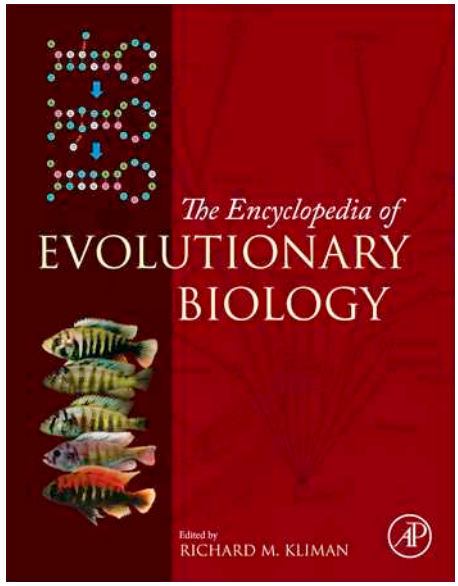

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Symbiosis, History of

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Glossary

Deism The idea that the universe follows natural, mechanical laws even though it was created by a deity. The deity is presumed not to intervene after its original creation act. Deism was introduced by Natural Philosophers and is foundational for nineteenth century Natural History schools.
Ecology The study of the 'household' of organisms, broadly conceived as including biotic and abiotic environmental interactions, often depicted in hierarchy theories ranging from populations and species to ecosystems, biomes, and biospheres.
Metamorphosis Pre-evolutionary idea that living organisms can transform, or change in form. Transformation and metamorphosis are precursors to transmutation and evolution theory.
Symbiogenesis Evolutionary mechanism that results from hereditary symbiosis.
Symbiont Any organism that engages in a symbiotic relation with one or more organisms – often used to designate the smaller partner in the symbiosis.
Theism The idea that a supernatural being has created the universe and intervenes in creation at will. This belief is foundational for the Semitic religions as well as early Natural Theology schools.

Defining Symbiosis

Symbiosis refers to the phenomenon whereby two or more organisms with distinct genealogical, evolutionary histories live in close association with one another (de Bary, 1878, 1879). Together, the host and its symbionts form a new biological entity that is sometimes called a *superorganism* (Spencer, 1876; Carrapiço, 2015), *holobiont* (Margulis, 1991; Guerrero *et al.*, 2013), or *symbiome* (Sapp, 2003: 33); and this newly formed entity is considered to be a single unit, either of *natural selection* (through its hologenome, Rosenberg *et al.*, 2007; Zilber-Rosenberg and Rosenberg, 2008), or of other evolutionary mechanisms. Symbionts can be acquired both vertically (during phylogenesis) and horizontally (during ontogenesis). When symbiosis becomes obligate and hereditary, it can lead to evolution by symbiogenesis (Margulis and Dolan, 2000: 157). But even without causing symbiogenesis, symbiotic associations can affect an organism's adaptation, reproduction and fitness, species extinction or speciation, and symbiosis can influence ecological systems (Brucker and Bordenstein, 2012; Margulis, 1991; Zook, 2015).

Is Nature 'Red in Tooth and Claw' or 'Social' – Origins of Symbiosis Research in Natural History Research and Its Relation to the Sociopolitical Sciences

Research on symbiosis originated in nineteenth century European Natural History Research. Natural History Research marked the beginning of the modern sciences and encompassed the physical, biological, and cultural sciences (Gontier, 2011). Rather than adhering to 'divine laws' specified in religious writings, utopian scholars such as Thomas More or Bernard Mandeville, and moral philosophers such as Thomas Hobbes, Adam Smith, David Hume, and Jean-Jacques Rousseau would search for 'natural laws,' and transition from a theist to a deist worldview. These moral philosophers are called Social-Contract theoreticians because they founded sociopolitical, secular thought by debating the fair and just distribution of 'public goods' and 'natural resources' across nations, the 'natural' 'division of labor,' and the 'common goods' (shared belief states) that socially bond individual citizens into a 'common wealth' (a nation) (Gontier, 2009).

Their theorizing on the 'naturalness' by which humans 'live together,' and what the most righteous sociopolitical societal structure is, would come to define liberal and social thought and lead to the rise of the major secular sociopolitical doctrines of the nineteenth and twentieth centuries (libertarianism, liberalism, socialism, Marxism (communism), communitarianism, national socialism, and democracy). These sociopolitical ideologies were formulated by drawing idealized analogies with the animal world (often in the form of fables), which in turn founded preliminary researches on 'animal societies' that developed into naturalistic, and eventually evolutionary research on biological species.

