Characterizing life: four dimensions and their relevance to origin of life research

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Abstract

The question 'What is life?' has been debated since antiquity, and continues to confound scientists and philosophers today. There are over 100 proposed answers to that question in the literature. Some authors continue to propose new answers, and others argue about whether or not we should just give up. Following several recent contributions to the latter 'meta-debate' about life, this chapter suggests a pluralist approach to characterizing life: multiple characterizations of life can co-exist, for different but often complementary purposes. After discussing the relevance of characterizing life for origin of life research, this chapter offers a new way to think about the landscape of characterizing life in terms of four conceptual dimensions: (1) treating life as an all-or-nothing phenomenon or as a matter of degree, and characterizing life (2) materially or functionally, (3) at the individual or community level, and (4) minimally or inclusively. Depending on which agenda is at stake within origin of life research—for example, explaining the actual origin of life on Earth, versus explaining how life could, in principle, emerge anywhere at all—the sorts of features we might want in a characterization of life can vary along these four dimensions.

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1.1. Introduction

What is life? This question has been a subject of debate for over 2,000 years. For readers unfamiliar with this debate, the following quotations give an immediate sense of the disparity of views involved:

> “[A]ll living systems are defined as organized molecular systems controlled by negative feedback with properties of equifinality, homeostasis, and self-maintenance”. [1.60] (p. 1037)

> “Life is a self-sustaining chemical system capable of Darwinian evolution”. (This is the well known ‘NASA definition’ of life, proposed several decades ago by Carl Sagan and popularized in subsequent discussion [1.25])

> “[Metabolism] characterizes all known life… something that does not metabolize cannot properly be regarded as being alive”. [1.6] (p. 121)

> “[There is] an urgent need for a better, comprehensive theory of life to better define the aims of [origin of life] investigations, that is, to define the phenomena whose spontaneous onset is being studied”. [1.53] (p. 1035)

> “Attempts to define life are irrelevant to scientific efforts to understand the origin of life”. [1.56] (p. 599)

The first three quotations illustrate several positions, among dozens, in the debate about the nature of life: what are life’s characteristic features, or how should we define life? Some answers focus on a set of properties, as in the first two quotations; others spotlight a single property, such as metabolism. By some counts, there are over 100 proposed answers in the literature [1.45] [1.59]. In response to this proliferation of views on the nature of life, in recent years a meta-debate has arisen about the whole project of defining life in the first place: is a definition of life necessary, important, or even possible? This is on display in the last two quotations, with their conflicting views on the value of defining life for origin of life research. The debate and the meta-debate about life continue actively today, spanning a range of fields including origin of life research, astrobiology, artificial life and philosophy. This chapter focuses on both debates with an eye to their relevance in origin of life research.

Some authors have suggested that biology needs a characterization of life. Tibor Gánti begins his influential book *The principles of life* with the claim that “[a]n answer to this question [‘What is life?’] is an indispensable precondition for the birth of theoretical biology” [1.18] (p. 1). Other authors have called that question ‘foundational’, ‘fundamental’, and ‘critical’ to biology [1.11] [1.15] [1.35]. These discussions assume that, given its designation as the core life science, biology must be invested in settling the question of what life is. Some biologists are certainly interested in that question. But contemporary biology in general does not need an answer to it, in order to get on with the vast majority of its theoretical and empirical business. The subject matter of biology—the living world and its associated phenomena—is clear enough without one. Classic counterexamples and borderline cases for accounts of life (discussed further in Section 1.2) do not, as such, create roadblocks in core biological research. For example, the lack of consensus on whether viruses are ultimately living, non-living, or in between is no matter of frustration for microbiologists studying bacteria and their viruses.

In contrast to biology at large, some overlapping fields cannot take for granted, or be indifferent to, the status of their subject matter as living or non-living. The subject matter’s status as such appears to be precisely what is at stake in a field like origin of life research; the same is true of astrobiology more broadly, artificial life and at least some subfields of synthetic biology. A recent report from a workshop gathering around 40 origin of life researchers urges the field to continue working to understand the nature of life, in order to “define the phenomena" whose origins are the field's very focus [1.53] (p. 1035). This idea is intuitively appealing. A definition of life sounds like an important conceptual precondition for success in fields whose primary aim is to explain, identify, or engineer the boundaries between the non-living and the living. On the other hand—and here the meta-debate referred to above comes in—Jack Szostak [1.56] objects that efforts to define life are unhelpful and irrelevant to the central aim of origin of life research, which is understanding the gradual transition from a world with only physics and chemistry to a world with biology as well.

This chapter suggests an inclusive perspective on approaches to characterizing life, following several recent contributions to the meta-debate about life. It then offers a new way to think about how life is characterized in terms of four conceptual dimensions, and discusses the bearing of those dimensions on characterizing life in the context of origin of life research. The rest of this book discusses origin of life research in detail, so this chapter will not spend much time introducing the field. Just a few points are important to note here at the outset. Origin of life research is highly interdisciplinary and diverse in its content and aims. While its most high-level aim can be summarized straightforwardly as explaining life's origins, there are many different threads of empirical and theoretical research in service of that aim. These are grounded in an array of different knowledge bases and methodological approaches, from fields including physics, chemistry, geology, paleontology, molecular and evolutionary biology, and artificial life. There are an impressive variety of research approaches across the field, from reconstructing the historical steps of life's presumed emergence on Earth approximately four billion years ago, to trying to understand the universal conditions for life to emerge from non-living matter anywhere at any time, to synthesizing life from scratch in the laboratory [1.53]. All of these backgrounds and approaches contribute, from various angles, to that larger aim of explaining life's origins.

1.2. The debate about (defining) life

In the western tradition, accounts of the debate about life trace it back several millennia to Aristotle, who distinguished the living from the non-living in terms of functions like reproduction and nutrition. Since then hundreds of others have weighed in, from early modern natural philosophers through to contemporary philosophers and scientists from a range of fields (for an excellent historical overview see [1.3]). Much of this discussion has focused on *defining* life: coming up with a condition (for example, metabolism) or a list of conditions (for example, reproduction, metabolism, and evolution) meant to draw a line between the non-living and the living. In the following subsections I briefly overview the long-standing debate about defining life, and a more recent debate about that debate itself (Section 1.2.1); I then suggest that we reframe this discussion around characterizing, rather than defining, life (Section 1.2.2).

