

¹Institut für Biologie, Abteilung Pflanzenphysiologie und Evolutionsbiologie, Universität Kassel, Kassel, Germany²Arbeitsgruppe Biologiedidaktik, Biologisch-Pharmazeutische Fakultät, Universität Jena, Jena, Germany

Physiological phytopathology: Origin and evolution of a scientific discipline

U. Kutschera^{1*}, U. Hossfeld²

(Received November 28, 2011)

Summary

In 1860, the German biologist Anton de Bary (1831-1888) elucidated the life cycle of the pathogenic oomycete *Phytophthora infestans*, which causes late blight in potatoes and was responsible for severe famines during the 1840s. In a book on this topic published 150 years ago, DE BARY (1861) established the scientific discipline of physiological plant pathology. Here we summarize the life and scientific achievements of Anton de Bary, who coined the terms “symbiosis” and “parasitism”, with reference to Charles Darwin’s (1809-1882) principle of descent with modification by means of natural selection. Then, we outline de Bary’s discovery of the cause of the wheat stem rust disease, which is attributable to infections with the fungus *Puccinia graminis*. Since ongoing pathogen-host plant co-evolution is well documented in nature, we conclude that “Nothing in phytopathology makes sense except in the light of Darwinian evolution”. Finally, we describe the value of basic research in the plant sciences with reference to practical applications, such as the maintenance and enhancement of crop yields and food quality.

Introduction

One century ago, the *American Phytopathological Society* published the first issue of a journal that persists to the present day. For the first page of this new periodical, the distinguished botanist and microbiologist Erwin F. Smith (1854-1927) was asked to write a tribute. To the surprise of some of his North American colleagues, in *Phytopathology* Volume 1 (No. 1), a German biologist was honoured in the following words: “Of all the personalities contributing to the advancement of plant pathology from its crude beginnings to the present time, none has been more interesting than that of De Bary, none more productive of important results. De Bary cleared the way for all that has followed in plant pathology and we must ever think of him with that reverence due a great master” (SMITH, 1911). In a subsequent biography of Erwin F. Smith, Anton de Bary was characterized as an excellent biologist “Gifted with brilliance and the instincts of a cautious experimental scientist, one who refused to admit or advance any truth as fact until proved by strict technical procedures” (RODGERS, 1952).

Anton de Bary (1831-1888) was one of several outstanding 19th century scientists who remains “in the shadow” of the famous British naturalist Charles Darwin (1809-1882). This is to a large extent due to the fact that he studied “lower organisms”, such as plasmodial slime molds, fungi, and plants (HOPPE and KUTSCHERA, 2010). In only one of the many books authored by de Bary references are made to “higher animals” (vertebrates) or humans (DE BARY, 1885). Moreover, it is rarely appreciated that it was Anton de Bary (1878), who defined the terms “symbiosis” and “parasitism” with reference to plants and Darwin’s principle of natural selection (KUTSCHERA and NIKLAS, 2004; 2005).

One hundred and fifty years ago, a little-known monograph on the potato late blight was published that inaugurated the scientific disci-

pline of experimental plant pathology (DE BARY, 1861). In this article, the achievements of Anton de Bary are outlined. Then, the origin and evolution of experimental plant pathology is discussed with respect to pathogenic fungi and bacteria. Finally, we describe theoretical and applied aspects of these international research agendas with reference to Darwin’s *Origin of Species* (1859, 1872).

The plant and fungi collector evolves into a laboratory scientist

Anton de Bary (Fig. 1) was born on the 26th of January 1831 in Frankfurt-Main, Germany. From 1849 to 1853 he studied medicine at the Universities of Heidelberg, Marburg and Berlin, where he earned his academic degree with an unpublished dissertation on a botanical subject. The title of this work of 1853, *De plantarum generatione sexuali*, indicates the primary interest of the young physician: plants and related sessile organisms. At the same time, the 22-year-old junior scientist, who was already an experienced plant and fungi collector, published his first monograph. In these *Researches on the*



Fig. 1: Photograph of the founding father of experimental plant pathology and his research object, potato plants (*Solanum tuberosum*), infected by the oomycete *Phytophthora infestans*. The name “infectious plant destroyer” for this pathogenic fungus was coined by Anton de Bary in 1876.