It is well-known that Darwin (Burrow, 1972; Barrett, 1977; Bowler, 1983; Smocovitis, 1996) was inspired by:

1. Adam Smith's liberal idea of free-market economy and his metaphor of the 'invisible hand';
2. Thomas Malthus's notions of 'scarcity of resources' and 'struggle for existence';
3. Herbert Spencer and Thomas Huxley's liberal ideas on sociocultural 'progress';
4. Jean Baptiste Lamarck's ideas of 'adaptation' and teleological progress in biology;
5. Francis Bacon's 'induction theory';
6. Charles Lyell's 'uniformitarianism'; and
7. Wilhelm von Humboldt and Auguste Schleicher's 'natural genealogies' of the Indo-European languages.

The early Darwinists did not distinguish the natural from the sociocultural sciences, and their evolutionary theories were a natural extension of sociopolitical, liberal Hobbesian thought – how the latter ideology defined the 'natural'

condition as well as the sociocultural and political life of humans and animals. For Hobbes (1651/2010), humans were like wolves, who in a 'natural state' found themselves at 'war' with other humans because they wanted to defend their individual freedom. Early Darwinists extended these ideas to the whole of nature and, in the words of Alfred Lord Tennyson, they saw nature as 'red in tooth and claw.' A struggle for existence results from a scarcity of resources, leading to a natural selection of the fit, at the expense of the maladaptive (Huxley, 1888; Bouglé, 1909).

Etymological analyses of symbiosis jargon demonstrate that, prior to the introduction into biology, many of the foundational concepts were also used to define sociocultural human relations and sociopolitical ideologies (**Table 1**). Early symbiologists, however, applied less-liberal or non-liberal, often socialist and communitarian language to characterize the living arrangements present in the natural world – ideas that were inspired by Rousseau's social-contract theory. Rousseau (1762/2001) understood humans as 'good natured' and inherently social beings that became corrupted by artificial societies. The human family, one of the basic units of law, is typified by its sharing of resources, and societal living is ideally characterized by reciprocal exchange and a fair (re)distribution of natural resources. Reciprocal and altruistic social rule-following enables the formation of a 'social-contract' that in turn allows for the establishment of a 'higher, common good' that founds the resurrection of the welfare state. As members of the welfare state, persons become citizens that create a community where, for the sake of the whole, individuals give up part of their freedom to live together. These social ideas were further developed by Pierre-Joseph Proudhon (1840, 1849) under the form of 'mutualism' (**Table 1**), and by Pyotr Kropotkin's (1902) work on 'Mutual Aid.'

The Sociopolitical Life of Animals: Commensalism, Mutualism and Parasitism in the Economy of Nature

Research on symbiosis in the animal world followed as an extension of these sociopolitical theories. Linnaeus introduced the concept of an 'economy of nature' in the eighteenth century (Egerton, 2015), and Haeckel (1866) developed these ideas further when founding the field of ecology. The 'division of labor' concept was introduced by the French naturalist Milne-Edwards (1827), in the context of orthogenetic developmental laws, in order to describe the origin of complex anatomical forms in a hierarchical (systems theoretical) perspective (D'Hombres, 2012).

As a forerunner of ecological thought, Pieter Harting, working at Utrecht University, wrote a Dutch work in 1862, 'On the industry (economy) of animals: for all those who love nature,' wherein he discussed the numerous crafts found in the animal kingdom, ranging from 'carpenters' to 'architectural builders' and 'cleaners.' By applying sociopolitical terminology, Harting (1862) conceptualized the 'economy of animals' in terms of 'distributions' of 'common and public goods,' as well as 'divisions of labor' that underlie a hierarchically structured animal society.

Harting's work inspired the Belgian Zoologist and Paleontologist Pierre Joseph van Beneden, a student of Cuvier, which in turn specify the nature of the *social* lives of animals, in particular how they establish communal living and how they share their food resources. In this context, he would introduce the terms *commensalism* (*commensaux*), *mutualism and parasitism* (**Table 1**).

