The movements of diatoms / by Jabez Hogg.

(8)

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The Movements of Diatoms.

By Jabez Hogg, M.R.C.S., F.R.M.S., etc.

THE remarkable movements exhibited by the Diatomaceæ have for a century or more continued to engage the attention of microscopists, and who, failing to offer a satisfactory explanation of the phenomenon, appear to have concealed their ignorance of the subject under a cloud of hypotheses.

In the October number of the "International Journal of Microscopy and Natural Science" the question is placed once more before us by Mr. G. H. Bryan, who ventures to offer a few very judicious remarks on a recently published paper by Mr. J. G. Grenfell, entitled "On Some Species of Diatoms with Pseudopodia,"* and his observations are confined to certain fixed forms of diatoms belonging to the genera *Melosira* and *Cyclotella*, both of which, when examined in the dried state, are seen to be furnished with a series of radiatory processes, perfectly rigid and non-contractile. Now, I entirely concur in Mr. Bryan's view, that these are, in no sense of the word, pseudopodia, neither are they, or can they be, regarded as organs of locomotion, and their discovery—which, by the way, is a very aged one—throws no light whatever

* This paper appears *in extenso* in the "Quarterly Journal of Microscopical Science" for Oct., p. 615, and the title it bears is "On the Occurrence of Pseudopodia in the Diatomaceous Genera, *Melosira* and *Cyclotella*."

on the debateable question, the movements of diatoms. These spinous processes have been described over and over again. Their composition is simple enough :—Organic matter, carbonate of lime, and a slight admixture of a silicated peroxide. They are apparently secreted by the diatom for the purpose of affording a rigid support to the gelatinous or protoplasmatic material outside the framework or skeleton. Very many genera besides *Melosira* and *Cyclotella* are known to possess similar spinous processes, which are stiff, non-retractile, and arranged symmetrically around the valves. The same kind of perfectly rigid spines are also a characteristic formation of many desmids—*Micrasterias*, *Arthrodesmus*, *Epithemia*, *Stephanosiæ*, and *Achnanthidium*. These appendages, however, bear no resemblance to the well-known pseudopodia of the lower Protozoa, and which are most undeniably organs of locomotion and prehension ; granular prolongations of the protoplasm, drawn out into thin threads, all preserving a greater or less degree of cohesion having direct contact with the body substance, and which the animal can at will thrust out and retract.

Mr. Grenfell states that the principal points to notice in the structure of the Melosira pseudopodia are their stiffness and non-retractility to ordinary observation. Why this qualification? He continues :—

"The dried slides show that the great majority of the pseudopodia are arranged fairly symmetrically round the margin of the valves in typical specimens. I counted forty-six as the actual number of radiating ribs on the valve of *Cyclotella*. Hence, there would appear to be a close connection between the number of the pseudopodia and the structure of the diatom, a point of very great importance.

"The pseudopodia vary a good deal in thickness. In this respect they agree with those of *Archerina Boltoni*" (of Lankester). This organism, however, belongs to the Algæ, and is filled with chlorophyll, and we learn from its discoverer "that it is associated with the non-nucleate *Gymnomyxa* (*Homogenea* or *Monera*)," and he further adds :—"I should not be surprised if some naturalists maintain that *Archerina* is a duplex organism, consisting of a moner-like animal Protozoon and a simple Algæ living together in constant association."

Mr. Grenfell, on the contrary, believes that "botanists will agree with him in thinking there is nothing plant-like in *Melosira* and *Cyclotella*."

It, therefore, appears to be unnecessary to prolong the discussion on these appendages or spines, since it will in no way help us in an inquiry into the motile organs of the Diatomaceæ.