* Corresponding author

smut fungi and the diseases that they cause in plants, with regards to cereals and other crop species, DE BARY (1853) summarized the current knowledge on this topic and postulated that only by means of proper experiments the true causes of these devastating plant diseases may be elucidated some time in the future.

In 1854, de Bary became a lecturer (Privatdozent) for botany at the University of Tuebingen. Only one year later (1855), the specialist for fungi and plants received an appointment as professor of botany at the University of Freiburg im Breisgau. At the Botanical Institute in Freiburg i. Br., which later became one of the leading centres for plant research in Germany (BRIGGS, 2010), the biologist published his seminal monograph on the potato blight (DE BARY, 1861). After twelve years of hard work, the famous scientist left Freiburg to accept a more attractive position at the University of Halle, where he stayed from 1867 to 1872. He spent his final and most productive years at the newly constituted University of Strassburg, where de Bary served as the first rector. The biologist died in Strassburg on the 19th of January 1888 as a result of a tumour infection (SPARROW, 1978; HORSFALL and WILHELM, 1982).

Anton de Bary started his career as a field naturalist, who collected plants and fungi in the nearby country side. Although he was formally trained as a surgeon, his interest in medicine was overshadowed by his drive to study plants, fungi and other “lower organisms” such as myxomycetes (DE BARY, 1859, 1864, 1866, 1884). He established sophisticated laboratory techniques to analyze the life histories of plant parasites, myxomycetes and other “primitive” living beings. Hence, Anton de Bary was a botanist, plant physiologist, myxomycetologist and phytopathologist (HOPPE and KUTSCHERA, 2010). Moreover, with the publication of his *Lectures on bacteria* (DE BARY, 1885), the laboratory scientist became one of the founding fathers of modern bacteriology.

Potato blight and the origin of physiological phytopathology

In a recent article entitled “Genome evolution in plant pathogens”, fungus-like parasites (oomycetes), such as the potato blight pathogen *Phytophthora infestans*, and their infection strategies are described

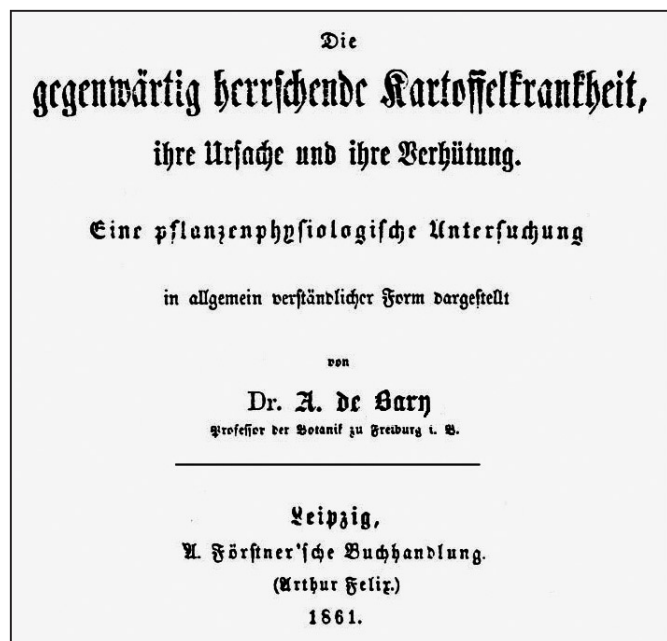


Fig. 2: Title page of Anton de Bary's monograph on the potato late blight. This book also contains recommendations how to prevent the spread of this devastating plant disease.

(DODDS, 2010). However, the author of this popular summary of potato blight research did not mention that, 150 years before his paper was published, the discipline of physiological plant pathology was established.

At that time, the life cycle of *P. infestans* was elucidated. This discovery, which was summarized in a seminal book, was published in November 1861 under the title *The currently spreading potato disease, its cause and its prevention. A study based on the principles of plant physiology* (Fig. 2). Herein the author inaugurated the discipline of experimental phytopathology, i.e., the scientific study of plant diseases (DE BARY, 1861).