For van Beneden,

> When taking a closer look at the animal world, it does not take long to find more than one analogy with human society. If I'm allowed to say so, there is not one social position found in human society that is not also found in the animal kingdom. Most of the animals live peacefully from the fruits of their labors, and exercise a profession that gives them life. But, at the sideline of these honest industrials, we also find miserable ones, who cannot do without the assistance of their neighbors, some of whom establish themselves as parasites in their organs, others as commensals (*commensaux*) that take profit from the gains (labors) of the honest. (Van Beneden, 1875: 2–3, my translation)

Commensals or *messmates* are merely companions at the table, they are allowed to dine with the host and feed on their neighbor's catch. They can live inside or onside their host (what we today call *endo- or ectosymbiosis*), and they can either live independently or forever remain fixed (today called *facultative and obligate symbiosis*). *Parasites* are those animals who live at the expense of their neighbor, they take advantage of their host and can endanger its life. *Mutualists* are animals that live onto one another without being either *parasites* or *messmates*. They receive 'asylum,' and either return 'mutual services' or develop 'sympathetic bonds' which attracts them to one another (van Beneden, 1873, 1875). van Beneden described such associations to exist throughout the animal kingdom, and he dedicated a chapter on the nature of *parasites* as causative agents of disease (**Figure 1**).

The different social living arrangements of animals, for van Beneden, demonstrated the existence of a Great Chain of Being, which in turn evidenced divine providence. He did not use evolutionary vocabulary, but he did assume that especially the 'fixed commensals' undergo 'metamorphosis.'

With the dawn of evolutionary thought, two distinct paradigms, one of competition and one of socialism would emerge to characterize societal living of human and other animals. Both paradigms were well-recognized in both the biological and sociocultural sciences as valid means by which to describe the natural world. In a review article written by Bouglé (1909), for example, in a volume commemorating the 50th anniversary of Darwin's *Origin*, competition and socialism were presented as distinct and complementary 'laws' by which biological and sociological phenomena evolve.

Herbert Spencer (1876), famous for interpreting natural selection theory as leading to the 'survival of the fittest,' would write on the social living arrangements amongst distinct animals from within the competitive paradigm. Spencer introduced the concept of the 'superorganic,' and investigated how different 'life forms' (biological species but also sociopolitical, cultural, and linguistic systems), brought forth a division of labor and a hierarchical organization of the natural world that enables a unilinear and evolutionary progressive way of living or being in the natural world. For him, the superorganic structure comprises a higher, societal whole, of which he sought out the social laws.

Table 1 Etymology of symbiosis jargon

Term	*Etymology*	*First usage in biology*
Consortia	Plural for *consortium,* from Latin *consors* (partner, wife, companion) and *consortio* (having the same destiny), first introduced in French as *consorte* in the fourteenth century to designate a husband's wife, and later in England, where, from the fifteenth century onward, it first became a legal term for 'the right of a husband to access his wife,' and later a term to designate larger associations and societies that are bounded by duties and rights (e.g., in the form of divisions of labor)	Introduced in botany to characterize symbiosis by Reinke (1873) and Famintsyn (1907)
Commensalism	From the French word *commencaux*, derived from fifteenth century, Middle Latin *commensalis* (coming around a table), and *cum mensa* (eating at the same table)	Introduced in zoology by Van Beneden (1873, 1875) in that meaning, as *commensaux*. In a first English translation of his major 1975 work in 1976, the *commensaux* were translated as *messmates*, which either derives from Middle English *mes* (for table, dinner, food, and eating together at the same table), or from the old French word *mesme* or *même* (which means even, same or equal)
Mutualism	Introduced in French in the late fifteen century as *mutuel*, derived from the Latin *mutuus* (reciprocal exchange). Originally, the word was used to designate feelings of both love and hate between individuals. The term roots the French words *mutuel* and *mutuellisme*, first introduced by Pierre-Joseph Proudhon (1840, 1849), to designate societal socialism in human and animal societies; and a year later in Brittan as *communitarianism* by John Goodwyn Barmby, to designate societal, communal lifestyles (*consortia*) with social care (e.g., social justice such as health care)	First introduced in biology by van Beneden (1875) in that meaning, and today characterized as one type of symbiosis
Parasitism	From the Greek word *parásit*os (a person or organism who lives at the expense of another, who receives free nourishment and protection). Introduced in natural and medical sciences from the Greeks onward. First reintroduced in Medieval French as *parasite* in the sixteenth century	In biological and biomedical sciences fundamental to describe pathogens, though the first introduction in this sense remains obscure. de Bary (1878) in botany, and van Beneden (1875) in zoology, already identified several microorganisms as causal agents of disease, ideas that would become reintroduced as foundational for the germ theory of disease in the late nineteenth century
Symbiosis	From Greek *sumbio*sis (companionship) and *sumbioun* (to live together). First reintroduced in German and English languages in the early seventeenth century, to designate 'communal or social life,' including the union or living together of distinct individuals as companions, also in marriage (community) as husband and wife. From the seventeenth century onward used to describe societal, community life	First introduced in botany, by Frank (1877) as *symbiotismus* in 1877, and as *symbiosis* by de Bary (1878, 1879)
Symbiogenesis	*Symbio-* stems from the Greek *symbiosis* and *-genesis* from *genesis* (origin, birth, production, generation, creation). Symbiogenesis means generation or evolution by symbiosis	First introduced in biology by Merezhkowsky (1905) and later also by Kozo-Polyansky (1924/2010), by Wallin (1927) as *symbionticism*, and by Sagan (1967)
Hereditary symbiosis	A symbiotic association that becomes permanently transmitted to future generations, foundational for symbiogenesis	First introduced by von Faber (1912) in Germany as 'erbliche Zusammenleben' (hereditary living together) of bacteria inside tropical plants. Translated into English as 'hereditary symbiosis' by Cowles (1915), and later adopted by Buchner (1921, 1939), Wallin (1927), Lederberg (1952), and Sagan (1967)
Symbiont/Symbiote	Derived from symbiosis to designate an organism that entertains symbiotic associations, first known use in 1887 in Germanic languages, and from 1909 in French as *symbiote*	The term symbiote was first introduced by Paul Portier (1918) in France
Synergy	From the ancient Greek *Synergia* (working together, cooperation, joint work, assistance or help). First introduced in the middle of the seventeenth century. By the mid-nineteenth century, used to designate group cooperation and communal group living that advances effects unobtainable by the individuals, which is why the whole becomes more than the sum of its individual parts	First introduced in biology in bio-economic, systems theoretical and hierarchical approaches to life (see e.g., Corning, 2013, 2014)
	References: http://www.oed.com/; https://www.wiktionary.org/; http://www.etymonline.com/	(Carrapiço, 2015; Gontier, 2015; Sapp, 1994)

