



Evolutionary Biology  
New Perspectives on Its Development 5

Anne Dambricourt Malassé *Editor*

# Self-Organization as a New Paradigm in Evolutionary Biology

From Theory to Applied Cases in the Tree  
of Life

 Springer

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# Evolutionary Biology – New Perspectives on Its Development

Volume 5

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Anne Dambricourt Malassé  
Editor

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Tree of Life

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*Editor*

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# Contents

<b>1</b>	<b>Introduction: Understanding the Origins and Evolution of Living Organisms—The Necessity of Convergence Between Old and New Paradigms . . . . .</b>	<b>1</b>
	Anne Dambricourt Malassé	
<b>Part I The Modernity of Old Paradigms</b>		
<b>2</b>	<b>Self-Organization Meets Evolution: Ernst Haeckel and Abiogenesis . . . . .</b>	<b>11</b>
	Georgy S. Levit and Uwe A. Hossfeld	
<b>3</b>	<b>D’Arcy Wentworth Thompson’s “Physico-Mathematical” Approach to the Investigation of Morphogenesis and Its Pertinence to Cognitive-Behavioral and/or Learning-Based Explanations of Evolution . . . . .</b>	<b>33</b>
	Adam C. Scarfe	
<b>4</b>	<b>From Dissipative Structures to Biological Evolution: A Thermodynamic Perspective . . . . .</b>	<b>91</b>
	Dilip Kondepudi, James Dixon, and Benjamin De Bari	
<b>5</b>	<b>Self-Organization at Different Levels of Metazoan Complexity in Comparative Genomic–Phenomic Context . . . . .</b>	<b>119</b>
	Valeria V. Isaeva	
<b>6</b>	<b>Instinct as Form: The Challenge of Bergson . . . . .</b>	<b>161</b>
	Stephen E. Robbins	
<b>Part II Modernity of Self-Organization and Emerging Paradigms</b>		
<b>7</b>	<b>Biological Evolution of Microorganisms . . . . .</b>	<b>187</b>
	Werner Arber	
<b>8</b>	<b>Self-Organization in Embryonic Development: Myth and Reality . . . . .</b>	<b>195</b>
	Stuart A. Newman	

---

<b>9</b>	<b>The Morphoprocess and the Diversity of Evolutionary Mechanisms of Metastable Structures . . . . .</b>	<b>223</b>
	Andrei I. Granovitch	
<b>10</b>	<b>Mesological Plasticity as a New Model to Study Plant Cognition, Interactive Ecosystems, and Self-Organized Evolutionary Processes . . . . .</b>	<b>253</b>
	Marc-Williams Debono	
<b>11</b>	<b>Quantum Fractal Thermodynamics to Describe the Log-Periodicity Law in Species Evolution and Human Organizations . . . . .</b>	<b>291</b>
	Diogo Queiros-Condé, Jean Chaline, and Ivan Brissaud	
<b>12</b>	<b>Sapiens and Cognition: The Optimal Vertical Nervous System—The Last Threshold of Self-Organized and Self-Memorizing Increasing Complexity from Gametes to Embryo . . . . .</b>	<b>307</b>
	Anne Dambricourt Malassé	
<b>13</b>	<b>Evolutionary Creativity . . . . .</b>	<b>359</b>
	Edgar Morin	



# Introduction: Understanding the Origins and Evolution of Living Organisms—The Necessity of Convergence Between Old and New Paradigms

1

Anne Dambricourt Malassé

For several decades now, the field of evolutionary biology has been envisioned as organized around a profound and fundamental divide: theories relying on strong selective factors and those appealing to weak ones only [...]. This Introduction calls for a new and more consistent paradigm that would make sense of the overall development of evolutionary biology, one based on a realignment of the alliance between all partners pursuing research in this area. —Richard Delisle (2021).

## Abstract

Global warming, the Anthropocene concept (Hamilton C, Nat News 536(7616): 251, 2016), the sixth mass extinction (Ceballos et al., PNAS 114(30):E6089–E6096, 2017), and the rapid progress in astrobiology looking for primitive life forms are raising the awareness of the actors of society toward evolution as the prime reality without which neither the biodiversity nor our species would exist, and our civilizations survive. This discernment leads us to a better understanding of the processes at the origin of the organization of dynamic structures and their reproductive properties, from the smallest cellular unit to the most complex interactions within the organism and then between organisms for the same unit

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of time and space. This awareness also encourages us to discern, over very long geological and cosmic time scales, principles of self-organization of complex systems and generic laws of adaptation and complexification.

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**Keywords**

Life · Evolution · Self-organization · Complexity · Emergence · Memory · Transdisciplinarity · Paradigms · Modeling · Epistemology · Basic and applied research

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**1.1 Introduction**

The transformism formulated by Jean-Baptiste Lamarck in 1801 at the National Museum of Natural History, Paris, and the “natural selection” formulated by Charles Darwin in 1859 were the premises of a general systems theory (Bertalanffy 1968), necessary to understand the self-organized processes with the transmission of acquired characters, but they did not master the physical explanations for abiogenesis or the emergence of the cellular cycle, the beginning of life. Since then, the development of technics and methods of knowledge acquisition, as well as critical thinking, have made it possible to develop numerous models for the distinct levels of organization, thanks to physical, chemical, thermodynamics, and mathematics formulations, each one questioning the analytical processes creating order and stability, but also instabilities with innovative emergences, up to the level of reflexive consciousness and its creative abilities.

The sciences concerned with time (instant, duration, memory), energy (conservation, dissipation), form (mathematics, physical laws), and signals (information) had their precursors with Ernst Haeckel (1834–1919), Henri Bergson (1859–1941), D’Arcy Wentworth Thompson (1860–1948), Alexandre Oparin (1894–1980), John Haldane (1892–1964), Claude Shannon (1916–2001), René Thom (1923–2002), and Ilya Prigogine (1917–2003), among other remarkable theorists of the nineteenth and twentieth centuries. Their research has contributed to the development of new theories and paradigms, such as the deterministic Chaos theory with nonlinear dynamic systems, near or far from equilibrium in living phenomena: dissipative structures and geometric and dynamic fractals. Cybernetics in systems theory developed during the twentieth century and applied to robotics or nonliving natural phenomena help to distinguish the living properties from the artificial intelligence (AI) created by the human mind. AI is cut off from the irreversible processes of biological evolution, which have been going on for 4 billion years. Human biology and cognitive abilities emerge from this, with the trace of this evolution in each cell, that a robot even hybridized with a human cell will never have. A robot is the artificial product of mathematical knowledge and not an innovation of biological evolution. For this reason, a fundamental reflection is necessary to discuss self-organization not only in biological ontogeny, well-accepted, but also in evolutionary gametogenesis, which is much rarer and that

raises difficulties at a conceptual level upstream of biological processes. Such difficulties are the processes of emergence, which become explicit with the origins of life.

Those scientific developments have been slowly integrated into the life sciences, to model the morphogenesis, the regulation of homeotic genes in the control of embryogenesis, the phylogenetic stability of ontogenetic geometric trajectories, the emergence processes, etc. The transdisciplinarity developed by Edgar Morin (Rigolot 2020) for half a century is a forthcoming method of the twenty-first century, allowing for the juxtaposition of such different fields of knowledge, in the acceptance of their differences and without mutual exclusion. The origins of life created the evolutionary properties of gametogenesis, and ontogeny and phylogeny are thus associated in recursive loops since phylogeny of gametes has created a great variety of ontogeny.

The volume divided into two parts does not claim to be exhaustive as the diversity of models varies according to the scales studied. Rather, it is meant to be representative of the immense scope of theoretical knowledge in need of attention, requiring a combination of open-mindedness, rigor, reflection, and the search for complementarity between explanatory models. These advances concern all scales of time and space in living systems, from complex molecular interactions and productions (memorized by transmission or innovative) to instinct, intuition, and memory until the self-reflexive consciousness.