In February 1861, the German botanist Anton de Bary documented in detail how the vegetative body (mycelium) of *P. infestans* spreads through the leaf tissue of infected potato (*Solanum tuberosum*) plants (Fig. 1). In a series of elegant experiments, de Bary recorded the symptomatic progression of the plant disease ‘late blight’ against the developmental stages of *P. infestans*. Based on these studies, which demonstrated a positive correlation between the life cycle of *P. infestans* and stages of plant disease progression, de Bary concluded that the oomycete is the causal agent of the disease of the potato plant.

In this monograph (Fig. 2), which was primarily based on his own research, Anton de Bary provided experimental evidence that potato tubers are infected by the fungus via the brown, blighted leaves and described the spread of the disease in the field. Specifically, DE BARY (1861) provided detailed drawings of cross sections through the leaves of infected potato plants, showing the vegetative structure (mycelium) spreading via the intercellular spaces of its host organism (Fig. 3 A). He also monitored the development of the conidiophores as they emerge from the pores of the stomata (Fig. 3 B) and the germination of isolated spores of *P. infestans* (Fig. 3 C). Based on

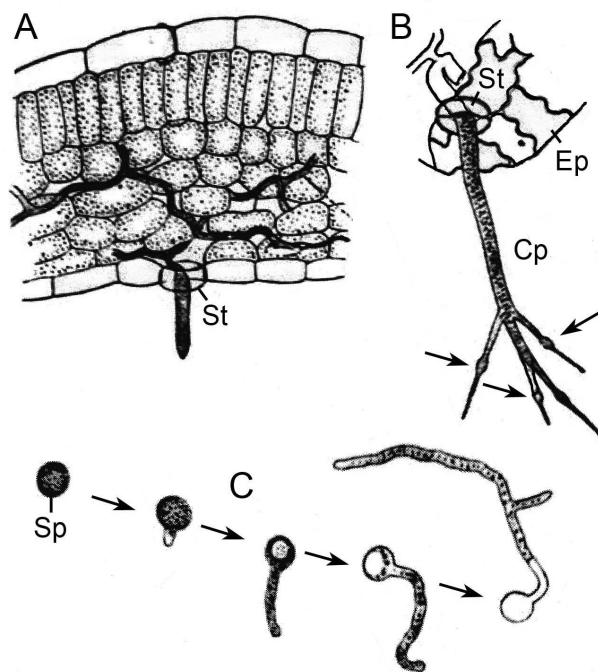


Fig. 3: The discovery of the life cycle of the late blight oomycete *Phytophthora infestans* by Anton de Bary. The mycelium of *P. infestans* in a leaf of a potato (*Solanum tuberosum*) plant (A), spore germination in liquid culture (C), and a conidiophore (with spore-containing conidia, arrows) that emerges from a stomatum on the underside of a leaf (B). Cp = conidiophore, Ep = epidermis, Sp = spore, St = stomatum (adapted from DE BARY, 1861).

these and other observations carried out according to the principles of experimental plant physiology, a scientific discipline established in Germany during the 1850s by Julius Sachs (1832-1897) (KUTSCHERA and BRIGGS, 2009, 2012), the author concluded that “The disease of the leaves, stems and fruits is caused by a pathogenic fungus, *P. infestans*, and the disease of the tubers occurs via infection from the leaves” (DE BARY, 1861). Moreover, the scientist, who was working at that time at the University of Freiburg i. Br., concluded that “It will never be possible to drive the parasite *P. infestans* to extinction ... however, a careful selection of uninfected tubers for agriculture will be sufficient to prevent large-scale spreads of this devastating plant disease” (DE BARY, 1861). At the end of the text, he informed agriculturalists how to prevent the re-occurrence of another, devastating potato blight epidemic, such as that in Ireland from 1845 to 1848, which caused crop losses and famine (ANDRIVON, 1996; READER, 2009; MATTA, 2010; SKELSEY et al., 2010).

Spontaneous generation of lower organisms?

It should be noted that de Bary used his empirical proof for the “fungal theory”, which states that *P. infestans* is the causal organism of potato blight, to refute the doctrine of spontaneous generation. In 1861, many scientists still believed in the emergence of “lower” or “primitive” organisms, such as *P. infestans*, from dead material under present-day environmental conditions. The doyen of phytopathology provided experimental data documenting that the oomycete developed only from its own spores and never appears *de novo*. With the publication of these evidence-based conclusions, which supported the corresponding “microbe-experiments” of Louis Pasteur (1822-1895), the belief in “generation without parents”, which had never been supported by unequivocal evidence, disappeared forever from

the scientific literature (MATTA, 2010). Hence, the origin of plant pathology 150 years ago led to the demise of a dogma that had been the topic of endless debates among naturalists and philosophers. In his book *On the Origin of Species*, DARWIN (1859, 1872) ignored the “spontaneous generation – debate”, because, in his view, the evidence for this concept had always been weak and controversial.