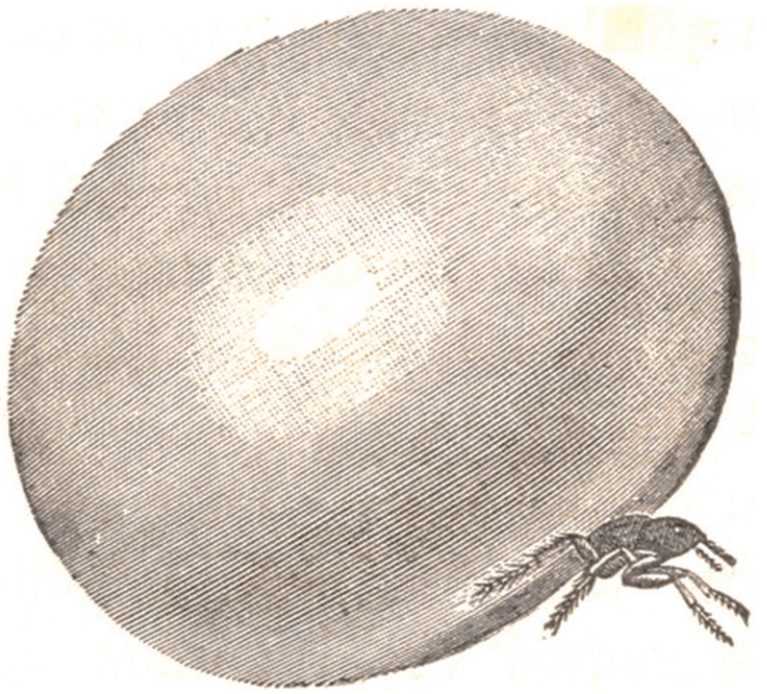

Figure 1 The swelling of a female chigoe flea (*Tunga penetrans*), a parasitic flea native to Latin America that partially penetrates the skin of mammals to breed, leaving an infectious blister. Used by Van Beneden (1875: 430) as an example of *temporary parasitism*.

Social Darwinians thus focused on competition, and many symbiologists understood these theories as direct extensions of liberal thought into biology. Symbiosis scholars critiqued by emphasizing that the sociopolitical and biological realms display many instances of social and mutualistic behavior, which they equally understood as 'lawful.'

