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The Contribution of de Bary to Our Knowledge of Myxomycetes

By G. W. MARTIN

The slime molds have been known scientifically for over two centuries. Even before Micheli's time, there is record of references to *Fuligo*, and in 1729 Micheli published recognizable descriptions and illustrations of several genera and species. Other pre-Linnean botanists studied the group, but it was not until Linnaeus had stimulated interest in things botanical (although, as is well known, he added nothing to our knowledge of the fungi and slime molds) that extensive study was devoted to the group. The work of Batsch, Bulliard, Schrader, Schweinitz and some of their contemporaries gave us a taxonomic basis for the species, while that of Persoon and Fries, especially the latter, established many of the genera essentially as they are understood today. By all of these students, with the possible exception of Fries, the slime molds were accepted as Gasteromycetes without question. This is not surprising when one considers that they were rarely examined with anything more powerful than a hand lens. The peridium, the powdery mass of spores, the form and structure of the capillitium when present,—all are strikingly suggestive of a puff-ball, and that they were related to the puff-balls was the obvious conclusion. True, the plasmodium had been observed and illustrated by Micheli, and Fries, at least, had personal experience of the difference between its behavior and that of the mycelium of the higher fungi. He relates with gusto an account of how he had placed a plasmodium of *Diachea elegans* in his hat, to find that in less than an hour it had covered the entire inside with its white net-work. Fries expressed his sense of the importance of the plasmodium by segregating the slime molds from the other forms he included in the Gasteromycetes on the basis of this one character. But even Fries retained them in the Gasteromycetes and there they remained until de Bary studied them.

De Bary's published work covers such an astonishing range of subject matter that it is not surprising that the part of it devoted to the slime molds should seem to form a comparatively insignificant proportion of his total achievement. The list of his contributions as cited by Jost includes 106 items. Of these, the titles of only six mention the slime molds, and incidental references to the group are not numerous in his other writings. He published, in all, three major contributions to the morphology and life history of the slime molds, one critical and largely polemical paper, and two general summaries

of the group, one in the *Morphologie* of 1866, the second in the *Vergleichende Morphologie* of 1884. All except the last belong in the earlier period of his activity. Nevertheless, from the standpoint of the special student of the slime molds, de Bary's contributions must always remain of the highest significance. As he justly states in his 1858 paper, up to that time there had been no important addition to the knowledge of the slime molds as summarized by Fries in the *Systema mycologicum* of 1829. Between 1858 and 1864 de Bary's investigations removed the group once for all from its position among the Gasteromycetes and established it as an autonomous group of organisms certainly far removed from the higher fungi, whatever may be the final decision as to his particular views concerning its true taxonomic position.

The first indication of his interest in the group appears as a brief reference in *Flora* in 1854 (Vol. 37, n.s. 12, p. 648), in a report of the meeting of the German Naturalists Society, where he is mentioned as describing the manner of germination of the spores of *Trichia rubiformis* (i.e., *Hemitrichia vesparium*), in connection with an account of the germination of the spores of certain smuts and their subsequent development. He was then twenty-three years old, and had already published ten papers on subjects ranging from mycology and plant pathology to the morphology of flowering plants, thus early demonstrating his wide range of interests. His germination experiments must have started him to thinking about the slime molds, for in 1858 there appeared in the *Botanisches Zeitung* a masterly account of a series of observations and studies on the life history of the slime molds, with special reference to *Fuligo septica* and *Lycogala epidendrum*, but including critical discussion of a number of other representative forms. In this paper he definitely states his conclusion that the slime molds are to be regarded as animals, allied with the rhizopods, and proposes for them the name Mycetozoa. The paper was at once recognized as of fundamental significance. It was translated into French by L. R. Tulasne and appeared in 1859 in translation in the botanical series of the *Annales des Science Naturelles*; unusual recognition for a young man of twenty-seven! It was only four years later, however, that he was to come before the French scientific public in an even more conspicuous manner, by the publication in the same journal of his prize-winning paper tracing the life histories of downy mildews and rusts.