1.2.1. The debate and the meta-debate

Many conditions for life have been proposed, giving rise to a range of ways to define life. These include biochemical definitions specifying that living things have signature biochemical features, such as being based on organic chemistry or nucleic acids; metabolic definitions focused on how living things exchange material and energy with their environments; thermodynamic definitions focused on how living things take in energy in order to create local order; and Darwinian definitions stipulating that life evolves by natural selection [1.3] [1.11] [1.52]. Throughout the history of this debate, when someone proposes candidate definitional criteria, someone else inevitably raises a problematic counterexample or borderline case. For example, if metabolism is claimed to be sufficient for life (in other words, if everything that metabolizes is alive), then candle flames arguably qualify as living; this seems problematic. If reproduction is claimed to be necessary for life (in other words, if something must be able to reproduce in order to qualify as living), then sterile hybrids like mules appear to be counterintuitively disqualified,[1] and viruses become a puzzling borderline case because they can reproduce only when infecting a living host, not on their own. The list goes on and on.

Other authors have surveyed extensively the landscape of proposed definitions of life, their shared and diverging features, and their various borderline cases and counterexamples [1.1] [1.3] [1.11] [1.29] [1.33] [1.35] [1.36] [1.41] [1.45] [1.52] [1.59]. I will not repeat their efforts here in detail, but will make just a few further summary points for the purposes of this chapter. First of all, that landscape is substantial, with by some counts as many as 100+ or 120+ proposed definitions of life [1.45] [1.59]. These vary widely in content. People keep proposing definitions of life, finding counterexamples, and coming up with new definitions. At some point in this debate, participants began talking past one another. This is compounded by the fact that the debate about life now takes place across a range of different fields, with all of their various journals and jargons and sub-specializations; these include origin of life research, astrobiology, artificial life, synthetic biology, philosophy of biology, and bioethics. So there is no consensus on a definition of life among origin of life researchers, let alone across disciplines with a stake in the matter.

In addition to the debate about which definition of life is the right definition, in recent years a meta-debate has been taking place about the whole project of defining life itself. The ongoing proliferation of candidate definitions has led some scientists and philosophers to dismiss defining life as hopeless, pointless, or otherwise doomed. There are at least four threads of this 'definition skepticism' (see further discussion in [1.54]). Carol Cleland argues that there are too many problems facing the project of defining life, including the sorts of counterexamples and borderline cases mentioned earlier. She says that we need a broader theory of life, not a strict definition, but scientists are in no position to formulate such a theory because our knowledge of life is based on a single sample: it all descended from the same common ancestor and is united by fundamental properties. It is difficult to look beyond this single sample in order to come up with a general theory, given our current absence of further samples as grounds for generalization [1.10] [1.11]. Second, Edouard Machery [1.30] argues that scientists from a range of fields rely on myriad definitions of life for disparate purposes, and there is no reason to think they will ever converge on a single, unanimous one; so the project of defining life (as a scientific theoretical concept, anyway) is pointless.

In a third thread of definition skepticism, Carlos Mariscal and Ford Doolittle [1.33] suggest that defining life is pointless for a different reason: they argue that the term 'life', properly understood, refers to an individual. The individual they have in mind corresponds to what Cleland called our single sample of life, namely, the spectacularly diverse but ultimately unified clade that is life on Earth [1.33]. A bit of background on the difference between individuals and kinds might be helpful here. Philosophers distinguish kinds, which are classes of things united by shared properties, from individuals. Individuals can be made up of many parts, but they are ultimately entities existing in space and time, whose parts are united by their shared history. A popular philosophical view is that biological species are in fact individuals,

[1] Actually, there are rare but real cases of fertile mules [1.49]. But even if we took this to suggest that mules need to give up their reign as long-standing counterexamples in the debate about life, the point could still apply to other sterile hybrids.

as just described, rather than kinds [1.19] [1.24]. If we understand species to be united by their shared evolutionary history as lineages, rather than by some essential property or properties shared by all of their members, this helps account for the dramatic variation we often see within species; especially striking examples include species with sexual dimorphism. With this background in mind regarding the difference between kinds and individuals, it makes sense to ask for definitions of terms referring to kinds (such as 'star' or 'biological taxon'). But it does not make sense to ask for definitions of terms referring to individuals (such as 'Polaris' or '*Homo sapiens*'). For this reason, Mariscal and Doolittle say that we should not worry about defining life (see also [1.23] for further discussion of the idea that life is an individual).

Fourth and especially relevant to this chapter, with its particular focus on origin of life research, is Szostak's definition skepticism mentioned in Section 1.1. He says that a definition of life is irrelevant to explaining the gradual transition from chemistry to biology. In particular, Szostak argues that any candidate point in that gradual transition where we might draw a boundary between non-life and life would be arbitrary; and, in any case, that drawing such a boundary does not enrich our understanding of that transition or its details [1.56].

1.2.2. Defining life is only one way to address the question 'What is life?'

Szostak is right. I will say more, below, about why. But it does not follow from his argument that the project of addressing the question 'What is life?', as a whole, is unhelpful and irrelevant to understanding the transition from a world of physics and chemistry to a world with biology. This is because Szostak's target is specifically the attempt to *define* life, or to "draw a line that divides the non-living from the living" [1.56] (p. 599). This is a relatively narrower project compared to the broader project of addressing the question 'What is life?'.

Definitions provide grounds for dividing some class of stuff from the rest of the world. A classic example is 'water is H_2O'. Philosophers usually think about definitions in terms of *necessary and sufficient conditions*: a definition of life provides conditions such that everything living has them (they're necessary) and everything that has them is living (they're sufficient). In other words, a proposed definition of life will draw a line between the non-living and the living. Many authors have this aim in mind. But many others proposing so-called 'definitions' of life are not proposing definitions at all, properly speaking, but instead something more like theories or models or accounts of life. These can take a number of different forms, and need not involve specifying necessary and sufficient conditions. For example, Gánti's famous chemoton model has been referred to as a definition of life, but it is arguably better thought of as a heuristic guiding theory development [1.22]. The heavy focus on defining life in the debate about life is unfortunate. It does not do justice to a much wider range of aims people have in mind when addressing the question 'What is life?' To the extent that answers to the question 'What is life?' take the form of something other than definitions (as Cleland argues they should), the other definition skeptics' problems look less problematic.

For the remainder of this chapter, then, I will refer to *characterizations* of life, a catch-all term meant to include theories and models and accounts as well as definitions of life. Other authors have used various terms to refer to what I am calling characterizations (but not necessarily definitions) of life, or a subset of them, including 'tentative criteria' or 'heuristics' for life, 'model-based definitions', 'provisional definitions' or 'operational definitions' of life [1.5] [1.11] [1.22] [1.31] [1.35] [1.36]; see also [1.26]. Unlike some of these other authors, I avoid even qualified versions of the term 'definition' here, in order to avoid the implied exactness and definitiveness of strict philosophical definitions. This leaves clearer room for working hypotheses or models of the nature of life, which best describes plenty of accounts of life which have elsewhere been labelled as definitions. By focusing on the whole range of attempts to characterize life, I suggest re-focusing our discussion of the debate about life: I am concerned here with the range of attempts to answer the question 'What is life?', which include, but are not limited to, defining life.

