English translation of Heinrich Anton de Bary's 1878 speech, 'Die Erscheinung der Symbiose' ('De la symbiose')

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English translation of Heinrich Anton de Bary's 1878 speech, '*Die Erscheinung der Symbiose*' ('*De la symbiose*')

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Abstract *Die Erscheinung der Symbiose*, meaning "the phenomenon of symbiosis" in English or "*de la symbiose*" in French, is a transcription of the 1878 lecture by the German botanist and mycologist Heinrich Anton de Bary in which he first used the term 'symbiosis' in a biological context. De Bary's speech was published in 1879 in German, later to be translated into French; though only fragments of his speech are available in English. Translating de Bary's lecture is timely because the field of symbiosis, especially with respect to microorganisms, is expanding and the importance of symbiosis is now recognized across the biological sciences. Researchers have now begun to sort through the early literature to uncover original thoughts pertaining to symbiotic interactions. We believe that having de Bary's lecture accessible to researchers in English will help enhance interest in the history of symbioses, document de Bary's pioneering contribution, and aid in establishing an understanding for whom the lecture was intended and when biological symbioses were first recognized. We present a short biography of Heinrich Anton de Bary, a full translation of his lecture, and conclude by briefly highlighting current endeavors in symbiosis research.

Keywords Symbiosis · *De la symbiose* · *Die Erscheinung der Symbiose* · Heinrich Anton de Bary

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1 Introduction

Heinrich Anton de Bary (Fig. 1), addressed by students and colleagues as Professor Anton de Bary or "The Professor", was born on 26 January 1831 in Frankfurt, Germany to August Theodor de Bary, a physician with a keen interest in botany, and Emilie von Meyer (Ahmadjian and Paracer 1986). In de Bary's early years, his father insisted he become a physician, and, in doing so, sent him to study medicine at Heidelberg University, Germany, and he later transferred to the University of Marburg, Germany (Horsfall and Wilhelm 1982). While in medical school, de Bary researched smut and rust diseases associated with cereals (field crops), which at the age of 22 led him to publish a book titled, *Untersuchungen über die Brandpilze und die durch sie verursachten Krankheiten der Pflanzen mit Rücksicht auf das Getreide und andere Nutzpflanzen* (de Bary 1853; English translation: *Studies on the smut fungi and the causes of plant diseases with respect to grain and other crops*). In his book, de Bary sought, and succeeded, to disprove the dogma of spontaneous generation. In that same year, de Bary received his medical degree with his dissertation titled, *De plantarum generatione sexuali* (English translation: *The sexual generation of plants*).

Following medical school, de Bary practiced medicine briefly until deciding to make botany his primary subject (Horsfall and Wilhelm 1982). Soon after, de Bary became an adjunct lecturer (or 'Privatdozent' in German) at the University of Tübingen Germany, where he assisted Hugo von Mohl, the German botanist and member of the Royal Society who coined the term 'protoplasm,' or the living content of a cell encompassed by the plasma membrane. At 24, de Bary succeeded Carl Nägeli, the Swiss botanist and chair of Botany at the University of Freiburg (Germany) who, perhaps, was most remembered for discouraging Gregor Mendel from continuing to investigate inheritance in plants (Sparrow 1978; Horsfall and Wilhelm 1982).

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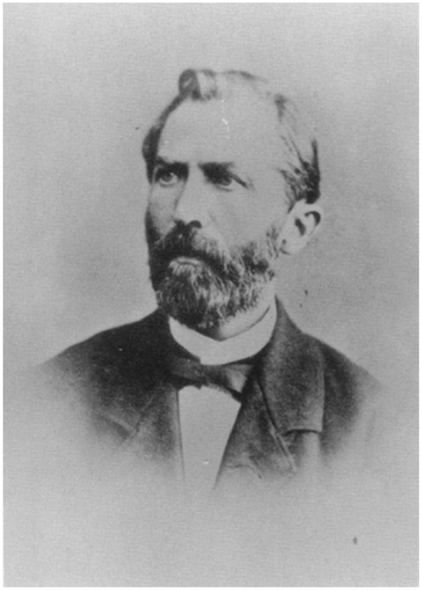

Fig. 1 Professor Heinrich Anton de Bary (originally in Sparrow (1978))