Pyotr Kropotkin (1902) pioneered by understanding 'mutual aid' as a 'law of nature' that complements the principles or 'laws' of natural selection (Kropotkin, 1902). The first two chapters of his magnum opus focused exclusively on the 'mutual aid' found in animals. In the remaining chapters, from invertebrates to humans, he lists hunting and breeding associations as examples of socialism that contradict the sociopolitical ideas put forth by Hobbes, Malthus and Huxley. Battling, what Kropotkin (1902) called 'Huxley's (1888) gladiator show,' where organismal beings are characterized as 'naturally' amoral and asocial beings, Kropotkin instead makes the case that mutual aid and the division of labor is as 'instinctive,' and 'natural' as 'struggle for existence' is. For Kropotkin, the law of mutual aid helps eliminate competition and aids in the struggle for existence, enabling the establishment of social and political laws that bond organisms in communal lifestyles characterized by reciprocal altruism and cooperation (for a discussion see Dugatkin, 2011 or Sapp, 1994).

At the beginning of the twentieth century, parallels between the sociocultural and natural world appear to have come into disuse. An exception is Hermann Reinheimer (1913, 1915, 1920), who would continue to draw explicit parallels between the biological and social world. He developed a 'bio-economic' view of evolution and also identified symbiosis as a 'law of nature' (for a modern-day account on bio-economics and *synergy*, see Corning, 2013, 2014).

Today, and from within an extended synthesis, the similarities between reticulate biological and sociocultural evolution are being rediscovered (Gontier, 2007, 2012; Hird, 2010a,b; Kressing and Krischel, 2013).

Botanical Lichenology Studies and the Introduction of the Symbiosis Concept

Symbiosis research entered botanical studies through the study of lichens. Lichens are chimeric organisms composed of distinct symbionts (**Figure 2**). They grow on trees or rocks, and closer analyses of their foundational structures demonstrate thread-like, interwoven networks that resemble hair braids ('*Flechten*').

Lichens were first studied in pre-evolutionary times when German botanists including Georg Franz Hoffmann (1760–1826) and Georg Friedrich Wilhelm Meyer (1782–1856) attempted to provide morphological and taxonomic classifications of lichens. Hoffmann (1787, 1790–1801) classified lichens as plants and especially Meyer (1825) assumed that lichens arose 'spontaneously' while he interpreted the different morphological life-stages in terms of 'metamorphosis.' Both scholars' research perpetuated some of the basic terminology still used today to describe lichen morphology.

After the introduction of evolutionary thought, the works of Simon Schwendener (1828–1919), Christian Ernst Stahl (1848–1919), Johannes Reinke (1849–1931), Albert Bernhard Frank (1839–1900), and Heinrich Anton de Bary (1831–1888) and his students, would clarify the exact morphological nature of lichens (Kärnefelt *et al.*, 2012: 10).

Schwendener (1867, 1868a, 1868b) was the first to propose that lichens are 'new plants' with 'new characteristics' that

Figure 2 Lichens are chimeric organisms consisting of fungi that live in intimate symbiotic association with algae and/or cyanobacteria. These are some of Schwendener's (1868a) early drawings of lichens that demonstrate the dual nature of the organism.

originate from a reciprocal and intricate relation between two different organisms. For Schwendener (1868a: 3, my translation), lichens:

> enable insight into previously overlooked or completely misunderstood living relationships between two large plant groups, namely "algae" and "fungi" ("Pilze"). The algae are willing to serve as nutrition for the fungus that controls the algae. Despite these counterpropositions, however, the organisms are so intrinsically and reciprocally connected that through their penetration and merging, they constitute new plants with a clear individual character. For that reason, many authors classify them into an independent group as lichens ("Flechten").

The French scholar Jean-Baptiste Édouard Bornet (1828–1911), who first described the phylogeny of red algae, confirmed the dual nature of lichens experimentally. Bornet (1873, 1874) was able to separate the individual organisms, and noticed that when several of the fungal spores of the species he studies are disabled to establish associations with algae, they either die or are unable to reproduce because they germinate on the algae. He also noticed that such associations are formed rapidly during ontogeny (Fink, 1913), and thus outside the germ line.

Nonetheless, Schwendener's hypothesis and Bornet's experiments were fiercely criticized by their contemporaries (e.g., Kröber, 1874; and see Sapp, 1994), even though Famintsyn and Boranetski were also able to separate the individual organisms in 1876 (Khakhina, 1992), and experimental work by Stahl (1877) resulted in the laboratory formation of lichens from associating fungal spores with algae.

In the same year that Bornet conducted his experiments, Reinke (1873) had referred to the chimeric lichens in vitalist and sociopolitical terms, as a '*consortium*' ((**Table 1**), a concept that in turn relates to the *synergism* concept). This can be interpreted as a precursor of systems theoretical hierarchy theory and ecological thought in general as it would be developed by scholars such as Jacob von Uexküll and Ludwig von Bertalanffy in the beginning of the twentieth century. Reinke (1895, 1908), a scholar trained in both theology and philosophy, opposed both Darwin's selection theory as well as Haeckel's monism, and favored morphogenetic explanations for lichen development.