The first part brings together chapters devoted to the modern relevance of nineteenth- and twentieth-century theories. The origins of life are analyzed since the abiotic phase with Georgy Levit and Uwe Hossfeld revisiting Ernst Haeckel (1834–1919) (Chap. 2). The authors recall that Charles Darwin never proposed a theory to understand the transition between an abiotic molecular environment and the formation of unicellulars necessary for the credibility of transformism. Ernst Haeckel postulated the spontaneous generations of monera, the precursor of Haldane-Oparin hypothesis, “we reconstruct Haeckel’s theory of abiogenesis as a self-organization theory and demonstrate its importance as an early attempt to discuss the origin of life in the post-Darwinian era.” In Chap. 3, Adam Scarfe develops the current influence of D’Arcy Thompson (1860–1948) calling in mind his Aristotelian and Kantian thinking patterns and his “physico-mathematical” approach of morphogenesis. The author refers to the Cambrian explosion under the angle of self-organized complex systems, referring to autopoiesis, teleology, and the hypothetical scenario of paleontologist Simon Conway Morris (1988) that “serves as a concrete example of how physico-geometrical factors entrain and/or present constraints that may canalize the behavioral selections of organisms.”

Ilya Prigogine (1917–2003) has demonstrated the compatibility between the production of entropy and the spontaneous organization of a dynamical system. These are the dissipative structures far from thermodynamic equilibrium. Since then, the Brussels school of thermodynamics has multiplied the examples of physico-chemical mechanisms whose behaviors resemble those of a living being engaged in an irreversible growth, the time arrow of life fighting against disorganization and death. Nonliving dissipative structures show that physicochemical components can

generate complex dynamic organizations ordered in their own space and according to their environment. In Chap. 4, Dilip Kondepudi, James Dixon, and Benjamin De Bari describe the remarkable formation of a worm-like structure capable of displacement. “We will see how some fundamental traits such as end-directed behavior, self-healing, and mutations, can be described in thermodynamic terms, as phenomena in self-organized non-equilibrium systems, called dissipative structures.”

The step of life requires properties missing in crystals that of self-memorization. A self-organization could not reproduce itself without its own memorization and the level of energy allowing the emergence of both its complexity and stability. The conditions are at least that of concentration thresholds of “islets” of complexities and energetical and informative interactions in permanent search of equilibrium. Those “islets” were composed of molecules whose properties allowed them to be recognized by other molecules to reproduce their information content, such as RNA and DNA, able to form membranes, produce energy, and synthesize proteins. Abiogenesis is a growing interest thanks to the search for exoplanets and studies of ancient Martian lake deposits with analysis of algal-like biota. “Our morphological and morphometrical investigations (. . .) suggest the presence of remnants of complex algal-like biota, similar to terrestrial procaryotes and/or eukaryotes; possible microorganisms that, based on absolute dating criteria used by other scholars, lived on Mars about  $2.12 \pm 0.3$  Ga ago” (Rizzo et al. 2021).

Understanding the dynamics of self-memorizations still has a long way to go, with the models of dissipative structures and basins of attraction and their attractors. The diversity of unicellulars and their chemical–energetic environments have favored the Cambrian explosion with the emergence of multicellular organisms. Chapter 5 addresses this new threshold in the evolution of life with Valeria Isaeva. The author follows the arrow of negentropic time by comparing the current cyanobacteria (colonial and filamentous prokaryotes) and the metazoans such as sea urchins and analyzes the physical properties (forces) that constrain the morphogenesis of an embryonic body plan (or archetype). The aim is a discussion to identify the correlations between genome and phenotype that determine the body plan, from the molecular scale to the organs, thanks to a multidisciplinary approach introducing forms, energy, and topology according to René Thom (1923–2002). Indeed “the central problem of topology is that of reconstructing the global from the local” (Papadopoulos 2020), Thom’s mathematics allows a more precise explanation of self-constrained dynamical systems and the emergence of new body planes coherent on the different spatial and temporal scales of ontology.

The first part ends with Chap. 6 on questions raised by Henri Bergson (1859–1941) still relevant: Stephen Robbins comes back to *Creative Evolution* (1907–1911) and “a pivotal discussion, the extreme complexity of instinctual behavior” such as Hymenoptera, which “‘knows’ precisely the three locations of motor–neuron complexes at which to sting a cricket such that it is paralyzed.” These observations require mechanisms of analysis and recognition of signals, therefore previous memories before finding innovative solutions: “Any theory of evolution, be it selection, self-assembly, or self-organization, is equally bound to address not only the origin problem of an organism’s structure but the correlated functional problem

of instinct.” The problem extends to intuition and memory and requires a consensus on the nature of consciousness, understood as a network of exchanges of signals, correctly identified, and therefore previously learned, memorized, and transmitted. Such complex processes have recently been described in the unicellular *Physarum polycephalum* (Broussard et al. 2019).

The second part of the volume presents contemporary models dealing with self-organization. Werner Arber describes harmless intestinal bacteria showing that “biological evolution occurs in microorganisms by consecutive steps of genetic variation [which] can be attributed to a process of self-organization that contributes to the permanent creation of appropriate biological capacities” (Chap. 7). Understanding the evolution of organogenesis under conditions of instability requires the distinction between cybernetics and living organisms affected by unpredictable fluctuations of global equilibrium and the ability of self-reorganization since fertilization. In Chap. 8, Stuart Newman discusses the concept of self-organization since the teleological formulation by Immanuel Kant in “*Critic of Judgement*” (1790) making the distinction between self-organization of non-living systems, living beings (embryogenesis), and the evolutionary processes that changed embryonic development. The concept has progressively replaced the metaphor of genetic program encoded in the DNA inspired by cybernetics in the 1950s. The emergence of new embryogenesis is not the one of a genetic program that assumes knowledge of the end (the final stage).

Life and the evolution of living organisms are not programmed robots, and fluctuations are innovative parameters that cannot predict bifurcations, but the complexity of gametes still misunderstood allows the reorganization of the ontogenetic memory and its hereditary transmission. Andrei Granovitch is engaged in a critical analysis of the synthetic theory (Neo-Darwinian doctrine) in which the notion of a highly integrated metastable system is missing, underlying that concept varies according to the scale of observation and regarding different evolutionary problems, adaptation, or transformation. In this Chap. 9, the author proposes to remove the doubt by unifying the distinct levels in a dynamical and dissipative system or morphoprocess and “a change of the evolutionary paradigm” to an “extended evolutionary synthesis.”

Chapter 10 addresses self-organization in the plant kingdom with the concept of biosemiotics, or exchanges of signals between animals and their environment, elaborated in the 1930s by the ethologist Jakob von Uexküll (1864–1944) and his concept of *Umwelt* (Uexküll 1982). Marc-Williams Debono confronts the paradigm with his work based on pioneering phytoelectrography experiments. The results demonstrate the essential role of the electrome within the dynamic coupling between the plant and its singular milieu. These new interfaces open a new field of investigation by revisiting the concepts of plant cognition and more generally of bio- or eco-semiotics.

The quantum world is in permanent agitation, but the long durations of cosmogenesis and biogenesis show universal principles of order or of structural stability (Bois 2002), which allow distinguishing a chronology, a continuity between two different instants and not a stochastic dispersion without reference or

information stabilized and reproducible. This information refers to nuclear forces and implies exchanges with the electronic orbital as developed in the nuclear-electronic orbital (NEO) approach (Hammer-Schiffer 2021).

Diogo Queiros-Condé, Jean Chaline, and Ivan Brissaud analyze in Chap. 11 a log-periodic law by showing its meaning and its relationship with fractality described by quantifying its length, time, and mass. Relying further on the work of Louis de Broglie's "hidden thermodynamics of the particle," they introduced kinetic-thermal chaining of lineage evolution that allows a fractal and quantum thermodynamic description of log-periodicity, which leads to what could be called a "*quantum thermo-fractality*" of the evolution of systems, especially species, astronomical, economic, historical, artistic, and social.