In 1867, de Bary and his wife Antonie de Bary (previously Antonie Einert) moved to Halle (Germany) to work at the University (currently, The Martin Luther University of Halle-Wittenberg), and subsequently replaced Diederich Franz Leonhard von Schlechtendal, the German botanist who co-founded *Botanische Zeitung*, a botany-centered academic research journal. Fittingly, de Bary later became a co-editor and then editor-in-chief of *Botanische Zeitung* (Sparrow 1978; Horsfall and Wilhelm 1982). After leaving University of Halle, de Bary moved to the University of Strasbourg (France) to continue his studies, which were, in fact, viewed as his most productive years (Sparrow 1978; Horsfall and Wilhelm 1982). Over the course of 33 years as a professor (1855 to 1888), de Bary trained more than 100 students who came from all corners of the globe to study in his laboratory (Fig. 2). In fact, de Bary viewed mentoring students to be one of his most important responsibilities, and persistently encouraged them to be self-reliant, to think critically, and to overcome difficulties and errors. Many of his students went on to become distinguished scientists and educators (Ahmadjian and Paracer 1986).

Aside from mentoring students, de Bary authored more than 100 publications on fungi and plant diseases: those on the parasitic oomycete, *Phytophthora infestans,* that infects potatoes, the fungal pathogen of wheat and other grains, *Puccinia graminis*, as well as studies of lichens. On 19 January 1888, de Bary passed away in Strasbourg, France, at the age 57 of cancer of the mouth (Balfour 1889; Horsfall and Wilhelm 1982), and at the time of his death was one of the most influential biologists in Europe (Sparrow 1978; Horsfall and Wilhelm 1982; Ahmadjian and Paracer 1986).

Over the course of a career lasting nearly 40 years, de Bary was very productive, not only writing more than 100 publications, but also completing several books, and describing six genera (*Aphanomyces* de Bary, *Aplanes* de Bary, *Echinostelium* de Bary, *Phytophthora* de Bary, *Piptocephalis* de Bary, *Pythiopsis* de Bary) as well as one species (*Phytophthora infestans* (*Montagne*) de Bary).

A few key landmarks highlighted de Bary's research achievements. Firstly, in 1877 he published a nearly 700-page book titled, *Vergleichende Anatomie der Vegetationsorgane der Phanerogamen und Farne* (English translation: *Comparative anatomy of the vegetative organs of the phanerogams and ferns*) that also included 241 woodcuts (de Bary 1877). This monumental study was translated by British botanists Frederick Orpen Bower, fellow of the Royal Academy who was awarded the gold medal of the Linnean Society and the Darwin Medal of the Royal Society, and Dukinfield Henry Scott, former president of the Linnean Society, a member of the Royal Swedish Academy of Sciences, who was also awarded the Darwin Medal of the Royal Society. Secondly, in 1866, de Bary published a ~300-page book titled, *Morphologie und Physiologie der Pilze*, *Flechten und Myxomyceten* (English translation: *Morphology and physiology of fungi*, *lichens and myxomycetes*; de Bary 1866), which he rewrote in 1884. Thirdly, de Bary's most important and innovative ideas resulted from his own ideas, namely, his definition of symbiosis: "a phenomenon in which dissimilar organisms live together" (de Bary 1879a, b; Ahmadjian and Paracer 1986).

In 1878, Professor de Bary was given the honor of an invitation to address the Association of German Naturalists and Physicians (de Bary 1879a, b). It was here, describing the intimate partnerships between algae or cyanobacteria (or both) and filamentous fungi, that Heinrich Anton de Bary introduced the term 'symbiosis' in a biological context. It is worthy to note that German botanist Albert Bernhard Frank used the word 'symbiotismus' in a 1877 manuscript and this may have stimulated de Bary. Furthermore, the term 'symbiosis' was incorporated into human linguistics in 1622; thus, de Bary's innovation was biologically centered (Richardson 1999). In 1879, de Bary's speech was privately published in Strasburg, Germany, by the Verlag von Karl J. Trübner publishing company as *Die Erscheinung der Symbiose* (de Bary 1879a). This seminal paper was translated into French (titled, *De la symbiose*) and published in *Vue Internationale des Sciences* (English translation: *International Journal of Science*) (de Bary 1879b), but only fragments have been translated into English (e.g., Ahmadjian and Paracer 1986; Sapp 1994). We hope that by providing a full translation, researchers at all levels as well as historians of science will gain a greater understanding of symbiosis and the origins of a discipline that investigates such a wide range of associations.

