

On the Origin of Space

Part 3D: Quantum Spatial Development - The Drosophila Embryo

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Abstract

Quantum dynamical space reveals itself in various forms within the initial phases of living organisms development. The chemical approach followed by the literature to identify the basic principles of morphogenesis appears then to be fundamentally incomplete by missing the holistic aspect of such developments, where the various cells interact on a spatial level with the principles of the interactions having nothing to do with chemistry. The early embryo of drosophila melanogaster gives key examples of such holistic physical interactions.

Keywords: drosophila, embryo, blastoderm, energid, bicoid, leptonic space manifold

Introduction

Can we apply the understanding of quantum dynamical spaces, i.e. space being built by its contents, as developed in [1] through [4], to the set of evolving biological cells called eggs, oocytes, zygotes and embryos, i.e. to the beginnings of living organisms? If we can do that in a meaningful way, we would obtain a strong confirmation about the existence of physical phenomena in Life not found anywhere else, as well as additional insight on how such processes run and are applied by Life. To this effect, we will take a number of pictures of developing systems drawn in the literature, and add a description of what is spatially going on in them. We shall look for logical physical explanations that complement existing descriptions, especially in areas where the research is presently stumped on the nature of the happenings. This article covers the early embryo of *drosophila melanogaster* as this system is a microcosm of key **physical** happenings that need description and evaluation in order to understand a number of physical facets fundamental to the existence of Life. The oocyte development and other developmental systems are evaluated separately. A short description of the first 5

stages of embryogenesis extracted from a large website is given in the Appendix to be used as a reference in the following text. [5] We describe *physical happenings* that mostly receive inadequate or no explanation in the literature as that literature covers almost exclusively only chemical facts. The physics appears left out, as if unnecessary or as a minimum incomprehensible, but yet it is the obvious key to the life of the organism. We will cover only a small part of this physics here, to give examples of the kind of physics involved, which is certainly not known classical physics.

a. Completion of meiosis [6. 7]

After mating, females release stored sperm from their seminal receptacles, so a sperm enters the micropyle shortly after the oocyte passes through the oviduct and while the egg is still in the uterus. As we have seen in the oocyte development, the first meiotic

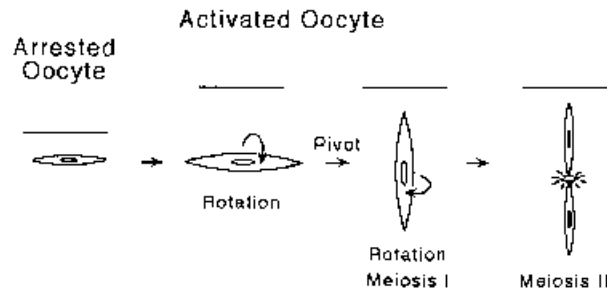


Fig. 1 – Rotation vs. cortex (line) [6]

division began then, and was arrested at metaphase I, with chromosomes (pronucleus) located in the cortical region near the anterior pole with the spindle aligned parallel to the egg surface. We have seen that a leptonic space manifold is tied to the chorion envelope generated by follicle cells. The follicle cells were sloughed off during the passing through the oviduct. Now any mechanical disturbance to this envelope disturbs this manifold and the spindle immediately rotates to a radial orientation vs. the egg cortex and resumes meiosis. (Fig. 1) *How such successive spindle orientations are achieved and maintained is an unanswered question in the literature (they are not even asked). These are definitely physical happenings, not chemical ones, and yet Life appears to depend on this kind of happening.*

Microtubules linking spindle poles to the oocyte surface have been implicated in the rotation and anchoring of the meiotic apparatus in other organisms (we will see such in another article about the *c. elegans* worm), but this is not the case in the *Drosophila* oocyte since the spindles lack astral MTs (i.e. lack centrosomes). However, a display of spindle assembly described as “complex” in the literature takes place, consisting of a transient array of MTs

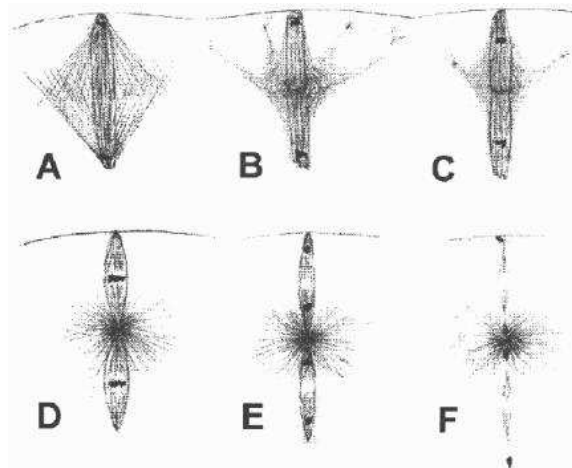


Fig. 2 – Meiosis I and II [8]

radiating from the equatorial region of the spindle toward discrete foci in the egg cortex. (Figs. 2B & C) The orientation of the spindle in Drosophila then also requires functional interaction with the oocyte envelope, a **physical function which is again unexplained**. We shall identify later the reasons for such happenings.

The subsequent meiosis II twin spindles (Figs. 2DEF) are arranged in tandem, end to end, and disposed perpendicular to the longitudinal axis of the egg, with the innermost spindle carrying the pronucleus that will join the sperm pronucleus. (The other 3 pronuclei will move to the egg surface where they disappear.) A *monastral* array of MTs is observed between these twin spindles at metaphase II, anaphase II and telophase II, making something that looks like a *central pole body*. (Fig. 3 - We shall note here that *the figure shows almost a perpendicular arrangement between the two lines of twin meiotic spindles*, something not reported in [7].)

