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The Classification of Diatoms (Bacillariaceæ)

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THE CLASSIFICATION OF DIATOMS (BACILLARIACEÆ).[1]

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There have been many systems of classification employed for the *Bacillariaceæ*, but very few of these have any valid claim, to be regarded as natural systems. They may be divided into three classes; (1) those based on the structure of the valves, of which Kuetzing's, Prof. H. L. Smith's, and that employed by Kirchner are examples; (2) those based on the form of the frond, the connecting membrane, and the gelatinous envelope, represented by Rev. Wm. Smith's; and (3) those based on the structure of the endochrome and the manner of forming auxospores, represented by that of Paul Petit. The following is a brief outline of the systems mentioned.

Kirchner divided the *Bacillariaceæ* into two groups[2] those whose markings are bilateral, that is, arranged on two sides of a longitudinal line or raphe, and[3] those with radial markings.

[1] Read before the Botanical Seminar of the University of Nebraska, March 21. 1896.

[2] Kryptogamen-Flora von Schlesien; Algen, 171. Breslau, 1878.

[3] Species Algarum, 1. Leipsic, 1849.

Those with bilateral markings he divided into two subdivisions the first comprising those with a central nodule, and the second those with none.

Kuetzing divided the *Bacillariaceæ* into three tribes; I, *Striatæ*, that is those with transverse striations; II, *Vittatæ*, that is those with longitudinal stripes; and III, *Areolatæ*, that is those whose surfaces are divided into angular areolæ. The first two tribes, *Striatæ* and *Vittatæ* he divided into two orders each, viz.; I, *Astomaticæ* and II, *Stomaticæ*. The *Astomaticæ* included those with no central nodule, or as he understood it, with no central opening, while the *Stomaticæ* included those with a central nodule. If the central nodule were really a stoma or aperture as Kuetzing considered it, this grouping might have been a natural one; for this difference in structure might have connoted important physiological differences, but it is generally conceded that the nodules are merely markings on the valves, and it is likely that they indicate nothing as to the physiology of the plant. So no higher groups than genera, or possibly species, can be based on this character. His third tribe, *Areolatæ*, he also divided into two orders; I, *Disciformæ* that is, those of a circular or angular form, and, II, *Appendiculatæ*, or forms with appendages, as *Biddulphia*.

The classification of Prof. H. L. Smith[4] is one that has had considerable following. Bessey's Botany[5] was the first American textbook to adopt and give an outline of the system. It was adopted by Van Heurck[6], Wolle[7] and De Toni[8]. To say the least, it is a good practical system of classification, and probably this is the most that can be said for it, though in some points it seems to approach a natural system. Smith divides the Diatoms into three tribes, the *Raphideæ*, *Pseudoraphideæ*, and *Cryptoraphideæ*. The *Raphideæ* are all supposed to possess a raphe. The *Pseudoraphideæ* are usually elongated, have no raphe, but in its place there is a blank space resembling a

[4] Conspectus of the Families and Genera of the Diatomaceæ in *The Lens*, I: 1 1872 and II: 65, 1873.

[5] Botany for High Schools and Colleges, Henry Holt and Co., New York, 1880,

[6] Synopsis des Diatomées de Belgique, 1885.

[7] Diatomaceæ of North America, 1890.

[8] Sylloge Algarum, 1891.

raphe. The *Cryptoraphideæ* are usually circular or angular and have nothing resembling a raphe. Upon the supposition that the raphe is an essential organ, and that it is present in one tribe, replaced by another structure in the second, and "hidden" in the third, this might be a natural classification. But if the raphe is known to exist only in the first tribe and its existence in the others is wholly theoretical, it will hardly serve as a character on which to base a classification. It is true that the genera brought together by this system appear to bear more or less relation to each other, but if we knew as little about Phanerogams as we do about Diatoms, we should think that a division of them into *Arboræ, Frutices,* and *Herbæ* placed related genera together, for it would be easy to see that *Salix* and *Populus* are related, and also that *Solanum* and *Physalis* are more or less closely allied. I venture to regard the *Raphideæ, Pseudoraphideæ,* and *Cryptoraphideæ* as having no greater naturalness than the divisions *Arboræ, Frutices,* and *Herbæ;* and it is to be hoped that they will soon be consigned to the same botanical limbo in which the latter have long since found obscurity.

