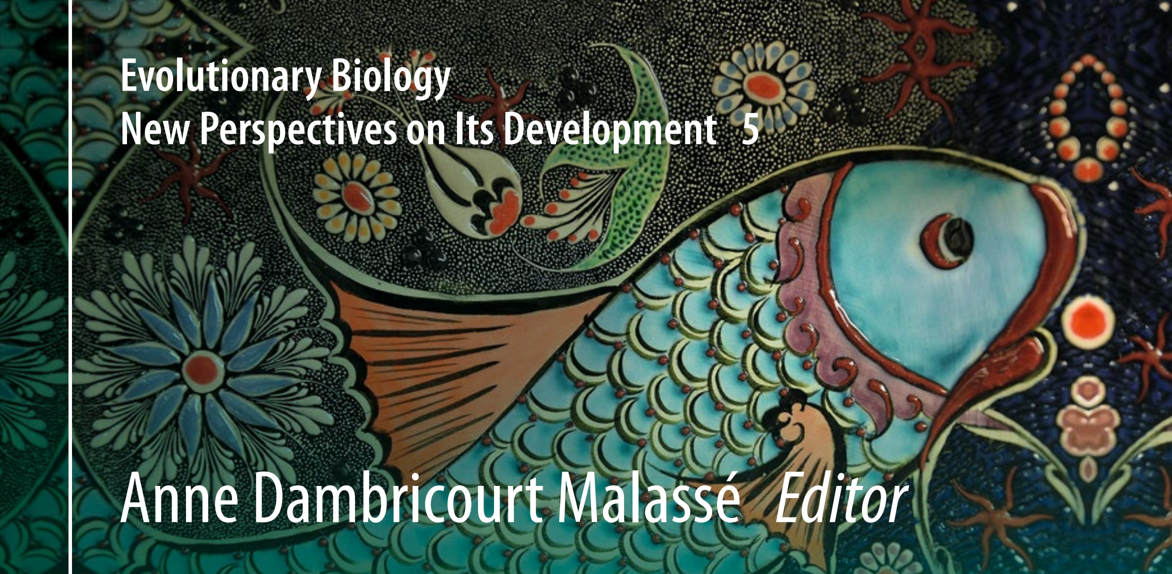

Evolutionary Biology
New Perspectives on Its Development 5

Anne Dambricourt Malassé *Editor*

Self-Organization as a New Paradigm in Evolutionary Biology

From Theory to Applied Cases in the Tree of Life

Springer

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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A. Dambricourt Malassé (ed.), *Self-Organization as a New Paradigm in Evolutionary Biology*, Evolutionary Biology – New Perspectives on Its Development 5, https://doi.org/10.1007/978-3-031-04783-1_2

Keywords

Abiogenesis · Ernst Haeckel · Self-organization · Evolution

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

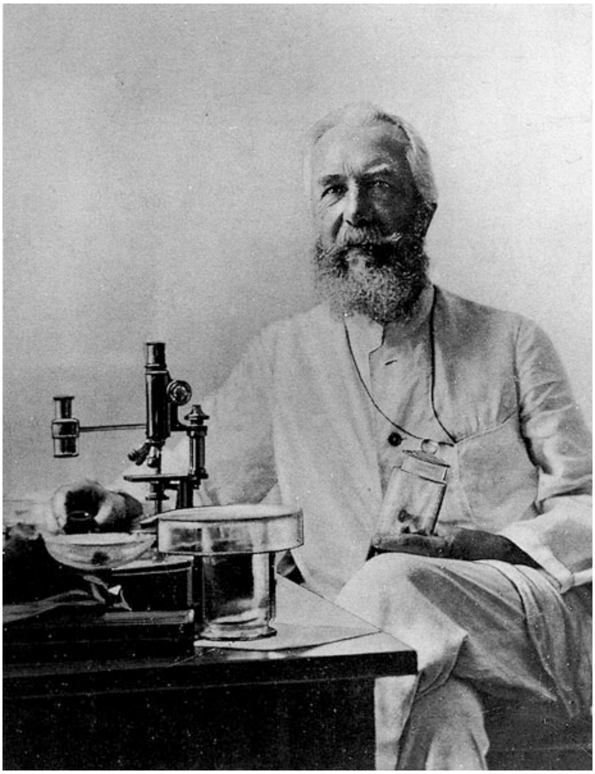


Fig. 2.1 Ernst Haeckel in his laboratory in the Buitenzorg Botanical Gardens on the Island of Java, 1901 (Courtesy: archive U. H.)

