ИССЛЕДОВАНИЯ

Symbiosis: "Living Together" in Chaos

Bradford D. Martin**, Ernest Schwab**

*La Sierra University, Riverside, CA, USA; Loma Linda University, Loma Linda, CA, USA; bdmartin@llu.edu
**Loma Linda University, Loma Linda, CA, USA; eschwab@llu.edu

Confusion has plagued the definition of the term symbiosis for over 130 years. Within a few years of coining the term in 1879 by Anton de Bary, some biologists started to redefine the meaning and usage of the term that simply means "living together." A lack of consensus ensued, resulting in a long history of disagreement on how to use this relevant and unifying biological term. This paper documents the history of the various definitions, the controversy and debates, and the attempts to unify biologists to a common definition and usage of symbiosis. In recent times, not much debate has occurred and a few biologists are now refusing to use this confusing term. However, most biologists continue to use symbiosis and the frequency in how it is defined in current general biology textbooks has intuitively evolved back towards de Bary's original definition. Some confusion may stem from the infrequent usage of endo-/ectosymbiosis terms to describe the level of intimacy and permanency in symbiotic interactions. Confusion in secondary symbiotic terminology, such as symbiont, commensalism, parasitism, parasitoidism, predation, grazing, herbivory, and carnivory, also exists and is discussed.

Keywords: symbiosis, symbiotic terminology, confusion, Anton de Bary, mutualism, commensalism, parasitism, parasitoidism, predation, grazing, competition.

Introduction

> The history of ideas is paved by constraints of language.
> Leo W. Buss, 1987

> We scientists shouldn't argue endlessly about the definitions of terms. We should try to use them unambiguously in ways that conserve their meanings for listeners and readers.
> R.A. Lewin, 1982

Symbiosis may be the greatest enigma in the history of biological terminology. Historically, there exists over 130 years of confusion in the definition of symbiosis (Sapp, 1994). Despite the protracted disarray with the various meanings, it is still used today, indicating its centrality to

biology. Some would argue that the confusion will never be resolved and that we must learn to live with the chaos by defining the term whenever it is used (Hertig et al., 1937; Whitfield, 1979; Bronstein, 1994; Wilkinson, 2001) and not to be concerned with multiple definitions (Whitfield, 1979; Lewin, 1982; Wilkinson, 2001). However, complex scientific language allows accurate communication, but only if the terms are clearly defined.

Most biological terms evolve as ideas and concepts change (Whitfield, 1979; Lewin, 1982; Sapp, 1994; Wilkinson, 2001). This change can lead to multiple definitions wherein the terms become somewhat ambiguous or abstract. Ideal language devoid of multiple meanings in biology is rare in practice (Keller and Lloyd, 1992). Although symbiosis may carry some conceptual abstractness, competing definitions exist that are relatively concrete. These definitions differ only in which species interactions are included under the scope of symbiosis. To add to the chaos of symbiosis proper, there is also a large amount of secondary confusion that has further distracted biologists from a general consensus on the main term.

A historical overview is needed to document the confusion in its complexity and completeness. This paper presents a detailed account of the multiple definitions and usages of symbiosis and its related terminology, revealing the extent of the confusion that has plagued biology for over a century. This article will focus primarily on individuals who were pivotal in the use and definition of symbiosis and related terms. The numerous quotes presented in this paper were necessary to convey the nature and tone of debate and controversy in the variable usage of symbiotic terminology.

Origin of the Term Symbiosis

The name symbiosis was coined by Anton de Bary (1879, p. 5; Fig. 1) and he defined it literally as the "living together of dissimilarly named organisms." He believed that it should include parasitic, commensalistic, and mutualistic relationships between different species (Hertig et al., 1937). De Bary was a plant pathologist, so he explicitly included harmful as well as beneficial interactions between species in his definition of symbiosis (Douglas, 1994). It appears that de Bary was not the one to introduce or foster the subsequent restrictive definition that created the initial confusion with his original broad definition.

Interestingly, Hertig et al. (1937, p. 327) states de Bary's "almost casual way in which the term was introduced in the 1879 symbiosis pamphlet, together with its use in the title, might give one the impression that it had been used previously in the literature." Sapp (1994, p. 6) contends that de Bary did not coin the term symbiosis, but rather it was Albert Bernhard Frank (1877; Fig. 2) who first used the word *symbiotismus*. Frank stated:

> "We must bring all the cases where two different species live on or in one another under a comprehensive concept which does not consider the role which the two individuals play but is based on the mere coexistence and for which the term Symbiosis [*Symbiotismus*] is to be recommended" (Frank, 1877, p. 195).

De Bary used the term *symbiose* (de Bary, 1879) and either term, *symbiose* or *symbiotismus*, would be valid equivalents to our current term of symbiosis. De Bary also referred to Frank (1877) in some of his writings. However, de Bary clarified the various associations that ranged along a continuum from parasitism to commensalism to mutualism (Sapp, 1994, p. 7). Although Frank appears to have coined the term, the literature overwhelmingly credits

de Bary with originating the term, as well as providing the broad definition that includes parasitism, mutualism, and commensalism (Hertwig, 1883; Pound, 1893; Schneider, 1897; McDougall, 1918; Hertig et al., 1937; Hegner, 1938; Scott, 1969; Read, 1970; Lewis, 1973; Hall, 1974; Cooke, 1977; Whitfield, 1979; Lewin, 1982; Goff, 1982; Boucher, 1985; Smith and Douglas, 1987; Margulis, 1990; Sapp, 1994; Bronstein, 1994; Douglas, 1994; Paracer and Ahmadjian, 2000; Wilkinson, 2001; Sharma, 2009). The failure to recognize A.B. Frank is further demonstrated by the following 1937 report on definitions of symbiosis:

> "Oskar Hertwig (1883) made it clear that it was de Bary who proposed the term, and the writer of this report has found no reference to it earlier than the symbiosis address" (Hertig et al., 1937, p. 327).

