

**Researches upon nemerteans and planarians / by Charles Girard. I.,
Embryonic development of Planocera elliptica.**

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RESEARCHES

UPON

NEMERTEANS AND PLANARIANS.

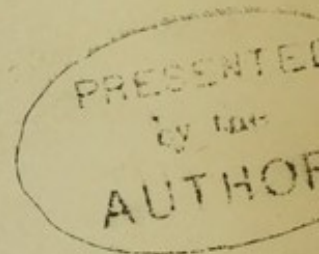
BY

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I.

EMBRYONIC DEVELOPMENT OF PLANOCERA ELLIPTICA.



PHILADELPHIA:

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January, 1854.

THE AUTHOR

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THE UNIVERSITY OF CHICAGO

TO

DR. JOHN C. WARREN,

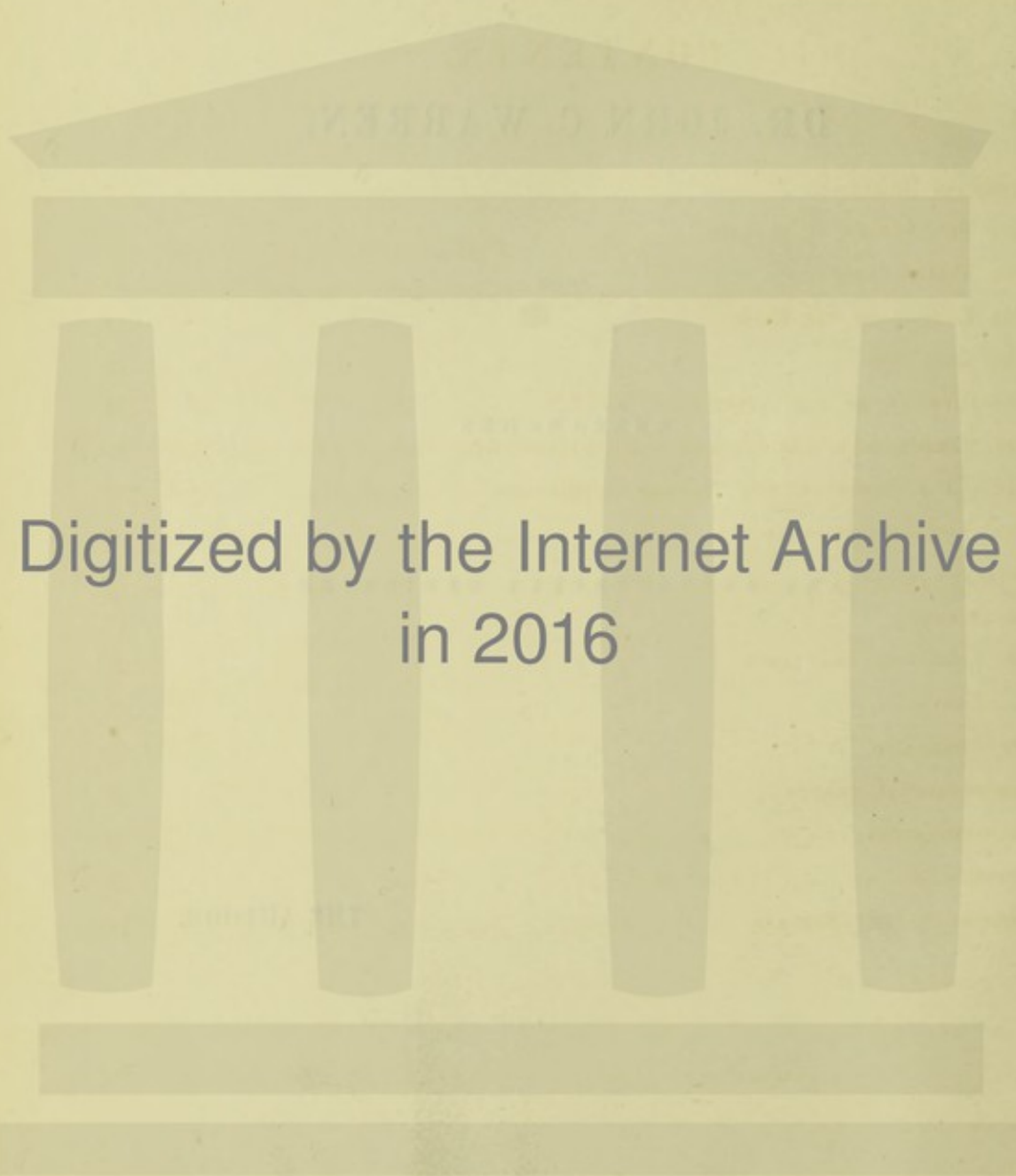
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PRELIMINARY REMARKS.

The observations recorded in the present Memoir were made chiefly in the spring of 1849, while assisting Prof. Agassiz in embryonic investigations upon several other types of the animal kingdom. The microscope used was his large Oberhäuser.

A historical sketch of these investigations was read before the American Association for the Advancement of Science, at its Cambridge meeting, in August 1849, and printed in its Proceedings in 1850.*

I then contemplated publishing without much delay the whole of my Researches upon the American Nemertians and Planarians, together with the embryology of their different types. But the time which I could devote subsequently to these investigations having become, by necessity, very much limited, and fearing that the chief object which I had in view in tracing them, and which was the starting point to new researches, would lose its actuality, I determined to issue these as a first part.

The species, the eggs of which constitute the subject of this memoir, is quite abundant in the harbors of Boston and Beverly, Mass., under the stones of the beach, where I have first observed it in the spring of 1847, and was since described by me under the name of *Planocera elliptica*. I am inclined to think that its range may be found to extend further north, and likely also further south.

All the drawings, except figs. 94—103, have been executed by myself from specimens under the microscope; the latter were made by Mr. A. Sonrel, from two models which I furnished him, representing the young Planaria immediately after its escaping from the egg. My original drawings have been admirably well reproduced on stone by the above named artist.

C. GIRARD.

Cambridge, Mass., September 1850.

* Proc. Amer. Assoc. Adv. Sc., 2d meeting 1849 (1850), 398, a French version of which subsequently appeared in the "Bulletin de la Société des Sciences naturelles de Neuchâtel (Switzerland), vol. ii. 1850, 300.

On the fifth of October, 1850, this memoir was read before the Boston Society of Natural History,* and referred to the publishing committee, which reported in favor of publication in its Journal whenever the funds of the Society could meet the expenses required by the illustrations.

At the suggestion of several of my New England friends, I withdrew the memoir upon my leaving the North, hoping to find a speedier way of bringing it before the public. But circumstances out of my control have occasioned a delay of three years, during which period several works of embryology have passed through the press, which, although not treating of the same special subject, would have induced me to modify some of the paragraphs of my original memoir, had I not desired to preserve the form in which it was originally written.

A few paragraphs, however, have been added to the chapter on the fecundation, and to the conclusion, in which I have felt it my duty to refute an assertion, since made, against the views I hold in regard to the systematic position of Planarians.

The first part of these Researches was originally published in the second volume, of the new series, of the "Journal of the Academy of Natural Sciences of Philadelphia."

C. G.

Washington, Nov. 1, 1853.

* Proc. Bost. Soc. Nat. Hist. iii. 1850, 348.

I.

THE EGG BEFORE IT IS LAID.

I have seen the egg when it was but a simple cell, which the most practiced eye could not have distinguished from the constituent cells of the organic tissues, had its situation and its further development not been a subsequent warrant of its true nature.

This first observation was made in the fall of 1848. The eggs, at that season, were undoubtedly primordial cells, formed according to the process to which I have called attention elsewhere.* These cells now, were to take a predetermined development, a given direction; in other words, lead a life independent of the life of the maternal body, endowed with a circle of activity of their own. From that time they become the initial centre of as many individuals, although still connected with the original matrix.

Indeed, during the ensuing winter, these primordial cells had already acquired such a development, that any one, familiar with the subject, could recognize an egg at the very first glance. Their size was considerably increased, and the germinative vesicle and germinative spot, being now present, there was no possibility of being misled in regard to them, even if the eggs, compared with the size of the organic cells, had not answered all objections.