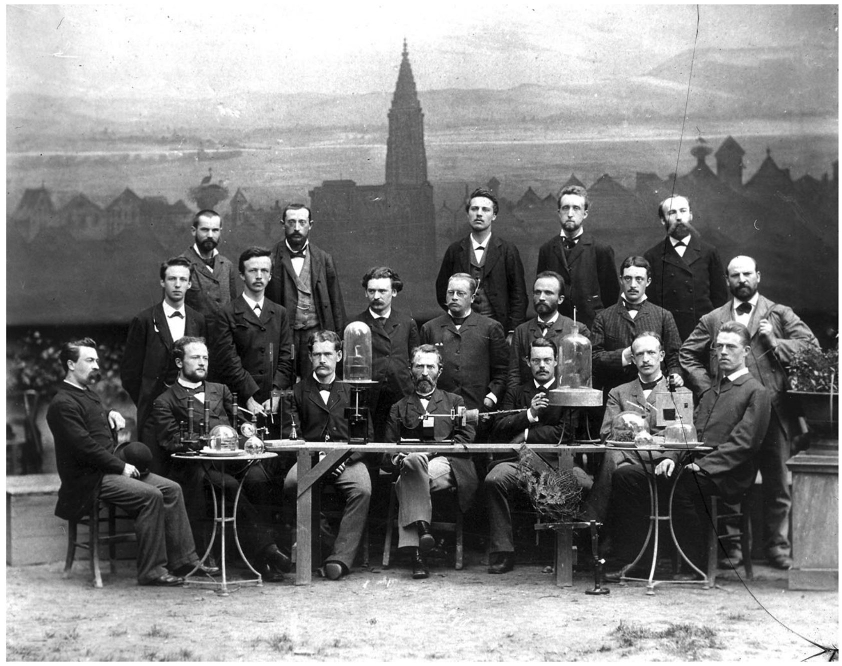

Fig. 2 Professor Heinrich Anton de Bary and members of his laboratory in Strasbourg, France

2 Translation

Die Erscheinung der Symbiose ('*de la Symbiose*')
[The phenomenon of symbiosis]
Lecture
Held at the meeting of the German Natural Scientists and Physicians in Cassel
By A. de Bary
Professor of Botany at the University of Strasbourg

Preface
The talk that is being published here was held at a general meeting of the Cassel Natural Scientists. It was intended for the named group of listeners, *i.e.* for natural scientists and physicians, in order to give them a compact summary of a large number of connected natural phenomena and general aspects for assessing these. With the customary copy in the daily paper of the meeting, I believed that the talk had been adequately recorded for the audience and for others for whom it might be of interest. I felt that an additional publication would be superfluous. And even now, in spite of having been requested to make the lecture available to a larger public, I would have declined if it had not been for a supplement of the *Augsburger Allgemeiner Zeitung* [Augsburg General Newspaper] no. 296, October 23, 1878, in which a critique by A.W. was published. Or perhaps I should rather call it a provocation. The remarks of the A.W. correspondent were not suited to give the reader an accurate impression of what the lecture intended to convey. It even contained a text in quotation marks that I was supposed to have said, but that was not in the lecture and that never could have been included. I feel that I owe the reader who has become interested in the subject matter, but is not familiar with relevant literature, a printed version of the subject matter as it is.
I do not believe that any further arguments with the A.W. correspondent are necessary. For readers who are not familiar with the subject matter, I have added foot notes with factual explanations.[1]
Strassburg, November, 1878.
A. de Bary

When I was trying to find a subject for this conference, I was studying two plants that live in a special relationship. This gave me the idea to talk about observations regarding dissimilarly named organisms that live together, in symbiosis, as we can call these associations. The present preoccupation with the subject, but also the consideration that similar relationships have become well known in the course of the past 10 years, are factors in deeming them to be of general interest. Thus, this talk will be a consideration of such symbioses, namely, the living together of differently named organisms. I have decided to bear with this subject, in spite of the fact that the topics at our meetings should deal with contemporary issues, critique and history of methods used in science and teaching. The presentation of current research results will certainly also be of general interest.

[1] We have not translated the numerous footnotes that are in the German but not in the French version, since they were not part of the original talk.

I am going to talk mostly about observations made in the plant kingdom; first, because the nature of these associations are easier to observe, and also because the corresponding phenomena found in the animal kingdom are already known to people present here, or can be read about in the popular book written by [Pierre-Joseph] van Beneden: *Animal parasites and messmates.*

I will not have time to talk much about this subject in the limited time that I have here, so I will simply indicate the main points, and explain them with good examples.

The most well-known and most exquisite example of symbiosis is holoparasitism, the state in which an animal or a plant is born, lives, and dies on or in an organism that belongs to a different species. This organism becomes the home of the parasite and provides the parasite with its entire nourishment. In one word, it is its host, and since the parasite attains its nourishment either from the body of the host or from the food it consumes, it lives off the organism. The relationships between the parasite and its host are, as we know, very diverse, particularly regarding the dependency of one on the other.