γ -tubulin transiently localizes to this central body, which also contains components of the Drosophila embryos centrosome (DMAP190 or CP190). Therefore, **this egg must contain a maternal pool of centrosomal components undetectable in mature inactivated oocytes**. However, these components are **unable to organize bipolar spindles**. The zygotic centrosomes essential for such spindles must be obtained from the male. We can only conclude then that

male gametes contribute more than just DNA to this zygote, and

indeed an essential *physical* part is contributed by them for the construction of the embryo.

Assembly of the above combination of spindles occurs by reorganization of the meiosis I spindle without its breakdown: The unusual disc- or ring-shaped central pole body forms de novo in the center of the elongated meiosis I spindle, followed by formation of the central spindle poles. The first step in forming the central pole body is the appearance of *puckers* in the center of the meiosis I

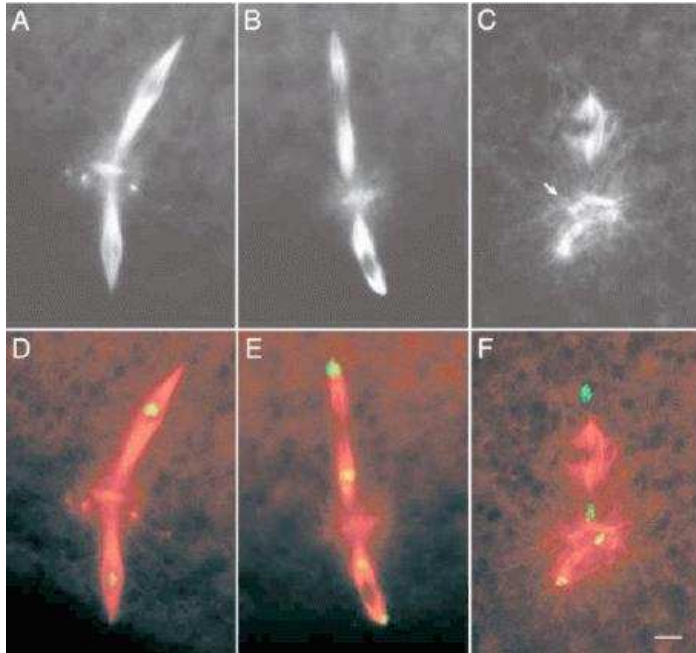


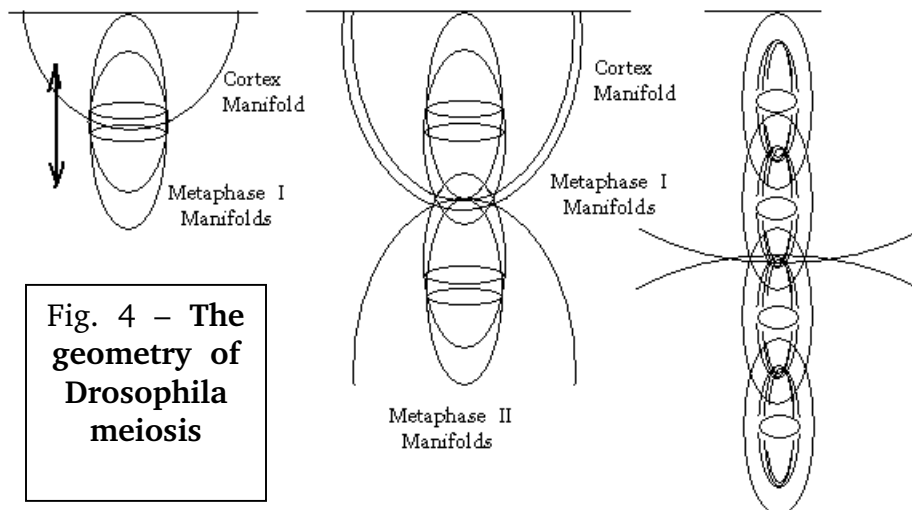
Fig. 3 – Meiosis II [7] - metaphase II (A,D) has a bright disk associated with foci of tubulin, and a ring-like structure in anaphase II (B,E). In early telophase II (C,F), the central spindle pole body (C, arrow) has enlarged into a ring that lies between the two central nuclei. MTs are red, nuclei are green.

spindle, followed by the pinching out from the spindle of a disc or *ring of microtubules* that becomes the body. Subsequently, the MTs arrayed to either side of the body narrow into poles, thereby forming the mature meiosis II twin spindles. Both central spindle poles become more tapered during progression through meiosis II, and the central pole body also changes in morphology, as the disc or ring becomes aster-like, then enlarges into a ring that lies between the two central telophase II nuclei.

The physics behind

[7] advances that the central pole body must be then a MT nucleating center for assembly of the central poles, and proposes a model based on MT “motors,” as is usual for the literature on that subject (such as [9]). We have a different idea: First, the initial anaphase I reorientation perpendicular to the cortex is due to the vanishing effect of the departed oocyte follicle cells on the zygote MT system at last: Now their leptonic space manifold breaks down into a set of isolated parts along the shell, one of them being around the female pro-nucleus (Fig. 4 left). This phenomenon is confirmed by looking at other species, which may show the *formation of isolated asters in that time period across the surface of the egg*. [10] The pro-nucleus then sees only the local cortex as the source of the leftover manifold. Thus one of the short manifolds of this nucleus (which has two sets of chromosomes then) has the same dimensions as the cortex manifold, and joins it, while the other manifold is perpendicular to the first, as usual for spatial leptonic systems based on kinetochores, like in mitosis, and thus perpendicular to the cortex manifold.

