blastoderma, początkowo jednolita (prócz bieguna tylnego, na którym leżą komórki pragenitalne), różnicuje się na:

1) materiał na serozę, który obejmuje biegun przedni, sięgając prawie do 1/2 długości jaja po stronie grzbietowej i do 1/3 po stronie brzusznej,

2) materiał na prążek i amnion, obejmujący pozostałą resztę powierzchni jaja.

Na granicy obu obszarów po stronie brzusznej pojawia się bruzda (zawiązek jamy amnionu), która następnie przesuwa się ku biegunowi tylnemu. Przesuwaniu temu towarzyszy silne spłaszczanie się sąsiadującego z bruzdą materiału na serozę. Wpuklenie się jego następuje dopiero w pobliżu bieguna tylnego.

Po zróżnicowaniu się blastodermy można zauważyć wywędrowywanie pojedynczych komórek blastodermy do żółtka.

Zarodek, początkowo w kształcie czaszy, przybiera następnie kształt pasa, sięgającego od bieguna tylnego do 2/3 długości jaja, a później wydłuża się tak silnie, że jego część przednia, z zaznaczonymi płatami głowowymi, prawie dotyka części tylnej. W późniejszym nieco stadium upłynnione żółtko wypełnia przestrzeń między serozą a workiem amnionu. Powierzchnię

nieupłynnionego żółtka poza prążkiem zarodkowym przykrywa cienka błona, histologicznie zbliżona do amionu.

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