Besides the germinative vesicle and the germinative spot, the nature of the contents already showed the egg: a vitellus or yolk, composed of small nucleated and homogeneous cells. These vitelline cells filling the whole of the yolk's sphere without any tendency of being more particularly crowded around the germinative vesicle (fig. 1—4). The vitellus itself was semi-transparent, owing to the small amount of its substance, then in process of formation.

The germinative vesicle is proportionally large and the germinative spot small, compared to the egg itself. The microscopic powers, then at my command, could not reach the structure of their contents.

A few weeks before they are laid, the eggs appeared as represented in figs. 5 and 6: nearly full grown. The mass of the yolk has increased so as to render the sphere entirely opaque (fig. 5). A transparent area, however, is seen upon one point where the germinative vesicle approximates to the surface of the sphere (fig. 6). At this stage of development, the germinative spot could no longer be perceived. The outline of the germinative vesicle itself became vague as if on the eve of disappearing also. It, however, does not disappear entirely before the eggs are deposited.

* Amer. Jour. of Sc. and Arts, 2d series, vol. ix. 1850.

II.

THE FECUNDATION.

The phenomenon of the fecundation is one of the most difficult to investigate experimentally, and one of the most difficult also for the mind to understand in its effects.

There is one feature in the egg's history which is well established by observations : an egg does not develope into a new being unless it has been previously fecundated.

In the fecundation there is a material action, which we may perchance witness the taking place of, and an immaterial act beyond the reach of our experiments.

Thus, it is necessary that the seminal fluid should come into contact with the eggs in order to effect the required act. The spermatic particles may then be observed in great activity moving all around the egg, now and then darting at it from various points and striking it ; when at last, they become so much exhausted that they remain immovable upon the egg until they vanish entirely away. Spermatic particles I have not seen penetrating into the egg, therefore they do not, to my knowledge, constitute any part of the future being, but they act upon its surface, totally disappearing afterwards. Such is the material act of the fecundation.

But, now, how are we to interpret that action? It causes a new being to be brought about, and which would not come forth without it : therein is the impalpable act of fecundation.

Spermatozoa have been observed by several embryologists within the vitelline membrane, and even in the vitellus, but observation has not yet defined the part which they play in the phenomenon of fecundation. Is their presence, in the egg, necessary to the fulfilment of that mysterious act? Do they constitute any integrant part of the future being? and if so, which part is it? Before any facts, answering the above queries, shall be experimentally demonstrated, no theory will ever have a chance of being adopted. The egg of *Ascidia* and that of *Planaria* are easily watched throughout their entire mass, and should a spermatozoon or spermatic particles penetrate into the vitellus, and constitute any part or portion of the future being, such a phenomenon could not escape the eye of a careful observer. If the union of the spermatic substance with the vitelline substance is a necessary act in the procreation of the embryo, that union is molecular and beyond the reach of observation with the optical apparatus now at our command : when the spermatic particles lose their activity and disappear to the observer's eye, they disintegrate into elementary molecules, in all probability minute cells, which enter the egg by endosmosis. That substance, in mixing with the vitelline substance, operates as a catalytic. For, no sooner has the phenomenon of the fecundation taken place, that the vitellus enters into the phases of the division, which is a mere kneading of the vitelline or embryonic substance.

That labor performed, the embryo issues forth out of the most homogeneous cellular substance, the substance of the vitellus.

Such, it appears to me, is the probable union, if union there is, of the elementary substance furnished by either sex in the procreation of a new being. The spermatic substance in its most intimate structure, does not differ materially from that of the vitellus; in both cases we may have minute cells, nucleated or not, transparent or semitransparent, very similar in general appearance.

What has just been said of the material act of the fecundation, was not observed upon the eggs of *Planocera elliptica*, the subject of this memoir, but in a species of *Ascidia*. When I shall investigate, for another memoir, the structure and functions of the sexual organs in Nemertians and Planarians, an opportunity may be afforded me to witness the fecundation in these two groups.

Among Planarians there are species in which every individual is provided with both sexes; there are others where we find each sex, represented by a different individual; accordingly the reciprocal action of these organs must take place in various ways.

In *Planocera elliptica*, each individual possesses ovaries and spermaries, that is to say, is an hermaphrodite. Whether two individuals are required to consummate the act of fecundation, as in the snails and slugs, I am not yet prepared to say.

In many species there are, properly speaking, no ovaries; the eggs are formed all around the ramifications of the stomach, whence passing through an oviduct into a pouch, supposed by anatomists to be a coital pouch. I have no settled opinion in regard to this organ, but I am satisfied that when in it, the eggs assume the last feature of intra-ovarian life.

The fecundation may either take place before or after the eggs are laid, according to their genera or species.

The spermatic particles of *Polycelis variabilis* I have observed, but shall describe them in connection with the development of its eggs on another occasion. Those of *Planocera elliptica* have hitherto escaped my notice. Their description would have been here in place.

III.

THE LAYING OF THE EGGS.

The spawning period lasts from the middle of May to the middle June, setting aside the precocity of some individuals, and the backwardness of some others.

When the animal lays its eggs, it creeps along the smooth surfaces of the submarine bodies, either stones, pieces of wood, or sea-weeds, &c. It leaves behind it a thin band of mucosity of the width of its body and in which the eggs are arranged in one layer,

side by side, in transversal rows (figs. 7 and 7 a). The eggs are ejected in certain quantities, and maintained a while under the flat body of the animal, which secretes the mucosity and gives to them this peculiar arrangement; a short time afterwards the bands may be isolated from the surface upon which they were fixed, and the eggs will remain in their respective places. They may be seen distinctly through the transparent and hardened mucus, which now has the appearance of a thin leaf of whitish glue. The length of the bands themselves varies considerably, as the animal may be disturbed and compelled to recommence another one somewhat apart from the first. Sometimes the interruption is so often repeated, that instead of continuous bands, we have a series of irregular patches, in which the linear arrangement of the eggs is no longer observed (figs. 9—11). This is particularly the case towards the end of the laying; the animal appears uneasy, impatient. It seems wearied from the labor of the spawning, and now takes no longer the same care of the last coming eggs.

The number of eggs deposited by one individual is very great, as is generally the case amongst all the lower and unprotected animals. It will lay at repeated times a day, and so during a week or two, as the eggs develop successively. It is even a necessity for some to be expelled, before the following ones can reach the oviduct and complete their growth.

There is but one yolk in each egg; a single case was observed in which two yolks existed, giving rise to two embryos, still in full life during the period of the motion, when last observed. They were equal in size, and therefore one of them was not separated from the other, as in fig. 14, unless the separation took place by equal parts. Further on we shall witness a case in which, out of a unique sphere, two embryos issued, though by an accidental process of the living fabric.

IV.

THE LAID EGG.

When observed immediately after they have been laid, the eggs are composed of the following parts: 1st, The yolk's sphere, with the germinative vesicle in its middle; 2d, A membrane surrounding the yolk or vitelline membrane; 3d, A zone of transparent albumen, and 4th, An external membrane, analogous to the so-called chorion, enclosing and limiting the whole egg (figs. 12 and 13).

The formation of the albumen and external membrane takes place during the passage of the eggs out from the oviduct. Whether in the oviduct proper, in the coital pouch, or in the cloaca, I am not prepared to say just now, from direct observations, but feel confident that I may solve the question ere long, in the pursuit of my investigations.

For a short time after the eggs have been laid we still observe a clear space towards one point of their surface, appearing however quite small on account of the increase of the vitelline substance, now filling up densely the whole sphere (fig. 13).

The absolute size of the eggs varies within certain limits; a few being found one third smaller than the usual size. The form itself is subjected to variations; generally circular, it sometimes elongates and becomes oblong or oval in some few.

V.

THE DIVISION OF THE VITELLUS.

The division of the vitellus or yolk commences about twelve hours after the deposition of the eggs, and last about twenty four hours. This phenomenon is subjected to a mathematical law as far as it affects the substance, but as there is already present a vital agent, the living principle of the forthcoming being, an allowance is made for variations. Let us consider the subject under both points of view.