Related to the definition of symbiosis, the field of study that encompasses symbiosis appears to have been defined relatively late in the history of symbiotic terminology by Clark Read in 1970.

Fig. 1. Anton de Bary

> "Although general study of symbiosis has not been dignified by a term to designate it as a field of research, it seems logical to refer to that field as symbiology" (Read, 1970, p. 1).

Other Parameters in the Definition of Symbiosis

Most biologists believe that de Bary's definition also implied that symbiosis included only interactions that are "intimate" (Hertig et al., 1937; Read, 1970; Trager, 1970; Goff, 1982; Douglas, 1994; Brooker et al., 2011; Reece et al., 2011; Russell et al., 2011; Solomon et al., 2011) or "intimate and permanent" (Hegner 1929; Caullery, 1952; Scott, 1969; Lewis, 1973; Hall, 1974; Whitfield, 1979; Thompson, 1982; Smith and Douglas, 1987; Howe and Westley, 1988; Margulis, 1990; Saffo, 1992; Bronstein, 1994; Starr et al., 2009; Miller and Levine, 2010; Stock et al., 2010; Freeman, 2011; Raven et al., 2011; Sadava et al., 2011), although biologists argue over this issue. Angela Douglas (1994, p. 1) states that de Bary "excluded associations of short duration" and that "insect pollination of flowering plants is not (a symbiosis)" and George Scott (1969, p. 2) explains "De Bary's broad concept of symbiosis clearly did not include associations in which interdependence is only of a secondary nature; nor did he consider chance associations of an ephemeral nature <…>" Conversely, Ahmadjian and Paracer (1986, p. 3) state "he included in his definition all cases of intimate associations, including epiphytes growing on trees and insects pollinating flowers." Also, "We consider pollination to be a type of symbiosis, as did de Bary" (Paracer and Ahmadjian, 2000, p. 11). Many other authors agree that de Bary defined symbiosis with a very broad definition that includes less intimate species associations (McDougall, 1918; Hegner, 1929; Read, 1970; Whitfield, 1979). Jan Sapp states:

> "<…> de Bary recognized that the term symbiosis might equally apply to looser associations such as that between pollinating insects and flowers and those between animals that search for food or shelter and animals and plants that supply it. He had no objections against making this generalization. To the contrary, he wanted to show that all these phenomena were related" (Sapp, 1994, p. 9).

This apparent contradiction in definitions is due to opinions of what is considered "intimate" or more importantly, a reciprocally influential interaction (Peacock, 2011). One author has even reversed a previous stance on intimacy being required for a symbiosis (Lewis, 1974, 1985).

Early Use of de Bary's Definition in the First 20 Years (1879–1899)

Only 14 years after de Bary coined the term, Roscoe Pound stated:

> "While mutualism, in the case of plants, can only exist with symbiosis, in the larger portion of cases of symbiosis there is no mutualism" (Pound, 1893, p. 509).

This clearly illustrates that Pound agreed with de Bary's broad definition. However, the confusion caused by the restrictive definition was obscurely initiated, as well as during this era he also stated:

> "Symbiosis in the strict sense and mutualism are often confounded, that is, the term symbiosis is often used to mean mutualism" (Pound, 1893, p. 509).

Less than 5 years later, biologists such as Albert Schneider (1897) acknowledged that etymologically the word symbiosis signified a living together and was therefore perfectly fit for use in the broader sense (Sapp, 1994, p. 32).

Misuse in the Next 70 Years: "Symbiosis = Mutualism" (1900–1970)

> "Equating symbiosis only with mutualism was a historical accident" (Ahmadjian, Paracer, 1986, p. 4).

Despite de Bary's clear definition with the inclusion of parasitism, some biologists continued to misinterpret the term symbiosis as a synonym for mutualistic or nonparasitic interactions. This stems from the common usage in language where symbiosis always implies a cooperative relationship that is beneficial to both parties (Boucher, 1985; Saffo, 1992). Less than 10 years after Pound (1893), continuation of this misinterpretation was discussed by Noël Bernard (1902):

> "<…> Bernard was reluctant to employ the term symbiosis since it 'had deviated from its etymological meaning,' to 'imply a useless finalist hypothesis'. The useless finalist hypothesis was 'symbiosis <…> taken in the sense of the association of two specifically distinct beings which harmonize their functions for the greater good of the community'" (Sapp, 1994, p. 78).

This was followed by a series of publications in the early 1900's (Hertwig 1906; Nuttall 1923; Meyer, 1925; Cleveland, 1926; Hegner, 1929) that perpetuated the misuse. Interestingly, Hertwig's (1906) restrictive view is a reversal from an earlier publication (Hertwig, 1883) in which he used de Bary's original definition (Hertig et al., 1937, p. 327). Also, Robert Hegner stated:

> "Symbiosis is a term that is frequently employed to describe a certain type of association between two species of organisms. This term was proposed by de Bary in 1879 for the constant, intimate, and mutually beneficial association of two organisms. Etymologically, symbiosis means simply 'living together', and hence should include parasitism and other types of association. Usually, however, symbiosis is used to imply the permanent association of two specifically distinct organisms so dependent on each other that life apart is impossible" (Hegner, 1929, p. 5).