Two further positions in the meta-debate about life bear mentioning here. A first says that we should be *pluralists* about characterizing life: that is, we should deny that the aim of characterizing life is necessarily to settle on a single unanimous characterization. There are different versions of pluralism, as a philosophical stance. The key point for our purposes here is that a pluralist about characterizing life accepts that multiple characterizations can co-exist for different purposes (for example, to guide different research agendas [1.5]), and denies that we should think of these as mutually exclusive answers to the question 'What is life?'

A second, related point is that characterizations of life are often tailored to particular research agendas, and open to revision as research progresses. This is a stark departure from the way most people typically think about definitions. The idea here is that given their roles in scientific practice, we should think of many characterizations of life as *working characterizations*. Other authors have called roughly what I am calling working characterizations 'provisional definitions' or 'operational definitions' of life. I agree with most of what they say, but avoid the term 'definition' for reasons mentioned above. Lucas Mix [1.35], for example, argues that provisional definitions of life are needed for progress in origin of life research and astrobiology. Leonardo Bich and Sara Green highlight that operational definitions of life "are connected to specific theoretical models which integrate sets of contextually relevant criteria for life that involve or enable observable or experimental operations (in the laboratory, on another planet, or in a software program)" [1.5] (p. 3). They say that operational definitions are operational in two senses: they are not set in stone, but open to changing over time as theory and experimental work advance, and furthermore they play an active role in guiding operations (research activities) in the fields which rely on them.

In addition to focusing on characterizations rather than definitions of life, I think both of the positions just mentioned—pluralism, and understanding characterizations as often provisional and open to revision—are the right positions. I will not argue for them at length here (but see [1.5] [1.22] [1.35] [1.36]). My focus for the rest of this chapter is on the question: How can different ways of characterizing life make a difference in origin of life research?

1.3. Does origin of life research need a characterization of life?

Even if origin of life research does not need a definition of life, there are several reasons a characterization of life might be important. One reason is that researchers might need one in order to achieve particular theoretical or empirical aims. Another reason is that they are just invested in understanding the nature of life. Many people are, and likely a higher percentage of people drawn to origin of life research (or to reading this book) are. In addition to assuming the reader is just interested, I will also discuss reasons to think that in origin of life research, characterizations of life are at least in the background and sometimes play an explicitly important role.

When astrobiologists search for life in the universe beyond Earth, they arguably need a characterization of life in hand. Without at least a minimal one, for example in the form of what Cleland has called 'tentative criteria' for life, there is no clear basis for search criteria or success conditions for finding 'life as we don't know it' elsewhere in our solar system [1.10] [1.43]. Compared to the goal of finding further samples of life in the universe, the situation in origin of life research might appear different. A characterization of life does not play the same role in setting search criteria or success conditions, at least not for the overarching agenda of explaining the emergence of life from non-living matter. In origin of life research overall, ‘life’ unifies under one umbrella a diverse array of theoretical and empirical research agendas. These all aim to contribute to our understanding of a series of transitions which occurred on Earth around four billion years ago, or which could in principle occur anywhere or at any time, or both.

For some agendas under that umbrella, however, characterizing life plays a clear role in setting success conditions. For example, some origin of life researchers aim to create life from scratch in the laboratory. Their goal is to better understand the transition from chemistry to biology by re-engineering or modelling it in the construction of protocells (see, for example, [1.14] [1.47]). Without an agreed-upon characterization of life, there are no agreed-upon success conditions for creating protocells. There is rough consensus among protocell researchers on understanding minimal cellular life (that is, the engineering target, a living protocell) in terms of three components: “the functional integration of metabolism, containment, and information processing” [1.48]. This means that at least the protocells community can agree on when their target has finally been reached. It does not mean that everyone, across all research communities, will be convinced that they have created life from scratch. And it is a rough but imperfect consensus, because some protocell-focused researchers characterize life differently [1.14]. In any case, this characterization of life as metabolism, container, and information processing is generally regarded as a shared blueprint for what goes into building a protocell, as well as a means of benchmarking progress towards doing so.

Unlike the works cited in the preceding paragraph, many origin of life publications do not have sections, or even sentences, explicitly addressing how the authors characterize life. This does not mean that there are no assumptions about what life is, and therefore characterizations of life, in the background. Consider the following example, from a different branch of origin of life research focused on identifying signs of the earliest life on Earth. Frances Westall and colleagues characterize and discuss the geology of a “hydrothermal-sedimentary context for the origin of life” [1.62]. The authors do not explicitly characterize life; this is not the sort of work that would be included in the lists cited earlier tallying up 100+ or 120+ characterizations of life in the literature [1.45] [1.59]. Nevertheless, characterizing life is at work in the background here. The authors begin their paper with an overview of what they take to be the basic requirements for prebiotic chemistry and early cellular life, in order to eventually show “that volcanic sediments could have played an important role in prebiotic chemistry and in the increasing complexity of prebiotic chemical systems eventually leading to the origin of life” [1.62] (p. 259). They go on to discuss “important processes for the emergence of life,” including cell formation and chemical evolution. They emphasize that their aim is not to explain how the first life forms emerged, but rather to advance our understanding of the physicochemical environmental preconditions for that emergence. But a characterization of life is still on display in their discussion: namely, one assuming that life involves (at least) contained cellular structures and complex evolving chemistry.

My point is *not* that works like this should actually be thought of as covert participants in the debate about life. These authors have plenty else on their agenda, and it would be misrepresenting their aims (in that paper, anyway) to include arguing about the question ‘What is life?’ among those aims. Rather, my point is that characterizing life is in the background in much of origin of life research, even when it is not considered an explicit aim or even an explicit point of interest. Discussions like that of Westall and colleagues assume characterizations of life as foundational background for their investigations of life's origins, even if the authors are not actively engaged in the debate about life.

This is where the difference between definitions and characterizations matters substantially. Some participants in the debate about life seem to think something like the following: if you're going to focus on life in your research, you had better have a definition of life. This is not true. Generically speaking, explaining the origins of X—where X came from, or how X came to be—does not necessarily require a definition of X. Astronomers and astrophysicists have disagreed about how to define planets. While this is an important question, debates about how to answer it do not hinder astrophysicists' efforts to explain how planets form; its answer just might end up constraining the set of particular entities that their explanations end up bearing on [1.7]. Biologists explain the evolutionary origins of species without settling on a unanimous definition of what species are. In fact, the idea of defining species is problematic and contentious for reasons which parallel the debate about whether life is a kind or individual, discussed in Section 1.2 [1.19] [1.24] [1.51]. But when we shift the focus of this discussion from strict definitions to characterizations, especially working characterizations, things look quite different. Scientists explaining the origins of life (or planets, or species, or any number of other things) will nearly always do so with some working characterization of life (planets, species) in mind, even if they reject the idea of trying to strictly define the theoretical terms in question, for any number of good reasons.