Generally the primitive yolk's sphere divides into two spheres of equal size (figs. 23, 24 and 25), then these two are subdivided, making four spheres (figs. 34 and 35), then eight spheres appear (figs. 38 and 39), then sixteen (fig. 43), and so on until the yolk's mass is so much subdivided that it presents the appearance of a mulberry, the *mulberry-shape* or last stage of the division of the vitellus. Such is the physical or mathematical law which governs the matter, as it will strike every one when observing the phenomenon of the division.

Now the variations. While the foregoing is taking place there are eggs in which the process of the division appears rather fanciful, as if the living principle was already assuming a marked preponderance over the matter itself, and subduing the latter to the power of organism. Thus in fig. 15 one point of the sphere is depressed: in fig. 16 the depression has become a groove. The sphere sometimes is split open as in fig. 17. Sometimes, again, a groove on one side and a slight depression on the other side are observed (fig. 18). Still others show two symmetrical grooves opposite each other and connected by a transverse line (figs. 19 and 20), which foreshadows a division of the mass into two halves, equal or unequal, symmetrical or asymmetrical, though never circular, as represented in figs. 21 and 22.

In October 1847, Dr. A. A. Gould observed in the eggs of *Eolis gymnota*, from the Boston harbor, cases in which the yolk was divided into three spheres. This fact was so new, and I may say, so unexpected, that it struck every one then present and interested in embryological researches, as indicating a new law or principle hitherto unnoticed in the division of the yolk. Now, a similar case may be seen here (fig. 29): three perfectly distinct spheres, of unequal size, it is true, but three spheres only. Figs. 27

and 28 exhibit the first step of this process. Sometimes, as in fig. 26, when the yolk is divided into two unequal halves, a third smaller, sphere may be seen making its appearance between them and growing larger, while one of the latter is diminishing.

Therefore, the fact that the yolk is sometimes divided into three spheres, during the process of the division, only indicates a modification of the general rule, and not a new rule.

Next we come to the number four, and instead of four equal parts, we have two small spheres, appearing like herniæ in the middle and on both sides of the two halves (fig. 30). Figs. 31 and 32 exhibit two other stages of the same phase. Occasionally the two halves elongate and repeat the process of lateral depressions and grooving (fig. 33).

Then comes the case with five spheres: a small one, with four of equal size (fig. 36). Six and seven will follow (fig. 37), then eight, which coincides with the mathematical number.

I have not seen any case with nine spheres; these, undoubtedly, have escaped my notice. We have ten (fig. 41), and eleven (fig. 42). Beyond these numbers it becomes difficult, if not impossible, to follow out the irregular process. Even in the regular course of the division, the number of the spheres is difficult to ascertain beyond sixteen (fig. 43), for, soon appears the mulberry shape (fig. 44), in which the now very small spheres of division are either equal or unequal in size.

Soon afterwards the mulberry shape itself vanishes, when the eggs reassume a form and an appearance similar to what it was previous to the division, with this difference, however, that the vitelline sphere has become a little larger (fig. 46).

It has been a matter of some controversy as to whether the spheres of division were surrounded by a membrane or not. When the egg was divided into four of these spheres, the latter could be distinctly separated from each other (fig. 35). The same was effectuated when eight spheres were present (figs. 39 and 40). There can be no doubt, therefore, that the spheres of division are perfectly independent of each other. Under a heavy pressure (fig. 40), the peripheric line of the spheres, or else their membrane, seems to penetrate into the mass where the central transparent spaces, although not clearly circumscribed by a membrane, are still present. I am inclined to believe that there exists a temporary cellular membrane, forming and disappearing alternatively during the labor of the division of the substance. For, the vitelline membrane in an egg in process of formation, is itself not more conspicuous, still the yolk's sphere is perfectly circumscribed, though not yet surrounded by either an albumen or a chorion.

VI.

THE GERMINATIVE VESICLE AND GERMINATIVE SPOT.

The process of the division of the yolk is no sooner started, than the germinative vesicle and the germinative spot disappear as vesicles; their contents, then, mix with the yolk. But whether this mixture has any influence upon the process of the division, is difficult to determine. For a long time embryologists thought that the division of the yolk was dependent upon the previous bursting of these vesicles, but one instance is known now, in which the germinative vesicle is still present, when the yolk is already divided into several spheres. I cannot help thinking that the germinative vesicle and the germinative spot or spots (for there are sometimes several germinative spots in other types), have no initial power towards the future stage of development, and that their existence during the first period of the egg's history, only reminds us of the origin of the eggs in the common laboratory of organic substances.

The contained matter of the germinative vesicle is transparent; its structure was beyond the reach of the microscopic powers at my command.

VII.

THE CLEAR SPACE IN THE SPHERES OF DIVISION.

Another phenomenon connected with the division of the yolk, be the division regular or irregular, takes place during this period of the egg's history.

The vitelline sphere is no sooner divided into two parts, than in the centre of each of these parts a clear space appears, and as the number of the spheres of division increases up to the mulberry shape, in the manner above stated, each of the spheres of division exhibits that clear space, however small those spheres may be.

In its general appearance, this clear space reminds us of the germinative vesicle, from which it differs, however, in not being circumscribed by a defined membrane, whence its vague outline, and also in being proportionally larger. That it has nothing in common with the germinative vesicle, is satisfactorily shown in the case where the latter still exists when the yolk presents several spheres of division, each of which being provided with its own clear space.

The clear space of the spheres of division, therefore, is a phenomenon which indicates in the egg something else than matter, a vital activity every where present in the yolk, endowed with the same power common to all organized beings, to act from the centre towards the periphery, to expend the matter, to work it for its own purpose, and model it according to its own wants and its own design.

VIII.

THE VITELLINE SUBSTANCE.

Meanwhile the egg is passing through its diverse periods, modifying the general aspect of its mass as a whole, the vitelline substance itself is undergoing a cellular process of multiplication and renewal.

It has been remarked above that at the end of the period of the division of the yolk, and which precedes immediately the period of the embryo, the vitelline sphere had grown larger. In the ovarian egg the vitelline substance is gradually increasing as shown by the growing opacity of the yolk (fig. 1—6).

When the egg has just been laid, the vitellus is composed of small homogeneous cells, though varying in size, but all provided with large nuclei (fig. 12, *a*). When divided into four spheres, the constituting cells have become heterogeneous; there are large cells, each containing several nuclei, and small cells with but one nucleus (fig. 35, *a*). Towards the end of the process of the division, the yolk cells are again small and more uniform amongst themselves (fig. 45, *a*).

These facts plainly show that an intimate elaboration is taking place within each cell; nuclei develop in them, which, by their own expansion, become perfect cells themselves, and in their turn producing internal nuclei. Cells, thus, increase in number, and by repeating the same process, accumulate in a larger and a more dense mass.

IX.

FLOATING CELLS.

As soon as the egg has passed through the phases of the division, transparent cells make their appearance, floating in the albuminous zone, between the vitellus and the outer membrane of the egg (fig. 45, 46, 48, 51, and 52).

These floating cells are of two kinds, each kind originating in a different manner.

§ 1. The larger of these transparent cells are originally formed within the yolk, finding their way out as shown in fig. 47, where three of them appear near the surface under the form of transparent herniæ. They once were vitelline cells, which outgrew their circle of activity under the influence of the central activity of the yolk. Their vital power being extinguished, they are now rejected as no longer useful.

§ 2. The small ones, much more numerous than the former (fig. 52), were likewise vitelline cells, which on being accidentally dropped from the surface of the yolk, and remaining in an isolated state without any work to perform, no longer under the influence of vitelline life, lost entirely their activity and vital power. They grew some-

what in size, and developed into epithelian cells, according to a general physiological law. If, perchance, they congregate immediately on being detached from the yolk and before they become epithelian, then, still in possession of their own cellular life, they, for a time, will constitute a little spheroid, which will acquire vibrillæ, in accordance with the organic law of development of a large portion of the animal kingdom. These little bodies are the so-called *Cosmella arachnoides*, described by Alex. Nordmann as parasitic animals in the ovum of *Tergipes edwardsii*, a nudibranchiate mollusc.* When this spheroid is of a certain size, it sometimes happens that a small embryo issues from it, with a shape altogether similar to the embryos formed by the entire mass of the yolk.