Wheat stem rust: Infection experiments and their consequences

In 1865, the 33-year old German botanist Julius Sachs published his famous book entitled *Experimental Physiology of Plants*. In this seminal work (SACHS, 1865), the junior professor summarized the state of the art of a young scientific discipline that later evolved into Plant Physiology, i.e., the systematic study of the processes which go on in living, green, chloroplast-bearing sessile organisms. It is well known that Anton de Bary was heavily influenced by the work of Sachs, who established, notably in his masterpiece *Lectures on the Physiology of Plants* (SACHS, 1882), high standards concerning how to perform reproducible experiments under controlled laboratory conditions (KUTSCHERA and BRIGGS, 2009, 2012; KUTSCHERA and NIKLAS, 2009). In the “shadow of SACHS (1865)”, de Bary published another major work wherein he used his experimental protocols from his potato blight studies in an even more sophisticated way. With reference to his earlier, descriptive work on the “Brand fungi”, i.e., pathogenic organisms associated with the rust disease in wheat (DE BARY, 1853), he turned his attention to the life cycles of these pathogens. In a major research paper that appeared in a little-known journal, DE BARY (1865) elucidated the complex development and the different spore forms on two unrelated host plants (a phenomenon known as heteroecism), in several species of rust fungi. With a focus on wheat (*Triticum aestivum*), he described the formation of