Some parasites are completely dependent on different hosts that may vary according to their developmental stages. That is the case of the Cestoda (tape worms), or the rust fungi on *Berberis*, the *Boraginaceae*, and the *Poaceae*. On the other hand, some parasites can live with very different hosts, but can also, at specific times of their life, live without hosts. This is the case for several blood sucking insects, for some fungi, and several parasitic insects. The muscardine fungus (*Botrytis bassii*), for example, does not spare any species of insects when it meets them at the right moment. However, it can also grow freely, without a host, and produces spores that will reach new victims. Intermediate relationships exist between these two extreme cases.

Another point to consider regarding the relationships between parasites and their hosts is the negative effect that the first has on the second during development. Antagonism, a fight, must occur between the two, depending on the nourishment uptake of the parasite. The course and the outcome of this fight can differ greatly. Sometimes the parasites barely affect the hosts, in several fish for example. On the other hand, disease and death can be caused immediately by the parasite, as is the case of humans infected by *Trichinosis*, or in potatoes infected by *Phytophthora*. However, different relationships exist between other organisms. They are similar to parasitism and are often classified in this category, but they are essentially different.

Many smaller animals live on larger animals and feed on their waste: epidermis that is exfoliating, feathers, hairs, etc. This is the case for several species of *Trichodectes* and *Philopteri*; they can feed from the skin mucus of the fish, like the *Arguli.* These are van Beneden's mutualists; they are in a relationship of mutual enhancement with their hosts. By living off the waste of their hosts, they take care of its hygiene.

Other small animals live in or near larger animals, to feed from the crumbs that fall from the table of the rich, from the left-overs of the food that the larger has attained for itself. They are the commensals of van Beneden.

It's clear that similarities exist between all of these relationships and strict parasitism; there are also intermediate degrees.

In the plant kingdom, the last two categories are less common. However, a careful study found mechanisms that are close to the mutualism of van Beneden with epiphytes that are very well represented in the tropical world by hundreds of orchids and aroids. These plants attach to the bark of the tree and use the products resulting from the exfoliation of the bark. We find these interactions everywhere in this country, like the moss growing on bark – not to mention the smaller species – plants that choose to live in the desquamination of the bark, some having no preference for a specific tree species, others preferring one species.

All plants with chlorophyll are highly independent of their host concerning their nutritional processes. We could at most consider these epiphytic organisms as commensals of their plant hosts; but this term could be applied to all non-parasitic plants growing in the same location, to the extent that they share carbon dioxide, water, and nutritive substances from the ground. Using van Beneden's strict definition of commensalism, it cannot exist in the plant kingdom.

This is enough to demonstrate that there are not strict parallels between phenomena observed in the two kingdoms. There are, moreover, among the plants, additional associations between differently named species that cannot be classified in the categories previously mentioned. The association between *Azolla* and *Anabaena* as mentioned at the beginning of this talk is such an example.

Azolla is the name of a genus of fernlike plants that look like large, foliated mosses and that grow on the surface of water as the duckweeds (*Lemnaceae*) do. The stem is very branched and linked to abundant roots, and has two rows of leaves that are closely spaced and oriented horizontally on the water surface. Each leaf is composed of two lobes, superimposed and spread at the surface of the water. Despite an exceptional peculiarity, the structure of this plant is not essentially different from other plants that have a similar lifestyle. On the lower surface (oriented towards the water) in the upper foliar lobe, there is a small opening leading to a relatively spacious cavity, which is covered by special hairs. In this cavity, lives a blue-green algae composed of a single row of cylindrical cells, elongated and embedded in a gelatinous sheath, as is characteristic for several groups of *Nostocaceae* and especially for *Anabaena*. When the leaves die, the *Anabaena* within also dies, according to what we have been able to observe. There are no other algae in this cavity. How does this unusual visitor, without exception, enter each leaf and where does it come from? It cannot be found outside of the plant, on the leaves of the adult, or even at the entrance of the cavity. It is only found in one other location: a little bit below the extremity of the branch, that still grows in length, as in other plants of the same family, and produces new leaves and new branches. This extremity is curved and shaped like a hook oriented upward. A concave space is located just below it and surrounded by the structures that will give rise to the leaves and the branches. This concave space is also inhabited by *Anabaena*. It is located just below the extremity of the young developing branch, and *Anabaena* immediately locates to the indicated place. The young leaves are in contact with the algae; the upper lobe is flat at the beginning, but then a bulge in the shape of an annular bead grows quickly and forms the cavity with its opening. As soon as this bulge starts to form, a part of the algae gets trapped in the center, and grows within the cavity. As the stem extends, this foliar part containing *Anabaena* becomes isolated from its first location. I have already told you that this interaction was first described by [Georg] Mettenius and [Eduard] Strasburger and that they found no leaf without a cavity, and no cavity without *Anabaena*. The following part is no less interesting. We know four species of *Azolla* that are quite similar, but clearly delineated by differences in their fructification. Two of these species are very common in America and Australia; the third one is in Australia, Asia, and Africa; the fourth one is, as far as we know, limited to the area of the Nile [River]. In all these species, and in all the samples that were studied, we found this association with *Anabaena* as described, and totally identical in all the details. Thus, it is not possible, so far, to distinguish the species of *Anabaena* according to the *Azolla* in which they were found.

