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XXXVIII.—*On a new Genus of the Family of* Volvocineæ.

By Dr. Ferdinand Cohn of Breslau.

[Concluded from p. 347.]

VIII. *Comparison of the Development of* Stephanosphæra *with the Formation of Swarming-cells in the other Algæ.*

Whoever has observed the active spores (*gonidia*) of certain Algæ which are formed by the division of a primordial utricle in the interior of a parent-cell, and after the rupture of the latter emerge into the water by the help of moving cilia, will at once perceive the perfect agreement of this phænomenon with the facts observed in the development of *Stephanosphæra*. The formation and evacuation of the swarming-spores, as I have observed it myself many times in *Achlya prolifera*, *Chytridium*, and *Conferva glomerata*, and others in *Ascidium*, *Bryopsis*, *Codium*, *Ectocarpus*, and the Fucoideæ, presents the exhibition of *swarming* and *streaming out* exactly as we have just described it in the microgonidia of *Stephanosphæra*. The swarming-spores of *Bryopsis*, *Chætophora*, *Stigeoclonium*, *Ulothrix* and *Draparnaldia* have such a complete agreement of form with those of *Stephanosphæra*, that it would not be possible to distinguish them if they were seen only singly and not at the moment of emerging from the parent-cell. All these spores of Algæ bear *four cilia* at the anterior extremity, like the microgonidia of *Stephanosphæra*; a condition which has not hitherto been observed in any true or pseudo-Infusorium. Other swarming-cells have exactly similar form, development and motion, but bear only two cilia, as in those of *Cladophora*, *Characium*, *Apiocystis*, *Phycoseris*, *Chætomorpha* and others. The treatise of G. Thuret on the moving spores of the Algæ (Ann. des Sc. Nat. 3 série, tom. xiv. 1850)

has very recently given us most excellent representations of this phænomenon, to which I refer every one who may wish to acquire a clear idea of this remarkable mode of propagation of the Algæ and aquatic Fungi*. Yet to be warranted in deciding this question, it is indispensable to make a direct and unprejudiced observation at least of the most important phænomena, which is so much the easier to effect, that, with the exception of the *Oscillatorieæ, Nostochineæ* and *Conjugatæ*, almost all the Algæ propagate by swarming-spores throughout the whole year. An independent examination is here the more indispensable to every one who wishes to acquire an unprejudiced opinion as to the organisms standing on the limits between the animal and vegetable kingdoms, since the phænomena here in question are totally different from anything elsewhere known in the vegetable kingdom, and must be regarded as *sui generis*. The macrogonidia of *Stephanosphæra* themselves also agree perfectly in structure and movement with the swarming-cells bearing two cilia which Nägeli has represented of *Tetraspora* (Einzell. Algen. t. ii. C. *f*), of *Characium* (*l. c.* t. ii. A. *k*), or of *Apiocystis* (t. iii. D. *b*); only the common enveloping cell and the combination into families of cells, which elsewhere occur merely in immoveable forms of Algæ, have not previously been observed in swarming-cells, and must be regarded as specific characters of the *Volvocineæ*, without this organization standing in any contradiction to their vegetable character.

The developmental history of *Stephanosphæra* is especially decisive for the position of the *Volvocineæ*, because of the essential agreement it exhibits with another organism as to the real nature of which no doubt has ever been raised.

One of our most widely diffused freshwater Algæ, *Hydrodictyon utriculatum*, is composed, as is well known, of large utricular cells, which are arranged reticularly in such a manner that three or four always meet in a point, and five or six bound each polygonal space. The green contents lining the walls of the individual cells, in which a great quantity of chlorophyll-utricles are imbedded, are transformed in the propagation into a very large number of swarming-cells, the structure of which was misunderstood until very recently, and was first revealed by the masterly history of its development by Alex. Braun in his often-cited

* Compare especially my drawing of the microgonidia of *Stephanosphæra* (fig. 19) with the figures which Fresenius has given of the swarming-spores of *Chætophora* (zur Controverse über die Verwandl. von Algen in Infusorien), or Thuret at pl. 16. fig. 5, pl. 18. figs. 6, 10 & 11, pl. 19. fig. 3, pl. 21. fig. 3, of his treatise above cited. See also "Sur les organes reproducteurs des Algues," par MM. Derbès et Solier, 'Ann. des Sc. Nat.' 3 ser. xiv. pl. 33, on *Draparnaldia*.