The same year, 1859, in which the translation appeared, he published in the *Zeitschrift für wissenschaftliche Zoologie* a complete account of his researches on the slime molds, submitting it to a zoological journal in order to emphasize his opinion as to the animal nature of these organisms. Besides greatly amplifying what had been presented in his earlier paper, he included critical and detailed dis-

cussions of the mature fructifications of representatives of nearly all the significant genera, as well as accounts of their development. This paper, commonly regarded as the first edition of his monograph on the Mycetozoa, aroused wide discussion and a certain amount of opposition. It was in order to meet the criticisms of his opponents that he published in *Flora* in 1862 an answer to the objections raised, amplifying certain of his observations and re-stating his position. In 1864 he published his book, *Die Mycetozoen*. This is often regarded as merely a second edition of his 1859 work, and is so listed in some of the bibliographies—indeed, de Bary himself so refers to it—but it was so extensively revised and amplified as to be in effect a new work. Cienkowski's studies, themselves stimulated by de Bary's work, had been published in 1863, confirming his conclusions and filling in gaps in the developmental history of the plasmodium. These results, and a number of new observations are incorporated in this book, which may be regarded as the culmination of his studies on the slime molds. He takes up in logical order the structure of the mature fructifications of the important genera, arranged in a new taxonomic sequence; the structure and behavior of the plasmodium; the process by which the latter develops into a fructification; the structure of the spores, their germination and subsequent development; the various resting stages; the relationships of the Mycetozoa, as a group, with other organisms. In the *Morphologie* of 1866 and the *Vergleichende Morphologie* of 1884 he added few original observations, but contented himself with the incorporation of the contributions of others, accompanied by critical remarks, often brief, but pungent. Aside, then, from their service in summarizing the knowledge of the slime molds and thus stimulating the study of the group, these later works are less significant than the earlier ones. It need not be supposed that he did not study them critically after 1864. Rostafinski's reference to de Bary's manuscript, both in the *Versuch* (1873) and in his monograph (1875), makes it evident that de Bary possessed unpublished data which he put at Rostafinski's disposal. But de Bary's fundamental contributions to the knowledge of the slime molds must be sought in the four papers appearing from 1858 to 1864. These contributions may be summarized under two main heads: first, his pioneer work on the morphology and life history of the group; second, the effect of his studies on taxonomic treatment.

To one brought up in the tradition of the microtome and the stained slide it is always illuminating to note the critical and detailed observations made by the older students on living material, or on temporary mounts treated with the simplest reagents. It calls to mind Buller's significant comment made as recently as 1922, "if the microtome had never been invented, the progress in our knowledge of the general organization of the hymenium of the Hymenomycetes would have been much greater by now than it actually is." Using

these simple methods, which, however, represented the most advanced techniques of his time, and applying them with unprecedented skill and accuracy of interpretation, de Bary described the sporangia of typical species of many genera with an accuracy and fullness of detail never before approached. He traced, step by step, the massing together of the strands of a plasmodium to form an aethalium, the progressive differentiation of the original homogeneous material into peridium, hypothallus and sporiferous region and, in the last, the final delimitation of spores and capillitium. He showed that the development of forms fruiting as separate sporangia or plasmodiocarps is merely a variation of the same process. Working from the other end of the life cycle, he showed that the spores of all species germinate in essentially the same manner, giving rise to one or sometimes two swarm-cells, that these divide repeatedly and finally fuse, forming first amoebae, then gradually enlarging into small amoeboid bodies which are essentially small plasmodia. This general sequence has never since been open to question. Later students working on this phase of the subject have contented themselves largely with amplifying de Bary's account and with supplying cytological details of the life cycle by the use of methods not known when de Bary worked on the group.