Chapter 12 presents the embryonic and phylogenetic origins of the vertical organization of our species, of which permanent bipedal locomotion is one of the many postnatal consequences (Anne Dambricourt Malassé). This discovery is replaced in its historical context that of the classification of species with Georges Buffon and Jean-Baptiste de Lamarck with the theory of evolution, two characters who have profoundly marked the naturalist tradition of the National Museum of Natural History (Paris). The discovery highlighted a dynamic architectural and morphogenetic unity between dental occlusion and the orientation of the axial endoskeleton that supports and protects the central nervous system from the brain stem. The process was demonstrated as early as 1987. The phylogeny matches with the curve of the increasing complexity of the brain, but the strengthening occurred according to a succession of long stable periods followed by increasing angulation thresholds. The first stage of the verticality was the *Hominidae* (vs semi-erect *Panidae* and *Pongidae*), the last one being ours (*sapiens*). The stability of the evolutionary trajectory does not conform to divergent representations of chaotic bifurcations and allowed us to infer memorization properties specific to gametes. The emergence of the operating chains at the threshold of verticality called here the *cerebro-cerebellar Rubicon*, and the symbolic thought would result in the integration of the cerebellum in the loops of cognitive reflection of the brain, necessary for the control of its balance, the stability of the organism, and to anticipate the fall.

Chapter 13 closes the volume with Edgar Morin who has devoted his life looking into human nature and its singularity in the evolution of life, namely the highest evolutionary degree of the reflexive consciousness of the world and oneself. His method is the most extensive transdisciplinary approach that can be conceived, from quantum mechanics to cybernetics, and human societies to ecosystems and reflexive consciousness. His approach is unified by a definition of the complexity that recognizes through the antagonisms, the manifestations of a single reality that assimilates these conflicts by self-organizing recursive loops, and from which new properties emerge. Fundamental research attempts to grasp these properties at the basis of emergence, and the mind, then, notes the ever-widening extent of the unknown of which it is itself a stakeholder, emerging from universal evolutionary creativity. Reflexive self-consciousness cannot objectively abstract from it. Confronted with all scales of its complexity, the awareness of the limits of the

consciousness is a recognition of its mystery that returns this last to its links with the evolution of the living complexity and those processes of emergence.

These 13 chapters illustrate the diversity of evolutionary processes according to the space-time scales considered, as well as the relevance of the avant-garde schools of thought during the nineteenth and twentieth centuries in explaining the processes of self-organization. Open to the physics of chemistry, to the thermodynamics, mathematics, then cybernetics, and quantum mechanics, their common denominators are the interactions between particles, atoms, and molecules, ordered into their form according to energy levels, capable of association, source of biochemical innovations with the natural creation of autonomous systems, and consequently a complexification of their environment and interactions. The concept of natural selection has paved the way to their discovery for an even finer approach to the threshold of the emergence of life and the modalities of the self-reproduction of unicellular that imply preexisting self-memorization properties. Those modalities have allowed adaptation to their environmental diversifications, fluctuations, and complexified interactions, and then emergences of complexified organizations into multicellular organisms. The concept of natural selection nevertheless is devoid of these looping processes of integration and self-amplification and does not match the natural logic of the creative complexity with memorization properties. Such living properties may react to the risks of Anthropocene extinction, thanks to innovative creativities, but also to the memory of processes proper to the different lineages, which were useful for their survival in the past.

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**Part I**

**The Modernity of Old Paradigms**



# Self-Organization Meets Evolution: Ernst Haeckel and Abiogenesis

# 2

Georgy S. Levit and Uwe A. Hossfeld

## Abstract

Although Darwin proposed a logically coherent theory of evolution, which presupposed the natural occurrence of initial life forms, he never offered a theory of the origin of life. This task was instead taken up by his German pupil Ernst Haeckel. In contrast to Darwin, Haeckel paid lots of attention to abiogenesis. Already in his first major Darwinian book, *Generelle Morphologie* (General Morphology), he postulated the origin of life on Earth by way of *archigonia*, i.e., spontaneous generations of *monera* (the most primitive structureless microorganisms) directly from inert matter. For Haeckel, all living organisms on earth evolved from monera, and until his very last publication, he admitted the initial occurrence of monera was a repetitive event; i.e., the very initial evolution was polyphyletic. This created a tension between his monistic and pro-Darwinian tendency toward strictly monophyletic explanations on the one hand and his theory of abiogenesis on the other hand. Essentially, Haeckel's concept was a self-organization hypothesis built into the framework of Darwinian theory, and it fits into the more comprehensive doctrine of Haeckelian philosophical monism as well. Although it appears archaic from the modern viewpoint, Haeckel's theory of abiogenesis contributed to the growth of experimental studies of abiogenesis in the early 1920s—for example, in the development of the Oparin–Haldane hypothesis. In his book, *The Origin of Life*, Aleksandr Oparin explicitly mentions Haeckel and discusses Haeckel's concept of abiogenesis in some detail. In this chapter, we reconstruct Haeckel's theory of abiogenesis as a self-organization theory and demonstrate its importance as an early attempt to discuss the origin of life in the post-Darwinian era.

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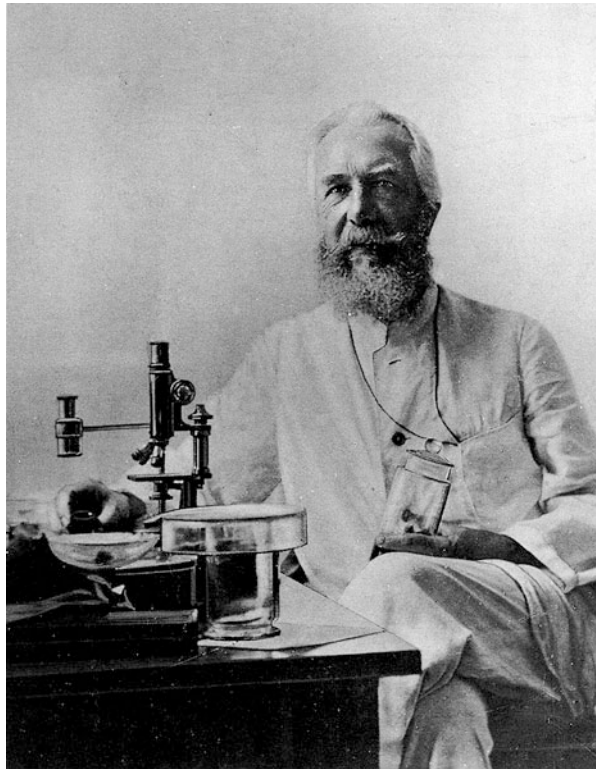
**Keywords**Abiogenesis · Ernst Haeckel · Self-organization · Evolution

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**2.1 Introduction**

Ernst Haeckel is known, first of all, as a crucial figure in the growth of Darwinian biology in the nineteenth century—as the “German Darwin” (Fig. 2.1). He was undoubtedly the major figure of the first Darwinian revolution in German lands and, arguably, on the continent as a whole. In his time, more people worldwide learned evolutionary theory from his publications than from any other sources, including Darwin’s own writings (Richards 2018). Haeckel’s popular scientific *Natural History of Creation* went through 12 editions, and *The Riddles of the Universe* sold more than 650,000 copies, “making it the most successful work of popular science in German history” (Finkelstein 2019). He defended and developed the Darwinian theory with unmatched passion and energy and created a conceptual framework within which the majority of Darwinians worldwide worked over subsequent decades. Contemporary biology and related sciences are unthinkable without terms

**Fig. 2.1** Ernst Haeckel in his laboratory in the Buitenzorg Botanical Gardens on the Island of Java, 1901 (Courtesy: archive U. H.)



and concepts introduced by Haeckel, such as “phylogeny,” “monophyletic,” “polyphyletic,” “ontogeny,” “biogenetic law,” or “ecology.” Moreover, his novel theories were encouraged and admired by Darwin himself (Levit and Hossfeld 2019). It was Haeckel who crucially contributed to the visualization of the Darwinian theory by designing multiple “phylogenetic trees” reflecting evolutionary pathways of various organismic groups, including humans.