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work (Verjungung, &c., 279), with which my own observations agree perfectly. The essential point in this is, that the contents of the large cells of *Hydrodictyon* are transformed in two ways: first, into a number of *large moving spores*, which are of globular form, send out two cilia from a colourless point, only tremble and jerk hither and thither within the parent-cell, and never leave this; after a brief swarming these attach themselves into a network in the interior of the envelope and secrete a rigid membrane which surrounds the whole; in this manner they, the *macrogonidia*, become *combined* into a *family of cells* and grow into a new net exactly like the original. Secondly, in other cells of *Hydrodictyon* the contents are converted into a far greater number of smaller *microgonidia*, 30,000 to 100,000 of which are developed in one utricle; these are spindle-shaped, possess *four cilia*, move very actively and quickly, emerge singly from the parent-cell into the water, and after a long movement pass into a condition of rest, without ever becoming united into a net-shaped family of cells.

Abstracting the differences which may be shown always between two genera, we detect the *same law of development*, that in *Hydrodictyon* as in *Stephanosphæra*, the bi-ciliated, less numerous macrogonidia arrange themselves into a *family of cells* already within the parent-cell, according to the character of the given conditions of the two genera, the cell-family being active in the *Volvocineæ* and immoveable in the *Protococcaceæ*; while the more numerous, more actively moving microgonidia with four cilia leave the parent-cell and enter upon a metamorphosis, the retrogradation from which to the normal type of the genus has not been observed yet here, or indeed in the microgonidia of any of the Algæ. Such an undeniable agreement of the law of development of *Stephanosphæra* with an undoubted plant like *Hydrodictyon*, which testifies to a near relationship, would be inconceivable if the former were to be regarded as of essentially different organization,—as belonging to quite another kingdom of nature*. Thus the developmental history of *Stephanosphæra* also furnishes the most convincing proof of the vegetable nature of this genus, and consequently of the *Volvocineæ* generally.

* Thuret has also observed in one of the *Dictyoteæ*, *Cutleria multifida*, besides large swarming-cells which are developed to the number of eight in a parent-cell and readily germinate, the formation of smaller, likewise moving cellules, which originate exactly in the same way, only by often-repeated division (to thirty-two?), and never germinate. Thuret regarded the latter as analogous to the spermatozoids; we should rather consider them as a proof that a simultaneous formation of macrogonidia and microgonidia occurs also in the higher forms of the marine Algæ (see Thuret, *l. c.* vol. xiv. pl. 31, and vol. xvi. pl. 1).

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IX. *On the Physiology of* Stephanosphæra.