Two years after van Beneden had introduced his work on the social lives of animals, Frank (1877) characterized the association between the organisms that make up lichens as 'symbiotismus,' and defined it in terms of 'coexistence' (Sapp, 1994: 6). In the subsequent two years, de Bary (1878, 1879) reintroduced the ancient Greek concept of *symbiosis* (**Table 1**) to characterize the dual nature of lichens, and defined symbiosis as "the living together of unlike-named organisms." By basing himself upon the experimental work of his former students, Famintsyn and Stahl, de Bary developed the first theoretical framework on the appearance of symbiosis in the plant kingdom; a framework wherein he made direct reference to van Beneden's work. For de Bary, botanical symbiosis demonstrated the closest affinity to van Beneden's zoological mutualism concept (Seckback, 2002; **Figure 3**).

van Beneden and de Bary set the scene for all later theorizing on symbiosis because their work became available to a wide scholarly audience. The former's work was translated into English, and the latter's was summarized in the writings of his students and collaborators whom included Andrey S. Famintsyn (1835–1918), Sergei Winogradski (1856–1953), Martinus Beijerinck (1851–1931), and Ernst Stahl and Andreas Schimper (1856–1901). Scholars would opt for de Bary's symbiosis concept, and van Beneden's distinctions repeatedly became understood as types of symbiosis that specified the nature of the symbiotic relation.

Symbiosis in *All* Animals, Plants, and Protists and its Significance for Evolution

Microscopic advances steadily enabled better visualizations of pro- and eukaryotic cellular morphology, and botanists

Figure 3 Some of the pioneers in Symbiosis research, from left to right and top to bottom: Pierre-Joseph van Beneden (1809–1894), Simon Schwendener (1829–1919), Heinrich Anton de Bary (1831–1888), Andrey Sergeevich Famintsyn (1835–1918), Albert Bernhard Frank (1839–1900), Pyotr Kropotkin (1842–1921), Andreas Franz Wilhelm Schimper (1856–1901), and Paul Buchner (1886–1978).

identified the numerous cellular organelles found in plant cells. Between the 1860s and 1880s, Julius von Sachs (1859), Gottlieb Haberlandt (1876), and Schimper (1883) documented the role plastids (*'chlorophyllkörner'* or chlorophyll grains and *'Farbkörper'* or pigment corpuscles) play in the formation of starch and the coloring of the plant's leaves. Schimper (1885) furthermore noted that chlorophyll bodies (*'chloroplastiden'* or chloroplasts) divide in ways similar to bacterial division and suggested a symbiotic origin for the latter. As such, he first drew attention to symbiosis as an *intracellular* phenomenon, a theme that was later repeated and expanded by Paul Buchner (1921), who dedicated a full book on intracellular symbiosis (Sapp, 2002).

Andrey Famintsyn (1889a,b, 1892, 1907), the father of Russian plant physiology and a student of de Bary, studied both lichens and chloroplasts from a symbiotic point of view. Famintsyn is considered one of the pioneers of symbiogenesis theory, because he emphasized the adaptive role symbiosis plays in evolution by enabling the synthesis of new *consortia* (**Table 1**).

Symbiosis research also progressed from within the biomedical and bacteriological sciences where bacteria became understood as parasitic agents of disease. Ferdinand Cohn published a first systematic classification of bacteria in 1872; in 1876, Robert Koch associated the *anthrax* bacterium with the Anthrax disease ('Milzbrand-Krankheit') in cows; Pasteur's work on the germ theory of disease was read before the French Academy of Science in 1878; and Charles Louise Alphonse Laveran, the discoverer of the malaria parasite, was one of the first to, in 1880, recognize parasitic protozoa as causative agents of disease (Gontier, 2015b).

The positive effects of symbiosis also remained a topic of interest, especially in what regards its impact on ecology and the biosphere. Frank (1885) first described 'root symbiosis' (*'Wurzelsymbiose'*) that occurs between fungi and the roots of trees and plants, and he introduced the concept of *Mycorrhiza* (Carrapiço, 2015). At de Bary's lab, Winogradsky (1893, 1895) discovered nitrogen-fixing bacteria in the soil, which he called 'autotrophic' for their ability to synthesize chemical elements instead of devouring organic matter.