In addition to being Darwin’s most influential and faithful disciple on the continent, Haeckel also significantly broadened Darwin’s scientific agenda. While Darwin largely constrained himself to the establishment of the theory of biological evolution, Haeckel aimed at the creation of a universal evolutionary theory explaining the evolution of the entire universe—a theory mobilizing all natural sciences and philosophy. Given these grand ambitions, Haeckel was compelled to offer a theory of life’s origins, whereas Darwin bracketed the issue in favor of his immediate theoretical interests: “Charles Darwin’s self-imposed task was the understanding of the evolutionary processes that underlie biological diversity, a task that epistemologically can be undertaken even if it provides no explanation of the origin of life itself” (Peretó et al. 2009). Although Darwin never came up with a proper theory of abiogenesis, his correspondence proves that he was speculating about it.<sup>1</sup> In the published works, Darwin was very cautious though; for example, he did not even mention microorganisms in the *Origin of Species* (Darwin 1859; Davies 2009), and it was Haeckel who first brought the Darwinian agenda to bear on the fields of microbiology and the origin of life (Kutschera 2016). Never afraid of brave speculation, Haeckel developed an idiosyncratic theory of the origin and early evolution of life which he regarded as a further extension of the Darwinian paradigm.

Haeckel’s theory of abiogenesis is not simply a matter of historical curiosity. There is a causal chain connecting Haeckel’s work with modern theories of life’s origins. Until very recently, it has seldom been recognized that Haeckel played a significant or even key role in shaping Alexander I. Oparin’s (1894–1980) theory of the origin of life from lifeless matter (Lazcano 2016). As argued by Kolchinsky and Levit (2019), Haeckel’s hypothesis contributed to the growth of experimental studies of abiogenesis in the early 1920s, the best known of which became the works of Oparin. In his path-breaking book, *The Origin of Life* (the earliest version was published in 1924 in Russian: Oparin 1924), Oparin acknowledges Haeckel’s view that spontaneous generation is a “logical postulate of philosophical natural science” (i.e., this concept follows logically from everything we know from natural science), although it is not yet proven by immediate experience, and discusses his concept of abiogenesis in some detail (Oparin 1941, pp. 48–49). At the same time, Oparin criticized Haeckel for making no principal difference between the occurrence of crystals and “anucleate monera.” He classified Haeckel’s views therefore as naïve and “mechanistic” and took issue specifically with the immediate emergence of living matter from inorganic substances: “This was Haeckel’s essential error” (Ibid., p. 49).

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<sup>1</sup>E.g., Letter no. DCP-LETT-7471, Darwin to J. D. Hooker (01.01.1871).

In the present chapter, we outline Haeckel's views on the origin of life and early evolution and explain his motivation for developing these ideas. We come to the conclusion that in developing his theory of abiogenesis Haeckel followed his monistic creed and established several speculative hypotheses in the absence of sufficient experimental and observational data.

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## 2.2 The Philosophical Background to Haeckel's Theory of Abiogenesis

Haeckel played a central role in the history of monism, which in his interpretation was simultaneously an ethical worldview and a research program in the natural sciences, ontology, and epistemology (Stewart et al. 2019). In contrast to Darwin himself, Haeckel tried to turn Darwinism into a universal worldview, a "philosophy." His universalism did not merely connect academic philosophy with science; it made philosophy and natural science into an inseparable whole. For Haeckel, "all true natural science is philosophy, and all true philosophy is natural science. All true science (*Wissenschaft*), however, is natural philosophy" (Haeckel 1866, Bd. II, p. 447; Hossfeld and Levit 2020).

At the core of Haeckel's doctrine was the concept of evolution as a universal phenomenon affecting everything from inert matter to man. He believed in the unity of body and soul and of spirit and matter:

We adhere firmly to the pure, unequivocal monism of Spinoza: Matter, or infinitely-extended substance, and Spirit (or Energy), or sensitive and thinking substance, are the two fundamental attributes, or principal properties, of the all-embracing divine essence of the world, the universal substance (Haeckel 1900, p. 21).

Monism guided Haeckel's work from his first major Darwinian book, the *Generelle Morphologie* (1866), to his last book, the *Kristallseelen* (Crystal Souls 1917). The adoption of *substance monism* as a scientific meta-methodology and basis for a new worldview (*Weltanschauung*) was Haeckel's major philosophical acquisition. *Substance monism*, such as materialist, idealist, or neutral monism, supposes that all concrete objects fall under one highest type (namely, matter, ideas, or neutral substance, respectively). Haeckel combined matter, energy, and psychoma (the world's soul) into the trinity of substance, thus embracing all basic physical and psychological phenomena within one doctrine. All three elements of the trinity had corresponding conservation laws: the conservation of matter, of energy, and of psychoma (or *Empfindung*: perception). In his last philosophical manifesto, *Gott-Natur* (*Theophysis*) (God-Nature [Theophysis] 1914: Haeckel 2008), Haeckel claimed that his universal concept of substance served to reconcile old and still continuing controversies between materialism, energetics, and panpsychism. From the epistemological viewpoint, Haeckel saw cognition as a "natural physiological process whose anatomic organ is our human brain" (Haeckel 2008, p. 48). For Haeckel, the only secure foundation for science was empirical

knowledge [Erfahrung, Empirie], and the ultimate objective of modern science was to cognize the “unconscious laws” governing the universe, as “everything happens with absolute necessity in accord with mechanical ‘causal’ laws” (Haeckel 2008, pp. 74–75).

Although Haeckel considered himself a part of the Spinozian movement, his own teachings centered first and foremost around the doctrine of the omnipresence of evolution (Hossfeld and Levit 2020). He proposed an all-embracing but organism-centered evolutionism, which took energetic, life-possessing matter to be its substantial, causal foundation. This proposal led him to adopt a kind of anthropocentrism rooted in pan-psychism, which expressed itself in a vectored, apparently teleological evolutionary development. Haeckel explicitly denied genuine teleology in biological evolution (and even introduced the term “dysteleology” as a doctrine of “goallessness” in evolution) (Haeckel 1866, Vol. II, p. 266ff), but the whole logic of his doctrine suggests inevitable progress toward “more perfect” organic creatures [Vervollkommnung]: “The notion of progress is the key of Haeckel’s evolutionary theory” (Dayrat 2003). Haeckel’s progressivism is not about the intrinsic tendency toward perfection, but follows from natural laws governing cosmic and organic evolution and the ontological structure of the universe. For Haeckel, “there was no teleological providence in the universe, only a naturalistic law of progress” (Di Gregorio 2005, p. 189), but the progress toward perfection followed from these laws such that gradual perfecting in biological evolution (*teleosis*, in Haeckel’s terms) is the *inevitable* result of natural selection (Haeckel 1900, p. 272). The transition from inert to living matter is a necessary logical link in this worldview.

Monism and evolutionary theory were, for Haeckel, parts of the same research program, labeled the “monistischen Entwicklungslehre” (the monistic doctrine of evolution). At the core of the monistic worldview was the idea of the fundamental unity and cognizability of the world. The strong connection between the concepts of evolution and monism can be seen in Haeckel’s work, *The Monism and the Link between Religion and Science. The Creed of a Natural Scientist* (1892). In a printed lecture known as the “Altenburg speech,” Haeckel asserted that the monistic idea of God is compatible with the natural sciences, and he recognized the spirit of God in all things. God cannot be seen as a personalized being anymore, namely an individual with a constrained spatial and temporal extension; instead, “God is nature itself” (Haeckel 1914 in: Haeckel 2008, p. 71). Furthermore, he claimed that the Truth, the Good, and the Beautiful are the three noble divinities before which we kneel. There will be new altars built in the twentieth century, Haeckel argued, to celebrate the “trinity of monism” (Levit and Hossfeld 2017).

Haeckel distinguished theoretical and practical monism. Theoretical monism was a worldview grounded in experience, “pure reason,” and science, with the latter based on evolutionism and proceeding from the unity of the universe. The theory of abiogenesis was part of theoretical monism (Krause 1984). Practical monism, on the other hand, was a set of ethical rules for a “reasonable lifestyle” in accord with theoretical monism.