There are a number of cases in which species closely related to the *Azolla-Anabaena*, commonly described as *Nostoc*, live in terrestrial plants, also in cavities, but with always less regularity than the described example. They can be absent, or can come from outside during the later stages of development. I only want to refer, as an example, to the roots of the cycads. This plant grows slowly and when relatively young begins to develop a thick tap root that becomes branched in and on the ground, as other roots do. At the base of the root – I do not know if this is always the case – one or two pairs of root branches develop. Generally or maybe always, they grow perpendicularly upwards, branch, change directions once or twice, and form spadiceous bulges at their extremities. Similarly, dichotomously branched roots appear later, often in abundance and very close to each other, on the branches of the tap root and spread on the ground. Frequently, but not always, *Nostoc* can enter between the cells of the dichotomously branched roots; this is followed by specific changes in the structure of the root branch. Under the bark, a parenchymal layer develops that barely differs from the roots in absence of *Nostoc*. Soon, this layer becomes an arched structure, held by thin strands between which are located large spaces. The strands are elongated cells of the parenchymal layer. The spaces are filled with abundantly growing algae. This is, again, a specific association; we know a number of others, but they are not as remarkable.

There is one form of vegetation, an extensive group, composed of thousands of species that is an association of two or three different species that also can only exist through this association. I am talking about organisms known as the lichens. Among them, you probably know the reindeer lichen and the Iceland moss. Everyone has also seen how, especially in the mountains, they may abundantly cover the surfaces of rocks, peat, and the trunks of the trees.

Most of us learned at school that lichens are cryptogams and their method of fructification is exactly that of the ascomycete fungi. Their structures are also very similar, except that they always contain cells with chlorophyll that fungi do not have. Because of this specificity, lichens can assimilate carbon dioxide, explaining their ability to live on naked rocks or other substrates deprived of organic compounds. Fungi deprived of chlorophyll require organic compounds.

The masses of green cells that characterize the lichens had the most unusual fate in the history of science, until it was demonstrated 10 years ago that they are not really part of the plant, which has the same vegetative and fruiting body as the fungus. They are algae that live and grow in association with fungi that cannot exist without this singular association. A specific species of fungus and a specific species of algae create in a unique association a specific lichen; without this association, the lichen would not exist. If the spores of the lichen, which are produced abundantly, are sowed under favorable conditions, only small fungi grow and quickly die. The fungi can only develop to lichens if they associate with the correct alga. Each species of lichen fungus only associates with a few species or with only one species of alga; among these fungi, many related species can form these associations.

However, the number of algae is lower than the number of fungi that can produce lichens, and lower than the number of the corresponding lichens; because according to [Agustín] Stahl's reports, it is clear that one single species of alga can be used by several or perhaps many fungal species to form many lichen species. I will have to come back to this subject to discuss the forms of the association and the relationships between the associated species.

When we observe more closely the phenomena described above, we find in the azollas and the cycads as well as in lichens, intimate associations of different species, but never an organization that fits one of the categories described at the beginning of this study. For the reasons that I have already explained, we cannot strictly speak of commensalism or parasitism.

The *Anabaena* of *Azolla*, and the *Nostoc* of the *Cycas*'s roots live in specific locations, but they do not live at the expense of their hosts; there is not even evidence that they take advantage of them. The *Nostoc* of *Cycas* can thrive excellently in water, even without having this hostel. When we artificially isolated it, the *Anabaena* of the *Azolla* also seemed to live in water without a living host, which has not yet been verified. We can theoretically assume this a priori for *Anabaena* as well as for the *Nostoc*-form. Not only because they have the same structure as plants with chlorophyll that can live without organic compounds, but also because we know many structures that look exactly like them, which means that there are many *Nostoc* and *Anabena* species that do not grow in living accommodations, but vegetate freely in water or on the ground.