Fig. 2. Albert Bernhard Frank

The above paragraph by Hegner reads exactly the same as in his 1938 edition, except for the removal of "for the constant, intimate, and mutually beneficial association of two organisms" (Hegner, 1938, p. 3). This correction indicates that he realized he had misquoted de Bary in the 1929 edition, deleted the inaccurate wording, and now recommends the original broad definition.

Others during this era misquoted or purposefully ignored de Bary's definition as seen in the following examples:

> "The term symbiosis as originally used by de Bary (1879) means living-together of two organisms on a partnership basis. <…> but each organism must receive some benefit from its partner or else the association is not one of symbiosis" (Cleveland, 1926, p. 51).

> "This term was created by A. de Bary in 1879, to designate the intimate and constant association of two organisms with mutual relationships assuring them of reciprocal benefits" (Caullery, 1952, p. 217).

Illustrations of deliberate change from broad to narrow usage are observed in the following instances:

> "In 1883 he [Oskar Hertwig] read a paper <…> He used the term *symbiosis* in precisely the same broad sense as de Bary, cited with approval van Beneden's term *mutualism*, and specifically included *parasitism* under *symbiosis*. However, in his textbook, 'Allgemeine Biologie' (1906), on page 392 he stated, in referring to associations with mutual benefit, that 'such a relationship the botanist de Bary has named symbiosis'" (Hertig et al., 1937, p. 327).

Lewin (1982, p. 254) states that Hertwig started using the restricted definition in 1883. This is not correct, as the above paragraph states it was 1906 when he abandoned de Bary's broad

definition in favor of the restricted definition. George Scott argued in favor of the restricted definition after acknowledging de Bary's clear definition in which parasitism was included:

> "Parasitism <…> De Bary described it as the most exquisite example of symbiosis – but when we note that the relationship between host and parasite is essentially one of unilateral or non-equilibrated symbiosis, there is room for doubt about its inclusion within the restricted concept of the term" (Scott, 1969, p. 3).

It would almost appear that this group of biologists hijacked symbiosis from its original intended definition by de Bary. The term endomutualism should have been adopted and used by these biologists to describe the symbiotic phenomena of their interest, but it appears absurd to rationalize that symbiosis = mutualism. In doing so, the broad categorical term (i.e. symbiosis) has been reduced to a synonym of one subset (i.e. mutualism).

Permission to Perpetuate the Confusion in 1937

After the misuse of symbiosis in the early part of the 1900's, the confusion became so distracting that in 1937 the American Society of Parasitologists appointed a committee to investigate and clarify the meaning of symbiosis and other related terms (Hertig et al., 1937). This committee concluded that:

> "Formal recommendation <…> as to future usage of the term symbiosis seems hardly necessary. It is obvious that de Bary should not be cited as having defined it in the sense of strict mutualism. It may be maintained by some that the wide usage has in fact thus narrowed the term, but this can hardly set aside the historically correct and still current usage in the broad sense. It follows that the present confusion necessitates the definition of the term whenever it is used" (Hertig et al., 1937, p. 328).

Although the committee states it did not make a formal recommendation, it essentially gave permission to all biologists to continue defining symbiosis according to their own personal preference and thus perpetuated or even exacerbated the confusion.

In more recent times, the restrictive view of symbiosis defined as only mutualism has continued (Burkholder, 1952; Caullery, 1952; Haskell, 1972; Whitfield, 1979; Lewin, 1982) and some have expanded this definition to also include protocooperation (Richardson, 1977), commensalistic and neutralistic associations (Pianka, 2000), or "no permanent stimulation of defensive reaction mechanisms" (Scott, 1969, p. 3). Others recognize both the restrictive definition and de Bary's definition (Bronstein, 1994; Barbour et al., 1999; Bush, 2003; Odum and Barrett, 2005; Krebs, 2009).

Frustration with Confusion is Not New

Frustration with the confusion of symbiotic terminology is not new, for both those who defended de Bary's broad interpretation, as well as those who accepted (sometimes in defeat) the newer synonymic definition for mutualism. As noted in the section on 1879–1899, the first expression of frustration was by Roscoe Pound, a de Bary proponent, when he acknowledged the confusion starting in the early 1890's where symbiosis in the strict sense and mutualism are

often confounded (Pound, 1893). W.B. McDougall (1918) also documented the early confusion by citing seven different published definitions and several proposed classifications of symbiosis, while thoroughly comparing these with de Bary's broad definition. He believes the confusion and restrictive definition resulted from de Bary's narrow focus of research in lichens, without elaborating upon a classification for all the various types of symbiotic interactions (McDougall, 1918, p. 250–252).

Even during the 1900–1970 era of the restrictive definition, some biologists who used the restrictive definition expressed that they did not like it. L.R. Cleveland wrote:

> "Parasitism proper, or in the general sense, according to fairly well-established usage, covers all three associations: commensalism, symbiosis, and true parasitism. It would be much better, however, to use the term symbiosis, which means living together, and under it include commensalism, mutualism, and parasitism. However desirable such a change in terminology may be, it is not an easy matter to make it, and I shall not attempt it at this time" (Cleveland, 1926, p. 52).

Two years after this, Hegner (1929) stated his displeasure with the restricted definition of symbiosis and reversed his restrictive view a few years later to de Bary's broader view, as noted earlier in the section on 1900–1970 (Hegner, 1938). Clark Read expressed this view:

> "The term used by De Bary was *symbiosis*, which means nothing more than 'living together.' <…> Although there is value in using the term symbiosis, in the general sense indicated above, many authors have applied it in a restricted sense to mutually advantageous associations" (Read, 1970, p. 3).