Szostak's reasons for saying origin of life research does not need a definition of life are compelling. But his target is the strict definitional project of drawing a hard dividing line between the non-living and the living. If we look at the project of 'defining life' more broadly, to include characterizing life, this should change the overall assessment. It suggests that, while a definition is not necessary, a characterization of life is nearly always in the background; the extent to which it is explicitly articulated varies; and it will at least sometimes be important and useful. My aim in the rest of this chapter is to look at how, to the extent that characterizations of life are articulated, it can matter how life is characterized.

1.4. Dimensions of characterizing life

Existing discussions of the debate about life have focused on the content of different characterizations, grouping them into clusters based on their shared focal features, such as evolutionary versus thermodynamic versus metabolic characterizations [1.27] [1.35] [1.41] [1.45] [1.52] [1.59]. Here I discuss something different: dimensions of varied strategies or commitments regarding *how* life is characterized.

The following four subsections focus on four such dimensions. The first regards a choice between treating 'living' and 'non-living' as dichotomous categories (i.e., drawing a line), or treating them as a matter of degree where there is a continuum from the non-living to the living. The second is characterizing life materially or functionally; this regards the extent to which material (commonly biochemical) particulars are specified. The third dimension is characterizing living individuals or living collectives; this regards whether the aim is to specify what makes a life form (typically an organism) living, or to specify criteria for populations, lineages or communities of life forms. The fourth dimension is characterizing life minimally or inclusively; this regards whether the aim is to capture all of the rich complexity of life as we know it, or a minimal conception applying only to the most basic or early life forms.

In each of the following subsections, after explaining the relevant dimension in more detail, I discuss how variation on that dimension can make a difference to characterizing life in the context of origin of life research. Most of these points will be conditional: to the extent that origin of life researchers explicitly endorse a characterization of life, it makes sense to endorse characterizing life one way rather than another way, according to the dimension in question. In particular, I suggest that (1) there is and should be an emphasis on characterizing life minimally and as a matter of degree (Dimensions 1 and 4); and (2) which way it makes sense to go on Dimensions 2 and 3 is up for debate, but which way is preferable can depend on the research agenda in question. My aim is not to assess characterizations of life along these dimensions, nor is it to judge which ways to characterize life are the best. Rather, it is to examine how variation along these dimensions affects the relationship between characterizing life and a variety of other aims and agendas in origin of life research.

1.4.1. Dimension 1: Dichotomy or matter of degree?

Many characterizations of life, and all strict definitions of life, treat living and non-living as dichotomous categories: they specify one or more criteria meant to draw a line, including what is living and excluding what is non-living. For example, Humberto Maturana and Francisco Varela say that "All that is living must be based on autopoiesis, and if a system is discovered to be autopoietic, that system is defined as living" (cited in [1.45]).[2] Drawing such a line in principle does not mean that, in practice, there will not be borderline cases or grey areas. For example, even if we have a clear understanding of autopoeisis in hand, it might be empirically difficult to say if some particular system in the world is autopoietic or not. But Maturana and Varela's definition of life implies that autopoeisis is the principled criterion for demarcating two categories, living and non-living.

An alternative to this sort of view is to treat what is living or non-living explicitly as a continuum or a matter of degree (see discussion in [1.1]). Christophe Malaterre's account of life [1.31] specifies five 'lifeness signatures'—individuation, replication, variation, metabolism, and coupling of these components—and says that different entities or systems can instantiate some or all these five features to varying degrees. Some things are paradigm living (maximally instantiating all five lifeness signatures), others are paradigm non-living (instantiating none of them at all), and others are in between (for example, instantiating some but not others, or all five but only partially). A laptop will not instantiate Malaterre's lifeness signatures. Chemical steps on the way to the origin of life, such as lipid vesicles or auto-catalysts, will instantiate some but not all five signatures, and some only partially. Living or proto-living systems will instantiate all five. So on this view, at its roots, "the tree of life dissolves gradually into non-living matter" [1.31] (p. 645); there is a grey area, rather than a hard line, dividing the living from the non-living.

A different characterization of life which also illustrates the 'matter of degree' view is Mark Bedau's account of minimal chemical life [1.2]. Bedau characterizes life in terms of three components: a container (localizing and integrating the life form), metabolism (using energy and resources from the environment), and program (replicated inherited information); this is based on Rasmussen and colleagues' protocell account of life [1.48], discussed in Section 1.3. Bedau proposes a Boolean possibility space of those three features and each of their nine possible relationships of mutual support and integration, which gives us a spectrum of

[2] 'Autopoiesis' refers roughly to self-generation and self-production [1.35].

possibilities shading from non-living to living. On these accounts there is no line between what is living and non-living. Life is a matter of degree.

One compelling reason to characterize life as a matter of degree, as opposed to a dichotomy, is that the borderline cases mentioned in Section 1.2 become non-issues. Viruses are a well-known borderline case for definitions of life, to the extent that metabolism or reproduction are regarded as definitional on many accounts, and viruses can metabolize and reproduce only while infecting a host, not under their own steam [1.9] [1.17]. On both matter of degree accounts of life discussed above, the in-between status of viruses is a feature, rather than a bug (so to speak). Bedau [1.2] represents viruses, while not infecting hosts, as a 'program' component lacking full functional integration with the other two components (container and metabolism). Viruses are therefore in between fully non-living and fully living. Malaterre puts viruses in the grey zone of his five-dimensional account because "they are capable of individuation and of coupling the reproduction of their most visible entities, virions, to the metabolic and replication processes of their cellular hosts" [1.31] (p. 655). There is no need to worry about whether transitional entities like viruses are living or non-living when life is explicitly characterized as a matter of degree, rather than a dichotomy.

In the context of origin of life research it makes sense to understand life as a matter of degree. As A. G. Cairns-Smith said decades ago, "Life, then, is not some absolute quality that would have suddenly appeared, it would have emerged gradually during early evolution… When you can see what is going on in such a progression you lose interest in erecting picket fences" [1.8] (p. 3). 'Erecting picket fences' pertains to defining life as understood in this chapter: providing necessary and sufficient conditions to draw a line between the non-living and the living. If life were characterized dichotomously, this would suggest that the origin of life is ultimately a story of crossing a clear line, where there was not life at all and then all of a sudden (more or less) there was. This conflicts with origin of life researchers' agenda of explaining a complex series of gradual transitions which occurred over a long time.