It is my intention to dwell more at length upon these loose cells in another Paper, now in preparation, and in which their physiological signification will be thoroughly examined.

X.

THE EMBRYO.

§ 1. Between the period of the division of the yolk and that of the first manifestation of the embryo, there is a period of apparent repose, which lasts from four to five days. The vitelline sphere seems to undergo no process of any kind; the labor is undoubtedly beyond the reach of our investigations, for, that something is going on in it, cannot be questioned for a moment: life once started, keeps acting until it ceases definitely its actions. During this period the vitelline mass, from opaque (figs. 46 and 47), acquires two transparent diameters (fig. 48), which are transformed into four transparent internal cavities (fig. 49), sometimes a single, but larger central cavity is observed (fig. 50), which is less distinct in others (fig. 52 and 53), probably in the latter the embryonic substance has not yet acquired all its transparency: a phenomenon at all events taking place during this period of rest and preceding that of motion.

§ 2. For, now the embryo begins to move, the most wonderful sight which an observer may behold. When numbers of them are witnessed at once, some may be seen revolving around an ideal axis forty turns a minute, whilst in others the movement is scarcely perceptible. And between these two extremes of motion, there are all intermediate degrees of velocity. According to the will of the animal, the velocity may be increased or diminished, so that the same individual moves alternatively with different degrees of velocity. When passing from one degree into another, this does not take place according to the mechanical law of uniform acceleration, but the two

* Essai d'une monographie du *Tergipes edwardsii*.—Ann. Sc. Nat. 3d Ser. V. 1846, 109, Pl. I.

extremes may succeed each other in both directions. The axis of rotation is changing as the form of the vitelline sphere itself temporarily changes, under the incessant contractions of the embryonic mass.

The direction, or movement of revolution is sometimes from right to left; in others, from left to right, in an horizontal plane. In some others again, that movement is either forwards or backwards in a vertical plane.* The embryo, therefore, is absolutely free, and can assume any position and turn in any direction. For, the direction itself may change almost instantly, that is to say, if an embryo moves now from right to left, the next moment it may move from left to right. I have repeatedly seen a vitelline sphere, artificially pressed out of its external envelope, continue to move as if still enclosed. When crushed to the isolation of the constituent cells, all of these, large and small, began to dance, turn, whirl independently of each other, as if controlled by an irresistible impulse of their own.

Another phenomenon which illustrates the independence of the cells, took place under my eyes. An embryonic sphere, while in motion, lost about one third of its substance, the cells of which became loose within the albuminous zone, and were carried by the current, around the remaining portion of the original vitelline sphere. These loose cells, after a while, congregated into a small sphere, and for a moment one would have thought that there were originally two embryos in the same egg, a large and a small one. Soon, however, the small sphere was destroyed by the other and its cells again loosened, when it rebuilt itself once more. But now it became a permanent little sphere, which, in its motion within the same area as the large one, caused many irregularities and perturbations, in the general movements of the latter.

We have here one of the most attractive and wonderful phenomenon which nature may display; a phenomenon hidden from the eye of the great multitude of men. How many are there, who, at a glance into that sanctuary, would feel powerfully impressed with the thought that a divine mind, an allwise Creator is the author of the small as well as of the great in the whole universe. A moment of simple reflection would convince them that such an activity like that which they thus behold, in a little sphere of organic substance, cannot be accounted for by the mere attributes of material forces.

§ 3. About twelve hours after the motion has begun, the embryonic mass, still circular in general form, assumes now two aspects in its substance: 1st. The central part, which is composed of large cells either transparent or semi-transparent, containing a milky fluid at divers degrees of development (fig. 55, *a. b. c.*); and 2d, the peripheric layer, composed of ordinary vitelline cells from the surface of which vibrillæ now will grow (fig. 56).

§ 4. The embryonic mass, after a lapse of another twelve hours, acquires a plastic

*The horizontal and vertical planes are here spoken of with reference to the observer's orientation.

elasticity by which the primitive spherical form is subjected to the most diversified though temporary variations. This fact is another evidence that cells may contract as well as muscular tissues, although the physiology of this function is not easily explained in the actual state of our knowledge on this subject.*

§ 5. The transformation of the spherical embryo into a symmetrical animal is effectuated by two forces, the material force and the organic force, by which a different development follows as either the one or the other of these forces prevails.

A. The embryonic sphere, being subjected to a rotatory motion around an axis, may elongate and assume an oblong shape (fig. 57), such as would be originated under the mathematical or astronomical law. Then one of the regions acquires a preponderance over the other, the embryo moves forwards, thus indicating a cephalic region. From this instant there are two sides, a right and a left (fig. 59 and 61): the body being flattened or depressed, very much resembling that of the parent. There are two eye specks upon the anterior region, the only organs as yet conspicuous. The little animal crawls about when caused to escape prematurely out of the egg's external membrane. Some individuals are provided with a caudal, others with a cephalic needle-like appendage, varying in length and more transparent than the body, which is provided with vibrillæ all around. The external layer of the body is also more transparent than the general mass (fig. 60 and 70). The same embryo may alternately assume the forms represented in figs. 66—68 and 70—74. The surface of the body is incessantly waving or undulating under the constant agitation of the centre.†

The material law, having predominated in the above cases, it gave origin to an anticipated development, which went on so rapidly as not to allow all metamorphoses to take their natural course; forms like those of the parents made their appearances within the egg's envelope.

The query now is, whether or not these embryos would live and grow into adult and perfect animals, duly representing their species, and capable of reproducing it? I may be mistaken, but I cannot help thinking that most of them would not survive, and that in their polymorphic and ever changing aspect we have the expression of a convulsive state of these organisms about to die out, a final struggle of a vital essence enveloped in an abnormal material body.

B. But now let us see what forms the organic law of development brings about. The first modification which the embryonic sphere undergoes, is a quadrangular shape (fig. 75), which somewhat elongates (fig. 76), when a transversal groove is formed below, dividing an anterior from a posterior region (fig. 78). Then a longitudinal groove appears, which divides the posterior region into two halves (figs. 77, 79 and

* I allude to the contraction of cells in jelly fishes (*Medusæ*) observed by Prof. Agassiz.

† In figs. 60—67 the embryos are represented not surrounded by the outer membrane of the egg. Indeed, they had not escaped naturally, but were forced out by pressure before hatching.

80). The embryo now elongates, becomes thinner, whilst its back rises (figs. 84, 86 and 87). Sometimes the anterior region is likewise divided beneath into two halves by the prolongation of the longitudinal groove, so that the entire lower portion of the body, when seen from below, exhibits four hillock-like elevations (fig. 85). The transversal groove now deepens and the back rises more and more (figs. 82, 83 and 89), until after a few days the embryo escapes, passing into the next period of its history, which is that of the larva.

A single instance of a caudal, needle-like appendage was noticed (fig. 91). But on account of the extreme transparency of those appendages, the perpetual and irregular movements of the embryos, they may have escaped my notice.

The internal organization of the hatched embryo is very simple, for nothing is to be detected in its interior except large transparent cavities (figs. 91—93), enclosed in a more dense layer of the enveloping substance, itself surrounded by an external more transparent layer.

XI.

THE EMBRYONIC SUBSTANCE.

What is here called *embryonic substance* is nothing else but the vitelline substance, which, as a whole, became the embryo itself, now moving within the egg's envelope. It is a never resting substance, undergoing the perpetual process of evolution, incessantly renewing itself by the development of its central parts and the decaying of the outer parts, in accordance with a physiological principle of the animal fabric.