D.L. Lewis stated that "Zoologists <…> and microbiologists <…> urge a return to the broad, de Bary concept but, within mycology, the dichotomy remains despite spoken <…> and written <…> pleas for integration" (Lewis, 1973, p. 262) and "I would like to hope that what follows will be the last word but am under no illusions that this will be the case!" (Lewis, 1985, p. 29).

M.P. Starr (1975), who proposed a radically different, broad approach to symbiosis, expressed a very high amount of frustration by stating:

> "The terminology presently used for labeling organismic associations is confusing, parochial, and highly imprecise. <…> It is logically and semantically monstrous to give both a class and an included subclass the same name, yet that has been the fate of the term 'symbiosis'; <…> 'Symbiosis' is an eminently appropriate term for the superclass of most of the phenomena under consideration here <…>. I have now come to the conviction that it is high time to reverse the semantic deterioration" (Starr, 1975, p. 1–3).

Two years later, Roderic Cooke described the restricted definition as erroneous:

> "<…> the term symbiosis has come to be erroneously restricted to associations that are characterized by mutualism. <…> Currently, there does, however, seem to be movement towards a restoration of its initial broad meaning, although even so there is some reluctance to apply it to associations that do not involve prolonged or permanent intimate contact <…> Symbiosis is, therefore, used here in the all-embracing sense to refer to *all* associations <…>" (Cooke, 1977, p. 4).

Although a promoter for the restrictive definition of symbiosis, due to a "growing consensus in the biological literature" (Whitfield, 1979, p. vii), Philip Whitfield stated he was perplexed with what was happening to the broad definition:

> "It will be necessary, though, to discuss the unfortunate confusion of terms which already exists in this area to perplex both student and research worker alike. <…> Thus it was an all-embracing term including the vast majority of interspecific associations between organisms. De Bary did not in any way constrain the breadth of his concept by reference to the way in which organisms lived together. <…> Unhappily this beautifully general term has been rendered almost unusable without further qualification because it came to be used for a more specific area of associations" (Whitfield, 1979, p. 6–7).

Following with a stronger position, R.A. Lewin stated "To urge us now to go back to original or outdated definitions is, I think, counterproductive" (Lewin, 1982, p. 259). Lynda Goff countered his argument in the same issue of Bioscience with "What better word could be applied to all the individual associations that fall along this continuum of physiological interactions than de Bary's term symbiosis" (Goff, 1982, p. 256). However, she was incorrect in saying "It is urged that the 1937 recommendation of the Committee on Terminology to the American Society of Parasitologists, to employ the term symbiosis in the broad and 'historically correct' context in which it was originally defined, be accepted once and for all <…>" (Goff, 1982. p. 256). The committee actually stated "Formal recommendation by this Committee as to future usage of the term symbiosis seems hardly necessary" (Hertig et al, 1937, p. 328). They recommended defining the term whenever it is used, due to the confusion (see "Permission to Perpetuate the Confusion..." above). Another inaccuracy, Lewin (1982, p. 256) states that Cooke (1977) recognized the generally accepted restricted usage, but deplored it as erroneous. Although deplored as erroneous, he personally continued to use a very broad definition, including neutralism (Cooke, 1977, p. 4).

D.L. Lewis strongly opposed opinions like Lewin's (1982) above and stated "because their view (Lewin and others) is often repeated in textbooks, it does not mean that it is correct!" (Lewis, 1985, p. 29). A few years later, Smith and Douglas (1987, p. 1) wrote "many biologists have subsequently equated symbiosis with mutualistic associations <…> However, this more restrictive use of the term is frequently difficult to apply to real associations. <…> For such reasons, de Bary's original definition of symbiosis is preferred by a number of biologists <…> and is adopted in this book." This was followed by Lynn Margulis (1990, p. 673) who added "Biology textbooks define symbiosis anthropocentrically—as mutually helpful relationships <…> However, the research scientists today studying symbioses embrace de Bary's original definition in modern guise: symbiosis refers to protracted physical associations among organisms of different species without respect to outcome". Mary Saffo agrees with this view and stated:

> "Several authors formally embrace <…> or even promote <…> de Bary's outcome-independent usage of symbiosis, but then focus on cooperative, benign, or non-pathological instances of symbiosis in ways which implicitly <…> or explicitly <…> exclude parasitism or pathogenic associations from the purview of symbiologists. <…> Thus, the current confusion does not stem from misunderstanding de Bary. It arises instead because we do not have a language to discuss benign or mutualistic interspecies interactions, including 'mutualistic' symbiosis; with this deficiency we tend to preempt the larger term for this restricted use" (Saffo, 1992, p. 20).

The problem that Saffo (1992) describes above is clearly illustrated by Angela Douglas (1994, p. 1) who discusses the problems with the term symbiosis and explains "no definition is universally accepted." She initially acknowledges that looser mutualistic interactions and parasitism should possibly be included, however, indicates that parasitologists do not accept this today. Ironically, she ends the discussion on terminology and the remainder of her book deals with mutualistic or nonparasitic interactions where she consistently and exclusively uses the term symbiosis when referring to these interactions.

It would appear from the history presented above that the claim by proponents of the restrictive mutualistic view of symbiosis is not at all a growing consensus other than for the early 1900's. In fact, it would appear to have been the opposite, at least for the more vocal researchers of those later times. The growing consensus may have reflected more of the textbook, informal, or conversational definitions that were popular during those periods.