The term mutualism would be best suited to define the life of the *Nostoc* that we have just talked about, if we accept that the host and the parasite are useful for one and other, *i.e.* do each other a few favors. It is, however, doubtful that there are mutual advantages to the partners. We can definitely say that they do not harm each other significantly, because, if this were the case, the association would not exist. It is likely that the host protects the little algae in different ways. But presently, we have no evidence of the mutual benefits that they could afford each other.

The usefulness of the relationships for the lichen partners varies, but also differs from that of the relationships observed in animals. Without making any huge mistakes, but only for very few of them, can we talk about real parasitism. This is because the fungus creates its home in or on the algae, the smaller partner, and lives at its expense. But even in the best scenario, the term parasitism is not strictly accurate. For most of the lichens, the relationship is quite different. The algae can usually live alone. We can not only artificially isolate it and observe its independent growth and reproduction, but we also often see the lichen algae in nature without its being part of a lichen. This is not the case for the fungus of the lichen. It cannot develop by itself, as already mentioned, and dies quickly if it does not find an alga. To grow and develop, the fungus needs the alga's carbon dioxide assimilates. However, it does not simply stay in or on the algae, it encloses it with its body, growing so extensively that for most of the lichens, it forms most of the overall mass. The alga only represents a small part, one tenth, or maybe less. According to this volume, the fungus would be the host, and the algae would be the tenant. But the host depends on the tenant to survive – it is what usually happens in real life. The tenant is given the best of care; not only is its growth not inhibited, but is even better than when growing alone; its growth is coordinated with that of the host. Finally, by penetrating deeply into the hard rock, the host is in charge of attaching the body to the substratum, but also for providing necessary components of volcanic ash to the joint household.

We cannot continue to discuss the extremely interesting detail regarding lichen structure and economy, but must limit the discussion to that which has already been said, adding that there are many diverse phenomena regarding the living together of organisms of different species that are associated with parasitism, mutualism, etc. They are too diverse and complex to be put into categories. Parasitism, mutualism, and lichenism are special cases in this establishment of associations in which the term symbiosis serves as a general description. Do we want to differentiate the main categories? We suggest two categories: the antagonist symbiosis in which the partners combat one and other, and the mutualistic symbiosis in which there is a reciprocal benefit for the symbionts, but here, again, we cannot define exact boundaries.

The boundaries are not well defined if we want to distinguish associations of symbionts that are strictly united for their common benefit in contrast to those that we can group under the term of sociability. Examples of the latter are very diverse. A Mexican bird, the cowbird, lands on the nose of a bison stuck in the mud and is on the outlook for mosquitoes that want to crawl into the animal's nose. Another example: On the mountain, Serra dos Orgaos, in Brazil, an aquatic plant, *Utricularia nelumbifolia*, which is probably insectivorous, lives on the arid rock slopes, a phanerogam with chlorophyll. It only grows in water, locked in the funnel-shaped center of the leaf rosettes of a member of the Bromeliaceae, common in these regions. It produces stolons, almost like those of strawberries that form a new plant when they reach another rosette. New flowers and stolons form on this new plant. These associations are similar to the ones we have referred to as symbiosis, but we can only use this term if we also use it for all the other relationships such as the ones that exist between the insects that enter the flowers and the flowers that receive the pollen from the insects, or between animals that look for food or for a shelter and the other animals or plants that provide them. I have no objection to this generalization, as I have tried to demonstrate the similarities between these associations.

With the proof of the similarities of these associations, the exceptional position occupied by certain parasites disappears, even though it may seem special among the close relatives. We also reject the old opinions that they were borne from the juices or rotten tissues of the host. And, similarly, the lichens also lose their position that at first glance seemed so exceptional.

[2] The lichenologists became extremely upset upon hearing of this algal-fungal interaction, feeling that their darlings were being degraded, convinced that it was unbelievable that lichens were not independent organisms, but rather – in their opinion – an illegal association between a fungus and an alga. The outrage ought to disappear, considering the fact that there is nothing illegal going on, but rather that these are special cases that occur everywhere in nature with a thousand different forms. We can only thank Schwenderer for clarifying the previously puzzling structure of lichens as such a unique form of symbiosis.

[2] The following text, the end of which will be marked by another footnote, was only in the German, but not in the French translation.

The proof that the examples discussed belong to the large number of interactions between different organisms is not in itself an explanation for the interactions, assuming that this is understood as one example of an empirical rule that had previously been seen as one isolated case. A real explanation can be gained if regarded from the same standpoint and within the same limitations as for other such phenomena of the same category. And conversely, they may contribute to understanding the entirety.