That the formation of macro- and microgonidia does not exhaust the whole series of forms which *Stephanosphæra* may pass through is proved by the following observation, which unfortunately I have not yet been able to complete. Having cultivated some *Stephanosphæra* for a long time in a little glass cup, in the way described in my essay on *Loxodes Bursaria* (*l. c.*), all the primordial-cells at length exhibited dark, thick, greenish brown contents, so densely filled with numerous granules that the two chlorophyll-vesicles could no longer be detected; their form was more or less globular, and the mucous radiating processes were entirely absent; their outlines were remarkably sharply defined, as if they had become surrounded by a rigid membrane. At the same time I remarked that the primordial-cells were no longer fixed immoveably at the periphery of the envelope-cell, never changing their relative positions; but *jerked backwards and forwards, finally tore themselves away from the envelope-cell, and then began to rotate slowly and lazily in the interior*. Soon after I saw the envelope-cell also burst at some spot and collapse; and the eight primordial-cells gradually emerged, one after another, as independent globes; they were now seen to be *enclosed in a pretty closely applied envelope*, through which penetrated two cilia, and hence they present the utmost resemblance to *Chlamydomonas Pulvisculus* (fig. 20). They moved about for some time in the water and *at length came to rest, losing their cilia and accumulating like little green Protococcus-globules at the bottom of the glass*. We therefore have here a motionless, perfectly plant-like stage of *Stephanosphæra*, such as we are acquainted with in *Chlamydococcus* and *Chlamydomonas*; the remainder of the *Volvocineæ* undoubtedly pass into a similar condition of rest, which is the means of their preservation when the water of ditches is dried up in summer. The emergence of single globes from the common envelope, in a form resembling *Chlamydomonas*, may also be readily observed in *Gonium* (Ehr. Infusor. pl. 3. fig. 1).

I conjecture that the motionless, Protococcoid cells of *Stephanosphæra* are the means for the preservation of the species when the water, as is always the case in the shallow hollows in stones, their natural station, is dried up for a long time and all the living inhabitants are precipitated on the stone. The observations of Major von Flotow have already demonstrated that the dried-up muddy sediment always reproduces *Stephanosphæræ* when water is again poured on to it. This *capability, of reviving from the dried condition*, is shared by *Stephanosphæra* with *Chlamydococcus pluvialis*, in which likewise the motionless cells remain

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living after being dried up for years and are capable of giving birth to moving forms, while the swarming-cells themselves are destroyed for ever by rapid desiccation. Herr von Flotow has sent earth with dried *Stephanosphæræ* to Dr. Rabenhorst in Dresden, who, in like manner, succeeded in reviving them by moistening; in this way the latter obtained abundant material for distributing *Stephanosphæra* under No. 102 of the 11th Decade of his 'Algen Sachsens resp. Mitteleuropas,' and thus to effect the more general diffusion of this remarkable organism*.

Since the moving *Stephanosphæræ*, as numerous experiments have taught me, are destroyed, just like the swarming-cells of *Chlamydococcus*, by rapid desiccation, I believe that the motionless, Protococcoid globes, the development of which I have just described, are the forms which do not lose their vitality by drying, but are capable, when wetted again with water, of going through a cycle of development, by which they return to the normal moving form of *Stephanosphæra*. Yet I must remark that I have not hitherto obtained sufficient material to observe the resting *Stephanosphæra*, and to trace the processes which occur in the revivification, and that in reference to this most important phænomenon I must leave a gap, which I hope to fill up next summer.

In conclusion I add a note on the mode by which I have succeeded in obtaining sufficient material for my observations, since this also is of physiological interest. At their stations the *Stephanosphæra*-spheres occur mingled with *Chlamydococcus*, but by no means in the abundance requisite for the investigation; and although green clouds do collect at certain points in the water wholly composed of our *Volvocineæ*, it is difficult to extract sufficient of them for examination, since they immediately start apart when touched. I succeeded in overcoming this inconvenience by a simple means, so as to bring thousands of these elegant organisms on to the object-holder at any moment. I took, namely, a flat bottle with a short narrow neck, and nearly filled it with the water containing *Stephanosphæræ*, stopped it with a cork, and then laid it horizontally so that the cork partly dipped in the water. In a few hours almost all the *Stephanosphæræ* in the water collected on the cork, which was covered with a green coat composed exclusively of the revolving spheres, while the rest of the water in the bottle contained only *Chlamydococcus* and scarcely any *Stephanosphæra*; so that when I wished

* I must observe, however, that some of the specimens compared by myself contained no *Stephanosphæra*. A few printed details are given with the specimens, gathered from information furnished in my letters, not intended for publication in this form and not revised by myself; they contain many and essential inaccuracies.