Attempts to Correct Terminological Confusion

W.B. McDougall (1918) was one of the first biologists to propose a unified approach to symbiosis. He recognizes three authors who influenced his proposed classification that includes *conjunctive* and *disjunctive* symbiosis (i.e. endosymbiosis and ectosymbiosis). He states:

> "The classification which is given below is believed to be at once simple enough in its conception and broad enough in its definition and scope to include all phenomena that should be embraced under symbiosis. Symbiosis is defined as the living together of dissimilar organisms. Any more limited definition proves unsatisfactory because of the difficulty of drawing lines of separation between kinds of phenomena among living things. Only by including all phenomena of the living together of organisms can this difficulty be avoided" (McDougall, 1918, p. 254).

To elaborate, he states that many authors who utilize the restrictive definition of symbiosis, include leaf cutting ants and their mushroom gardens as an example of symbiosis. He points out that this is essentially no different than a man and his vegetable garden, and only a short step away from a cow and the grass upon which it feeds. H.C. Cowles agrees stating "The term is much needed <…> for there is no other term of such broad and general nature" (Cowles, 1921). Interestingly, both authors state that mutualism does not exist, and that such apparent beneficial relationships are simply reciprocal parasitism (McDougall, 1918).

Paul Burkholder (1952) also entered the symbiosis discussion by introducing his famous table with a complete list of biologically possible species interactions, symbolized by +, -, and 0 effects in "on" and "off" conditions. Interestingly, "He initiated a long history of the confusing use of the terms symbiosis and parasitism by equating them with outcomes and by describing 'symbiosis' as only a mutually beneficial interaction" (Tuininga, 2005, p. 266).

M.P. Starr (1975) was one of the more recent outspoken biologists to try to unify symbiotic terminology by reversing the common restrictive definition of symbiosis and proposing a revolutionary, broad system based on criterional continua. He considered all species interactions to be symbiotic and that they blended together on spectra for eight evaluated criteria: 1) spatial, 2) relative size, 3) temporal, 4) necessariness, 5) independence, 6) nutritional, 7) specificity, 8) harmful or beneficial effects, and 9) integrational criteria (Starr, 1975, p. 7). His system views symbioses to be interactions between two organisms (more than two was considered to be *hypersymbiosis*) that are alive at least from the initial interaction. Also, the interaction can be transient to persistent as well as interspecific or intraspecific (*heterosymbiosis* vs. *homosymbiosis*). Richard Dawkins also believes in including intraspecific associations (Dawkins, 1976, p. 197). Starr's scheme allows for intermediate categories and doesn't emphasize one aspect of the relationship above others. However, some continua are not as yet quantifiably assessable. He has been criticized by Philip Whitfield who believed that Starr's classifications do not telescope down to easily handled labels and that they could not supplant the old labels (e.g. parasite, predator, mutualist, commensalist, etc.).

He maintained that these old names, no matter how fuzzy their definitions may be, are essential for concise communication (Whitfield, 1979, p. 14).

Ten years later, D.L. Lewis approached the symbiosis confusion by ingeniously modifying Starr's (1975) scheme. He proposed a symbiotic continuum that evaluated criteria on: 1) fitness, 2) duration, 3) relative size, 4) physical contact, 5) specificity, 6) nutrition, 7) interdependence, and 8) integration (Lewis, 1985, p. 34). These correspond closely with Starr's criterional continua, but are more refined. The fitness continuum of Lewis includes six types of interactions: competition, amensalism, agonism, neutralism, commensalism, and mutualism (Lewis, 1985, p. 34). Antagonism is defined as including competition, amensalism, and agonism, while agonism is subdefined as including only predation and parasitism (Starr, 1975, p. 7; Lewis, 1985, p. 30).

A broad view of symbiosis does not usually include competition, amensalism, and neutralism, although Lewis (1985) argues that within the definition of de Bary, a living together of dissimilarly named organisms, there is no reason why the concept should not be extended to include them. Several general ecology authors agree with this expanded broad definition as well (Kormondy, 1996; Odum and Barrett, 2005; Krebs, 2009; Sharma, 2009). However, like Starr (1975), Lewis also considers intraspecific interactions and transient associations to be symbiotic. His concept of symbiosis merely requires two organisms to have an effect on each other's fitness. He maintains that by adopting the above view:

> "<…> symbiotic interactions become universal, <…> and can merely be contrasted with asymbiosis—interactions with the non-living (abiotic and dead) environment <…> This is what should happen to the concept of symbiosis. In this way <…> the discriminatory value of the word *symbiosis* is downgraded by its very broadness. It can be withdrawn from the semantic melee involving mutualism, parasitism, etc. but persist as the term for interactions in the widest possible sense. With this much debated concept safely on the sidelines, attention can instead become focused more sharply on different aspects of biological interactions" (Lewis, 1985, p. 31).

Lewis (1985) treads on the fuzzy borders of symbiosis and asymbiosis by including saprotrophy (although in parentheses) in a nutritional continuum with necrotrophy and biotrophy. He admits that saprotrophy by definition is asymbiotic, but points out that it is difficult to draw lines between it and necrotrophic interactions (Lewis, 1985, p. 33). For example, when a prey is killed and the killer continues to feed upon it after its death, the continued relationship is essentially an integral part of the nutritional continuum along with saprotrophy. This would also apply to mutualistic interactions in which organisms culture others as food (e.g., ants and fungus gardens, ruminants and their microsymbionts, humans and crops) and pollination foraging (e.g. nectar-feeding may be regarded as a saprophytic trait and feeding on pollen as necrotrophic) (Lewis, 1985, p. 36). Smith and Douglas (1987, p. 2) also use a modified Starr (1975) approach to describing characteristics of symbioses.