Haeckel’s monistic creed, which brought him into open conflict with traditional religions, determined the internal dynamics of his theoretical system including issues

concerning the origin of life. In his popular treatise, *The Riddle of the Universe*, Haeckel introduced abiogenesis in the chapter on “The Unity of Nature,” summarizing its logical steps in the chapter’s abstract: “The monism of the cosmos. Essential unity of organic and inorganic nature. Carbon-theory. The hypothesis of abiogenesis” (Haeckel 1900, p. 260). He called the first spontaneously generated living bodies on earth, “monera,” and he claimed: “But as these remarkable Monera are from one point of view of the greatest interest, so from another they deserve general attention from the inestimable importance which they possess of affording a mechanical explanation of vital phenomena, and especially for a Monistic explanation of entire organic nature [our italics]” (Haeckel 1869, p. 223). There were three elements of this monistic creed that were crucial for Haeckel in this respect: (1) the universe is a united whole evolving in a certain direction; (2) the direction of the world’s evolution is of dysteleological (as opposed to teleological) nature and is determined exclusively by natural laws; (3) natural laws embrace not only “mechanical” (material) processes, but also psychoma that makes Haeckel’s understanding of “natural laws” much broader than in contemporary science. Proving abiogenesis was therefore absolutely essential for Haeckel. If there is no abiogenesis, the world is not a united whole and the monist creed fails. If there is no abiogenesis, life is a product of supernatural forces and evolution is a teleological process.

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### 2.3 Spontaneous Generation and Early Evolution in Haeckel’s Writings

Haeckel began speculating about the origin of life and looking for the most primitive organismic forms before he published his magnum opus, *Generelle Morphologie der Organismen* (Haeckel 1866). In a letter to Darwin from November 11, 1865,<sup>2</sup> Haeckel described *Protogenes primordialis*<sup>3</sup> as one of the most primitive types of Rhizopoda [eines der allereinfachsten Geschöpfe], the “organism without organs.” Haeckel emphasized that *generatio aequivoca* (spontaneous generation)<sup>4</sup> of such a “protein clump” [Eiweiss-Klumpen] is clearly intelligible, and if true, this would contribute to solving the difficult problem of the beginnings of the evolutionary theory.

In the *Generelle Morphologie*, Haeckel already presented a coherent theory linking planetary and organismic evolution. The metaphysical foundation for his theory was the notion of the unity of organic and inorganic nature, which, Haeckel believed, was “empirically proven” (Haeckel 1866, Vol. II, p. 447). Combined with

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<sup>2</sup>“Letter no. 4934,” accessed on June 10, 2021, <https://www.darwinproject.ac.uk/letter/DCP-LETT-4934.xml>

<sup>3</sup>*Protogenes primordialis* is a moneron Haeckel believed to have observed in 1864 in the Mediterranean by Nice (Nizza) (Haeckel 1865).

<sup>4</sup>Haeckel deployed the terms “generatio aequivoca” and “generatio spontanea” interchangeably; see, e.g., Haeckel (1866, Bd. II, p. 34).

Haeckel's belief in the "almighty" causal law governing all of nature "without exceptions," the idea of the "absolute unity of nature" rendered abiogenesis a logical necessity. As he believed in building his theory on the ground of empirical observations, Haeckel was forced to establish a theory compatible with available biological data.

Haeckel published his theory in the mid of the controversy between Louis Pasteur and Felix Pouchet generated by Pasteur's experiments on spontaneous generation (Farley and Geison 1974). Haeckel was critical of both sides in the controversy and claimed that *plasmogonia* (spontaneous generation) was not yet proven, although it was theoretically impossible that Pasteur would ever be able to prove its nonexistence (Haeckel 1866, Vol. II, p. 34). In clear support of Pouchet, Haeckel proposed the existence of a group of very primitive microorganisms, which he called monera (plural): "A *Moneron* was defined as a primitive form of life consisting of undifferentiated protoplasm and lacking a nucleus" (Rupke 1976). Nothing is as important as the discovery of monera for explaining the origin of life, Haeckel argued (Haeckel 1870, p. 178). Being a "missing link" between macroorganisms and lifeless matter, monera became the crucial element of Haeckel's concept of abiogenesis. Monera, Haeckel claimed, were absolutely homogeneous, structureless organisms, which served as the stem forms (i.e., parent forms) [Stammform] from which all other organisms evolved by way of differentiation (Haeckel 1866, Vol. I, p. 179). Monera spawned directly from inorganic liquid in the same way that crystals appear in their mother liquor [Mutterlauge]. In 1866, Haeckel was uncertain whether spontaneous generation of monera and their subsequent evolution into higher organismic forms was an ongoing process or whether it happened only in the remote past (Haeckel 1866, Vol. II, p. 33, Vol. XXIII, p. 367).

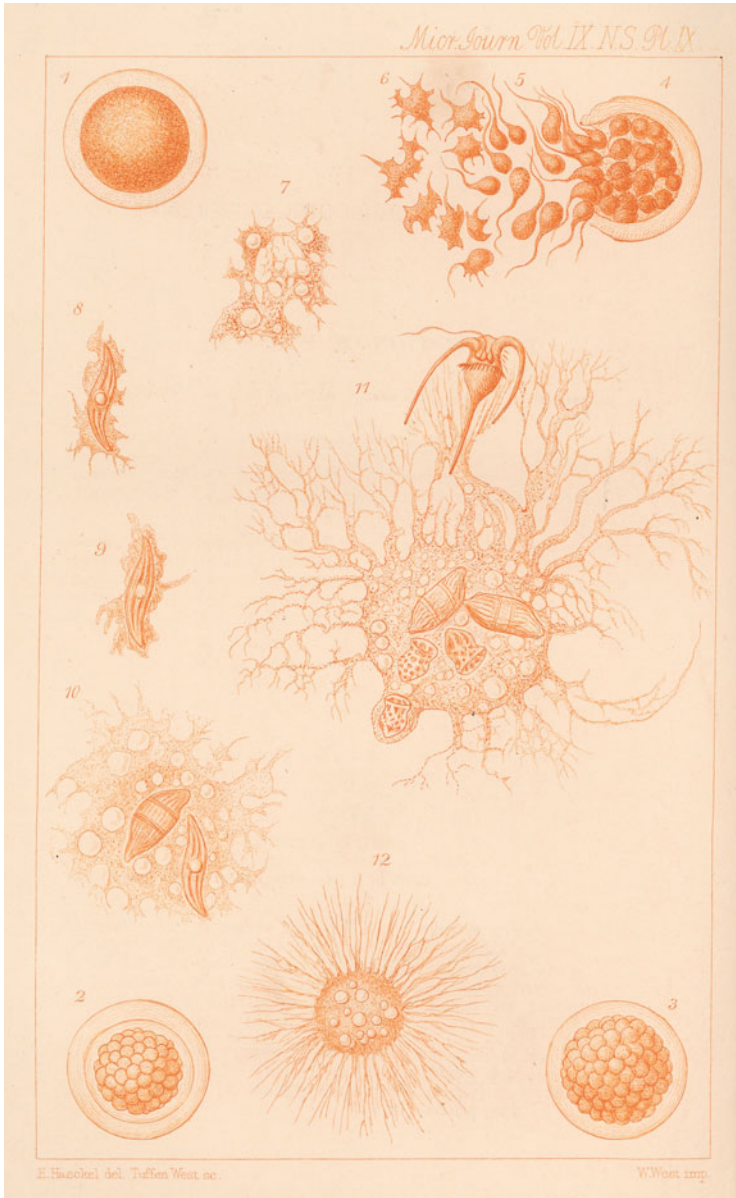
In the *Generelle Morphologie*, Haeckel introduced several terms he would continue to employ when discussing the origin of life. The term *autogonia* was used as a synonym for spontaneous generation [Urzeugung] (Haeckel 1866, Vol. I, p. 179). Specifically, the autogonia hypothesis suggested that structureless monera spawned immediately from the interaction of inorganic substances in a primordial liquid. Another important notion Haeckel introduced was *plasmogonia* (Haeckel 1866, Vol. II, p. 34), which is another kind of parentless procreation of organisms. The difference between autogonia and plasmogonia is that, in the latter case, monera spawn not directly from inorganic matter, but from an organic liquid [organische Bildungsflüssigkeit]. An umbrella notion embracing both kinds of spontaneous generation was *archigonia* (Haeckel 1866, Vol. II, p. 33), which explains why Haeckel called the first monera, "archigonian parent forms." This sophisticated terminological hierarchy was important for Haeckel, because he did not exclude that monera would be spontaneously generated from lifeless matter even today. If this is the case, they would occur in liquids saturated by organic substances, via plasmogonia. In the late publications, Haeckel tended to see the occurrence of monera as a double-step process (first appear organic substances and then monera out of this organic substances) even in the ancient times.