Here the difference is the fact the manifolds are generated from the chromosomes side since there are no centrosomes/centrioles. One anastral pole then sticks to the cortex side *acting as a base*, and the other moves away from it. The nuclear manifold on the cortex side inflates to the point of forming intersections with the manifold from the cortex, thereby the side MT foci observed. (Fig. 4 center)



4 center)

Now to the meiosis II part: Each pro-nucleus separates its chromosomes again, thereby starting to generate *two new leptonic manifolds* within the

meiosis I manifolds, one reaching inward of the egg, and the other outward, starting to give a “puckered” array of MTs at their intersection, an intersection that subsequently grows into a ring (as actin does in cleavage furrows during mitosis). There is no centrosome effect here at all. γ -tubulin and other parts of centrosomes are attracted there merely by the manifolds intersection as the kinetochores inflate more their manifolds, and thus come and generate more MTs with no real purpose. (Fig. 4 center and right) The angle seen between the two lines of twin spindles demonstrates that expansion of manifolds forces a folding between the two lines as the central nuclei get closer.

b. Fertilization at last

Fusion of parental gametes occurs in the inner ooplasm. How does the female pronucleus reach the interior of the egg? Our physical answer is that the egg innermost pro-nuclear kinetochores have generated two small leptonic space manifolds, one of which is reached first by being the closest, and is merging now with the manifold of corresponding dimensions inflated by the sperm centrioles (apparently only centrioles can generate such necessarily large manifolds from far inside the egg). The smoothing of the stretched manifold curvature brings the pro-nuclei together for final joining of the gametes at the center of the egg. The observed filamentous cytoplasmic connections developing between the cortex and the egg center is a telltale of the stretched manifold connections generated by the sperm MTs supporting the developing manifold along the way. The 3 other pronuclei are tied to the envelope manifold and its ultimate deflation brings these bodies to their fate.

To confirm this analysis, we will quote [10]:

“In the vast majority of animals, the centrosome is disassembled during gametogenesis in males and females and then reassembled soon after fertilization, requiring components from both sperm and egg. During spermatogenesis, the centrosome is stripped of the pericentriolar material and its ability to nucleate microtubules, but retains the centriole and its ability to replicate. Conversely, during oogenesis, the centrosome loses its ability to replicate but retains the pericentriolar material, whose components become dispersed throughout the cytoplasm.” We have seen that indeed in *Drosophila* oocyte the centrosome disappeared at the end, but centrosomal material remains in a dispersed manner.

“Thus, zygotic centrosome assembly at fertilization utilizes the sperm’s centriole and the egg’s pericentriolar material. The sperm basal body is a single centriole that disassociates from the sperm immediately after entry in the egg and becomes associated with maternally supplied centrosomal proteins. The sperm-derived centriole serves two functions during early development: nucleating zygotic centrosome formation, and selection of the female pronucleus from among the four female meiotic products in the egg. As the *Drosophila* oocyte completes meiosis, the newly assembled centrosome duplicates and nucleates two distinct foci of microtubule arrays. These arrays interact with the innermost of

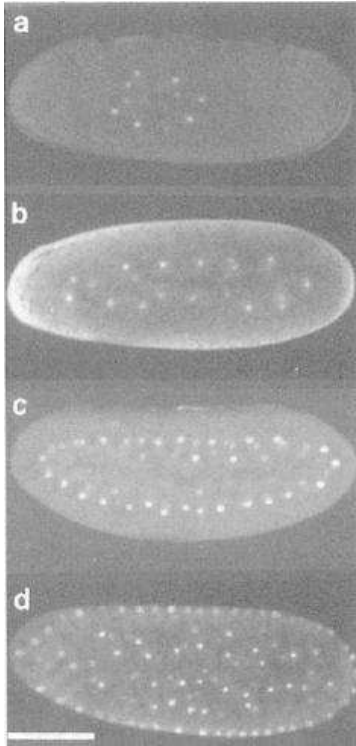
the four female meiotic products, which becomes the female pronucleus. ***The microtubule arrays appear to serve as tracks for migration of the female and male pronuclei towards each other.***

The female spindles are anastral and separated by a ring-like ‘central spindle pole body’ that lies between the chromosomes. During anaphase/telophase, the innermost nucleus migrated away from the other three meiotic products. This innermost migrating nucleus becomes the female pronucleus while the polar bodies and the central pole body remain in the cortical region. Because meiosis appears identical in fertilized and unfertilized eggs, this suggests that the sperm does not play a critical role in female pronuclear selection and migration. Instead, it appears that the central pole body may play a crucial role. Mutations that disrupt the central pole body in *Drosophila* eggs result in defects in meiosis and/or pronuclear migration and fusion. The central pole body may function in female pronuclear selection by acting as a tether to prevent the other three meiotic products from migrating into the interior of the egg, where the gametes fusion and mitotic divisions are initiated.” Yes, as we have seen, ***the 3 outward bodies are tied to the envelope manifold***, and if there is no sperm, then the innermost pronucleus will drift away from the envelope. If, furthermore, asters develop from the envelope, there is then a potential for parthenogenesis, but that’s not the case of *Drosophila*.