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to examine them I had only to take out the cork, and a drop of the water adhering to it furnished me with all the stages of development of our organism simultaneously in very large numbers. After a short time the *Stephanosphæræ* had again assembled on the cork. I may remark in passing, that there is scarcely any sight more beautiful under the microscope, than a large number of these elegant crystal-like spheres crowded together, rolling through the water in all directions like revolving wheels, with their bright green and often curiously branched wreaths of primordial-cells, sometimes exhibiting themselves as rings, and sometimes as zones, sometimes rotating round a centre, and at others rolling away in the strangest curves.

I made some experiments to investigate more closely the cause of accumulation of the *Stephanosphæra* alone on the cork, and this furnished me with a sufficient explanation of the behaviour of the spheres towards light. When I placed water filled with *Stephanosphæra* and *Chlamydococcus pluvialis*, in a shallow porcelain saucer in a window, a green band was soon found at the margin of the fluid turned towards the window, and this was almost exclusively composed of *Stephanosphæra*, while at the opposite side the *Chlamydococcus* had collected, but with scarcely a single *Stephanosphæra*. Since the side of the water turned towards the window was kept in shadow by the projecting margin of the saucer, and thus constituted the *darkest* part, while the *brightest* point was on the opposite side, it followed that the *Stephanosphæra* avoids the light, and accumulates at the darkest part of the vessel, as is also shown by the collection under the shadow of cork. When I next covered the side of the saucer turned towards the window with a strip of wood, so that this part was kept quite dark, while the opposite side of the saucer was not overshadowed by it, within two hours all the *Stephanosphæræ* removed from the darker margin at which they had previously collected, yet did not repair to the opposite illuminated margin, but arranged themselves in a *green line going transversely across the water*, which corresponded accurately to the limit between the deep- and half-shadow of the slip of wood,—a position the more striking, since green microscopic plants when uninterfered with collect always at the margins alone and never in the middle of the water. When I placed the slip of wood so that it reached across from the front to the back, from the darkest to the lightest place, the green band was seen neither on the margin next the window nor on the opposite; but the green cloud of *Stephanosphæræ* soon appeared on each side of the strip of wood outside its central shadow. Repeated experiments gave the same result with the greatest certainty. From these facts it follows, that *the moving spheres of* Stephanosphæra *seek the darker*

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part of the vessel, avoiding however a total absence of light and assembling in preference in a moderated light or half-shadow. Since other Algæ and Infusoria exhibit a different behaviour towards the light, we thus possess a means of *sorting*, to a certain extent, the microscopic inhabitants of a specimen of water, as I did the shade-loving *Stephanosphæræ* from *Chlamydococcus*, which ordinarily seek the brightest light.

X. *Summary of the Results.*

I conclude my essay with the diagnosis of the new genus which has formed its subject:—

Algæ.

Order Palmellaceæ. (*Chamæphyceæ*, Kütz.)

Family Volvocineæ.

Stephanosphæra, nov. gen. (Wreath-globe.)

Stephanoma? Werneck, according to Ehrenberg's paper in Gesellsch. naturforsch. Freunde' (Spenersche Zeitung, vol. xxviii. April 1846).

Trichogonium? Ehrenb. *l. eod.*

Stephanosphæra in Rabenhorst's 'Algen Sachsens,' Dec. xi. No. 102.

Gen. Char.—A family of cells, rotating and moving throughout life; composed of *eight* green primordial-cells, bearing *two* active cilia, arranged at equal distances in a *circle passing round*, enclosed in a common, hyaline, *globose* vesicle; propagated both by *macrogonidia* originating from *eightfold* division of each of the green cells, and bearing two cilia, congregated into eight octonary families, and *very numerous* smaller *microgonidia*, produced by *multifold* division, turning round first within the common vesicle by the action of *four cilia*, and then escaping singly.

Spec. Char.—*Stephanosphæra pluvialis*, n. s. Green cells globose, elliptical or fusiform, often running out into mucous rays at both ends. Diameter of the cells = $\frac{1}{330}$th to $\frac{1}{190}$th of a line (0·0065 to 0·012 mm.); diameter of common vesicle = $\frac{1}{80}$th to $\frac{1}{40}$th of a line (0·028 to 0·055 mm.).