Other authors' thoughts run parallel with Lewis (1985) in contrasting similarities between predation and detritivory/saprobism (synonyms for saprotrophy) and how it stretches the boundaries of our understanding of symbiosis. Krohne (2001, p. 245) states that some ecologists consider a broad definition of predation to include herbivory, detritivory, parasitism, and carnivory. Begon et al (2006, p. 225) recognizes five main categories of species interactions: competition, predation, parasitism, mutualism, and detritivory. They discuss that detritivory can be denoted by +/0, since the detritivore benefits, while its food that is dead already is unaffected. They also state that "The general term applied to +/0 interactions is 'commensalism', but

paradoxically this term is not usually used for detritivores." Brewer (1994, p. 223) concurs that saprobism is similar to "less personal kinds of commensalism." Ricklefs (2008, p. 290) also denotes detritivory as a +/0 species interaction and recognizes only four main categories: competition, consumer-resource (predation/parasitism), detritivore-detritus, and mutualism.

K.A. Pirozynski (1987, p. 439) expressed concern, in his book reviews of Ahmadjian and Paracer (1986) and Smith and Douglas (1987), of their de Baryan concept of symbiosis defined simply as the living together of differently named organisms. He states "Swallowed whole 'symbiosis' is in danger of becoming a catch-all category in as much as evolution in biotic environment is the rule rather than the exception."

Mary Saffo (1992, p. 17) encourages the retention of the broad de Bary definition of symbiosis, but one that is outcome-independent. She proposes the term *chronic endosymbiosis* to label these symbiotic interactions that are mutualistic, benign, nonparasitic, or poorly understood (Saffo, 1992, p. 22). She objects to using simply endosymbiosis because Douglas and Smith (1989, p. 350) used the term to describe benign associations in which they explicitly excluded parasitism. This outcome-independent perspective does not preclude the use of outcome-dependent terms like parasitism, commensalism, and mutualism.

P.A. Abrams (1987) discusses how previous interspecific interaction classifications have often been incomplete, have suffered from ambiguously defined categories, and/or have wrongly equated categories of populational effects (e. g. +/– with possible mechanisms of interaction, such as predation or parasitism). For example, equating all –/– effects with competition and all +/– effects with predation or parasitism may have caused ecologists to ignore a variety of important interaction mechanisms. Abrams states that there are only six possible pairs of +, –, and 0 symbol combinations to represent the various interaction types between populations of two species. Various authors have often mixed and matched effects and mechanisms in their classification schemes. Abrams believes it appropriate to divide major categories defined by effects into subcategories based on mechanism, and states that four of the six categories of most classifications do not have any mechanistic connotations. New terms for –/– and +/– interactions will be necessary if ecologists want words that refer to those interactions in a generic sense and Abrams did not propose any (Abrams, 1987, p. 278).

Return to de Bary's Definition (1971–2011)

A gradual progression towards de Bary's original definition has been occurring over the past 40 years, particularly the past 20 years. This may have been initially influenced by the discussions of Starr (1975) and Lewis (1985), followed by growing agreement and adoption by many other prominent biologists into the 1990's. Ahmadjian and Paracer concur with this observation:

> "Interspecific associations, or symbioses, occur when two different species of organisms depend on each other for food, shelter, or protection. <…> At the present time, the original intention of de Bary is being honored by most scientists and symbiosis is once again being defined broadly" (Ahmadjian and Paracer, 1986, p. 1–3).

Today, all ten current editions of general biology textbooks cited in this article, explicitly or implicitly, define symbiosis in a broad sense similar to de Bary's definition (Starr et al.,

2009; Mader, 2010; Miller and Levine, 2010; Brooker et al., 2011; Freeman, 2011; Raven et al., 2011; Reece et al., 2011; Russell et al., 2011; Sadava et al., 2011; Solomon et al., 2011). The primary literature also continues to support this trend (Moran, 2006). As noted before, Kormondy (1996), Odum and Barrett (2005), Krebs (2009), and Sharma (2009) promote an expanded de Bary definition like Starr (1975) and Lewis (1985). However, with this growing consensus to return to a broad definition, some authors have recently started to avoid using symbiosis entirely (Krohne, 2001; Molles, 2010; Miller and Spoolman, 2012).

Confusion Due to the Lack of Usage of Endo-/Ectosymbiosis

Beyond the arguments of Starr (1975) and Lewis (1985), speculations on why confusion exists and has persisted so long are few. We believe that some of the confusion stems from a lack of consistent usage of endo-/ectosymbiosis terms. These terms have been thoroughly discussed and defined as early as the 1950's as seen in the statement below by Maurice Caullery:

> "One is led, indeed, by the constancy of the association and of the relationships between the associates to consider as cases of symbiosis the regular association of two definite species without the fusion of individuals with one another; we shall designate these associations by the term ectosymbiosis, in contrast to the typical form of symbiosis, where there is interpenetration of the two associates with the formation of a mixed complex, which we shall call endosymbiosis" (Caullery, 1952, p. 219).

Starr (1975, p. 9) further emphasized the need to describe symbiosis as either ecto- or endosymbiosis. Many others have further endorsed this system to clearly describe the type of symbiosis (Lewis, 1985; Smith and Douglas, 1987; Sapp, 1994; Paracer and Ahmadjian, 2000; Nardon and Charles, 2004). Smith and Douglas (1987) and Lynn Margulis both further describe the need to discern endosymbiosis as either as extracellular or intracellular:

> "Nature abhors a pure culture; symbioses, whether ecto- or endocellular, are the rule rather than the exception" (Margulis, 1980, p. 271).

It is critical that biologists use these prefixes in order to better describe the level of intimacy and permanency in symbiotic interactions. The inconsistent use or omission of these descriptors is common and further obscures a student's ability to fully and accurately comprehend the entire scope of symbiosis or the ability of researchers to communicate effectively and efficiently.