At a very early period in the history of the microscope, the movements of Diatoms and Desmids engaged the attention of observers. Possibly the objects themselves attracted and received more attention than any other class of objects simply from their beauty of form and value to microscopists as test objects. Most of them are believed to possess a motile power of some sort in a greater or less degree. Motion is not confined to those species in which the fully-formed frustules have already entered on an independent stage of existence. The same motile power is seen in connection with concatinate forms :—*Synedra*, *Schizonema*, etc.—which move on a fixed extremity—and another species, *Bacillaria* —united in a brotherhood of frustules—which maintain an almost incessant gliding motion, forwards and backwards. There is, in short, a very considerable diversity in the manner and extent of motion manifest in the specified genera, although none possess it in an equal degree to very many of the unicellular desmids, and the more active spores of the Algæ—all of which are endowed with a series of very motile vibratile cilia, arranged at one or both ends, not unfrequently covering the whole of the cell, as seen in the Volvox, a marvellous creation, and truly a wonderful world in miniature.

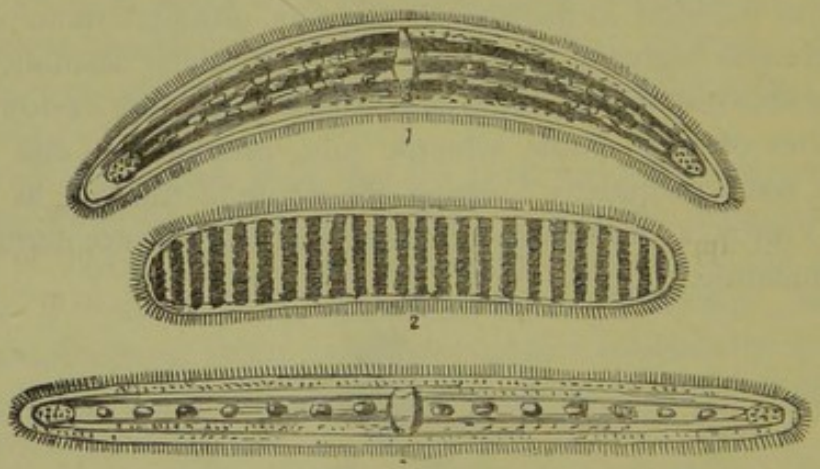
Ciliated Zoospores of an Algæ.

Some few years before Schultze published his observations on the movement of diatoms, the question had already engaged my

attention. During the summer months of 1854, I was in constant communication with the late Rev. Lord F. G. Osborne on the vibratile cilia of Closterium. Each had at the same time observed in

A diagrammatic representation of the "attached tongues of cilia" in *Closterium lunula*, as originally drawn by the late Rev. Lord Sidney Godolphin Osborne, 1854, who believed the cilia were closely associated with the active cyclosis, seen by the aid of direct sunlight, moving in vacuole at either apex of the frond.

Closterium lunula that the whole of the frond appeared to be alive; the active cilia driving the granular matter and the chlorophyll in a continuous stream throughout the length and breadth of the cell. The granular cyclosis at each extremity maintaining an apparently independent rotatory motion. There was, however, no



This diagrammatic drawing is introduced solely with a view of showing the arrangement of the cilia lining the frustule, the outer limiting homogeneous membrane—so generally overlooked from its transparency—having been omitted for the purpose of rendering the ciliary bodies attached to the inner membrane, more palpable.

Fig. 1.—Closterium lunula.
,, 2.—Surirella constricta.
,, 3.—Navicula viridis.

escape of these granular bodies or zoospores.* The ciliary action in *Closterium* more nearly resembling that of the branchial action of the mussel or oyster than that of *Vallisneria* or *Nitella*, the whole frond brilliantly glittering with granular bodies lashed by active cilia. Encouraged by the success which had attended my investigations of desmids, I was led to look for them in the Diatomaceæ. Ehrenberg, having now abandoned his theory of an expanding, snail-like foot projecting from the central opening in *Navicula*, *Surirella*, *Gemma*, etc., announced the discovery of ciliary processes, situated along the lateral openings of the frustule, capable of extension or retraction at intervals. Kutzing, a reliable observer, partially acquiesced in this view. He was of opinion "that the openings or pores in the siliceous valves gave exit to gelatinous substances, analogous with that thrown out during the act of self-division, and which often persists when the act is completed, as observed in *Coeconeis*, *Melosira*, *Cyclotella*, *Fragilaria*, etc."