Obs. Revives after desiccation.

Inhabits hollow stones filled with rain-water, in company with *Chlamydococcus pluvialis*: Salzburg, *Werneck*?. Zambra, *A. von Frantzius*; Hirschberg, *Von Flotow*.

The principal results of my investigations may be pretty accurately comprised in the following statements:—

1. *Stephanosphæra* is a new genus of the group of *Volvocineæ*, and only essentially differs from *Pandorina*, *Gonium* and *Volvox* through the law of arrangement of the internal green globes.

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2. It is formed of eight equivalent green *primordial-cells*, which are arranged at the circumference of a circle; these are enclosed in a common *envelope-cell*, in which they stand at the equator, near the circumference.

3. The envelope-cell is of perfectly spherical form, and is composed of a structureless, completely closed cellulose membrane, filled with limpid contents (water ?).

4. The eight primordial-cells are globular, cylindrical or spindle-shaped, and are composed of the universal nitrogenous protoplasm of vegetable cells, which is coloured green by chlorophyll, and rendered opake by numerous fine granules (starch or protoplasm ?); they ordinarily enclose two chlorophyll-utricles containing starch. They are not bounded by any rigid membrane.

5. The substance of the primordial-cells becomes prolonged, especially at the two ends, into radiating and often ramified mucous filaments, which are retracted in the course of vegetation; the protoplasm-filaments occur also in other *Volvocineæ*, and have been differently interpreted in them (as hairs, tails, a vascular system, intercellular passages, &c.).

6. Each primordial-cell bears two cilia at the point turned outwards, and these penetrate, through orifices in the envelope-cell, into the water, and cause the movement of the entire organism.

7. The laws of the movement agree with those of the swarming-cells of Algæ, and Astomous or Anenterous Infusoria; it consists of a rapid rotation round the axis of the envelope-cell, which does not take place in any given direction, and of a simultaneous screwing forward, by which the *Stephanosphæra* runs through manifold curves in different planes.

8. The propagation takes place by division of the primordial-cells inside the envelope-cell. Each primordial-cell separates, by successive septa, first into two, then into four, and lastly into eight secondary cells; from this last division proceeds a permanent generation, while the two preceding were only transitional generations; the eight secondary-cells originating from one primordial-cell arrange themselves at the circumference of a circle, each developing two cilia, and remain united, secreting a common envelope over their surface, which, at first appressed and tabular, becomes removed away and acquires a spherical form through absorbing water. In this propagation by macrogonidia eight exactly similar young *Stephanosphæræ* originate in each envelope-cell of the parent organism. More rarely, the second division forms a permanent generation, and then the envelope-cell contains only four primordial-cells.

9. In the propagation by microgonidia, which commences in a similar manner, when however it is only the sixth or seventh

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generation which becomes permanent, the secondary-cells produced by the multifold subdivision separate from each other; they are smaller, spindle-shaped, and bear four cilia, by means of which they move very actively, even inside the parent envelope, and after breaking out of this, move freely and singly through the water, without ever secreting an envelope-cell, and giving rise to the production of a family of cells.

10. At certain times the individual primordial-cells develope a special membrane inside their envelope-cell, closely enclosing them; they then break away, move at first in the interior of the envelope, and finally emerge free into the water as *Chlamydomonas*-like globes; after a short swarming these pass into a Protococcoid condition of rest.

11. It is probably this resting condition which alone of all the forms of development of *Stephanosphæra* possesses the power, after being dried up from water, of being revived by a new addition of water, and causing the origin of new moving generations; but the process here in question has not yet been completely observed.

12. The *Stephanosphæræ* avoid both bright light and complete darkness; they seek moderately lighted spots and half-shadow.