This latter point speaks to why Szostak was right. At least in origin of life research, it does not make sense to draw a hard line. Szostak's criticism is that such line-drawing is antithetical to the project of explaining the gradual transition from chemistry to biology, precisely because "as one focuses experimentally on any of the 'defining' properties of 'life', the sharp boundary seems to blur, splitting into finer and finer sub-divisions" [1.56] (p. 599). But while this is a clear strike against defining life, we should not read this as a call for origin of life researchers to abandon the question 'What is life?' Rather, Szostak's point highlights the need to characterize life as a matter of degree, not a dichotomy, in order to be consistent with everything else we know about the origin of life (see [1.43] for discussion of why characterizing life dichotomously might be at least more appealing, if not the best theoretical move, in other areas).

1.4.2. Dimension 2: Material or functional?

Some proposed characterizations of life focus on material particulars. For example, Altstein (cited in [1.41]) says that life is "the process of existence of open non-equilibrium complete systems which are composed of carbon-based polymers and are able to self-reproduce and evolve on the basis of template synthesis of their polymer components"; Perret [1.44] says that life is "a potentially self-perpetuating system of linked organic reactions, catalyzed step-wise and almost isothermally by complex and specific organic catalysts which are themselves produced by the system". Other characterizations of life are purely functional, inviting an open-ended range of material or even digital instantiations of life. For example, contrast

Perrett's materially detailed characterization above with a minimal, purely functional one like "life is self-reproduction with variation" [1.59]. The latter could be instantiated by familiar carbon-based Earth life, silicon-based life, self-replicating computer programs, and any number of other systems, chemical or otherwise.

This dimension of material or functional characterization need not go one way or the other. It comes in degrees: some characterizations specify fine-grained material details, some are permissively functional, and many are in between. For example, Perrett's "linked organic reactions" specifies a more fine-grained material feature than the NASA definition's permissively material criterion that life is a "chemical system"; and some are purely functional without any material specification.

Unlike with dimension (1), there is no striking reason why origin of life researchers should necessarily go one way or the other on this dimension. But compared to other fields invested in characterizing life, origin of life researchers are in a particular but qualified position to characterize life materially: to the extent that their aim is to explain the origin of life as we know it on Earth. Which way characterizations of life go on this second dimension can track (at least roughly) a difference between two agendas in origin of life research. Some research focuses on explaining the details of how, where, or when life as we know it actually emerged on Earth around four billion years ago. Some research seeks to explain something broader: how life could possibly emerge anywhere in the universe at any time. We can call these, respectively, *how-actually explanations* and *how-possibly explanations* of life's origins.[3]

To the extent that specifically material characterizations of life seem appealing, they seem appealing in the context of how-actually explanations of life's origins. Life on Earth descended from a common ancestor and shares common biochemical features, like nucleic acids with a phosphate backbone and amino acids with left-handed chirality. There is debate about how these biochemical features came about and the extent to which they are genuinely universal constraints; for example, regarding the priority of an RNA world in the origin of life [1.20] [1.39], the universality of nucleic acid biochemistry [1.40], or the necessity of phosphorus-based biomolecules [1.42] [1.63] [1.66]. Not everyone agrees on how to explain even the most basic material details of life as we know it, let alone life at large. But there are constraints on how much departure we can imagine from biochemistry as we know it, once the earliest progenitors of life on Earth began to form. So, those aiming to give how-actually explanations of life's origins are in a position to endorse specifically material as opposed to functional understandings of life (compared to, for example, researchers attempting to detect 'life as we don't know it' in other solar systems [1.43], or to create living computer programs [1.37]).

On the other hand, if the aim is to give a how-possibly explanation of life's origins, a less specifically material characterization of life seems more appealing. One need not go all the way to a purely functional characterization which would count computer programs as living.[4]

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[3] These are distinct explanatory agendas, but they are not mutually exclusive; focusing on how-possibly explanations of life's origins is compatible with trying to explain the details of how life actually emerged on Earth.

[4] The extent to which one should is open for debate; some discussions talk about computer programs as if they are living and some accounts of life argue for explicitly including them. I will not get into that debate here, but see, for example [1.3] [1.64].

But to the extent that life could, in principle, depart from biochemistry as we know it, it makes sense to characterize life in a way that allows room for this.

One could also argue that even a how-possibly explanation of life's origins calls for a material characterization of life. Steven Benner [1.4], for example, argues that polyelectrolytes, in addition to being key biomolecules of life as we know it, are necessary for life in principle.[5] So, my claim is not that how-possibly explanations will necessarily call for less material characterizations of life. Rather, it is that when one aims to provide only a how-actually explanation of life's origins, a strongly material characterization of life is suitable; to the extent that one aims, in addition or instead, to provide a how-possibly explanation of life's origins, the suitability of strongly material characterizations becomes debatable. The crux of that debate is just how far we can stretch the boundaries of biochemistry as we know it (see, for example, [1.42] [1.63] [1.66]).

1.4.3. Dimension 3: Individual or collective?

Most attempts to characterize life have focused on separating living things, like tardigrades and crocodiles and protocells, from non-living things, like chairs and rocks and liposomes. This is a natural way to understand the question 'What is life?'—in terms of what makes living individuals living. But while that question is often interpreted as asking what distinguishes a living organism from a non-living thing, a number of authors treat living populations [1.1] [1.54] or even the whole biosphere [1.16] [1.28] as the focal unit. Some of these characterizations of life are based on properties which by definition can apply only to collectives of individuals, or collectives of individuals over time. An example of the former sort of property is variation; an example of the latter is evolution. Variation and evolution are focal properties in many popular characterizations of life, and the bearers of those properties are living populations, not individuals.[6]

Some characterizations of life apply only to individuals or to collectives; others include both individual-level and collective-level properties. An example of the latter is Malaterre's five-dimensional account of life [1.31], discussed above in Section 1.4.1. Malaterre characterizes life in terms of four features of individuals (individuation, metabolism, replication, and coupling of components) and one feature of collectives or populations of living things (variation). Other examples include Francis Crick's [1.13] three-feature account of life in terms of self-reproduction, evolution, and metabolism, and Gánti's [1.18] inclusion of features of both individuals (metabolism, growth) and collectives (capacity for evolution) in his criteria for life.

There is no obvious reason in principle to prioritize characterizing living individuals versus collectives, and a few authors explicitly argue that characterizations of life should apply at both the individual and collective levels. For example, Kepa Ruiz-Mirazo and colleagues [1.50] argue that autonomy characterizes living individuals such as organisms, while open-ended evolution characterizes living systems like the biosphere. Bedau [1.1] argues that supple

[5] A polyelectrolyte is a biopolymer with a repeating charge in its backbone; DNA and RNA molecules are examples, among many others.