Haeckel presented a mature classification of various monera and a description of their morphology in a lengthy journal paper entitled, *The Monograph of Monera*

[*Monographie der Moneren*], published 2 years after *Generelle Morphologie* (Haeckel 1868). In 1869, an English version of the *Monograph* appeared in the *Quarterly Journal of Microscopical Science* (Haeckel 1869) (Figs. 2.2 and 2.3). In the *Monograph*, Haeckel emphasized that monera were the most simple and primitive [unvollkommenere] of all imaginable life forms (Haeckel 1868, p. 64); even purely theoretically, there could be no organisms simpler than monera. He even hesitated to label monera as organisms as they are not constituted by smaller parts. A most primitive moneron is not a cell (as it is not yet separated into the nucleus and the plasma), but a homogenous protein body in a solid–liquid aggregate state having no rigid geometric characteristics, but becoming spherical when resting and experiencing no external influences. Monera, as structureless plasma globules, are, for Haeckel, proof that an ultimate separation between the two kingdoms of plants and animals is impossible, as they (monera) are so indefinite that they can equally serve as the origin of both plants and animals. Accordingly, Haeckel placed them into the kingdom of Protista along with Rhizopoda, amoeba, diatoms, etc. (Ibid., p. 65).

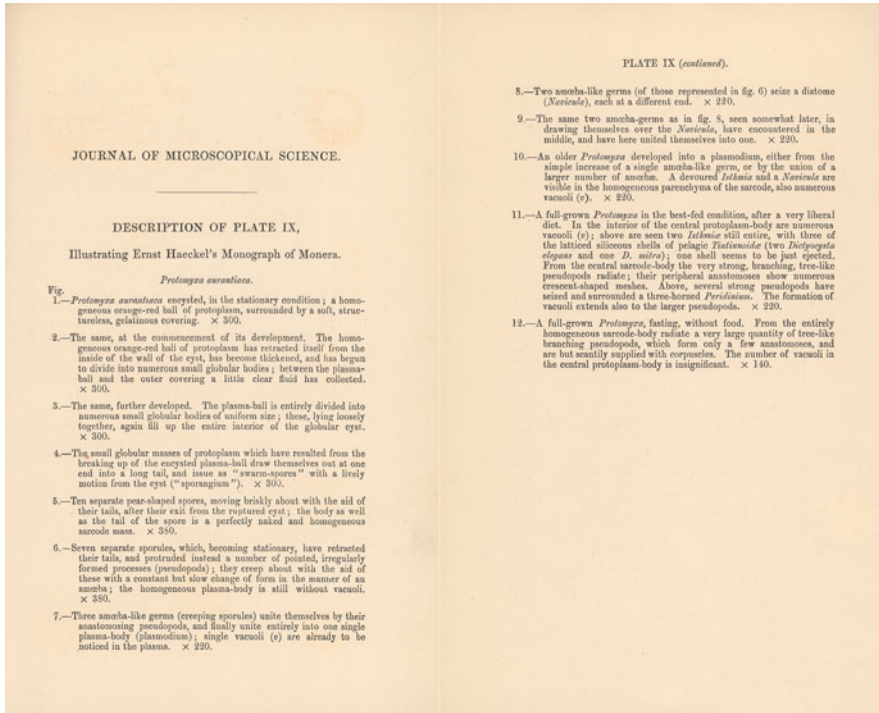
It is important to emphasize that monera, for Haeckel, were not a matter of mere theoretical speculation. The first moneron was discovered by Haeckel in 1864, “and the number has gone on steadily increasing ever since,” as one of Haeckel’s contemporaries, the French protozoologist Aimé Schneider noticed (Schneider 1873). The immediate impulse to write the *Monograph* came from “new observations” Haeckel made in the winter of 1866/1867 on the coasts of the Canary Island Lanzarote, already after completing *Generelle Morphologie*. From a contemporary scientific perspective, Haeckel’s monera were relatively macroscopic organisms; for example, *Protogenes primordialis* (one of the first monera he described) was between 0.1 and 1.0 millimeters in diameter. As Schneider commented: “This little creature, hardly visible to the naked eye, and, at most, as big as a small pin-head, is of a fine orange-red color, consists of a perfectly homogeneous and transparent mass of jelly, and offers the paradox of *an organism without organs*” (Schneider 1873). As monera live in water, they are able to move by means of protoplasm contractions and building of pseudopodia. They propagate by fission, in an asexual mode (Ibid., p. 130).

Already in the *Monograph of Monera*, Haeckel claimed the extraordinary importance of his monera theory for the hypothesis of spontaneous generation: “If the natural history of the Monera is already, on these grounds, of the highest interest as well for morphology as for physiology, this interest will be still more increased by the extraordinary importance which these very simple organisms possess for the important doctrine of spontaneous generation, or archigony” (Haeckel 1869, p. 30). In the follow-up to the *Monograph* published 2 years later and entitled *Nachträge zur Monographie der Moneren* (Supplement to the Monograph of Monera), Haeckel added a special chapter, “Die Moneren und die Urzeugung” (Monera and the Spontaneous Generation), where he summarized his theory of abiogenesis and early evolution (Haeckel 1870, pp. 177–182). Haeckel begins by establishing a theoretical connection between his hypothesis and Darwin’s theory of descent and emphasizes that “every thinking reader” of Darwin’s book should have been asking



**Fig. 2.2** Plate IX from Haeckel's "Monograph of Monera": (Quarterly Journal of Microscopical Science, Vol. IX, 1869). The plate depicts one of the new monera Haeckel found on the coastline of the Canary Island Lanzarote. The orange-colored "Rhizopod-like" organism was found on empty shells of *Spirula peronii*





**Fig. 2.3** Detailed description of the Plate IX from Haeckel's "Monograph of Monera" illustrating the development of spores by *Protomyxa aurantiaca*. Haeckel characterized the generic character of *Protomyxa* as follows: "A simple shapeless protoplasm-body (with the formation of vacuoles), which protrude ramifying and anastomosing pseudopods. Reproduction by zoospores, which combine together into plasmodia" (Haeckel 1869, p. 340)

himself "where the first simplest proto-form [Urform]" is coming from (Ibid., p. 177). It is this proto-form, Haeckel argued, that gave rise "to all other organic forms" by means of Darwin's natural selection. Haeckel emphasized that the theory of the origin of life is a "necessary and integral constituting part of the universal evolutionary theory" (Ibid., p. 177). It is a "natural bridge" between the Kantian-Laplacian theory, which provides causal explanations of cosmic evolution, and evolutionary biology, which provides causal explanations of the origin of plant and animal species. The essence of the hypothesis is that a moneron consists of structureless protein binding, which appears directly from the lifeless substances of the primordial liquid by adapting to its immediate environment (Ibid., 178). We have observed the occurrence of various carbon compounds in our laboratories so many times, Haeckel argued that it is easy to imagine protein compounds occurring under natural conditions as nature is more powerful than any laboratory. He even hoped that 1-day monera could be produced synthetically (Krause 1984, p. 62).

Haeckel summarized the specific character of carbon compounds in a so-called carbon theory, which, he emphasized, was monistic:

The peculiar, chemico-physical properties of carbon—especially the fluidity and the facility of decomposition of the most elaborate albuminoid compounds of carbon—are the sole and the mechanical causes of the specific phenomena of movement, which distinguish organic from inorganic substances, and which are called life, in the usual sense of the word. (Haeckel 1900, pp. 262–263).

Abiogenesis for him was the occurrence of the living protoplasm out of inorganic carbonates in the form of monera. Monera are held together by purely mechanical forces. Furthermore, the concept of ontogeny is not applicable to the simplest monera (such as *protamoeba* and *protogenes*),<sup>5</sup> as they do not develop, but simply grow larger, analogous to inorganic crystals. When a moneron achieves a certain body size, it splits into two parts simply due to the weakening of the molecular cohesion forces; i.e., it is a purely mechanical process far less sophisticated than cell division.