With the taxonomy of the slime molds in a more specialized sense, de Bary seems not to have been greatly concerned. He was, however, intensely interested in the broader questions of relationship, both within the group and between the slime molds and other organisms. In his first paper he very positively states his conviction that the slime molds are animals, renaming them Mycetozoa as more in harmony with their true nature than the old term Myxomycetes. And, as mentioned, the first of his longer studies was published in a zoological journal. But even in these two papers he recognizes that the traditional conception of all living things as either animals or plants loses much of its validity when primitive organisms such as these are considered. In his 1859 paper the subtitle refers to the Mycetozoa as included among "der niedersten Thiere." In 1864 the subtitle reads "der niedersten Organismen." The change is significant. By 1864 he had become much less emphatic and specifically states that the matter is of slight significance. In 1866 he was willing to include them with the Fungi in a work of general scope, in 1884 adding the bacteria, and while he makes it plain that he is not suggesting relationship, he is obviously recognizing traditional association. He could scarcely have done this had he felt that the slime molds were definitely animals. In our day, when such suggestive connections between the lower fungi and various animal-like forms are coming to light it is interesting, but perhaps unprofitable, to speculate to what conclusions a de Bary might arrive concerning the phylogeny and relationships, not only of the slime molds, but of the fungi

in general. It is safe to say that his views would not be the mere dogmatic and uncritical repetition of traditional beliefs so often seen in the textbooks and treatises of this day, as of his.

De Bary's sequence of genera illustrates well his willingness to leave conventional paths when he felt sure of his ground. He departs widely from Fries's classic treatment, and his families and the order of the genera are in substantial agreement with those adopted by later students until very recently. Rostafinski, working in de Bary's laboratory, did propose some radical changes in the order of the genera in his *Versuch* of 1873, but in the Monograph of 1875 he reverts to de Bary's scheme, and this general arrangement has been maintained in the standard works of the Listers, Macbride, and Hagelstein which are in wide use today. Other taxonomic schemes have been proposed from time to time and it is probable that some changes will be generally agreed upon. After all, few taxonomic arrangements have persisted for a longer time. The problem of the relationship, if any, between the slime molds, the Acrasieae, the Labyrinthulales and similar groups de Bary left unsolved, and in that condition it still remains.

One suggestion made by de Bary is interesting in the light of more recent work. In his 1859 paper, he suggested that perhaps many of the amoebae commonly found in water and in damp plant detritus may be merely stages in the life cycle of some of the Mycetozoa. This is put forward merely as hypothesis—de Bary is always clear-cut in his distinction between hypothesis and verifiable fact—but it is suggestive as illustrating the play of his mind upon his subject matter. Later he recognized that his original statement was too broad, but insisted that some of the amoebae occurring in such situations are more than likely myxamoebae. I cite this merely to illustrate the point that for any modern worker in mycology or related fields, a careful study of de Bary's writings is sure not only to give an indispensable historical background, but also to be a rich source of suggestion and stimulus.

In the short space of six years, busily occupied at the same time with other important problems, and working in laboratory quarters which would now be regarded as utterly inadequate, de Bary laid the foundation for a modern approach to the slime molds. His accomplishment is marked by what he left undone as well as by what he did. Recognizing that the taxonomic treatment of the group as Fries left it was adequate for his immediate purposes, he devoted himself to fundamental studies on development, and to the correlation of the phenomena he discovered with the morphological structures that must always be the basis of taxonomic treatment. By so doing, he cleared the way for a sounder taxonomy which would add a consideration of significant microscopical characteristics to the more obvious

morphological features used by the older systematists, and would interpret the latter in the clearer light of a knowledge of the peculiar developmental history of the forms.

In the field of letters, a work tends to be regarded as a classic insofar as its appeal is permanent and universal rather than ephemeral and local. In this sense, few scientific works become classics, and when they do it is as likely to be on account of their literary as of their scientific qualities. Among themselves, scientists use the term in a more circumscribed sense. If a work is complete within its self-imposed limits; if the facts which it presents, whether old or new, are accurately stated and subjected to critical analysis; most important of all, if it is the medium through which new ideas are presented, it deserves to be called a scientific classic. De Bary's studies on the slime molds, especially those of 1859 and 1864, unquestionably conform to these standards.

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