Secondary Symbiotic Terminology Confusion

Disagreement on terms other than symbiosis has created distractions that have contributed to the confusion. For example, the terms symbiont versus symbiote, symbiont is a commonly used term, but symbiote is supposedly more etymologically correct. De Bary coined the term *symbiont*, however, *symbiote* is the Greek word for "companion" and therefore more philologically correct (Meyer, 1925; Cleveland, 1926; Hertig et al., 1937; Read, 1970; Starr,

1975; Nardon and Charles, 2004). Apparently, symbiote is more commonly used in French literature, while symbiont is more commonly used in English, German, and American literature (Hertig et al., 1937).

> "*Symbiont* is the form coined by de Bary. Webster's Dictionary gives *symbiont* as the preferred form (derived from a participle of the corresponding Greek verb) whereas symbiote is listed as a synonym or variant <…> *symbiote* is derived from the Greek *sumbiotes,* meaning 'one who lives with,' 'companion,' 'partner,' whereas *symbiont* has no Greek original <…> The matter is apparently one of taste and usage rather than correctness" (Hertig et al., 1937, p. 328).

Another example of terminological confusion occurred with commensalism, coined by P.J. van Beneden (1876). He referred to a commensal as a "messmate" (Starr, 1975), whereas in recent times many authors, if not most, have extended it to include benefits other than nutritional (Abrams, 1987, p. 80).

Parasitism is another perplexing term in symbiosis because of its wide usage in an agonistic +/– connotation. Robert Hall (1974) argues that a parasite is simply an organism living in or on another organism from which it obtains food and therefore could result in beneficial, neutral, or harmful effects to the host. He supports his argument with others that have used or recognize the term in a broad sense (Pound, 1893; Cleveland, 1926; Hegner, 1929; Odum, 1971; Trager, 1986). For example, Cleveland (1926, p. 52) used the term "parasitism proper" and "true parasitism" to distinguish between the broad definition and the restricted harmful definition. Hall (1974) proposes "pathogenism" as the term to better describe harmful relationships of a parasite. Parasitism would then include mutualism, commensalism, and pathogenism. Interestingly, he supports the broad de Bary interpretation of symbiosis and therefore this would make parasitism synonymous with symbiosis. Conversely, there is evidence that the broad interpretation was not the original definition of parasitism. Boucher et al. (1982) reveal that van Beneden's (1875) original use of the word parasitism was in the harmful connotation. Van Beneden (1875) wrote "we find others who mutually provide each other services, it would be most unflattering to call them all parasites or commensals. We consider it fairer to call them *Mutualists,* and thus mutualism takes its place beside *commensalism* and *parasitism*" (Boucher et al., 1982, p. 317). Three years later, Alfred Espinas (1878) included a chapter in his doctoral thesis titled "Accidental societies between animals of different species: Parasites, Commensals, Mutualists" (Boucher et al., 1982, p. 317). Currently, many biologists mix various components from the above definitions. For example, many believe that parasites do not disrupt or seriously diminish the performance of their host even though they take nutrients from the host. Furthermore, parasites that produce disease are called pathogens (Paracer and Ahmadjian, 2000).

Paul Burkholder (1952) utilizes the terms above, but introduced several new terms to describe various combinations of +, –, or 0 species interactions. He proposed commensalism for +/0 interactions, but *allotrophy* for 0/+ ones; amensalism for –/0 interactions, but *allolimy* for 0/– ones; instead of competition for –/– interactions, he uses *synnecrosis*; and lastly, parasitism for +/– interactions, while predation for –/+ ones. Very few authors have adopted allotrophy, allolimy, and synnecrosis, as well as Burkholder uses symbiosis for +/+ interactions, not mutualism.

Terms more peripheral to the more restrictive definitions of symbiosis have also created confusion (e.g. predation, parasitism, parasitoidism, and grazing). Starr (1975, p. 2) discusses various conflicting usages of the term "predator" yielding an assortment of meanings consisting of various mixtures of components such as 'feeds on', 'causes death of', 'consumes', 'destroys',

'eats', 'pursues', 'hunts', 'pounces on', 'kills', 'captures', 'uses as food', 'seizes', 'exploits'. He uses another string of descriptors for parasitism to illustrate similar variability. Many general biology, general ecology, and general parasitology authors, implicitly or explicitly, recognize parasitism as being very similar to predation (Kormondy, 1996; Pianka, 2000; Krohne, 2001; Odum and Barrett, 2005; Roberts and Janovy, 2009; Starr et al., 2009; Molles, 2010; Brooker et al., 2011; Russell et al., 2011; Miller and Spoolman, 2012) and some equate parasitism as a form of predation (Dodson et al., 1998; Stiling, 1999; Krebs, 2009; Smith and Smith, 2009; Mader, 2010; Raven et al., 2011; Sadava et al., 2011). To complicate matters, some authors discuss grazing, parasitoidism, carnivory, and/or herbivory in comparison to predation and parasitism (Brewer, 1994; Stiling, 1999; Pianka, 2000; Krohne, 2001; Odum and Barrett, 2005; Begon et al., 2006; Ricklefs, 2008; Smith and Smith, 2009; Molles, 2010; Brooker et al., 2011; Freeman, 2011; Reece et al., 2011; Russell et al., 2011; Sadava et al., 2011), often with very different interpretations in how they relate to one another. To illustrate the confusion, Brooks and McLennan (1993, p. 2–3) use a definition for the term parasite as "all those creatures which find their nourishment and habitat on other living organisms <…> without destroying it [the host] as predators do their prey". The group "parasite" would then include certain organisms that many biologists would not consider to be parasites in the traditional sense, e.g., vampire bats, some mosquitoes, and all herbivores, while excluding organisms normally considered to be parasites, e.g., intestinal nematodes (Trichostrongylidae) that feed on intestinal bacteria and protozoans not host tissue. Paul Stiling (1999, p. 268) discusses how intimacy and lethality are factors to consider when classifying predators, parasites, parasitoids, and grazers. This is now being introduced in general biology textbooks (Brooker et al., 2011). Begon et al. (2006) and Thompson (1982) agree with these factors, other than the latter author considers parasitoidism as a form of parasitism.