Beijerinck, another student of de Bary, also found *Rhizobia*, nitrogen-fixing, symbiotic bacteria present in the roots of legumes, and he was the first to point out their importance for agriculture (because rhizobia-rich roots and soil makes for fertile soil). Beijerinck is considered one of the founders of virology, and in nineteenth century academic circles, also de Bary (1861) was mostly known for his studies on plant diseases and for reporting on the life cycle of the fungus *Phytophthora infestans* that is parasitic on potatoes thereby causing potato blight (Gontier, 2015b).

Symbiosis found its way to America with the works of Roscoe Pound (1893) and Albert Schneider (1897) who integrated animal with plant studies in more general, and especially ecologically-oriented works on symbiosis (Sapp, 1994). Schneider (1897) first generalized de Bary's notion of symbiosis to *all* life forms, and he averred that symbiotic associations can occur between *more* than two individuals. He opens his work, 'On the phenomena of symbiosis' by saying that

> *All* living organisms manifest a more or less intimate biological interdependence and relationship. In fact, their very existence depends upon this condition, therefore no organism, no matter how simple or how complex its structure may be, is the result of a wholly independent phylogenetic development. (Schneider, 1897: 923, my emphasis)

Like Famintsyn, Schneider speculated about the evolutionary significance of symbiosis, when it first arose in

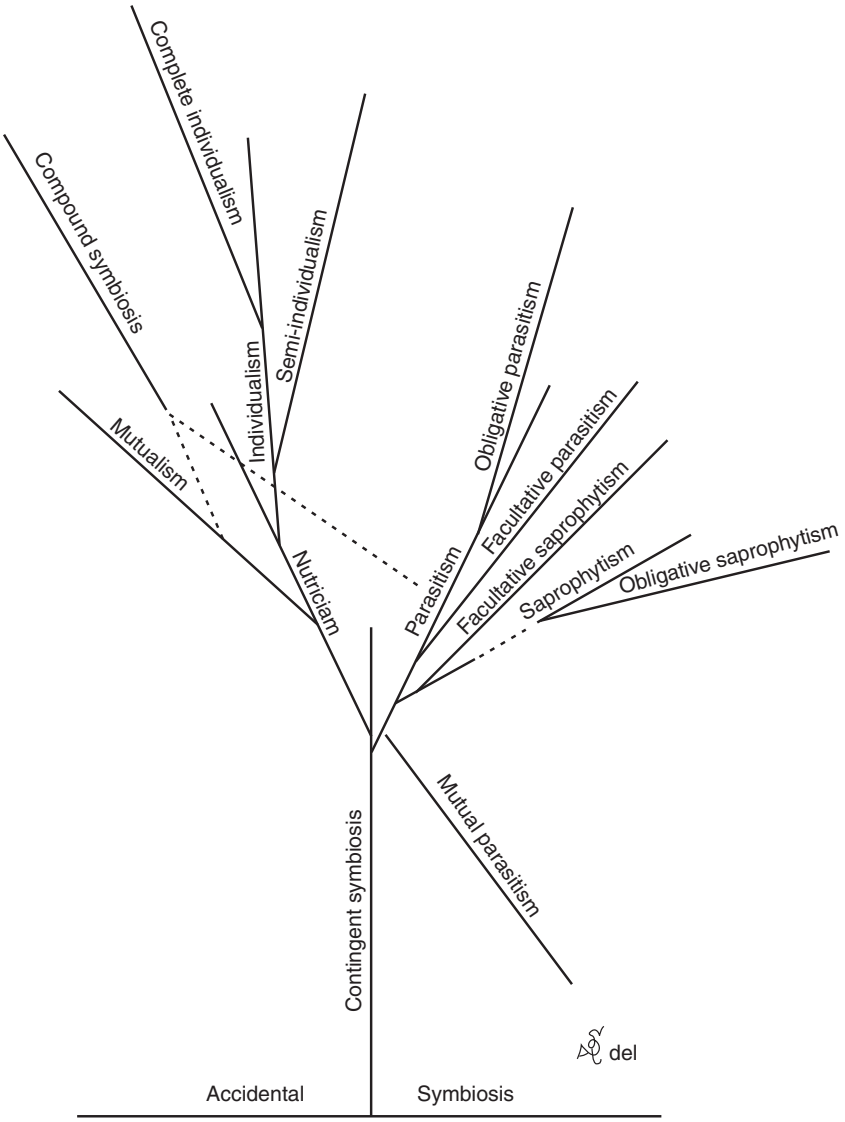

Figure 4 Schneider's phylogeny of the various types of symbiosis that evolved as an adaptive response to nutritional problems induced by the scarcity of resources and the struggle for existence.

time, and how it relates to natural selection. By associating symbiosis with a 'loss or acquisition of assimilated food-substances,' he understood symbiosis in nutritional terms, as an adaptive response to the struggle for existence that exists because of the scarcity of resources. In other words, for Schneider, it was hunger and a drive to reproduce ('food requiring and reproductive life-action of the organism'), that by necessity engaged organisms in forming symbiotic associations.