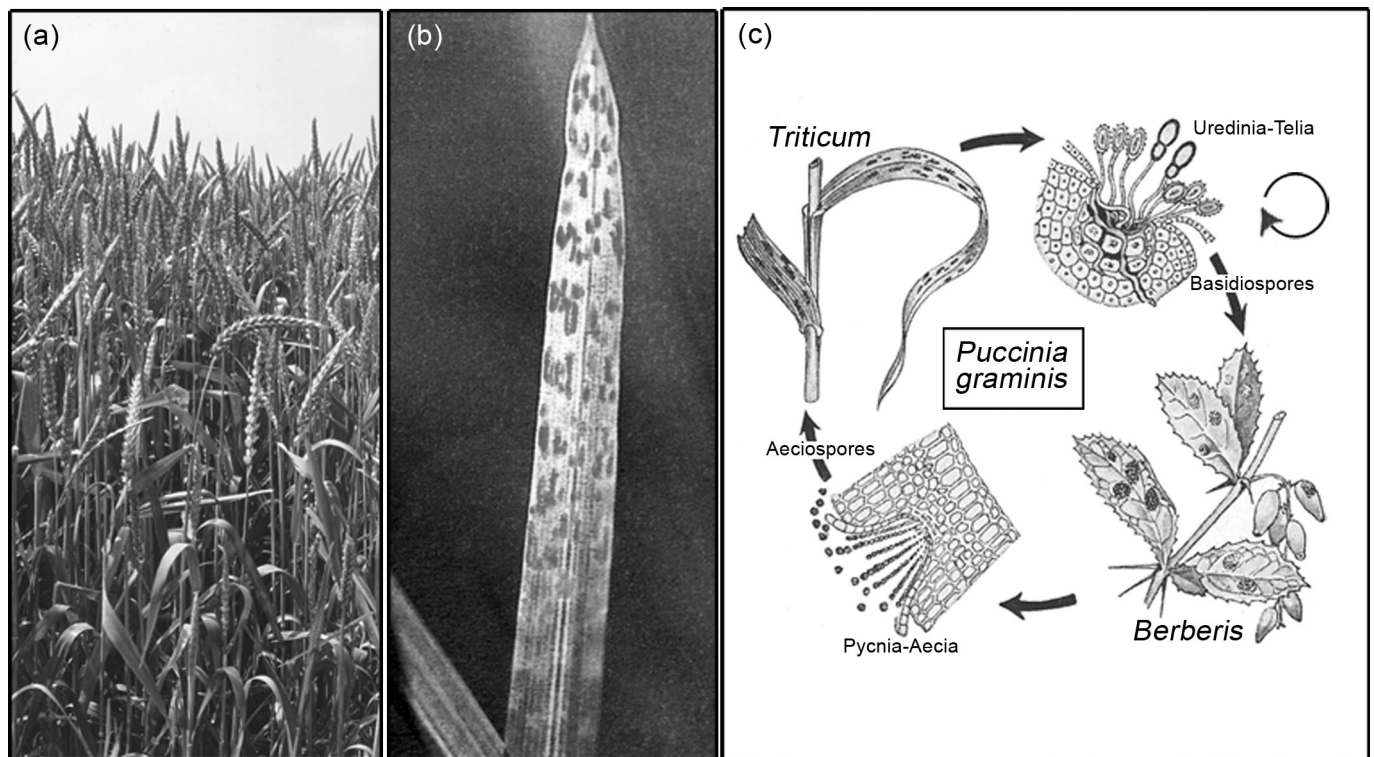


Fig. 4: Healthy wheat (*Triticum aestivum*) plants in the field (A) and a dying wheat leaf (B) that is infected by the pathogenic fungus *Puccinia graminis*, which causes this plant disease (stem- or cereal rust). Diagram of the life cycle of *P. graminis* via uredinia-telia (C). These propagules spread asexually on the infected *Triticum* plants (circle), release basidiospores that infect barberry (*Berberis vulgaris*) plants, where they reproduce sexually via pycnia-aecia, and finally re-infect wheat plants via aeciospores. Anton de Bary, who elucidated this grass (*Triticum*) host 1- alternate (*Berberis*) host 2- cycle, recommended removing barberry plants in the vicinity of wheat fields to prevent the spread of the cereal rust.

the brownish uredia and uredospores of the stem rust, which is caused by the fungus *Puccinia graminis* (Fig. 4 A - C). Based on de Bary's seminal work of 1865 and subsequent studies, the complex life cycle, with alternation of generations on different host plants, has been elucidated in detail. Due to the elegant studies of DE BARY (1865) we know that the common barberry (*Berberis vulgaris*), as well as a grass species, is required for the stem-, black- or cereal rust (*Puccinia graminis*) to complete its life cycle (DREWS, 2001). During the spring and early summer, stem rust infections on wheat and other cereal species (Fig. 4 A, B) produce dikaryotic urediniospores. These propagules, which are produced within the uredinia, are distributed by the wind to nearby conspecifics. Here they germinate on the stems or leaves and then infect their new host plant through the stomata. This asexual summer circle, which spreads the infection over wide areas, is indicated in Fig. 4 C as a circle. At the end of the growing season, the cereal rust produces dikaryotic teliospores, which, during the next spring, develop into basidiospores. These propagules can not infect cereal plants. However, they are carried by the wind to a second host plant, barberry (*Berberis vulgaris*) and related species. There, the basidiospores infect young leaves via the penetration of the epidermal cells. The resulting infection structures (pycnia or spermagonia), which represent the sexual stage of the life cycle, form, after fertilisation, so-called aecia. These structures produce aeciospores, which are carried by the wind to cereal plants. After infection, the aeciospores develop into uredinia, and thus the next life cycle of the pathogenic fungus *P. graminis* begins (Fig. 4 C). The elucidation of this "sophisticated" (i.e., evolved) life cycle of a plant pathogen, that still causes severe problems in Africa today (SINGH et al., 2008), originated with the work of DE BARY (1865). These insights were based on careful infection experiments and the use of different host plants and spores (DREWS, 2001). One practical consequence rapidly emerged from this elegant work: the systematic removal of barberry plants close to crop fields. It should be noted that Anton de Bary's research was based on the principles of experimental plant physiology (see the sub-titles of the monographs DE BARY, 1861 and 1863), a scientific discipline that was still in its infancy when the botanist-mycologist carried out his seminal work.

Conclusions: A de Baryian view of phytopathology

The German biologist Anton de Bary (Fig. 1) was one of the first to employ the emerging principles of experimental botany to study the causes of diseases in major crop species, such as potato and wheat. Based on detailed analyses, he elucidated the life cycles of pathogenic fungi, concluded that these eukaryotic microbes are the causative agents of disease development, and hence became the founding father of experimental plant pathology. This scientific discipline originated 150 years ago with the publication of a monograph on potato blight (DE BARY, 1861) (Fig. 2).