The process of multiplication by self-division as seen in *Closterium*. Separation takes place through the median line and is here represented as nearly complete.

Professor Smith, in his "Synopsis of Diatomaceæ," remarks upon the appearances described, that the presence of hairs apparently over the whole of the frustule, he has noticed in nearly every instance, but in no case has he detected any motion in such hairs, and he therefore infers that they are a parasitic growth, such as the mycelium infesting decaying Algæ, and he concludes as follows:—"I am inclined to believe that the movements of diatoms are owing to forces operating within the frustule, and are probably connected with the endosmotic and exosmotic action of the cells. The fluids which are concerned in these actions must

* Our joint observations were published in the "Transactions of the R.M.S.," 1855, p. 233, and in the second edition of my book on "The Microscope," p. 411—12, 1855, and subsequent editions.

enter and be emitted through the minute foramina at the extremities of the siliceous valves, and it may readily be conceived that an exceedingly small quantity of water expelled through one opening would be sufficient to produce a movement in bodies of so little specific gravity as that of all the diatoms."

Nägeli and Siebold propounded a modified mechanical or endosmotic and exosmotic theory, and which certainly requires some amount of imagination to render it intelligible, while it would be better expressed by the adoption of the chemical term, diffusion, and by means of which our atmosphere is maintained in a uniform and salubrious condition for the support of life on the earth's surface. By the action of light the diatom is enabled to separate the oxygen and give off carbonic-acid gas, an action which may impart sufficient force to produce movement in the spindle-shaped or ellipsoidal cell. It does not, however, touch the fringe of the process whereby the *Gomphonema* or the *Schizonema* eject their young fully-formed fronds through a very narrow opening at the top of a non-elastic, gelatinous sac. The young frustule, so far as I can determine, derives no assistance or motive power from the flaccid walls of the parent sac; but on nearing the opening it gains its freedom by a steady, jerky series of well-directed efforts, and at length swims off with vigorous action. One word as to the stipulate processes of these and cognate species. These are clearly emanations from the frustules, and not the frustules from the stipes, as described by some observers. In very fresh specimens, *Cocconema* were seen in different stages of growth. A brood of younger, mixed in with more fully-formed frustules, enclosed in the normal, parental, gelatinous sac, were furnished with extremely delicate stipes, and although detached from the cluster they exhibited no motion whatever. These bodies require very careful illumination for their detection, but the free condition of young and old alike confirm my view that the formation of the stipe proceeds concurrently with that of the siliceous skeleton. The spinous processes of other genera, we may surmise, indeed are sometimes seen to start from a minute nodule; and here the staining process, the borax carmine, or some aniline dye, materially assists our observations, and with the 1–12th or 1–16th immersion any remaining doubt will be dispelled.