It is true, however, that in the *Raphideæ,* there seems to be a trace of naturalness in the system. The author begins with the bilaterally symmetrical forms, that is those in which the raphe is a median line, as for example, *Navicula.* Those with the raphe at one side of the center, as in *Cymbella,* he considers a modification of the first type by a curving of the frustule and thus bringing the raphe nearer the concave side. And in the third division the raphe has approached so near to the concave margin that it fuses with it, as in *Amphora.* If this is to be considered simply as a modification of a typical form, it means little. But if this modification shows the course of development from the *Navicula* form to the *Amphora* form, it means a great deal. In *Navicula* and *Cymbella* two auxospores are formed from two mother cells without conjugation, and in *Amphora* two auxospores are formed from two mother cells by conjugation. It is probable that the method of reproduction found in the derived form is a development from that found in the primitive form. If then the *Amphora* form has developed from the *Navicula* form, there is reason to believe that the formation of auxospores without conjugation is the primitive method, although Murray[9] holds that the formation of auxospores by conjugation is probably the original method, and that their formation without conjugation is the derived method.

Wm. Smith[10] divided the Diatoms into two tribes in the first of which the frustules are free, and in the second imbedded in a gelatinous envelope. Under the first tribe he makes five subtribes, depending upon the form of the connecting membrane and the relation of the frustules to each other. The second tribe he divided into four subtribes based on the form of the fronds. This arrangement seems not only extremely artificial but also very impractical. Nothing about Diatoms is more variable than the form of the fronds; and where it is at all constant, such a system places closely related genera far apart; for example, *Cymbella* and *Encyonema*, *Nitzschia* and *Homœocladia* are placed in separate tribes, while in structure they are very similar, the main difference being that in *Encyonema* and *Homœocladia* the frustules are arranged in rows, while in *Cymbella* they are free or stipitate and in *Nitzschia* they are free. This method of classifying Diatoms may be likened to a separation of Grasses into those forming a dense sod and those not forming a sod; or of Dicotyledons into those exuding a resinous fluid and those that do not. Wm. Smith places *Gomphonema* in his first tribe, that is, the one having no gelatinous envelope; but some species of *Gomphonema* are stipitate while others are enclosed in an amorphous mass of jelly. The latter species would have to be placed in his second tribe, thus dividing the genus. It would lead to even greater difficulty than this, for the same species is sometimes stipitate and sometimes imbedded in a gelatinous envelope.

Of all existing systems that of Paul Petit[11] seems to approach

[9] An Introduction to the Study of Seaweeds, p. 195, 1895.

[10] For a synopsis of Smith's classification see Pritchard's History of the Infusoria, 101, fourth edition, 1861.

[11] Liste des Diatomées et des Desmidées observées dans les Environs de Paris precedée d'un essai de classification des Diatomées. Bull. Soc. Bot. France, tom. XXIII–XXIV, Paris, 1877.

An Essay on the Classification of the Diatomaceæ translated by F. Kitton, Monthly Microscopical Journal and Transactions of the Royal Microscopical Society, XVIII, 1877, pp. 10, 65.

Pfitzer, Die Bacillariaceen, in Schenk's Handbuch der Botanik, Breslau, 1882.

most nearly to a natural one because it is based on characters having physiological significance. It is based primarily on the structure of the endochrome, and secondarily on the method of forming auxospores and the general shape of the frustules. Van Heurck does not employ this system in his *Synopsis* because of the large number of fossil specimens and those from deep-sea soundings to which it could not be applied. But this is not a valid objection, for all the genera are represented by modern species, and these are sufficient for a basis of classifications, and since the specific characters are based mainly on the structure of the valves, there will be no trouble with the fossil forms. The following synopsis of Petit's system includes the higher divisions only.

I. *Bacillariaceæ coccochromaticæ.*

With numerous endochrome granules.

A. Frustules concentrically constructed. One mother cell forming asexually a single auxospore. *Melosireæ*, etc.

B. Frustules bilateral, one or two mother cells forming two auxospores, as far as known asexually. *Fragilarieæ*, etc.

II. *Bacillariaceæ placochromaticæ.*

With one or two large endochrome plates.

A. One endochrome plate lying against the convex valve; one mother cell forming one auxospore asexually. *Cocconeideæ.*

B. A single endochrome plate extending diagonally across the cell cavity, or lying next the girdle. Two auxospores formed from two mother cells, with or without conjugation. *Nitzschieæ. Amphoreæ, Cymbelleæ*, etc.