The emergence of symbiosis, for Schneider, was a process that required long periods of evolutionary time. He assumed that individual organisms evolved first, and because of their independent evolution, they were originally not equipped to form such relations, so they had to evolve them over the course of evolution. Schneider tried to synthesize natural selection theory with symbiology, in a 'coevolutionary,' 'ecological sense' *avant là lettre*. He described how symbiotic partners developed morphological adaptations to facilitate the symbiotic relationship, that went from parasitic and facultative to obligate and mutual.

Mimicry, for example, was a type of 'mutual adaptation,' a mutually evolved symbiosis. Other examples were the relation between the male and female reproductive cells, as well as the relation between mothers and their developing embryos. Schneider also brought symbiosis to entomology, by discussing numerous cases of symbiosis in insects and between insects and plants.

In his small but rich paper, he furthermore provided a layout for new terminology, by expanding the various types of symbiosis, and by pouring them into an evolutionary taxonomy (Figure 4). Schneider appears to have been engaged in reconstructing the evolutionary genealogy of the various types of symbiosis that evolved over the course of evolution.

Reduction of Symbiosis Studies to Ecology and Developmental Biology until the Advent of Symbiogenesis Theories

In 1885, Auguste Weismann developed his *Keimplasm* theory of descent that stated that hereditary traits are only transmitted through the germ line. It put a halt to neo-Lamarckian and evolutionary developmental studies, that because of their focus on ontogenetically acquired traits, became less and less understood as relevant for the study of evolutionary phylogenesis. Weismann's ideas were later synthesized with Theodor Boveri's and Walter Sutton's chromosome theory that identifies the chromosomes as bearers of hereditary traits. The rediscovery of Mendelian hereditary laws, and advances in theoretical and experimental population genetics as well as molecular genetics caused symbiosis to be studied from within fields such as ecology and developmental biology rather than evolutionary biology.

Symbiosis became understood as an ontogenetic or developmental, adaptive behavioral response to nutritional problems brought forth by the scarcity of resources and the struggle for existence. Nonetheless, in the margins of standard, Neo-Darwinian evolutionary theory, the evolutionary significance of symbiosis would remain studied by scholars who investigated cytoplasmic inheritance (for a discussion see Sapp, 2003; Gontier, 2015a) as well as ecological interactions (for a discussion see Egerton, 2015).

Some of the most important symbiologists at the beginning of the twentieth century were Frederick Keeble (1910), Paul Buchner (1921), Maurice Caullery (1922), George Nuttall who founded the *Journal of Hygiene and Parasitology* in 1901 and 1908, Lemuel R. Cleveland (1923).

Eventually, the recognition that 'hereditary symbiosis' can lead to symbiogenesis, and idea introduced by von Faber (1912) and brought to an English readership by Cowles (1915) and Buchner (1921), would reintroduce symbiosis studies into evolutionary biology.

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See also: Coevolution, Bacterial-Phage. Commensalism, Amensalism, and Synnecrosis. Cooperation and Public Goods, Bacterial. Lichen-Forming Fungi, Diversification of. Mutualism, the Evolutionary Ecology of. Plant–Pollinator Interactions and Flower Diversification. Predation and Parasitism. Sperm Competition. Symbiogenesis, History of. Symbiosis, Introduction to

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http://www.dnai.org/timeline/
DNA Interactive, Cold Spring Harbor Laboratory (features animations and historical timelines on the discoveries of the biochemical nature of DNA).

http://iss-symbiosis.org/
International Symbiosis Society (International Society that groups symbiologists).

http://www.nature.com/nrmicro/index.html
Nature Reviews Microbiology (Journal that regularly features review articles on symbiosis and related topics such as the microbiome and viriome).

http://www.asm.org/index.php/choma3/71-membership/archives/7852-significant-events-in-microbiology-since-1861
Significant Events in Microbiology 1861–1999, American Society for Microbiology (features major events and timelines in symbiosis, lateral gene transfer, genetics, and biomedical sciences).

http://www.springer.com/life+sciences/evolutionary+%26+developmental+biology/journal/13199
Symbiosis Journal (Official Journal of the International Symbiosis Society).