Haeckel developed a detailed systematics of monera. In 1870, he counted 16 different species of monera arranged into eight genera (Haeckel 1870) of which the most important from the viewpoint of the origin of life became the genus *Bathybius*, consisting of one species, *B. haeckelii*. In 1870, Haeckel believed that this marine benthic amoeboid organism, discovered by Thomas Huxley in the Atlantic Ocean and defined as a new moner,<sup>6</sup> was the nearest living relative of the ancestral monera (Haeckel 1870, p. 181; McGraw 1974; Rupke 1976). As *Bathybius* was not just a single organism swimming in the ocean, but a thick biomat-like layer covering the “deepest parts of the sea bottom,” Haeckel regarded *Bathybius* as very strong evidence in favor of continuous spontaneous generation, a Lamarckian view that the spontaneous generation of life from lifeless matter is a repetitive event. Otherwise, Haeckel argued, it would be very difficult to explain the origin of this “protoplasma blanket” (Haeckel 1870, p. 181). Yet, to the end of the 1870s, Haeckel abandoned this belief. His rejection of the *Bathybius* hypothesis in his 1880s publications may be seen as one of the factors, which biased him toward the view that the occurrence of life is not an ongoing process. His late masterpiece *Systematische Phylogenie* (1894–1896) does not mention *Bathybius* anymore (Di Gregorio 2005, p. 437). As Haeckel never explicitly explained his decision to eliminate any mentionings of this fictitious discovery from the late publications, Rupke labeled the end of the *Bathybius* story a “silent exit” (Rupke 1976).

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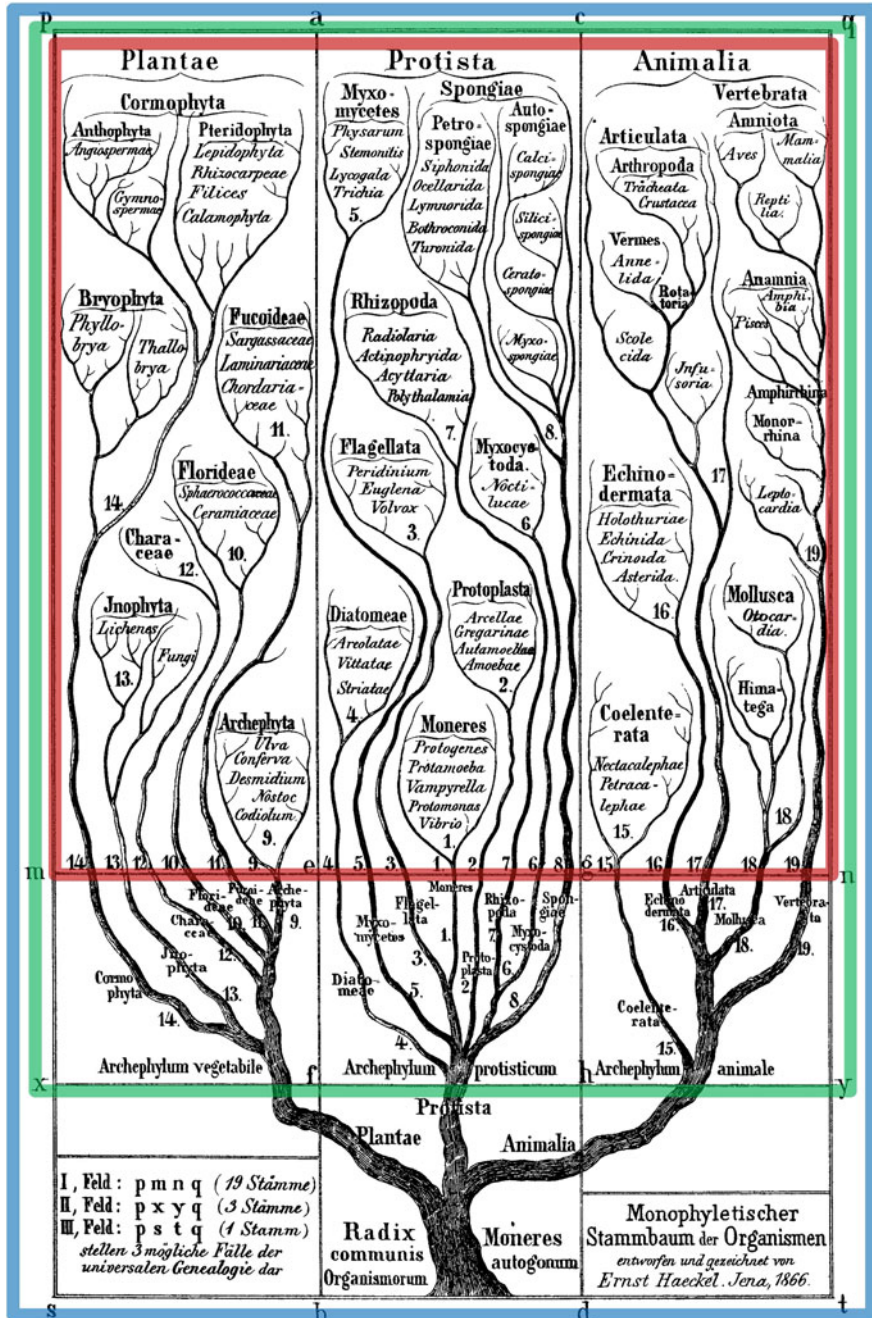
<sup>5</sup>Protamoeba and Protogenes are two genera belonging to the most primitive kind of monera. The genus Protamoeba consisted of five species, three of which were found in the freshwaters near Jena. The genus Protogenes consisted of only one species discovered in the Mediterranean, which Haeckel labeled *P. primordialis*.

<sup>6</sup>“I propose to confer upon this new ‘Moner’ the generic name of *Bathybius* and to call it after the eminent Professor of Zoology in the University of Jena, *B. haeckelii*” (Huxley 1868).

## 2.4 Trees and Bushes: Polyphyletic vs. Monophyletic Evolution

Haeckel's hypothesis, clearly expressed in early writings, that monera are continuing to spontaneously generate and evolve to higher forms even today (Haeckel 1866, 1868, 1869, 1870), was at odds with the Darwinian notion of strictly monophyletic evolution. Besides, strict monophyletism was better compatible with Haeckel's very own monism as the perfect unity of the world required perfect unity of life and of its origin. From the other side, if monera are simple homogenous aggregates of organic matter held together by purely mechanical forces—if they are, in fact, something between proper organisms and inert matter—it is difficult to explain why they should not arise repetitively in both the past and present. This contradiction created a tension which Haeckel never fully overcame, although his bias toward perfectly monophyletic evolution is well known (e.g., Haeckel 1887, p. 46; see also Levit et al. 2022). As Olivier Rieppel emphasizes, Haeckel “never rejected the polyphyletic origin of life through multiple spontaneous generation events” (Rieppel 2011). Benoît Dayrat even claims that Haeckel coined the very terms “monophyletic” and “polyphyletic” to discuss this question of whether the whole organic world owes its origin to a single instance of spontaneous generation or to several (Dayrat 2003).

In *Generelle Morphologie*, Haeckel formulated three hypotheses describing possible relations between the spontaneous generation of monera and living organisms (Fig. 2.4). His first hypothesis suggested that one single species of monera arose through autogonia. All other organisms, without exception, are descendants of this one monera species and compose a single phylum [Phylon] (1866, Vol. I, p. 199). His second hypothesis supposed that autogonia resulted in the creation of two different monera species, one of which was vegetative [vegetabilische] and the other of which was animal [animalische]. According to this hypothesis, all plants are descendants of the vegetative monera, and all animals have their origin in the animal monera (1866 Vol. I, p. 200). The third hypothesis suggested that there were “more than two different monera-species,” which gave rise to “more than two independent stems [Stämme] of organisms” (1866 Vol. I, p. 200). Haeckel considered this “the most probable of all three hypotheses” [bei weitem wahrscheinlichste von allen drei] and never completely abandoned it. Although in 1866, Haeckel “did not yet introduce the technical term polyphyly,” the third hypothesis clearly expressed the concept of polyphyly, which is the idea that “a variable number of independent phyla” originated from separate events of spontaneous generation (Rieppel 2011). In this case, each of the three kingdoms would be defined as “one single natural stem (phylum)” [ein einziger natürlicher Stamm (Phylum)] originating from an “independent spontaneously generated stem-form” [selbstständige autogone Stammform] (1866, Vol. II, XXXI). Haeckel was even open to the thought that there may be more than three monera and that a certain monera species could be, for example, a common stem form (common ancestor) [gemeinsame Stammform] of all vertebrates or of all coelenterates: “In our view it is most probable that each of the major stems [Hauptstämme] or phyla of animal and plant kingdoms evolved [entwickelte sich] from a separate monera stem-form” (Haeckel 1866, Vol. I, p. 185). According to this view, all major stems are descendants of “autogone” (independently generated)