In his famous publication on symbioses and pathogens in plants, DE BARY (1878) pointed out that only a Darwinian perspective yields meaningful conclusions – in other words, "Nothing in plant pathology makes sense except in the light of Darwinian (adaptive) evolution".

Anton de Bary's studies on potato blight and wheat stem rust highlight the practical value of basic research with respect to the maintenance of stable crop yields and food quality (ORBACH, 2011; KUTSCHERA and WANG, 2012). His insights concerning the mode of infection and the spread of plant pathogens in the field led to measures to prevent these epidemics from occurring in the future. Moreover, DE BARY (1861, 1865) explicitly pointed out that it will never be possible to completely eliminate pathogenic micro-organisms such as *Phytophthora* or *Puccinia*, because these living beings will always find ways to adapt to new environmental conditions via rapid microevolutionary processes. This classical "Darwinian view" of phytopathology was

correct. Today we know that dynamic plant-microbe co-evolutionary events occur (KUTSCHERA and NIKLAS, 2004; KUTSCHERA, 2009). Hence, new pathogens, such as the recently described modified stem rust strain *Puccinia graminis* race Ug99, which has a devastating impact on wheat production in Africa (SINGH et al., 2008; DODDS, 2010; MCCLUNG, 2011), can not simply be eliminated. These pests will continue to cause severe crop losses in those regions of the Earth where food production is steadily threatened by plant diseases, insect calamities, droughts, and civil wars.

Acknowledgements

We thank two anonymous reviewers for helpful comments on the manuscript. This work was supported by the Alexander von Humboldt-Stiftung, Bonn, Germany (AvH-fellowship Stanford 2010/2011 to U. K.).

References

- ANDRIVON, D., 1996: The origin of *Phytophthora infestans* populations present in Europe in the 1840s: a critical review of historical and scientific evidence. *Plant Pathol.* 45, 1027-1035.
- BRIGGS, W.R., 2010: A wandering pathway in plant biology: From wildflowers to phototropins to bacterial virulence. *Annu. Rev. Plant Biol.* 61, 1-20.
- DARWIN, C., 1859: *On the Origin of Species by means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life.* John Murray, London.
- DARWIN, C., 1872: *The Origin of Species by means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life.* 6th edn. John Murray, London.
- DE BARY, A., 1853: *Untersuchungen über die Brandpilze und die durch sie verursachten Krankheiten der Pflanzen, mit Rücksicht auf das Getreide und andere Nutzpflanzen.* GWF Müller, Berlin.
- DE BARY, A., 1859: *Die Mycetozen. Ein Beitrag zur Kenntnis der niedersten Thiere.* *Z. wiss. Zoologie* 10, 88-175.
- DE BARY, A., 1861: *Die gegenwärtig herrschende Kartoffelkrankheit, ihre Ursache und ihre Verhütung. Eine pflanzenphysiologische Untersuchung in allgemein verständlicher Form dargestellt.* A. Förster'sche Buchhandlung (Arthur Felix), Leipzig.
- DE BARY, A., 1863: *Ueber die Fruchtentwicklung der Ascomyceten. Eine pflanzenphysiologische Untersuchung.* Wilhelm Engelmann, Leipzig.
- DE BARY, A., 1864: *Die Mycetozen (Schleimpilze). Ein Beitrag zur Kenntnis der niedersten Organismen.* Wilhelm Engelmann, Leipzig.
- DE BARY, A., 1865: *Neue Untersuchungen über die Uredineen, insbesondere die Entwicklung der *Puccinia graminis* und den Zusammenhang derselben mit *Aecidium berberidis*.* *Monatsberichte der Königlich-Preussischen Akademie der Wissenschaften Berlin* 65, 15-49, 205-215.
- DE BARY, A., 1866: *Morphologie und Physiologie der Pilze, Flechten und Myxomyceten.* Wilhelm Engelmann, Leipzig.
- DE BARY, A., 1878: *Über Symbiose.* *Tageblatt der 51. Versammlung Deutscher Naturforscher und Ärzte in Cassel 1878*, 121-126. Druck von Baier & Lewalter, Cassel.
- DE BARY, A., 1884: *Vergleichende Morphologie und Biologie der Pilze, Mycetozen und Bakterien.* Wilhelm Engelmann, Leipzig.
- DE BARY, A., 1885: *Vorlesungen über Bakterien.* Wilhelm Engelmann, Leipzig.
- DODDS, P.N., 2010: Gene evolution in plant pathogens. *Science* 330, 1486-1487.
- DREWS, G., 2001: The developmental biology of fungi – a new concept introduced by Anton de Bary. *Adv. Appl. Microbiol.* 48, 213-227.
- HOPPE, T., KUTSCHERA, U., 2010: In the shadow of Darwin: Anton de Bary's origin of myxomycetology and a molecular phylogeny of the plasmodial slime molds. *Theory Biosci.* 129, 15-23.
- HORSFALL, J.G., WILHELM, S., 1982: Heinrich Anton de Bary: Nach einhundertfünfzig Jahren. *Annu. Rev. Phytopathol.* 20, 27-32.