13. The organization and development of *Stephanosphæra* agree essentially with those of *Chlamydococcus pluvialis*, the vegetable nature of which has been placed beyond doubt by recent researches. The only distinction consists in the type of the latter genus being represented by a simple cell, while that of *Stephanosphæra* and the rest of the *Volvocineæ* is represented by a family of cells.

14. The mode of propagation by micro- and macrogonidia in *Stephanosphæra* exhibits the most unquestionable analogies with an evident plant, *Hydrodictyon utriculatum*, and testifies to the near relationship of the two genera.

15. All the other *Volvocineæ*, as well as *Stephanosphæra*, are to be regarded as plants, and their organization can be understood and judged of naturally only according to analogy with vegetable cells.

EXPLANATION OF PLATE VI.

Fig. 1. Polar view of a *Stephanosphæra* with large globular primordial-cells.

Fig. 2. The same in the equatorial view, the points of the primordial-cells run out into mucous filaments.

Fig. 3. Polar view of a *Stephanosphæra* with eight smaller, distantly placed primordial-cells: *a*, envelope-cell; *b*, *b*, primordial-cells.

Fig. 4. The same in the equatorial view; the primordial-cells running out into variously ramified mucous filaments; the two front (interior in the figure) ones exhibit the points from which the cilia arise.

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Fig. 5. Equatorial view as in fig. 4; the primordial-cells are more crowded into one hemisphere of the envelope-cell.

Fig. 6. Polar view; only six primordial-cells exist, but the upper two are twice as large as the others.

Fig. 7. Polar view; the envelope-cell contains only four primordial-cells, the product of the second division having become a "permanent generation."

Fig. 8. Commencement of the formation of macrogonidia; the primordial-cell * is still unaltered; the cell ** exhibits a flow of the contents towards the two ends; the primordial-cell in the middle has divided into two, the rest already into four secondary cells.

Fig. 9. All the eight primordial-cells have divided, in the four secondary cells of the second "transitional generation."

Fig. 10. The division already advanced to the third "permanent generation," so that each primordial-cell has separated in eight wedge-shaped pieces.

Fig. 11. The young *Stephanosphæræ* produced by the division have become more organized, the colourless connected mass of protoplasm in the middle having been gradually constricted and cut off; they already begin to move inside their envelope: at *a*, two are seen in the side view.

Fig. 12. The division completed and the eight young *Stephanosphæræ* rotating in the common envelope.

Fig. 13. A young *Stephanosphæra* just emerged; its cilia are only visible by the eddy they produce in the water.

Fig. 14. A similar one killed by iodine, in the polar view; it exhibits the cilia and the common envelope-cell which is closely applied to the periphery of the primordial-cells.

Fig. 15. A somewhat older *Stephanosphæra*; the envelope-cell still has the form of a flat, tabular spheroid, and therefore appears as an ellipse in the equatorial view.

Fig. 16. Commencement of the formation of microgonidia; the eight primordial-cells dividing in a higher power of two.

Fig. 17. The eight original primordial-cells have been broken up into their microgonidia, which swarm about in the common envelope.

Fig. 18. The same stage as in fig. 17; one primordial-cell, *a*, has taken on the formation of macrogonidia and become developed into a young *Stephanosphæra*, which rolls along among the crowd of microgonidia.