We left the vitelline substance when its structure reappeared homogeneous during the last stage of the division of the yolk (fig. 45, *a*). Now, as soon as the embryo revolves (figs. 52 and 53), its substance again is heterogeneous (fig. 54). There are very small cells (*a, a*), in which no nuclei as yet appear to exist; others, somewhat larger (*b, b, b, b, b*), exhibit very distinctly their nuclei. These nuclei, by expansion, become hollow, and appear now themselves like cells, within a mother cell: without nuclei first (*c, c, c*), afterwards become nucleated (*d, d*). Some larger cells show several nuclei in each (*e, e, e*), the latter growing hollow, transform into new cells (*f, f, f, f, f*), which, in their turn, become nucleated (*g, g, g*), showing the third generation of cells previously to the bursting of the grandmother cell, which is going to take place. A few large oily cells (*h*), are intermingled with these.

Further onwards, the embryonic substance assumes two aspects (fig. 55). 1st. The centre is composed of large cells, some with an oily (*c*), others with a milky contents (*b*), and still others in which nucleated cells are in the process of formation (*a*). 2d. The periphery or surrounding layer is homogeneous and composed of small nucleated cells. Upon the outer surface vibrillæ are next formed, originating from the peripheric cells themselves (fig. 56).

I scarcely need allude to figs. 81 and 82, *a* as illustrating the permanent activity of the embryonic substance, for they show the same process of cellular life as in fig. 54. The proportional size and the degree of development alone differing, hence more important in other respects.

The substance, in the larval state, is still more heterogeneous than in the embryo, and continues to be such; there is no return towards that uniform structure of the vitellus as observed during its formation, and before and after its division. The future labor of the organism is *diversification*.

The substance, in the chrysalis state, I have not been able to examine thoroughly.

XII.

THE LARVA.

The larva retains the plastic nature and assumes the polymorphic outlines which we have noticed in the embryo. The preponderant forms assumed are already foreshadowed some time before the latter breaks its outer envelope (fig. 84—91). It still moves with all degrees of velocity, mayhap more rapidly, being now free from all obstacles and allotted to steer in almost any direction which opens itself before it.

The forms, however, of the larva are not quite as diversified as were those of the embryo. Its plasticity is more of a temporary character, affecting rather the regions one after another, than the general outline itself.

A few days after their breaking out of the egg, the larvæ appear under two typical shapes. In one the back or middle upper region is concave, whilst both extremities are somewhat elevated; it has a *camel-like* outline (fig. 94). In the other, the back is convex, very elevated and both extremities declivous; the outline is *dromedary-like* (fig. 99). In both forms the sides are rounded, and the anterior region is much narrower than the posterior one, as exhibited by the figs. 95—98 and 100—103. The under part of the body does not differ otherwise from its appearance in the embryo, except that the grooves are deeper, and consequently rendering the hillock-like elevations more prominent, making the animal to appear as if supported by three pillars or columns (figs. 96 and 103). In both forms also, cases may occur, which are already to be observed, though but slightly indicated in the embryo, in which the anterior region is divided, causing four of these pillars or processes to be present. Figures of these were not deemed necessary; fig. 85 conveying a correct idea of the fact here alluded to. When such, however, happens to be the case, the anterior region is as broad as the posterior one.

The rapid motion of the larvæ, prevented my seeing them either at rest or even permanently, in the focus of the microscope; their small size requiring a high magnifying power, reduced considerably the field of vision. Attempts at fixing

them between two glasses proved unsuccessful: the little creatures being constantly crushed under the slightest pressure. Hours after hours were spent, the eye over the microscope, in order to form a complete idea of their outlines, until I was prepared to carve models of their shapes, from which models, figs. 94—103 inclusive, were drawn by Mr. A. Sonrel. This circumstance is mentioned to account for their artistic appearance; also to explain their being mere shaded outlines, without any attempt for exhibiting their structure. As copies, in natural size, of my models, they are proportionally a little larger than the other figures.

The body of the larva is semi-transparent, in which no organs are as yet to be discovered; the eye-specks alone, dark brown, are very conspicuous. Vibrillæ still cover the whole surface of the body, but are especially developed around the prominences of the back and belly. Indeed, when speaking of back, belly and sides, it is in reference to the eye specks, which we consider as appertaining to the anterior region, for, in their motion, the larvæ keep in no permanent position or orientation. Almost any of the regions may be directed forwards; it is a perpetual rolling rather than a headwards progression; no region yet predominates exclusively over the other regions.

Towards the eve of the larval life, the larvæ are no longer moving in open medium. They keep nearer the bottom of the vessel, move slower, but are still subjected to those contractions of their body, which alternately and temporarily modify their shape.

XIII.

THE CHRYSALIS.

That larva which was seen so lively, so active, so plastic, so polymorphic, becomes a mummy-like body, an immoveable chrysalis (fig. 104), eight or ten days after it first began to revolve as an embryo (fig. 52, 53 and 55).

This chrysalis is an elongated, slightly curved body, semicylindrical in shape, concave above and flat below, as shown by a transverse section (fig. 105). Opaque at both extremities, whilst the middle region remains transparent, no organs are discernible in any of the regions. The external envelope, or case, is a tough membrane, through which the microscope can hardly penetrate. When crushed between two glasses, the cellular contents then escape, leaving the case empty.

I am not prepared to give any information in relation to the length of time which the animal remains in this state, having lost a great number of these little bodies which could scarcely be distinguished amongst the sand and organic substances always floating in the water; and when the latter had to be changed, many of them were unavoidably lost. On this account my investigations, have come to a temporary close at this point of their history.

For a time, I was still in doubt as to whether these singular chrysalis-like bodies

were really a normal state of existence in the embryogeny of Planarians, or an abnormal one, in consequence of the limited space in which the larvæ had been kept. But soon afterwards, having had an opportunity to observe the same bodies out at sea, in their natural element, there could be no hesitation in regarding this chrysalis state as a natural period in the genetic development of *Planocera elliptica*.

How long this period will last, is a question now to be investigated; also, whether the perfect animal is the next step, or whether there are other stages of development, or other metamorphoses.

XIV.

CHRONOLOGICAL SKETCH.

In 1849, a chronological narrative of the development of *Planocera elliptica* was read before the American Association for the Advancement of Science,* and subsequently before the Society of Natural Sciences of Neuchâtel, Switzerland.†

October 1848.—The eggs exist as organic cells, similar in every respect to the cells constituting the organic tissues at large.

December 1848.—From simple primordial cells, the eggs have grown to a semi-transparent sphere, containing some vitelline substance, a germinative vesicle and a germinative spot. The eggs can no longer be mistaken for primordial organic cells (figs. 1—6).

May 1849.—The eggs, still within the maternal body, have become opaque by the increase of the vitelline substance, which conceals now entirely the germinative vesicle, visible only upon the compression of the egg (figs. 5 and 6).

May 25, A. M.—Laying of the eggs. These consist of an external envelope, a zone of albumen and an opaque vitellus, occasionally showing a central clear space indicating that the germinative vesicle is still present. The germinative spot, however, has already disappeared (figs. 12 and 13).

May 25 P. M.—Commencement of the phase of the division of the yolk (fig. 15).

May 26 P. M.—That division comes to a close. The egg reassumes its primitive appearance (fig. 46).

May 27—31.—State of repose, preparing the embryo properly so called (figs. 47—50).

June 1.—The yolk or embryo begins to revolve, and will keep in motion until it shall be transformed into a chrysalis (figs. 52 and 53).

June 2.—Large transparent cells are formed in the centre of the embryo, still spherical in form, whilst upon its surface vibrillæ now appear (figs. 55 and 56).

*Proc. Amer. Assoc. Adv. Sc. second meeting, held at Cambridge, in August 1849. Cambridge 1850, 398.

†Bull. de la Soc. des Sc. Nat. de Neuch. II. 1850, 300.

June 3—5.—The embryonic sphere loses its primitive form by the flattening of one of its poles. From this flat surface several cones rise up, between which a groove is formed, which opens the sphere. The little creature is now symmetrical (figs. 75—93).

June 6.—Escaping of the embryos from the eggs as larvæ. The latter are polymorphic and endowed with a plastic elasticity by means of which they pass from one shape into another. At this stage of their development the larvæ of *Planariæ* resemble infusoria of the genera *Kolpoda* (figs. 94—103) and even *Paramecium* (figs. 57—65).

June 14—16.—The lively larvæ transform into an immoveable chrysalis-like body (figs. 104 and 105).