The first of these assumptions is obvious, and it goes without saying that regarding the explanatory aspects, the theory of evolution as developed by Darwin is meant. Only this theory, which includes the principles of breeding, is able to provide a scientific explanation for the phenomena that we have discussed. Any further discussion of this point would be superfluous. And, I do not need to mention the limits that the explanation temporarily has regarding the attributes of organized substance and the prevailing lack of knowledge of the physiological fundaments known under the collective name of adaptations of normally combined processes. Within these limits, on the basis of the theories of evolution and breeding, we can understand the habits of the cowbird and of insects that visit flowers, the relationship between *Azolla* and *Anabena*, the interactions of the lichens and of parasites, but also the peculiarities of morphology and structure that originated historically from successively inherited phenomena.

If these phenomena can be subordinated to the theory of evolution, then they are evidence for the theory and contribute to its totality. A closer examination of symbioses shows that a more important contribution can be found elsewhere. We have ample reason to agree with Darwin to say that successive adaptations and the correlating changes of morphology and transformations of organisms occur, and must occur, as a consequence of the influence of the environment on the organisms and on their capacity for transformation. Through the interactions of these two main factors, we can explain the forms and mechanisms that presently exist.

Most of these morphologies and mechanisms are fully developed and inherited traits; the transformations through which they originated did not occur before our eyes and we are not in the position to make them arbitrarily appear and disappear. Their origin lies in prehistoric times, a period which can be only more or less accurately determined. Regarding the azollas, for example, the development of the cavity in which *Anabena* resides arose before the spatial separation and thus differentiation of the four present-day species. We attain information regarding the processes involved in development of the present conditions from our experiences with variability, the capacity for transformation of species, from results of intentional breeding, in part through comparison of parallel existing morphologies, from predetermined inherited morphologies and from embryonic developmental states.

Of all the environmental factors, the effects of dissimilarly named organisms on one and other are particularly outstanding and are strong reciprocal determinants of morphology and behavior. The morphology and features of both the flowers that bees frequent and that of their visitors, the relationship of the azollas with their anabenas, and a thousand similar relationships can only be understood as a result of mutual adaptations. These cases can also be inherited, predetermined states. There are many other examples which confirm our expectations that symbioses are determinants of morphology.

It would take far too much time to remove the azollas from the cavities of *Anabena*, aside from the fact that it would not make any sense. There would be the insurmountable difficulty that removal of the little guest would undoubtedly injure the delicate structures of the host. However, there are not any better examples.

Many strict parasites influence the morphology of their hosts. Wolf's milk (*Euphorbia esula*) completely changes its morphology following intrusion of a parasitic fungus that totally transforms the form of the summer shoots. A similar freeloader fungus (*Aecidium elatinum*) intrudes into the buds of the European silver fir (*Abies pectinata*) [*Abies alba*]. The uninfected branches have horizontal, bilateral branching and evergreen leaves. The branches occupied by the intruder grow upright with whorled ramifications, losing their leaves every year and developing new ones every spring, developing little fir trees on the intact branches that can become 10 or more years old.

The parasites are directly responsible for these changes in morphology. They do not occur when the parasites are absent. They can be intentionally induced and prevented. Perhaps these examples should be disregarded since they border on pathogenicity; and since they have similarities to the formation of galls and tumors, their exemplary status is weakened – but admittedly not more than that. Where does the border between pathological and non-pathological transformation differ more than a conventional differentiation?

We'll refrain from further consideration of such examples, because this is not necessary.[3]

As mentioned earlier, when *Nostoc* enters the dichotomous roots of the cycads, the structure of these roots changes considerably. Large spaces appear in the compact parenchyma of the roots to house the visitor; they are formed by a specific orientation of the growing tissue and do not appear in the roots in absence of the visitor. We saw something similar, but more obvious, with the algae and the fungi that produce the lichens. We have already talked about the features of the fungi. The alga is considerably modified when it unites with its companion. The orientation of growth that influences the shape is modified. A gelatinous stem that *Nostoc*, the algae of

[3] This is the end of the text that is present in the German, but not in the French, text.

gelatinous lichens, produces is flat or slightly spherically shaped, branching regularly into a fructicose body. The chlorophyll cells, round or elongated, found in *Pleurococcus* and *Stichococcus*, change their shapes as soon as the lichen-fungus captures them. The orientation of their divisions can gradually change, but are variable depending on the fungus with which it associates.