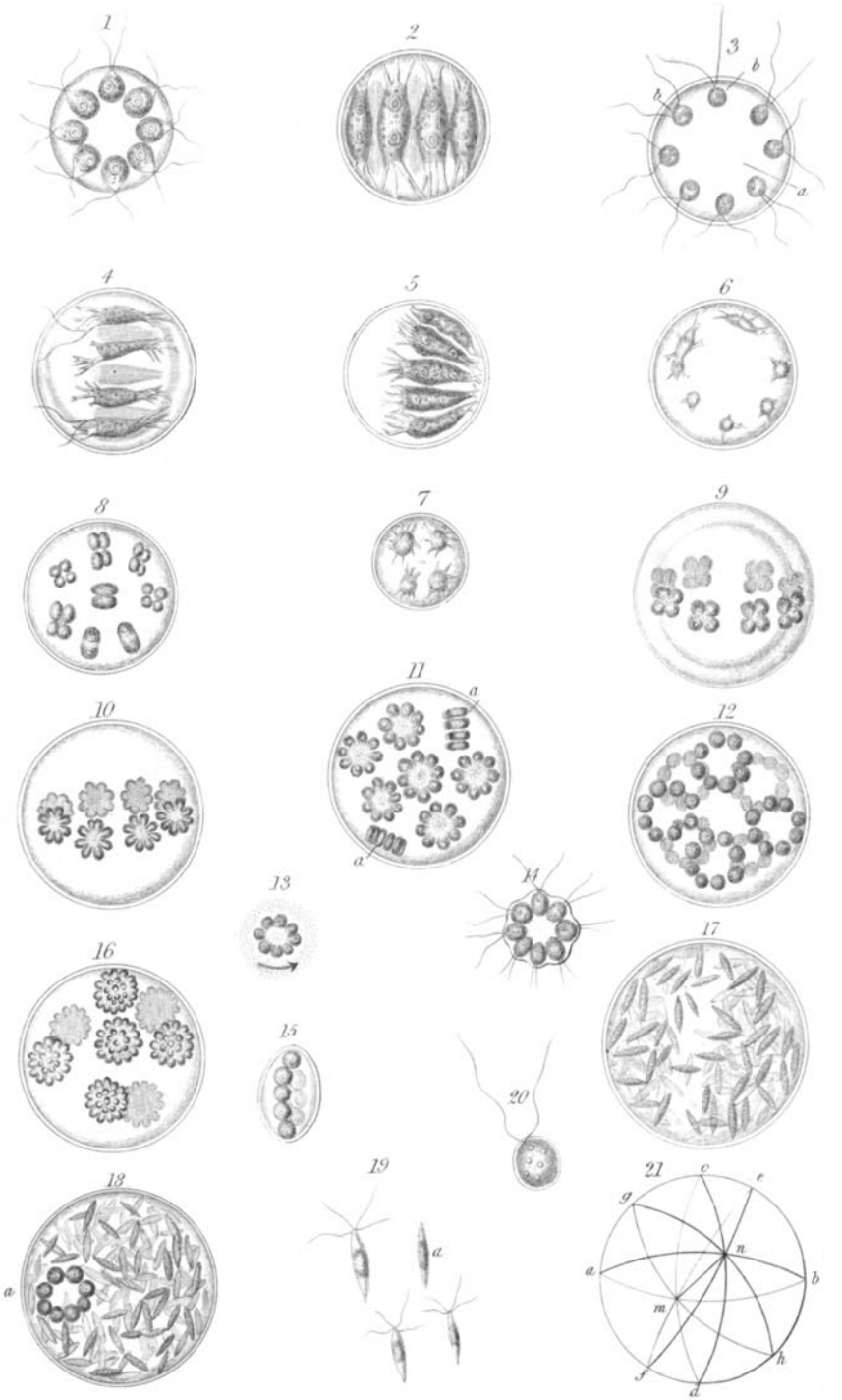
Fig. 19. A few microgonidia after their exit from the envelope-cell: *a*, moving actively in water; the rest killed with iodine and exhibiting four cilia.

Fig. 20. A primordial-cell, which after secreting a special coat in a *Chlamydomonas*-like condition, has emerged from the common envelope-cell to pass subsequently into a state of rest.

Fig. 21. Diagram to illustrate the laws of division in the macrogonidia of *Stephanosphæra*; first the septum *a, m, b, n*, is formed, then the second through *c, m, d, n*,—these two generations are "transitional;" the eight cells produced by the septa *h, m, g, n* and *e, m, f, n*, become a "permanent" generation.

The figures are represented magnified 300 times, except fig. 19, which is 500 times.

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