The further progress of development I have not yet been able to trace out.

XV.

RECAPITULATION.

§ 1. The egg of *Planocera elliptica* passes through a series of successive periods, each of which may be thus characterized :

I. PERIOD OF EVOLUTION. This period embraces the time which elapses between the origin of the egg and the laying. The egg originates like the organic cells. It generates its own mass around a new centre of attraction until it becomes capable of leading an independent life. During this period the egg is dependent upon the mother, and has its growth.

II. PERIOD OF PREPARATION. Embraces the time which elapses from the laying of the egg to the first manifestation of the embryo. The egg is full grown; the vitelline mass divides, works and kneads its substance, and prepares it for the future being. During this period the vitellus is in a state of rest, in other words, immoveable, but is no longer connected with its parent.

III. PERIOD OF THE EMBRYO. Embracing the time which elapses between the first manifestation of the embryo and its escaping from the egg envelope. The vitelline sphere is in motion and assumes various shapes.

IV. PERIOD OF THE LARVA. Lasts from the escaping of the embryo from the egg, to its transformation into a mummy-like body. The young animal moves freely about in the surrounding medium, still assuming divers shapes.

V. PERIOD OF THE CHRYSALIS. It commences when the lively larva, losing its polymorphic shape, becomes an immoveable body, simple and uniform in external appearance. The end of this period is not known.

§ 2. The organic process which is performed throughout the successive periods in the history of the egg of *Planocera elliptica*, is the most simple of the animal economy : The egg commences as a cell ; in it, neuclei are formed, the points of departure of the vitelline cells proper, which multiply by *exogenesis*. These vitelline cells, simple and homogeneous at first, enter into a process of *diversification*, from the instant that the organic vitelline sphere has received the impulse of development, by which a new individual is called into existence. Once started, this diversification of the constituent organic cells proceeds onwards, until the new being has completed its growth ; when all the organs, which its sphere of action involved, have reached that degree of fulness or completion, necessary to fulfil the end contemplated in the plan of structure to which the animal belongs.

XVI.

CONCLUSION.

§ 1. The investigations which I have traced upon Planarians have led me to their removal from the class of Worms, where they had ranked hitherto, into the division of mollusca, and more particularly into the class of Gasteropoda.* The embryological grounds for my so doing are the following :

The embryogeny of Gasteropod molluscs, and more particularly of Nudibranchiata has such a striking resemblance with that of the Planarians which I have examined, that any one familiar with the subject will acknowledge its evidence. Thus the division of the vitellus in *Polycelis variabilis*, as observed by me several years ago, although not published yet, seems almost an exact copy of the same phenomenon in *Acteon viridis* of the coast of France : when the yolk is divided into four spheres, four smaller ones will appear opposite, and then the latter will remain stationary whilst the former will follow out the process of the division.

In *Planocera elliptica* the division of the yolk does not differ apparently from the same phenomenon in *Acteon chloroticus* of New England, and likewise in several species of *Eolis* and *Doris*, as well as *Triton*. There is the most striking resemblance in that respect between *Planocera elliptica* and *Eolis gymnota*, in the cases in which the yolk divides into three spheres instead of four.

The vitellus, as a whole, transforms itself into an embryo ; there being no embryonic layer distinct from any other portion of its mass.

* Essai on the Classification of Nemertes and Planaria, &c.—Amer. Jour. of Sc. and Arts, 2d Series, xi. 1851, 41, and Proc. Amer. Assoc. Adv. of Sc., third meeting held at New-Haven in August, 1850, Washington, 1851, 258.

The embryos move within the egg, and their body is surrounded by vibrillæ, both in Planarians and Nudibranchiata, and during the earliest period of their existence they resemble each other most.

Planarians and Gasteropods undergo a larval life, during which they assume forms or shapes very different from those of the adults.

There is now the state of chrysalis which has not yet been observed among Gasteropods.

§ 2. An opinion adverse to the views which I now entertain respecting the systematic position of Planarians has been published* under the heading of "Zoological Notes from the correspondence of Prof. Agassiz."

With all the respect which I have for the zoological learning of that naturalist, I may be permitted to examine critically his brief reasoning. Planariæ, in his estimation, belong to the *same natural group* as intestinal worms. He saw embryos of Planariæ resembling the polygastric infusoria—*Paramecium* and *Kolpoda*; he alludes to a paper read by himself at the Cambridge meeting of the American Association for the Advancement of Science, held in August 1849, in which he showed their identity, whilst, according to the records of that meeting,† that paper was neither read nor printed; the title only appeared.

The dismemberment of the Class of Infusoria, discussed in the "Zoological Notes," is foreign to my subject.

Now that that dismemberment, even if rational, should tend "to show the correctness of Blanchard's views respecting the Planariæ," I most candidly confess that I cannot see the bearing. For, in admitting it, the same bearing would be true, applied to the class of Medusa, and Medusæ, on the same ground, would belong to the *same natural group* as the intestinal worms.

Furthermore, you may cast a glance at page 135 of the "Principles of Zoology" of the same author, compare the figure he gives there of a young Medusa, with fig. 62, accompanying the present Memoir, and decide which is most *Paramecium-like* of the two.

§ 3. In the third Part of these Researches I propose to illustrate the anatomical and physiological grounds for placing the Nemertians and Planarians in the division of Mollusca, when I shall also examine and discuss the opinion and observations of authors upon the same subject.

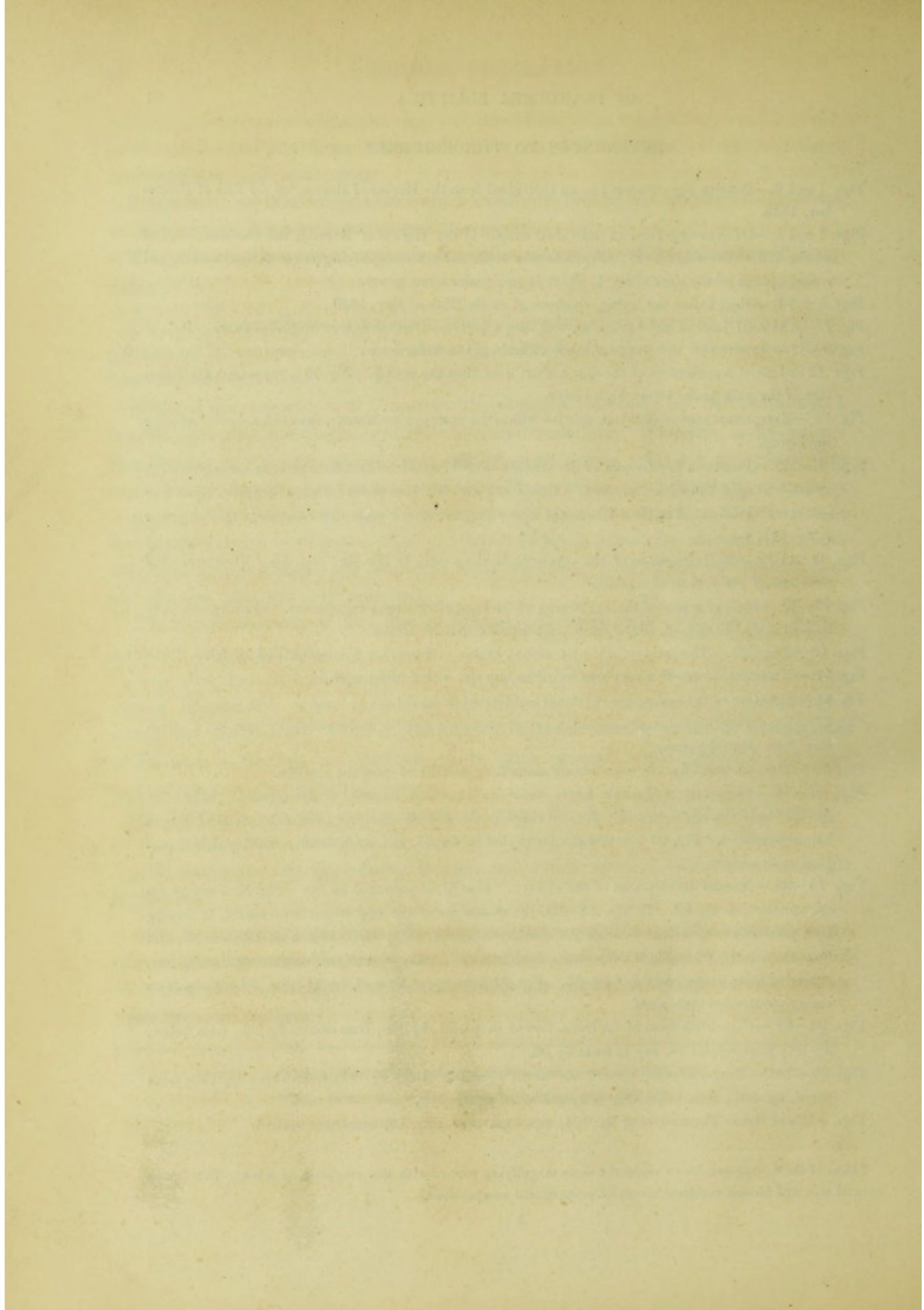
* Amer. Jour. of Sc. and Arts, Second Series, vol. xiii. 1852, 425.