[6] Of course, we could talk about variation within an individual as well; for example, regarding the differentiation of parts or cell types in a multicellular organism. But this is not the sense of 'variation' that the accounts of life discussed here tend to have in mind.

adaptation (akin to open-ended evolution) is the key feature of what he calls the primary form of life, or the living processes and evolving systems that give rise to individuals. He characterizes living individuals as entities whose existence is "explained in the right way by a supplely adapting system."

In origin of life research, explaining the origin of living individuals and the origin of evolving populations are often treated as two (big) pieces of the same puzzle. The aim is to explain a complex series of transitions from a world without biology as we know it, to a world with it. Views differ on which transition came first, and the details of how they occurred. But for the most part, the emergence of Darwinian evolution and the emergence of living individuals are treated as two key parts of the same overall process which calls for explanation (but see [1.58] for an argument for treating the origin of life and the origin of evolution separately).

Research on life's last universal common ancestor (also known as LUCA) bears mentioning here. Whatever properties LUCA had and whenever it occurred, there is general consensus that it was after the origin of life itself, but this research area overlaps strongly with origin of life research. There is debate about whether we should conceptualize LUCA as a population, a community, or a single organism; there is also debate about whether LUCA was genuinely living or not [1.12] [1.32]. This suggests that the present dimension of characterizing life has some bearing here. To the extent that these two debates about LUCA intersect—regarding its status as a collective or an individual, and as non-living or living or in between—characterizing life collectively or individually could make a difference.

A conceptual complication for Dimension 3 is the controversy, at least in biology and philosophy of biology, around what constitutes an individual in the first place. So far, I have been using 'individual' to refer to what typically comes to mind when we think of individual organisms, such as bacteria, octopuses, or human beings, and 'collective' to refer to populations or communities of such individuals. This glosses over important complexities of characterizing and identifying biological individuals. There are fascinating conceptual puzzles and borderline cases here, and extensive literature about them (see, for example, [1.46], and Section 3 of [1.55] gives a nice condensed overview of recent debate). A relevant complexity to mention here is the debate about to what extent we should think of certain collectives, for example, symbionts and their hosts, as individuals of sorts, or as 'superorganisms' [1.65]. A few discussions of life treat what I call collectives, above, as individual organisms [1.61] (p. 437). For the purposes of this chapter, my main aim in distinguishing individuals from collectives is to separate the sorts of things that metabolize from the sorts of things that undergo Darwinian evolution. Bacteria, octopuses, and human beings metabolize; only collectives of these (and of many other kinds of things) evolve.

1.4.4. Dimension 4: Minimal or inclusive[7]

Many characterizations of life focus on capturing all the complex richness of life as we know it, from ancient simple life to today's complex multicellular life. Alexander Oparin argued for characterizing life inclusively (and despite qualms about his describing humans as the culmination of biological development, I quote him here for the relevant point about inclusivity): "for an exhaustive understanding of life it is necessary to have an understanding of the whole gamut of its characteristic features, starting with those extremely elementary ones,

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[7] I am grateful to Mark Bedau for the idea to discuss this as a separate dimension.

with which the first living beings were endowed, and finishing with the most complicated manifestations of higher nervous activity in animals and man, in which the biological stage of the development of matter culminates" [1.38] (Chapter 1). On the other hand, some characterizations of life focus more narrowly on criteria for only the most minimal life forms, such as protocells [1.2] [1.47] [1.48], often to guide a particular research agenda—in this case, the one discussed in Section 1.3 of creating minimal chemical life from scratch in the laboratory.

This dimension of defining life minimally or inclusively pertains primarily to the 'individual' side of Dimension 3 (individual or collective). One could focus on characterizing only minimal living things, such as protocells at the origin of life, or one could focus on characterizing any and all living things, from the minimal to the more complex, such as contemporary multicellular organisms. This minimal or inclusive distinction applies secondarily to the 'collective' side of Dimension 3, insofar as a characterization of living collectives could have in mind collectives of only minimal life forms, or of any life forms inclusively.[8]

Origin of life research has a particular stake in characterizing life minimally, in service of its agenda of explaining how life originated from non-living matter. For other areas where characterizing life matters, an inclusive characterization might be called for. These include astrobiology's search for life on other planets, where understanding as much as possible about the diversity of life as we know it arguably better sets us up to recognize life as we don't know it. Another example is in applying biocentric theories in environmental ethics, which say that we have moral responsibilities towards all living things [1.57]. In order to know what qualifies for our sphere of moral consideration, we would need an inclusive characterization of life. In contrast, origin of life research is concerned with explaining the series of events giving rise to the first rudimentary life forms. As such, a minimal characterization of life is apt.

In the discussion of Dimension 1 above, I said that characterizing life as a dichotomy is inconsistent with the view that the transition from non-living to living matter is gradual rather than abrupt. Unlike in the case of Dimension 1, there is no particular inconsistency in characterizing life inclusively as opposed to minimally. One could be invested in explaining the origin of life from non-living matter, and at the same time interested in understanding and characterizing what life is inclusively, beyond its origin and early stages. The point here is just that for at least some projects within origin of life research, there is a particular and appropriate focus on characterizing life minimally. Similarly, some philosophers with a particular interest in the origin of life have focused on characterizing life minimally rather than inclusively [1.2] [1.31].

1.4.5. Summary discussion of the dimensions

A final point to underline about the dimensions of characterizing life is that they are not all binary. Dimension 1 is binary; it can go one way or the other. Definitions (and some other characterizations) of life imply dichotomies, where there is a line dividing the living from the non-living. When they do not draw lines, characterizations of life allow for a grey area, where the living and non-living are on some sort of continuum. Dimensions 2–4, however, are not

8 We could also talk about collectives themselves minimally or inclusively. This is beyond the scope of this chapter, but interesting and important for bigger discussions of Darwinian populations and which sorts of systems can do things like replicate and evolve [1.21].

binary either/or choices. Life criteria can be specifically material, permissively functional, or anywhere in between; characterizations can combine features of individuals and collectives [1.50]; and characterizations can be explicitly minimal, explicitly inclusive, or neutral on the matter. So the four dimensions do not imply a straightforward possibility space of 16 ways to characterize life. Rather, we can think of these as four axes along which approaches to characterizing life can be compared.