In these plants, and in the case of *Cycad*, pathological changes do not occur, not only because we do not have conventions to agree on what is healthy and what diseased, but also because there is no evidence of a decrease in vital energy, of faster death, nor any evidence of a sickly state. Instead, the reports written by Stahl have demonstrated that right after their association with the fungus of the lichen, the cells of the algae become much larger, contain more chlorophyll, are stronger in every way. Beyond doubt, according to data that have been known for a long time regarding the structure of the lichen, all of these characteristics are retained for the entire life of the lichen, sometimes for several dozen years.

Here, and in many more examples that I could have mentioned, we can see changes in morphology that we cannot explain as pathological in the mutual relationships between symbionts with dissimilar names. The researcher can arbitrarily make these changes appear or disappear by uniting or separating the symbionts. But, because the phenomena that we have described as symbiosis are only specific cases among the many relationships that exist between organisms, these are merely a contribution to understanding the entirety of associations between organisms. By themselves, these phenomena may not seem to be important, and for some people it might have appeared unnecessary to pay attention to them; they are however of great value because they are experimentally accessible.

The theory of evolution has often been criticized for its lack of experiments; this charge is wrong, because, as has often been emphasized, we can find important reports that support this theory in the breeding of animals and plants. Independently of the importance that we give to natural selection, which results in gradual changes of the species, it is desirable to see the opening of a new field for experiments. That is why I wanted to bring your attention to these experiments, even if only to clarify some of the observations. I have not talked about any new observations. All the examples that I have mentioned are well known. Evidences to support the fundamental theory that we have talked about are found everywhere. We just have to carefully look around.

3 Concluding remarks

Since Heinrich Anton de Bary's address to the Association of German Naturalists and Physicians in 1878, the recognition and appreciation for symbiotic partnerships and associations has greatly expanded. Over the following ~130 years (*i.e.*, until the present), our comprehensive knowledge of symbioses stems from various systems, including: (1) the bobtail squid *Euprymna scolopes* and its bioluminescent bacteria *Vibrio fischeri* (Nyholm and McFall-Ngai 2004); (2) hard corals and zooxanthellae (Muller-Parker and D'Elia 1997); (3) the gutless deep-sea tubeworm *Riftia pachyptila* and sulfur-oxidizing bacteria (Cavanaugh et al. 1981); (4) isoptera (termites) and their microbiome (Warnecke et al. 2007); (5) *Leguminaceae* and root-based nitrogen-fixing bacteria (Franche et al. 2009); (6) lichens (Nash 2008); and (7) mycorrhiza (Harley and Smith 1983); numerous other examples of symbiotic interactions are discussed by Egerton (2015).

A common characteristic of these symbioses is that symbionts associate with a specific species of bacterium or (more accurately) a community of bacteria and other microbes (fungi, viruses, bacteria, and archaea). Moreover, each partner provides a nutritional and/or metabolic advantage to the other, which might be termed altruism. For example, most aphids (plant lice) harbor intracellular bacteria of the genus *Buchnera*, where the primary role of the bacteria as a vector for nitrogen recycling is to provide amino acids to the host, while the host supplies the symbiont with nutrients via phloem sap, vertebrate blood, or wood (Douglas 1998).

In recent years, the field of symbiosis has focused on understanding partnerships between the host and its microbiome: the collection of bacteria, fungi, viruses, and archaea intimately associated and specific to the host. Mediating this revolution are advances in sequencing platforms (i.e., next generation sequencing) and corresponding bioinformatics techniques (i.e., metagenomics) (Jumpstart Consortium Human Microbiome Project Data Generation Working Group 2012; Shokralla et al. 2012). In brief, studies using these techniques show that bacterial symbionts are critical, if not essential, players in development, immunity, regeneration, and disease resistance (McFall-Ngai et al. 2013; Bordenstein and Theis 2015; Gilbert et al. 2015; and references therein). A synthesis of host-microbe studies led to proposing the holobiont or hologenome theory of evolution, which states that the collection of host and symbiotic microbes is a unit of selection and a product of co-evolution (Margulis 1991; Zilber-Rosenberg and Rosenberg 2008; Rosenberg et al. 2009; Bordenstein and Theis 2015).

The term 'symbiosis' first applied to biology in 1878 by de Bary is now accepted without question by the life sciences, and these intricate partnerships are thought to be a major driving force in evolutionary biology, as hosts and their symbiotic microbiota acclimate on short timescales and potentially adapt over long-term timescales. The recognition that dissimilar organisms can live harmoniously in close association with one another has had a more significant impact than de Bary could have realized, and the extent to which this is the case is likely beyond the scope of our present understanding. By publishing de Bary's 1878 speech in English, we hope this scientific landmark will be more widely recognized for its significance, its forward thinking, and as the origin of all studies on symbioses.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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