C. Two endochrome plates lying next the two valves. Two mother cells forming two auxospores by conjugation. *Eunotieæ, Synedrieæ, Surirayeæ.*

D. Two endochrome plates lying next the two girdle bands; two mother cells forming two auxospores without conjugation. *Amphipleureæ, Naviculeæ*, etc.

Although Petit's system is by no means perfect, it is at least a step in the right direction. He bases it upon characters that have some physiological significance, while the other systems are wholly or in greater part based on merely accidental characters. A clue to the genetic relationships of Diatoms, as of other plants, will be most certainly found in their method of reproduction. The shape of the frustules, or their markings, will serve for specific, or in some cases for generic characters, but they have no significance that will warrant their use in the erection of higher groups. Absolute shape and size will not serve as definite characters, for a single species between one auxospore stage and the next varies greatly in both these respects. Owing to the peculiar mode of cell division in which each new valve is formed inside the old one, each new frustule is smaller than the parent, hence the size gradually decreases until an auxospore is formed. Schumann[12], out of 470 species found ten in which the length of the largest was five times that of the smallest; twenty-nine in which the largest were from three to four times as long as the smallest, and the rest showing less variation. The variation in form is even as great as the variation in size. This is probably due to the difference in the thickness of the girdle, *i. e.* the part of the valves that overlaps, in different parts of the frustule. *Navicula iridis* Ehr. is a good example of a variable species. Its different forms have been described as species by most writers. In the typical form the valves are elliptical with gracefully curved margins. The first variation from this type has apices cuneate, and a still further deviation shows them acuminate-cuneate; and from this it varies to rostrate or capitate; and a diminution in size goes step by step with this change in form. These forms are represented by *Navicula iridis* Ehr., *N. amphigomphus* Ehr., *N. affinis* Ehr., *N. amphirhynchus* Ehr., and *N. producta* W. Sm. If the overlapping portions of the valves are slightly thicker near the ends than elsewhere, this variation would be the necessary result, for each new valve formed inside an old one would be slightly constricted opposite this thickened place, at first changing the rounded ends to cuneate, and as the narrowing pro-

[12] Pfitzer, l. c., p. 441.

ceeded still further, the cuneate form would become rostrate and a still further narrowing would give a capitate form. So form and size, although they have a certain significance, are not to be considered infallible characters.

The geological records throw no light upon the relationship of the *Bacillariaceæ*, for when this family first appeared, we find the same genera, and largely the same species as in our modern ones. This is probably due to the fact that their ancestors lacked the siliceous covering, and hence were not preserved. Diatoms evolved the same as all other plants until they developed their shells, but these put a stop to their further evolution, at least they show no trace of evolution since their first appearance. So the question arises whether the Diatoms represent the ends of several closely related genetic lines the further development of which was stopped by their siliceous shells, or whether we may trace the development of one form from another. The former supposition is the more probable, for the form of the earliest fossil specimens is identical with that of modern specimens of the same species; and the same genera are found among fossil as among modern Diatoms. If one genus of Diatoms developed from another, we ought to find the more primitive forms in the earlier strata, for there is little chance that their remains would not be preserved had they existed. But instead of this, Diatoms of all forms appear almost simultaneously. We may conclude then that the *Bacillariaceæ* represent the silicified ends of several closely allied genetic lines and that they have not changed in form since they acquired their siliceous covering. The structure of the valves it follows will tell us practically nothing of their relationship.

There are five methods by which auxospores are formed[13]. In the first the protoplasm of one frustule simply escapes from the valves, grows to a certain size, and then invests itself with new valves. In the second, two auxospores, instead of one, are formed in the same way by the dividing of the protoplasm of a single plant. In the third, the protoplasm of two Diatoms unites to form an auxospore. In the fourth, the protoplasm of

[13] Murray, l. c.

two Diatoms emerges from the valves, and placed by side, but without conjugation, forms each an auxospore. In the fifth, two Diatoms divide transversely and the two halves of each conjugate, each half with the corresponding half of the other and thus form two auxospores. Before any truly natural classification can be made the significance of these various modes of producing auxospores must be understood. Whether the sexual or the asexual method is the primitive one must be known, or whether the different methods are so many expedients to overcome the difficulties imposed upon these plants by their siliceous shells. At present our knowledge of the structure and physiology of Diatoms is not sufficient to enable us to construct a perfectly natural system of classification, and until something better is proposed, Petit's may well be adopted, for although it is not wholly natural, it is more so than any which has preceded it.