“We found that, immediately following entry, the sperm was initially rod shaped with two closely associated asters. It is very likely that these microtubule asters are organized by paternally derived centrioles. After sperm entry, the rod-shaped sperm nucleus become spherical in its transformation into a male pronucleus. At this point, it possesses two paternally derived centrosomes. The female pronucleus migrates towards the male pronucleus without acquiring asters. When the two pronuclei fuse, the product contains only the paternally derived asters.” This description indeed matches our analysis, but we can explain the motion of the female gamete toward the male, unlike the reference. In the case of asters generating across the envelope of the egg (which is not the case of *Drosophila*), the fused gametes have space manifolds that take over the entire egg, and thus the subsequent disappearance of the other asters.

c. Initial nuclear divisions and coherent migration to the surface

Each nucleus will control a small patch of cytoplasm called an *energid*, containing a nucleus, a centriole, microtubules and actin microfilaments among other things. During the ensuing ***rapid mitotic nuclear cycles***, the centrioles (supplied by the male gamete) start to lose their orthogonal arrangement in metaphase, move apart during anaphase and become widely separated at telophase. At the same time, the pericentriolar material of the centrosome expands and flattens, splitting into two units at late telophase. [11] Thus each nucleus at the end of these early mitoses has two separated centrosomes containing a single centriole from which a daughter centriole starts to bud. ***This means that these centrioles cannot be participating in the manifold building as normal mitoses do.*** We shall see later the reason why.



Now we go over the move of the initially dividing nuclei from the center to the periphery of the egg. *The 500 nuclei coming from the first nine (9) rounds of mitoses, and their energids, form a synchronous whole system, something unexplained by classical physics, as no common mechanical system can be seen here between the spindles, like the “fusome” in the oocyte development.*

The divisions are accompanied by *two temporally distinct nuclear movements* leading to the formation of a syncytial blastoderm with a uniform monolayer of cortical nuclei. The first of these movements is a *stepwise axial expansion*, occurring during division cycles 4-6 *at prophase and prometaphase*, and spreading the nuclei from a spheroid to a hollow ellipsoid underlying the cortex. (Figs. 5ab) This is followed by *cortical (outward) stepwise migration* during cycles 7-10 *at telophase and early interphase*,

Fig. 5 – The coherent move to the surface. ([12], Fig. 1) Anterior is left. Location of nuclei is shown. Nuclei remaining in the embryo interior = yolk vitellophage nuclei. Between nuclear cycles 4 and 6 (a = cycle 5 and b = cycle 6) the nuclei become distributed along the anterior-posterior axis through the process of *axial expansion*. During cycles 7 through 10 (c = cycle 8 and d = cycle 10) nuclei move in a *cortical migration* synchronously toward the surface to form the syncytial blastoderm.

which places the nuclei in a uniform monolayer at the cortex. (Figs. 5cd) These two movements differ in their geometry, velocity, cell-cycle dependence, and *protein synthesis requirement*, and are thus mechanistically distinct. During the cortical migration (and only then), a network of inter-digitating anti-parallel microtubule arrays connects the migrating nuclei and yolk nuclei located deeper in the embryo. Cortical migration is then proposed by [12] to be driven by microtubule-dependent forces that repel adjacent nuclei, leading to a girth expansion of the nuclear ellipsoid established by the axial expansion.

It will be noted here that axial expansion is not seen occurring separately in *Sciara* embryos, another species, (see [13], Fig. 1 not reproduced here) even though the developments of *Drosophila* and *Sciara* are parallel. *In Sciara however the egg is closer to spherical.* We will conclude that this separate expansion in *Drosophila* is much more likely coming from nuclei space manifolds evening out the location of their common surface vs. the envelope of the egg. This is confirmed by checking the distances of the edge of the energids domain (Fig. 6). *How could the limited-size energids know where they are as a whole*

vs. the envelope, unless the space manifolds they sustain sense this overall position?

[12] identify this axial motion to be independent of MTs and correlated to protein synthesis by the nuclei, with actin effecting the force, of course without any hint about how the directionality of the force could be effected. For the cortical migration they see the action of MTs as “molecular forces separating” the nuclei from yolk nuclei, as if local molecular actions could ever effect such a non-local behavior. Let’s see now what is spatially going on.

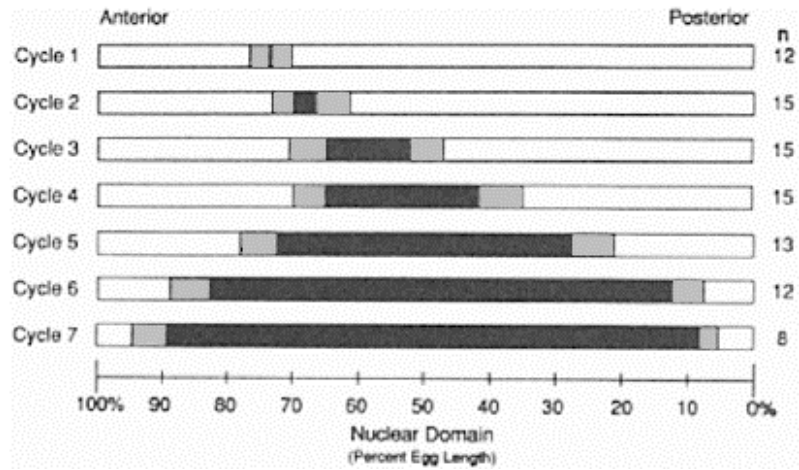


Fig. 6 – Domain occupied by nuclei vs. egg envelope ([12], Fig. 2, n= number of embryos analyzed)