To summarize the above conclusions about how, and to what extent, each dimensions can make a difference in origin of life research:

- Regarding Dimension 1: origin of life researchers should characterize life as a matter of degree, not a dichotomy. This is compatible with understanding the transition from non-life to life as gradual.
- Regarding Dimension 2: to the extent that the focus is on explaining the origin of life as we know it on Earth (a how-actually explanation), origin of life researchers are in a special position to emphasize strongly material characterizations of life, compared to other fields with a stake in characterizing life.
- Regarding Dimension 3: this dimension does not necessarily make a difference in and of itself. But in some threads of origin of life research focused explicitly on characterizing individual organisms versus collectives of organisms—if the status of those entities as living or non-living is at stake—an individual or collective characterization of life can make a difference.
- Regarding Dimension 4: origin of life researchers have a particular stake in characterizing life minimally, rather than inclusively. However, unlike with Dimension 1, there is no incompatibility between explaining the origin of life and characterizing life inclusively.

1.5. Conclusion

Two further explanatory dimensions of origin of life research are not addressed above, and bear mentioning, namely, questions about where and when life originated. In the context of how-actually explanations of life's origins, key questions include: in what environment(s) (for example, ancient hot springs or deep-sea hydrothermal vents, and when exactly, did life emerge on Earth? In the context of how-possibly explanations of life's origins, key questions include: in what sorts of environments could life emerge (does it have to involve water, or specifically hydrothermal conditions)? I do not think that any of the four dimensions discussed above make a difference to these questions in and of themselves, beyond the point made in Section 1.4.2 about material characterizations of life having priority in the context of how-actually explanations of life's origin, and how-possibly explanations tending to favor less specifically material characterizations of life.

But even so, characterizations of life (they need not be definitions) are in the background in origin of life research, even when they are not explicitly foregrounded or debated. It is interesting and important to draw this to the surface, regardless of whether or not one wishes to engage with the debate about defining life. The considerations discussed above reinforce the idea that despite *defining* life being arguably unnecessary for explaining the origin of life, *characterizing* life plays an at least implicit, and sometimes explicit role in theoretical and empirical efforts in origin of life research.

A final point to note about the four dimensions is how they reinforce pluralism about characterizing life, discussed in Section 1.2—though note that I have focused on a different angle of pluralism here, namely, pluralism in strategies or commitments in how life is characterized, rather than in the specific criteria featured in characterizations. For example, however we carve up what counts as a living individual or a living collective (Dimension 2), it is clear that some properties (such as metabolism) can apply only to individuals, other properties (such as evolution) can apply only to collectives, and other properties (such as self-regulation) could apply to either. This allows us to see how there is no in-principle conflict in having multiple co-existing characterizations of life at once. Some, such as metabolic characterizations, might apply to individuals, and others, such as evolutionary characterizations, might apply to collectives; these can be compatible [1.50]. Adding the rest of the dimensions to this example supports a call for accepting, and learning from, the proliferation of proposed characterizations of life.

References

1.1. Bedau, M. (1998) Four puzzles about life. *Artificial Life* 4(2), 125–140.

1.2. Bedau, M. (2012) A functional account of degrees of minimal chemical life. *Synthese* 185(1), 73–88.

1.3. Bedau, M. A. and Cleland, C. E. (eds.) (2010) *The Nature of Life: Classical and Contemporary Perspectives from Philosophy and Science*. Cambridge University Press, Cambridge, UK.

1.4. Benner, S. A. (2010) Defining life. *Astrobiology* 10, 1021–1030.

1.5. Bich, L. and Green, S. (2018) Is defining life pointless? Operational definitions at the frontiers of biology. *Synthese* 195(9), 3919–3946.

1.6. Boden, M. A. (2003) Alien life: how would we know? *International Journal of Astrobiology* 2(2), 121–129.

1.7. Brusse, C. (2016) Planets, pluralism, and conceptual lineage. *Studies in History and Philosophy of Science Part B: Studies in History and Philosophy of Modern Physics* 53, 93–106.

1.8. Cairns-Smith, A. G. (1990) *Seven Clues to the Origin of Life: A Scientific Detective Story*. Cambridge University Press, New York, USA.

1.9. Cleland, C. E. (2007) Epistemological issues in the study of microbial life: Alternative terran biospheres? *Studies in History and Philosophy of Biological and Biomedical Sciences* 38(4), 847– 861.

1.10. Cleland, C. E. (2012) Life without definitions. *Synthese* 185, 125–144.

1.11. Cleland, C. E. and Chyba, C. F. (2007) Does "life" have a definition? In: *Planets and Life: The Emerging Science of Astrobiology*. W. T. Sullivan and J. A. Baross (eds.), Cambridge University Press, Cambridge, UK: 119–131.

1.12. Cornish-Bowden, A. and Cárdenas, M. L. (2017) Life before LUCA. *Journal of Theoretical Biology* 434, 68–74.

1.13. Crick, F. (1981) *Life Itself: Its Origin and Nature*. Simon & Schuster, New York, USA.

1.14. Dzieciol, A. J. and Mann, S. (2012) Designs for life: protocell models in the laboratory. *Chemical Society Reviews* 41(1), 79–85.

1.15. Farnsworth, K. D., Nelson, J. and Gershenson, C. (2013) Living is information processing: from molecules to global systems. *Acta Biotheoretica* 61(2), 203–222.

1.16. Feinberg, G. and Shapiro, R. (1980) *Life beyond Earth: The Intelligent Earthling's Guide to Life in the Universe*. William Morrow, New York, USA.

1.17. Forterre, P. (2010). Defining life: the virus viewpoint. *Origins of Life and Evolution of Biospheres* 40(2), 151–160.