- KUTSCHERA, U., 2009: Charles Darwin's *Origin of Species*, directional selection, and the evolutionary sciences today. *Naturwissenschaften* 96, 1247-1263.
- KUTSCHERA, U., BRIGGS, W.R., 2009: From Charles Darwin's botanical country-house studies to modern plant biology. *Plant Biol.* 11, 785-795.
- KUTSCHERA, U., BRIGGS, W.R., 2012: Root phototropism: from dogma to the mechanism of blue light perception. *Planta* 235, 443-452.
- KUTSCHERA, U., NIKLAS, K.J., 2004: The modern theory of biological evolution: an expanded synthesis. *Naturwissenschaften* 91, 255-276.
- KUTSCHERA, U., NIKLAS, K.J., 2005: Endosymbiosis, cell evolution, and speciation. *Theory Biosci.* 124, 1-24.
- KUTSCHERA, U., NIKLAS, K.J., 2009: Evolutionary plant physiology: Charles Darwin's forgotten synthesis. *Naturwissenschaften* 96, 1339-1354.
- KUTSCHERA, U., WANG, Z.-Y., 2012: Brassinosteroid action in flowering plants: a Darwinian perspective. *J. Exp. Bot.*, in press.
- MATTA, C., 2010: Spontaneous generation and disease causation: Anton de Bary's experiments with *Phytophthora infestans* and late blight of potato. *J. Hist. Biol.* 43, 459-491.
- MCCLUNG, C.R., 2011: Plant biology: Defence at dawn. *Nature* 470, 44-45.
- ORBACH, R.L., 2011: Research vital to economic growth. *Science* 331, 1113.
- READER, J., 2009: *Potato: A History of the Propitious Esculent*. Yale University Press, New Haven.
- RODGERS, A.D., 1952: *Erwin Frank Smith. A Story of North American Plant Pathology*. Philadelphia: American Philosophical Society, Philadelphia.
- SACHS, J., 1865: *Handbuch der Experimental-Physiologie der Pflanzen*. Wilhelm Engelmann, Leipzig.
- SACHS, J., 1882: *Vorlesungen über Pflanzen-Physiologie*. Wilhelm Engelmann, Leipzig.
- SINGH, R.P., HODSON, D.P., HUERTA-ESPINO, J., JIN, Y., NJAU, P., WANYERA, R., HERRERA-FOESSEL, S.A., WARD, R.W., 2008: Will stem rust destroy the world's wheat crop? *Adv. Agron.* 98, 271-309.
- SKELSEY, P., ROSSING, W.A.H., KESSEL, G.J.T., VAN DER WERF, W., 2010: Invasion of *Phytophthora infestans* at the landscape level: How do spatial scale and weather modulate the consequences of spatial heterogeneity in host resistance? *Phytopathology* 100, 1146-1161.
- SMITH, E.F., 1911: Anton de Bary. *Phytopathology* 1, 1-2.
- SPARROW, F.K., 1978: Professor Anton de Bary. *Mycologia* 70, 222-252.

Address of the corresponding author:

U. Kutschera, Institute of Biology, University of Kassel, Heinrich-Plett-Str. 40, D-34132 Kassel, Germany / Department of Plant Biology, Carnegie Institution for Science, Stanford, California 94305, USA. E-mail: kut@uni-kassel.de