The physics behind

The fact protein synthesis is tied to both axial motion and cortical migration leads us to identify the nuclear space manifolds seen earlier in meiosis without centrosome. We see now further that *such manifolds expand when the DNA is in a state of protein synthesis*. Their spherical expansion is forcing the relocation lengthwise in the ellipsoid of the egg envelope due to the spatial constraints. (Fig. 7) Centrosomes have not yet started the development of their own manifolds. When they do (at a specific gene duplication cycle), they accomplish two things:

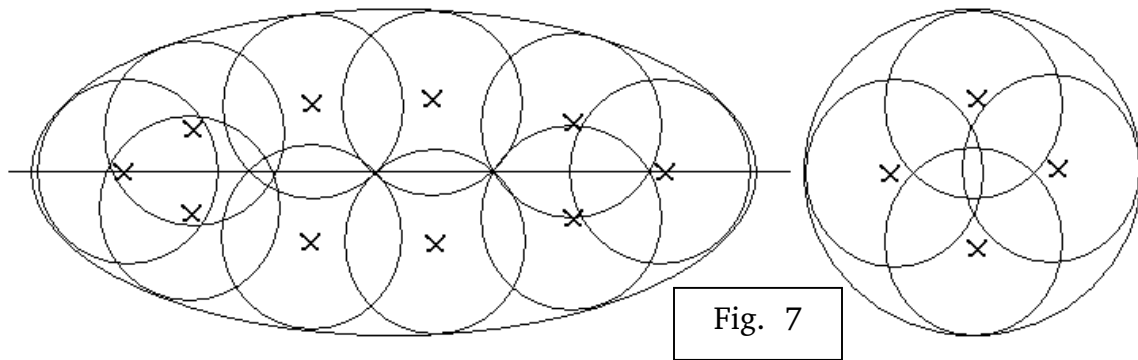


Fig. 7

(1) They maintain a 3D distance between nuclei that nuclei on their own can’t maintain, and this due to the simple geometrical fact that *an axis of symmetry is introduced by their manifolds*: (Fig. 8) *The nuclei have then no choice but to remain on a surface instead of being located anywhere in a bulk volume*. This fact has been verified in the case of unfertilized *Sciara* em-

bryos ([13]) where centrosomes are unavailable, as then nuclear collisions happen and thus a totally unviable embryo grows.

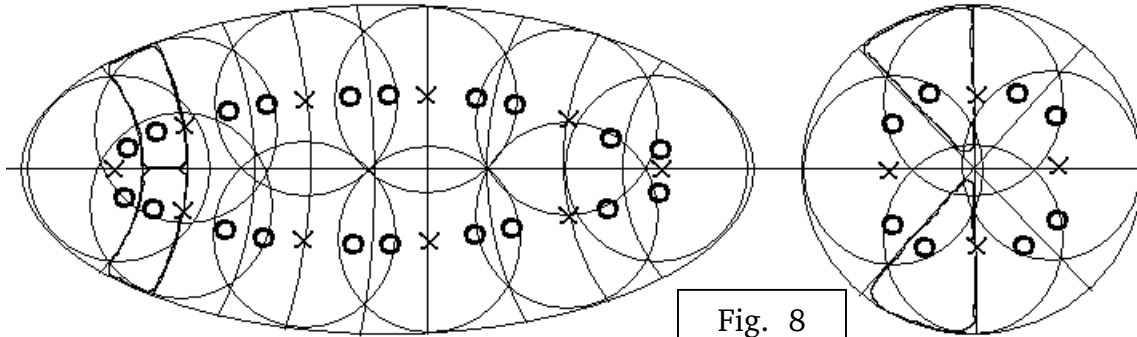


Fig. 8

(2) They effect the coherent expansion called the cortical migration experienced by the ellipsoid of the nuclei. As [12] identifies, this is a MT system expansion *restricted by the nuclear (protein synthesis) time period*. (This restriction will be further studied in a subsequent article.) *Spindles are indeed observed being aligned on the surface of the ellipsoid so their manifolds can expand on both sides of the surface*. The asters move toward the surface as in mitosis, but here from the center axis of the ellipsoid instead of the metaphase plate as they are forced into a wedge shape (Fig. 8 right) giving more room to expand toward the surface.

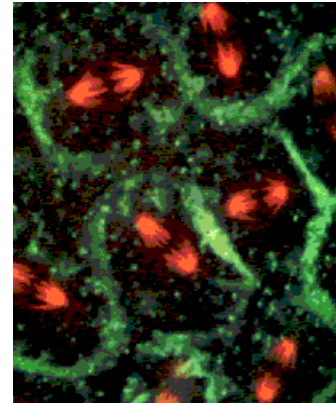


Fig. 9 - **Energid domains** ([14]) – Actin microfilaments (green) form the edges of the energid domain in a “pseudocleavage furrow” that surrounds the mitotic spindles (red).