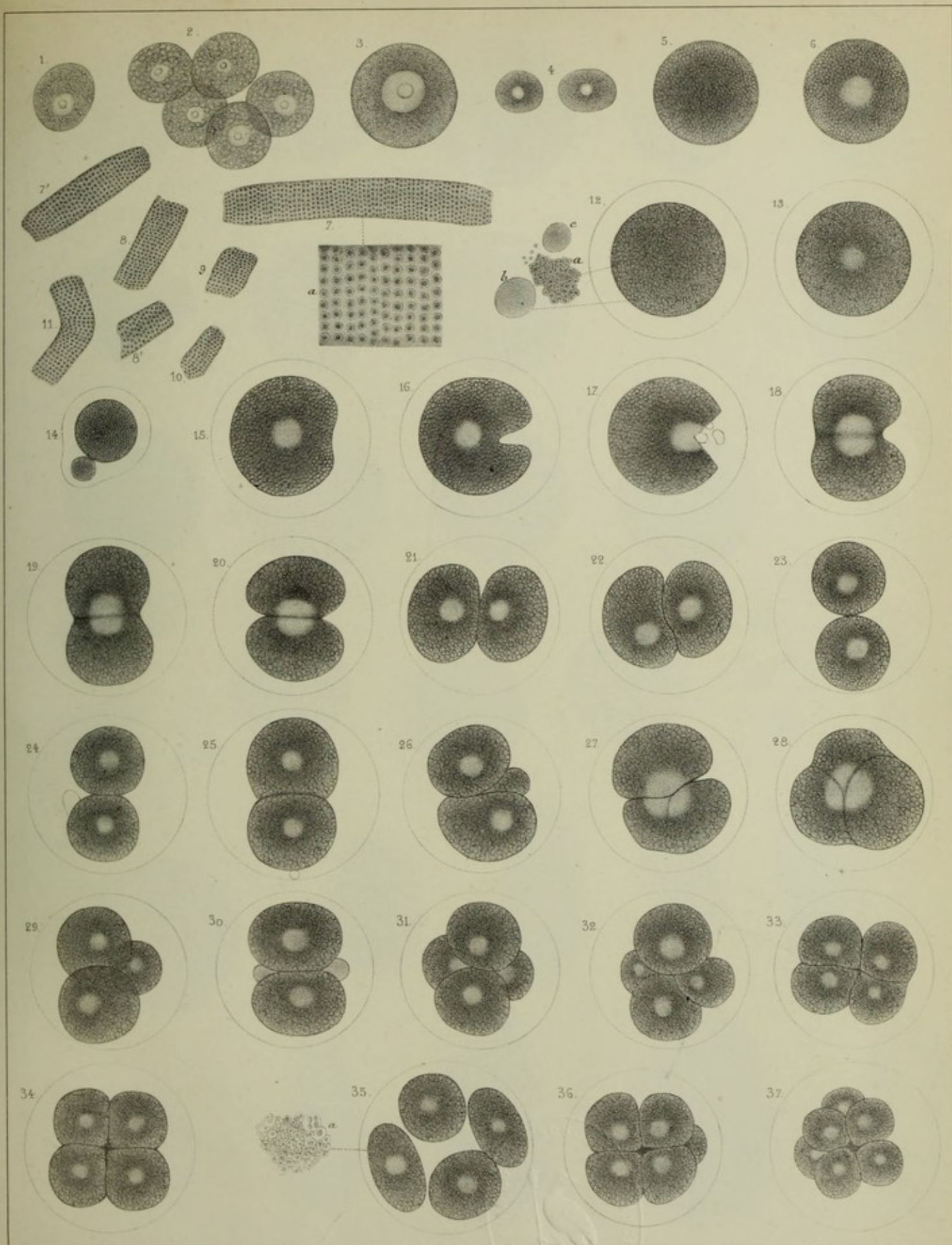
† Proc. Amer. Assoc. Adv. of Sc. Second Meeting, 1850, 433.

REFERENCES TO THE FIGURES.*

- Figs. 1 and 2.—Ovarian eggs observed in an individual from the Harbor of Boston, on the 22d of December, 1848.
- Figs. 3 and 4.—Ovarian eggs from an individual caught in the Harbor of Beverly, and likewise observed on the 22d of December 1848. Fig. 3 is seen under the same magnifying power as fig. 1 and 2, and represents one of the eggs of fig. 4, which is seen under a low power.
- Figs. 5 and 6.—Eggs before the laying, as observed on the 25th of May, 1849.
- Fig. 7.—A regular band of laid eggs in natural size, a portion of which is seen magnified in *a*.
- Fig. 8—11.—Interrupted and irregular bands of laid eggs in natural size.
- Figs. 12 and 13.—Appearances of the eggs a short time after the laying. Fig. 12 *a* represents the structure of the yolk under a very high power.
- Fig. 14.—Exceptional case of two yolk spheres within the same egg membrane, observed a short time after the laying.
- Figs. 15—43.—Phases in the division of the vitellus. Fig. 17 exhibits three floating cells issuing through an artificial split caused by pressure. In figs. 24 and 38, transparent herniæ are seen upon the spheres of division. Fig. 35 *a* illustrates the structure of the yolk under the same optical power as fig. 12 *a b c*.
- Figs. 44 and 45.—Mulberry shape of the yolk with floating cells, in fig. 45. Fig. 45 *a* illustrates the structure of the yolk at that period.
- Fig. 46—49.—State of repose of the egg during which the yolk becomes transparent. Floating cells may be seen in fig. 46 and 48, whilst fig. 47 exhibits transparent herniæ.
- Figs. 50, 52 and 53.—The embryo, when its motion begins. Numerous floating cells in fig. 52.
- Fig. 51.—Exceptional case of a very small vitellus or yolk, with floating cells.
- Fig. 54.—Structure of the embryonic substance as observed in fig. 53.
- Fig. 55.—The embryonic substance assuming two characters, a central and a peripheric one; *a b c*, structure of the central portion.
- Fig. 56.—The embryo of fig. 55, more highly magnified, in order to show the vibrillæ.
- Figs. 57—74.—Temporary embryonic forms under an abnormal impulse of development, artificially pressed out of the egg membrane. Any of these forms will successively assume the series of shapes here represented. Fig. 69 is a case similar to that in fig. 51, but much further developed, and proportionally smaller.
- Figs. 75—93.—Normal development of the embryo. Fig. 81, structure of fig. 80. Fig. 82 *a* represents the structure in fig. 82. In figs. 84—93, the membrane of the egg is not represented, it having been purposely broken open to allow the embryo to escape. Fig. 82 is seen from below in 86, and from above in fig. 87. Fig. 85 represents, from below, the case where four protuberances are extant, instead of three as represented in fig. 86. Fig. 92 is an upper view of fig. 91. Fig. 93 represents an embryo contracted upon itself.
- Figs. 94—98.—Camel-like form of the larva viewed in profile, fig. 94; from above, fig. 97; from below, fig. 98; from behind 95, and in front fig. 96.
- Figs. 99—103.—Dromedary-like form of the larvæ, viewed in profile fig. 99; from above fig. 100; from below, fig. 101; from behind fig. 102; and in front, fig. 103.
- Figs. 104 and 105.—The chrysalis; fig. 104, seen from above; fig. 105 transverse section.