Contramensalism is a relatively new term proposed to describe +/– interactions, which includes predation, parasitism, and herbivory (Arthur and Mitchell, 1989; Hodge and Arthur, 1996). However, there are problems with this proposed term: 1) herbivory is trophic term and not a synonym for *grazing* (Stiling, 1999), as well as predation is not all carnivorous; 2) they omitted parasitoidism from their definition; and 3) Hodge and Arthur (1996) acknowledge that "-mensal" literally means "table" and therefore has a trophic connotation, yet recommend contramensalism usage for non-trophic mechanisms as well. They also object to the usage of *exploitation* for +/– interactions (Lidicker, 1979) due to overlap in meaning with competitive –/– interactions. Possibly the use of *agonism* (as a subset of *antagonism*) as proposed by Starr (1975) and Lewis (1985) would be more appropriate, as well as predating these other purposed terms.

Conclusion

The purpose of this paper was to illuminate the issues and difficulties that have plagued the term symbiosis. Providing this historical summary should reignite the discussion that will ultimately bring a necessary solution to the confusion in symbiotic terminology. It would appear that some resolution has been quietly progressing over the past few years, despite any efforts to bring about change. Confusion in symbiosis and its related terminology has probably been due to the complexity and abstractness of biological phenomena in nature. David Wilkinson states:

> "With symbiosis, the textbook distinction between mutualism and parasitism is not always clear in nature, so it's perhaps unsurprising that the terminology mirrors these confusions" (Wilkinson, 2001, p. 485).

Various species interactions can be described along a continuum between two extremes. Terminology used to label the type of symbiotic interaction often is lacking to describe the dynamic and gradual transition between typological states. Philip Whitfield agrees with this thought:

> "Man's attempts to categorize associations between organisms will never produce a system of non-overlapping groups. <…> To this extent the categories can never be mutually exclusive pigeon-holes in which particular relationships must be placed. <…> The 'spectrum' image is often used to obviate some of the difficulties in the pigeon-hole concept. It suggests that association types are distributed along an axis of interactions. This alteration in imagery is helpful in that it incorporates the possibility of intermediate association types. <…> If we substitute a multi-dimensional space for the interaction axis, <…> Association types that are widely and discontinuously separate in one dimension can have mutually overlapping zones of intermediate forms in a different dimension. <…> This holistic view of associations corresponds in many ways to that recently expounded by Starr" (Whitfield, 1979, p. 3–6).

It may be best that the restrictive definition of symbiosis has faded somewhat into the recent past. Every definition of symbiosis must draw a line in the continuum of "living together". Therein lies the beauty of a broad definition, maybe much more inclusive than de Bary had intended.

Spending several lectures in a course on terminological confusion is a poor use of time and money in educating biology majors. Students see through the confusion and wonder why there is such a lack of consensus between subdisciplines on such a basic concept. How much time have researchers invested in trying to understand the confusion or convince others of a better way to view symbiosis? However, as long as such confusion persists, discussions will be necessary to attempt to resolve or at least minimize the unnecessary confusion. Times are different today in our understanding of symbiotic phenomena and there is resurgent interest with new perspectives in the field. It would appear that another attempt is in order, but it needs to be simple and integrative. Until all avenues have been exhausted, we should not be willing to accept the *status quo* or join the ranks of those who avoid the term. Should most or all biologists eventually avoid the use of symbiosis because of this prolonged and hopeless confusion, it will be a sad end to a beautiful term that simply means "living together".

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Симбиоз: «сосуществование» в хаосе

Брадфорд Д. Мартин*, Эрнест Шваб**

*Университет Ла Сьерра, Риверсайд, Университет Лома Линда, Лома Линда, США; bdmartin@llu.edu
**Университет Лома Линда, Лома Линда, США; eschwab@llu.edu

Путаница сопровождает термин «симбиоз» уже более 130 лет. Его ввел в 1879 г. Антон де Бари, обозначив им «совместную жизнь». Но уже через несколько лет биологи начали употреблять этот термин по-другому. Отсутствие консенсуса стало причиной долгих дискуссий о том, как использовать этот важный и комплексный биологический термин. Данная статья представляет историю различных определений, научных дискуссий, попыток привести биологов к единому пониманию «симбиоза». В последнее время споры в целом затихли, и некоторые биологи даже полностью отказались от использования этого сложного термина. Тем не менее большинство натуралистов продолжают говорить о «симбиозе», и чаще всего именно в его первоначальном значении, предложенном де Бари. Разногласия появляются в связи с не слишком часто использующимися выражениями эндо- и экозосимбиоз, описывающими степень близости и постоянства симбиотических взаимодействий. Существует и продолжает обсуждаться некоторая неопределенность в использовании вторичных терминов, таких как симбионт, комменсализм, паразитизм, паразитоиды, хищничество, травоядность, плотоядность.

Ключевые слова: симбиоз, неопределенность терминологии, Антон де Бари, мутуализм, комменсализм, паразитизм, хищничество, травоядность, конкуренция.