It is also significant here to recognize a pattern of SEGMENTS in the development, that will be amplified later with maternal gene products located at the surface of the embryo. The existence of such *precise physical spatial boundaries* will be of vital importance in making the later fuzzy chemical patterning *as precise as Life requires*.

d. The pro-blastoderm

When at the surface, the end of each mitosis leads to actin accumulation within a membrane bulge that lies above each newly formed daughter nucleus, called an “actin cap,” which subsequently expands in interphase to fuse with other caps and form the pseudocleavage furrows that surround the next mitotic spindles. (Figs. 9 and 10)

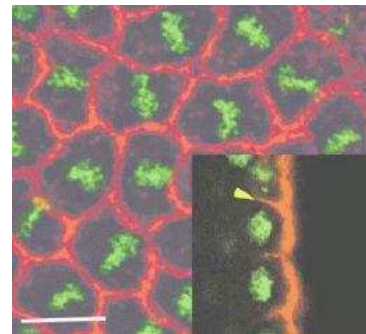


Fig. 10 ([15], Fig. 5c)

Centrosomes specify the position of actin-based interphase caps and furrows. However, [14, 15] have observed centrosome-

coordinated assembly of actin caps and actin reorganization into furrows during interphase to be **not blocked by microtubule disruption**. Centrosomes would then coordinate assembly of cortical actin caps through a **microtubule-independent mechanism**.

Afterwards, in the interphase to the 14th mitosis, cell membrane furrows invaginate in a process called **cellularization across** the syncytial blastoderm where the nuclei become almost isolated within a **cellular blastoderm**. However, there are still openings to the common cytoplasm. This quasi-partitioning is done by invagination of the oocyte membrane powered by microtubules. Cleavage furrows turn into furrow canals, and then actin microfilaments pull a curtain of membrane down around the bottom of the energids. (Fig. 11) A true blastula, i.e. a monolayer of cells surrounding a fluid-filled *blastocoel* containing the yolk, is formed only by the time of gastrulation.

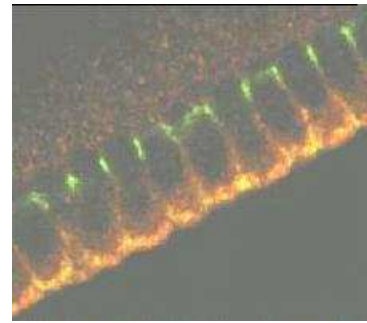


Fig. 11 ([15], Fig. 3c)

The physics behind (as much as we can tell)

We will advance from the above sparse experimental facts that

(1) The initial nuclei (up to 200) go through a variation of mitosis where the centrioles do not function as leptonic space manifold generators since they are only partly constructed (Fig. 12). They only follow the synchronous nuclear division process operating on its own with or without the help of centrosomes, with manifolds of its own, as it is well known to happen in less evolved systems.

(2) The migration to the surface of the embryo is first a nuclear system leptonic space operation involving manifolds, then with centrosomes bringing axes of symmetry to the

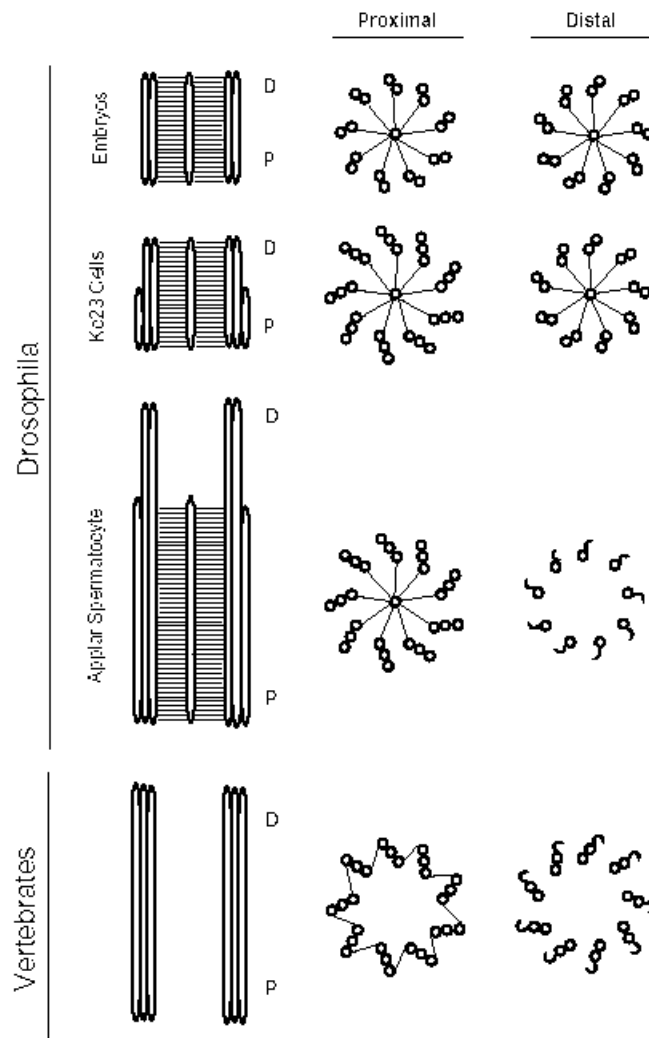


Fig. 12 – The partial centrioles of *Drosophila* ([16])

manifolds. The central cytoplasm expands synchronously and divides in “energids” squeezing themselves out of the center (bringing the centrosomes/centrioles with their nuclei). It will be noted that 2 differentiations already happen: the *pole cells* and the *yolk cells*, and this last differentiation is not covered by the literature – what drives this differentiation? It cannot be a chemical gradient as there is no such thing when this occurs.