**Fig. 2.4** Monophyletic stem tree from *General Morphology* [Generelle Morphologie] (Haeckel 1866, Vol. II, Table I). Color lines are added by us. Although entitled by Haeckel “Monophyletic Stem-Tree of Organisms,” this stem tree, in fact, includes three different diagrams illustrating three hypothetical “universal genealogies.” I. Rectangle “p m n q” represents 19-stem model (red line). II. Rectangle “p x y q” represents 3-stem model (green line). III. Rectangle “p s t q” represents 1-stem

monera, which evolved by means of divergence of characters and natural selection (Vol. II, 419). Elsewhere in the *Generelle Morphologie*, Haeckel writes: “The protoforms themselves, which form roots of the single stems, arose completely independently of each other via spontaneous generations [ . . . ]” (1866, Vol. II, p. 394).<sup>7</sup>

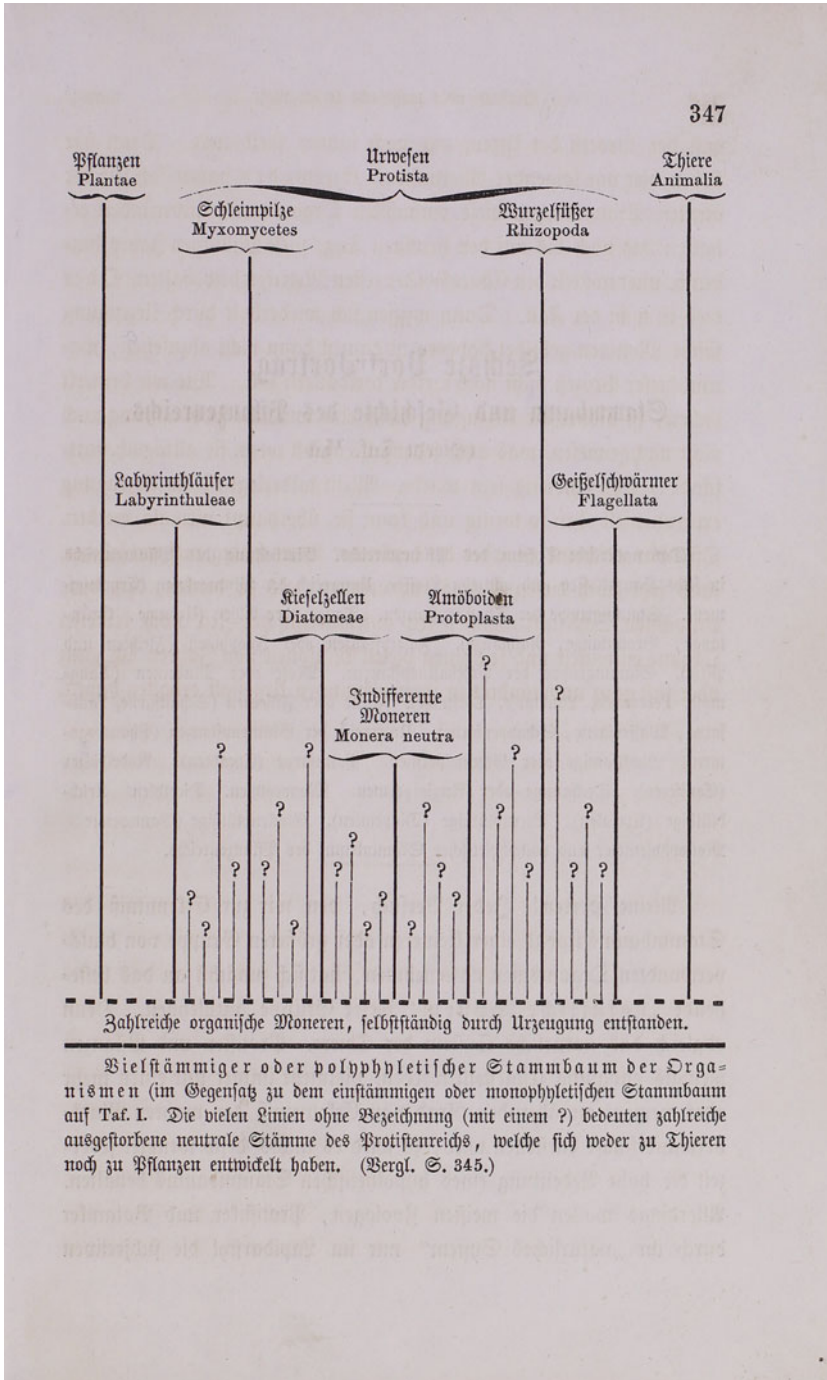
Neither Haeckel nor Darwin considered the polyphyletic origin of life as a danger for evolutionary theory. The British master himself did not exclude the possibility that animals and plants could have descended from distinct progenitors (Richards 2008, p. 137). Haeckel followed in Darwin’s footsteps: “Whether we finally assume a single common parent-form (the monophyletic hypothesis), or several (the polyphyletic hypothesis), is wholly immaterial to the essence of the theory of descent”, and it is equally immaterial to its fundamental idea what mechanical causes are assumed for the transformation of the varieties” (Haeckel 1879b, p. 3). Even Haeckel’s successor in Jena, Ludwig Plate (1862–1937), the leading Darwinist of his time (Levit and Hossfeld 2006), wrote in 1925 in a paragraph devoted to the origin of life that “polyphyly [Vielstämmigkeit] does not arise any serious objections against evolutionary theory” (Plate 1925, p. 144).

In the first and several subsequent editions of the *Natürliche Schöpfungsgeschichte* (*The Natural History of Creation*), Haeckel argued along the same lines (e.g., Haeckel 1868, 1879a, 1880). In the first German edition of the text, Haeckel repeated the idea that monera, which we observe today, could have existed since the “primordial time,” or alternatively, that spontaneous generation could be a repetitive process, and if so, it would be hard to deny that they could well be generated even today (Haeckel 1868, pp. 345–346). He illustrated the hypothesis of repeated spontaneous generation with a polyphyletic stem tree diagram (Fig. 2.5).

In the English edition of the book, titled *The Evolution of Man* (Haeckel 1879c), Haeckel emphasized again that the issue of the origin of life corresponded to the issue of the spontaneous generation of monera: “In the definite, limited sense in which I maintain spontaneous generation (*generatio spontanea*) and assume it as a necessary hypothesis in explanation of the first beginning of life upon the earth, it merely implies the origin of Monera from inorganic carbon compounds” (Haeckel 1879c, Vol. II, pp. 30–31). As in the *Generelle Morphologie* and *Monograph der Moneren*, he again admits that it is “very possible” that Monera will be “produced daily by spontaneous generation” (Haeckel 1879c, p. 32). In the seventh German edition of the *History of Creation*, Haeckel still employed the terms phytomonera [Phytomoneren], neutral monera [neutrale Moneren], and zoomonera [Zoomoneren] while admitting that distinct kinds of monera could be responsible for the origin of plants and animals. Haeckel also presented a modified diagram illustrating the

<sup>7</sup>German original: “Urformen selbst aber, welche die Wurzel der einzelnen Stämme bilden, sind gänzlich unabhängig von einander durch Geueratio spontanea entstanden, wie wir bereits im sechsten und siebeuten Capitel erläutert haben.”

**Fig. 2.4** (continued) model (blue line), i.e., all living organisms origin from a single-kind moneron (single common parent form). In 1866, Haeckel considered the model I (multi-monera model) as the most probable (Krause 1984, p. 64)



**Fig. 2.5** Polyphyletic stem tree from the first German edition of the *History of Creation*; it illustrates the idea of multiple independent spontaneous generation of monera and their evolution