It is quite clear that neither the mechanical nor the chemical hypothesis of the movements of diatoms affords a tangible explanation of the interesting motile power whereby *Bacillaria paradoxa* pursues its uniform action, and of which nothing approaching to a satisfactory explanation has been offered. This organism, when first placed under the microscope, is seen as a united band—50 or 100 in number—of transparent frustules, without any apparent motion of any kind. But in a short time the bright illumination and slight heat communicated to the mass soon sets it in motion. First one frustule, then another, slowly glides forward, until the mass is converted into a continuous chain, extending over the whole field of the microscope. When it has attained to the end of its tether, it then commences a retrograde movement, and the several frustules resume their allotted place with as much regularity and order as a well-drilled regiment of soldiers. In the next half-minute the same process of extension is gone through, and this continues to recur so long as the specimen is kept under observation. The force exerted by each individual frond must be considerable, as it will thrust aside any larger obstacle that may lie in its way with perfect ease and without changing its course. The aggregate band is enclosed when first seen in a gelatinous sac, and this plasmic, homogeneous envelope is so very transparent and colourless that it is only defined under high powers of the microscope, or by careful staining. This wonderful movement of the *Bacillaria* is undoubtedly a vital one, which no mechanical or chemical theory affords a conception of; it altogether differs from that well-known gliding, rolling movement of the amœba. The movement of one segment upon another, however, is not exclusively confined to the *Bacillaria;* it is exhibited by some other genera, but in a less degree. *Fragilaria*, *Grammatophora*, *Diatoma*, etc., have a link-like connection, the alternate or opposite angle of each frustule being united by a narrow isthmus or band. Other deviations have been observed, and which seems to me to leave the question of motile power in diatoms involved in very considerable doubt and difficulty.

The movement by cilia, arranged along either the sutural opening or at the extremity of the frustule, has, as I have endeavoured to show, not been disproved, and it will not be

denied that even a limited ciliary action carries with it a far more reasonable explanation than that of any other hypothesis set forth, even under the sanction of so eminent an authority as Professor Smith was admitted to be, but who pinned his faith to the "highest powers" of his day, but which are no longer so, and have been indeed entirely superseded by the homogeneous immersion objective with its high-angled aperture, and consequently far greater resolving power.

The years 1882—83 found me once more deeply interested in the movements of diatoms, and the outcome of my further observations were embodied in a paper which I communicated to the Belgian Microscopical Society, and which subsequently appeared in the "Transactions of the Society," 1883. At this period I was fortunately tolerably well supplied with *Navicula*, *Pleurosigma*, *Pinnularia*, and other spindle-shaped genera, and which on all occasions exhibited very active movements. The former were seen to force a passage through masses of mineral matters lying in their course; and with a jerky effort, directed again and again, ultimately removing it or forcing a way through the obstacle. On adding a particle of colouring matter to the cell-contents, the diatom arrested the minute granules as they approached. The same occurred when a minuter body approached, as *Palmoglæa*, and it was rapidly trundled, as it were, along the sutural opening in a longitudinal direction, and in the contrary direction to that in which the diatom was moving. Again, two frustules of equal size, in attempting to cross each other's path when the action was decidedly of an intermediary or restraining character, and on suddenly relinquishing their apparent hold of each other they separated with a bound. The movements I was a witness of in no way deserved Professor Smith's description—that of a "languid roll." *Pinnularia* were very numerous and active in my gatherings. Each frustule was furnished with two colourless contractile vesicles, placed on either side of the median nodule; these appeared to me to be reflexed inwardly upon their outer margins. The intermediary space of the frustules were filled with granular matter and a rich yellowish-brown endochrome. Nägeli states that the colourless vesicles referred to contain a nucleus and a nucleolus. Schleiden is of opinion that the nucleus is primarily

concerned in the original formation of the cell as well as in its subsequent self-division and multiplication. I dwell upon this because, on staining the frustules, I believe that at this point I detected the protrusion of a colourless, contractile protoplasm, which, on careful examination, appeared to partake either of the whip, flagellum, or pseudopodial character. But I am free to confess that my later examinations of these frustules have not enabled me to finally confirm and settle observations made ten years ago, although I have resorted to the various staining processes quite recently referred to in Mr. Grenfell's paper.

It appears to me that the long-debated question of the movements of diatoms is in a fair way to be solved. It would be strange indeed if it were not so, as the doubt which existed about the motile organ of a far more difficult body (the *bacterium termo*) has long since been removed. Its active flagellum has not only been seen by a small body of indefatigable workers at the microscope, but it has been photographed; and it seems to me to require no prophetic power to foresee that we are on the very threshold of discovering the motile organ or organs of that most charming class of objects, the Diatomaceæ.