(3) The segmentation of the embryo has already started with the move of the nuclei to the surface.

(4) Cellularization corresponds to a change in the centrioles as *mitoses 10 through 13 are asynchronous*: We have a cell differentiation much before cells are seen as differentiated, and this with centrioles becoming effective. The observed waves of mitoses starting from clearly defined locations at the anterior and posterior of the embryo is a strong indication of *differentiation waves* where each pro-cell is being told to go to the next developmental stage. Such waves have been studied in other species, and have been thought by some to be the basic tool of differentiation when nuclear division synchronism is no longer possible. [17] Here these waves are seen as needed since **individual organs must appear**, and synchronism is impossible due to different functional requirements for these organs. This change must be originating from the genetic development across all nuclei (timed in number of divisions), with the origin of the wave most likely coming from the two nuclei that start the latest division cycle first, and these must be the ones with the largest expansion room available, i.e. nuclei at or near the ends of the ellipsoid. *Centrioles then bring (as a whole) spatial and time memory that the nuclear system does not have, so organs can have their own synchronization, both in development and in maintenance.*

(5) The process of “actin caps” and “pseudocleavage furrows” is a continuation of what happened at the center of the egg, where a partial mitotic cleavage occurs between parent and child nuclei. Actin senses the space manifolds intersections generated by nuclei (and thus don’t need MTs to do their work), but such manifolds are concentric to the divided chromosomes since there is no extra generation by the centrioles. At the surface there is also a membrane only on one side of the spindle (parallel to the surface), so these manifolds expand at a relatively long distance on the internal side (until the far cortex at the border with the yolk), and no actin is located there. The addition of centriolar function would permit the collective attraction of actin across mitoses farther internally into the cytoplasm through deeper-going manifolds until the membrane almost surrounds each nucleus, with full closing only happening at the start of gastrulation. The results are then the described cap and partial furrow, with the cells becoming elongated reflecting the subjacent space manifolds.

(6) As wide cytoplasmic bridges remain between nuclei, using the common pool of cytoplasm and its MTs, the presence of proteins induced by maternal

mRNA deposited in the thin cytoplasm lining the surface membrane at the ends and top/bottom of the oocyte starts the genetic (MT-helped) diffusion, and thus the differentiation process, as we recall now from the literature, to put color to the already established segmental space manifolds.

e. Differentiation by pattern formation (see [17] for example)

Bicoid mRNA was at the anterior part of the oocyte membrane all the way back from the oocyte time, held there by microtubules tied to the membrane **in the large and thin 2D open cytoplasmic shell**. (The inside of the embryo is mainly yolk.) After the formation of the syncytial blastoderm bringing cytoplasm there in a thin layer, this mRNA begins to be translated into the *bicoid* protein (a transcription factor). The peculiar situation created allows a *chemical gradient* by diffusion through the thin very large open sheet of cytoplasm. However, microtubules are required to randomize the motion of large gene molecules so they can quasi-randomly move, as we have seen earlier in the oocyte case. Life as a rule does not otherwise use random processes, except when Life wants to disappear (e.g. in apoptotic processes – cell death). Such won't be the case in most other developmental situations, where differentiation agents are actively transported through **centriole-guided quantum systems**. It must be also noted that the origin of the sensing by large molecules of different concentrations has been largely unexplained, except for certain differential chemical affinities between molecules that would realize this sensing. In any case, the presence of leptonic space manifolds tightly squeezed in segments as we have seen will provide the precision required for the differentiation.

Conclusion

Through the study of *Drosophila* it becomes obvious that **the nuclear system is a fundamental factor in development**, not only chemically but **physically**. We have seen the function of the nuclear-generated fusome in the oocyte building. We see here an early embryo developing essentially without the intervention of centrioles, but with centrosomes used for the initial spatial arrangement. The MT system is in effect directed from the chromosomes area for cell divisions and other specialized functions. The literature has little accurate and detailed information on the physical/structural aspects of development, and even less when it comes to physical events tied to the nucleus. This is unfortunate as these aspects are what makes the whole systems we see around us and are us. This situation can be understood as coming from the strange physical behaviors observed that have no correspondence with classical physics effects, and it is very difficult to design experiments without the foresight coming with a meaningful theory.

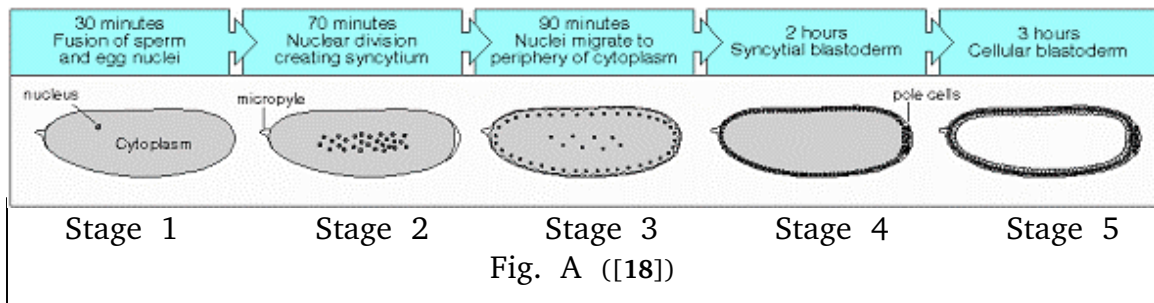
We have not gone into the workings of the nucleus itself as the experimental information is very scant there, but things such as the *synaptonemal complex*, are strange structures that CANNOT be explained also with our known laws of

chemistry or physics. With a few hints as we have obtained here, we will attempt to develop a better understanding of that area in a future article.