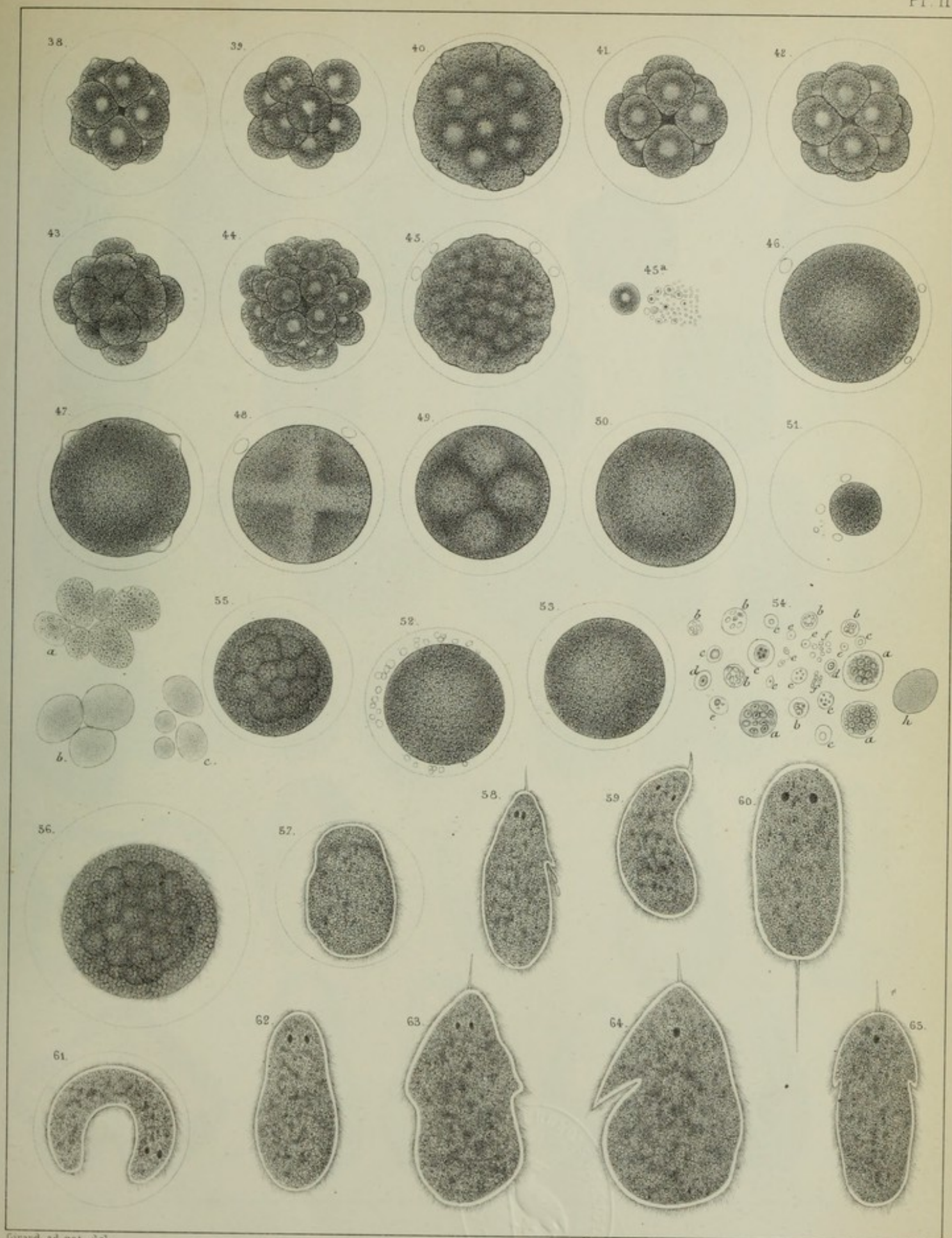
*Most of the figures are drawn under the same magnifying power, with the exception of a few. The figs. in natural size will furnish excellent means of proportional comparisons.





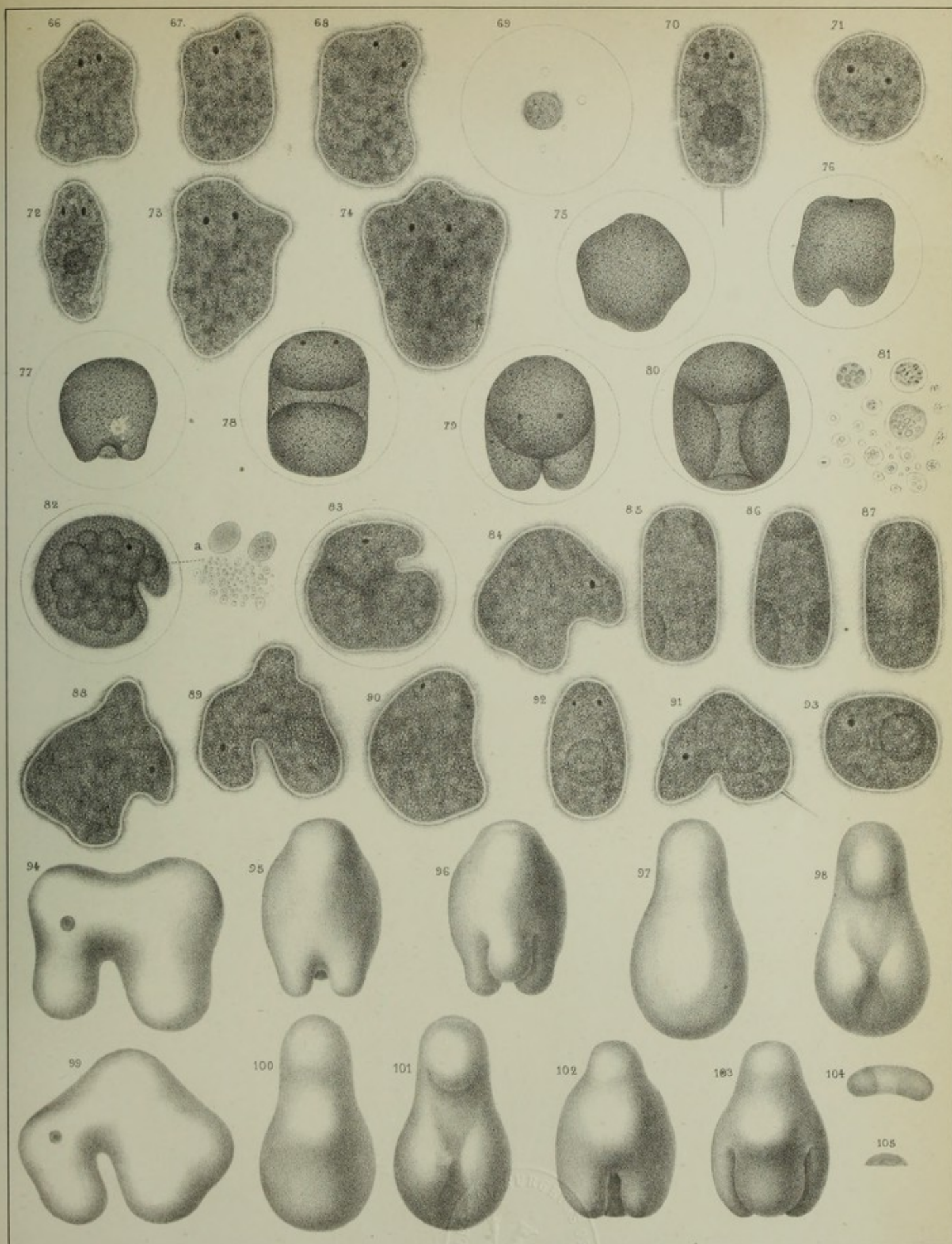
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