1.18. Gánti, T. (2003). *The Principles of Life*. Cambridge University Press, Cambridge, UK.
1.19. Ghiselin, M. T. (1974). A radical solution to the species problem. *Systematic Biology* 23(4), 536–544.
1.20. Gilbert, W. (1986). Origin of life: the RNA world. *Nature* 319(6055), 618.
1.21. Godfrey-Smith, P. (2009) *Darwinian Populations and Natural Selection*. Oxford University Press, Oxford, UK.
1.22. Griesemer, J. (2015) The enduring value of Gánti's chemoton model and life criteria: heuristic pursuit of exact theoretical biology. *Journal of Theoretical Biology* 381, 23–28.
1.23. Hermida, M. (2016) Life on Earth is an individual. *Theory in Biosciences* 135, 37–44.
1.24. Hull, D. L. (1976) Are species really individuals? *Systematic Biology* 25(2), 174–191.
1.25. Joyce, G. F., Deamer, D. W. and Fleischaker, G. (1994) *Origins of Life: The Central Concepts*. Jones and Bartlett, Boston, USA.
1.26. Knuuttila, T. and Loettgers, A. (2017) What are definitions of life good for? Transdisciplinary and other definitions in astrobiology. *Biology & Philosophy* 32(6), 1185–1203.
1.27. Kompanichenko, V. (2008) Three stages of the origin of life process: bifurcation, stabilization and inversion. *International Journal of Astrobiology* 7(1), 27–46.
1.28. Lovelock, J. (1979) *Gaia: A New Look at Life on Earth*. Oxford University Press, Oxford, UK.
1.29. Luisi, P. L. (1998) About various definitions of life. *Origins of Life and Evolution of the Biosphere* 28, 613–622.
1.30. Machery, E. (2012) Why I stopped worrying about the definition of life . . . and why you should as well. *Synthese* 185(1), 145–164.
1.31. Malaterre, C. (2010) Lifeness signatures and the roots of the tree of life. *Biology and Philosophy* 25, 643–658.
1.32. Mariscal, C. and Doolittle. W. F. (2015) Eukaryotes first: how could that be? *Philosophical Transactions of the Royal Society B: Biological Sciences* 370(1678), 20140322.
1.33. Mariscal, C. and Doolittle, W. F. (2018) Life and Life only: a radical alternative to life definitionism. *Synthese* 197, 2975–2989.
1.34. Maturana, H. R. (1981) Autopoiesis. In: *Autopoiesis: A theory of the living organization.* M. Zeleny (ed.), North Holland, New York, USA: 21–33.
1.35. Mix, L. J. (2015) Defending definitions of life. *Astrobiology* 15(1), 15–19.
1.36. Oliver, J. D. and Perry, R. S. (2006) Definitely life but not definitively. *Origins of Life and Evolution of the Biospheres* 36(5–6), 515–521.
1.37. Olson, E. T. (1997) The ontological basis of strong artificial life. *Artificial Life* 3(1), 29–39.
1.38. Oparin, A. I. (1964) *Life: Its Nature, Origin, and Development*. A. Synge (trans.). Academic Press, New York, USA.
1.39. Orgel, L. E. (2004) Prebiotic chemistry and the origin of the RNA world. *Critical Reviews in Biochemistry and Molecular Biology* 39, 99–123.
1.40. Pace, N. R. (2001). The universal nature of biochemistry. *Proceedings of the National Academy of Sciences of the United States of America* 98(3), 805.
1.41. Pályi, G., Zucchi, C. and Caglioti, L. (eds.) (2002) *Fundamentals of Life*. Elsevier, Paris, France.
1.42. Parke, E. C. (2013). What could arsenic bacteria teach us about life? *Biology and Philosophy* 28(2), 205–218.
1.43. Parke, E. C. (2020) Dimensions of life definitions. In: *Social and Conceptual Issues in Astrobiology.* K. Smith and C. Mariscal (eds.), Oxford University Press, Oxford, UK: 79–91. Oxford University Press.
1.44. Perret, M. (1952) Biochemistry and bacteria. *New Biology* 12, 68.

1.45. Popa, R. (2004) *Between Necessity and Probability: Searching for the Definition and Origin of Life*. Springer, Berlin, Germany.
1.46. Pradeu, T. (2016). The many faces of biological individuality. *Biology & Philosophy* 31, 761–773.
1.47. Rasmussen, S., Bedau, M. A., Chen, L., Deamer, D., Krakauer, D. C., Packard, N. H. and Stadler, P. (2009) *Protocells: Bridging Nonliving and Living Matter*. MIT Press, Cambridge, MA, USA.
1.48. Rasmussen, S., Bedau, M. A., McCaskill, J. S. and Packard, N. H. (2009). A roadmap to protocells. In: *Protocells: Bridging Nonliving and Living Matter*. S. Rasmussen, M. Bedau, L. Chen, D. Deamer, D. Krakauer, N. H. Packard and P. Stadler (eds.), MIT Press, Cambridge, MA, USA: 71–100.
1.49. Rong, R., Chandley, A. C., Song, J., Mcbeath, S., Tan, P. P., Bai, Q., & Speed, R. M. (1988) A fertile mule and hinny in China. *Cytogenetics and Cell Genetics* 47(3), 134–139.
1.50. Ruiz-Mirazo, K., Peretó, J. and Moreno, A. (2004) A universal definition of life: autonomy and open-ended evolution. *Origins of Life and Evolution of the Biosphere* 34, 323–346.
1.51. Ruse, M. (1987) Biological species: natural kinds, individuals, or what? *The British Journal for the Philosophy of Science* 38(2), 225–242.
1.52. Sagan, C. (1970) Life. In: *Encyclopaedia Britannica.* Encyclopaedia Britannica, Chicago, USA: 1083–1083A.
1.53. Scharf, C., Virgo, N., Cleaves, H. J. II, Aono, M., Aubert-Kato, N., Aydinoglu, A., Barahona, A. et al. (2015) A strategy for origins of life research. *Astrobiology* 15(12), 1031–42.
1.54. Smith, K. (2018) Life as adaptive capacity: bringing new life to an old debate. *Biological Theory* 13(2), 76–92.
1.55. Suárez, J. and Stencel, A. (2020) A part-dependent account of biological individuality: Why holobionts are individuals *and* ecosystems simultaneously. *Biological Reviews*, brv.126.
1.56. Szostak, J. W. (2012) Attempts to define life do not help to understand the origin of life. *Journal of Biomolecular Structure and Dynamics* 29(4), 599–600.
1.57. Taylor, P. (1986). *Respect for Nature: A Theory of Environmental Ethics*. Princeton University Press, Princeton, USA.
1.58. Tessera, M. (2011). Origin of evolution versus origin of life: A shift of paradigm. *International Journal of Molecular Studies* 12(6), 3445–3458.
1.59. Trifonov, E. N. (2011) Vocabulary of definitions of life suggests a definition. *Journal of Biomolecular Structure and Dynamics* 29(2), 259–266.
1.60. Tsokolov, S. (2010) A theory of circular organization and negative feedback: defining life in a cybernetic context. *Astrobiology* 10(10), 1031–1042.
1.61. Vaneechoutte, M. and Renato, F. (2009) From the primordial soup to the latest universal common ancestor. *Research in Microbiology* 160(7), 437–440.
1.62. Westall, F., Hickman-Lewis, K., Hinman, N., Gautret, P., Campbell, K. A., Bréhéret, J. G., Foucher, F. et al. (2018) A hydrothermal-sedimentary context for the origin of life. *Astrobiology* 18(3), 259–293.
1.63. Westheimer, F. (1987). Why nature chose phosphates. *Science* 235(4793), 1173.
1.64. Wilke, C. O. and Adami, C. (2002) The biology of digital organisms. *Trends in Ecology & Evolution* 17(11), 528–32.
1.65. Wilson, D. S. and Sober, E. (1989) Reviving the superorganism. *Journal of Theoretical Biology* 136(30), 337–356.
1.66. Wolfe-Simon, F., Davies, P., and Anbar, A. (2009) Did nature also choose arsenic? *International Journal of Astrobiology* 8(2), 69–74.