Finally, the diffusion mechanism described at length in textbooks to promote Life as a classical physics effect is but a very small part of the physical effects used by Life, and even this kind of effect, when used, depends on quantum processes through the quasi-random motion of MTs that are specifically activated to develop the conditions required to permit further order for Life.

Appendix [5]

Stage 1 lasts for about 25 min and begins once the egg has been laid, and ends when the first two cleavage divisions have been completed. The fertilized egg displays homogeneously distributed yolk granules and egg cytoplasm; only the periphery of the egg, occupied by a thin rim of periplasm, and a cytoplasmic island located dorsally within the anterior one-third of the egg containing the fertilized nucleus, are yolk free. (Fig. A)



Stage 2 lasts for about 40 min. During this stage cleavage divisions 3 - 8 take place. A characteristic of this stage is a significant retraction of the embryo from the vitelline envelope. This leads to the appearance of two empty spaces (perivitelline space), one at the anterior and one at the posterior pole of the egg. Retraction of egg cytoplasm begins when four zygotic nuclei are present; they are consistently located in the anterior one-third of the egg, surrounded by cytoplasmic islands called “energids” and therefore clearly separated from the yolk particles. Each nucleus does control its island. Each energid has a nucleus, a centriole, microtubules and microfilaments; with the actin microfilaments forming the edges of the energid domain

During divisions 3 to 5, the nuclei and their energids tend to move posteriorly; by the 5th cleavage, zygotic nuclei occupy an ellipsoid field in the center of the egg, between 20 and 80% of the egg length.

From this point on the nuclei begin to move peripherally, advancing stepwise, at a rate of about 10 μm per divisional cycle. By the end of the 8th division, the majority of nuclei are evenly arranged on an ellipsoidal surface about 35 μm beneath the membrane. Some nuclei remain centrally located and others drop out from the periphery to give rise to the *vitellophages* (yolk nuclei fighting bacteria). At the end of the 8th mitosis there are about 200 nuclei populating the periphery and about 50 yolk cells.

Stage 3 lasts for about 15 min. Polar bud formation and nuclear division 9 take place during this stage. Polar buds are formed around the nuclei located at the posterior pole of the embryo. They are the first signs of pole cell formation, which takes place in stage 4. Here, these polar buds divide once. The earlier posterior space is now occupied by the pole cells. The end of this stage is defined by the appearance of a clear cytoplasmic rim at the periphery of the embryo.

Stage 4 lasts approximately 50 min. It is the **syncytial blastoderm** stage in which blastoderm nuclei perform the last four cleavage divisions (10th through 13th). The nuclear divisions are now *metasynchronous*: **Mitoses 10-13 progress in waves which usually originate at two different sites, one near the anterior and the other near the posterior egg and move centripetally.** The duration of cleavage divisions 10-13 increases also progressively, from approximately 8 min to 20 min.

The living embryo has a clear rim peripherally, within which blastoderm nuclei are readily discernible. (Fig. B) Blastoderm nuclei are located peripherally, causing the egg surface to bulge out during divisions, causing the appearance of so-called "somatic buds," something also called "actin caps."

The polar buds divide again in syncytial division 10. Immediately after this second division the buds pinch off, forming 12-14 pole cells. The pole cells are the first cells to form in the embryo. Thereafter, pole cell mitoses exhibit a slower cycle than that of the dividing syncytial blastoderm nuclei [indicating the start of centrioles fully functioning].

Stage 5 is "*cellularization.*" The anterior space from step 1 vanishes. Blastoderm cell formation takes place, while blastoderm nuclei elongate considerably (40 min). Cellularization occurs by means of the introgression of membrane furrows to separate single blastoderm nuclei. This is a rapid process, and is accomplished within 30 min at 25°C. Blastoderm nuclei are spherical at the onset of cellularization but elongate considerably as the process continues, increasing in length from 3-4 μm to 10-15 μm .

Blastoderm cells around the perimeter of the entire egg at this stage are not completely isolated since they still maintain connected with the syncytial cortical cytoplasm through wide cytoplasmic bridges. These connections are finally lost during gastrulation.

All somatic blastoderm nuclei and cells have the same shape and do not show any apparent differences between particular egg regions. At the end of the stage, pole cells begin to shift their position dorsalwards. At the same time, midventral blastoderm cells acquire an irregular, wavy appearance, darkening at their interface with the yolk (closing of cells is at that point).

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Following stages: The above precedes gastrulation forming the mesodermal and the anterior endodermal primordia. Both cell shape and size will show considerable regional variations in later stages.

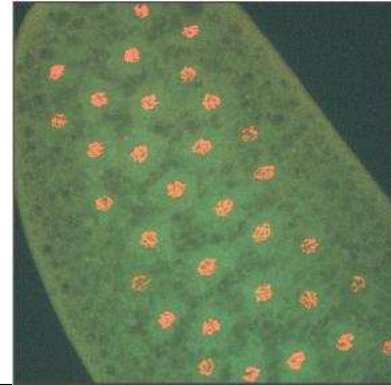


Fig. B – Syncytial blastoderm with energid domains

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