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.[1] 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).

[1] 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.

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 Entwickelungslehre" (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 supranatural forces and evolution is a teleological process.

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,[2] Haeckel described *Protogenes primordialis*[3] as one of the most primitive types of Rhizopoda [eines der allereinfachsten Geschöpfe], the "organism without organs." Haeckel emphasized that *generatio aequivoca* (spontaneous generation)[4] 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

[2] "Letter no. 4934," accessed on June 10, 2021, https://www.darwinproject.ac.uk/letter/DCP-LETT-4934.xml

[3] *Protogenes primordialis* is a moneron Haeckel believed to have observed in 1864 in the Mediterranean by Nice (Nizza) (Haeckel 1865).

[4] 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

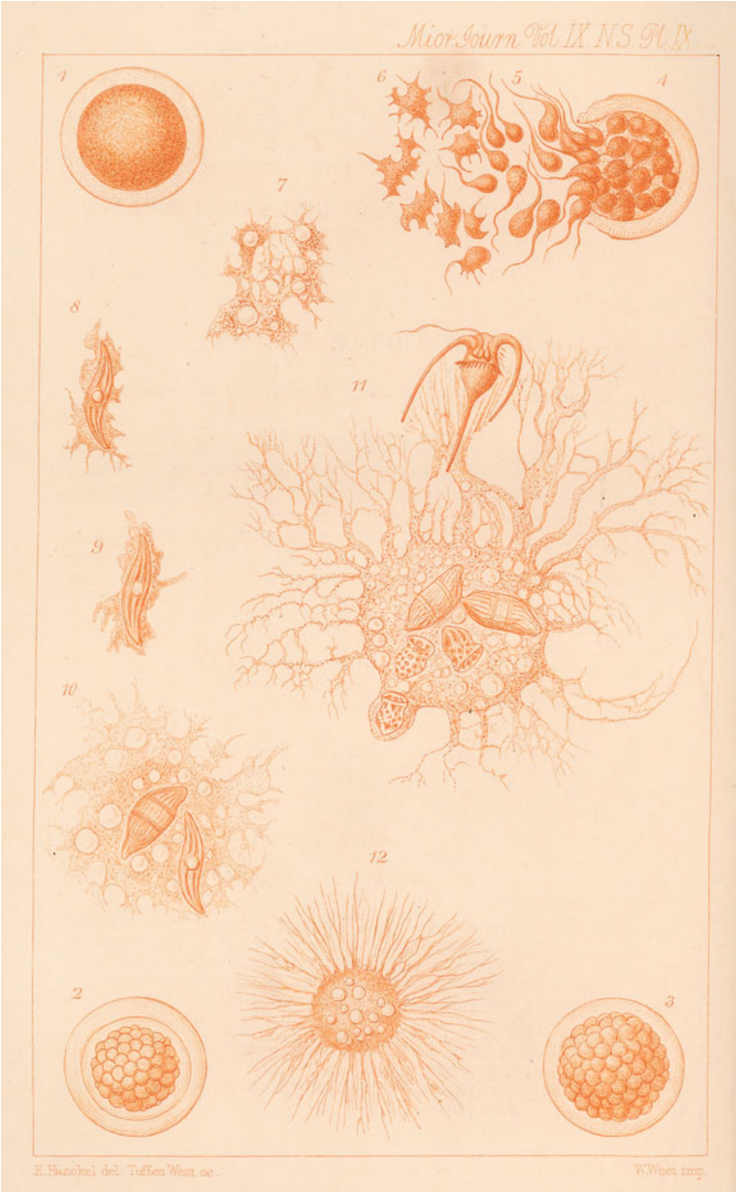
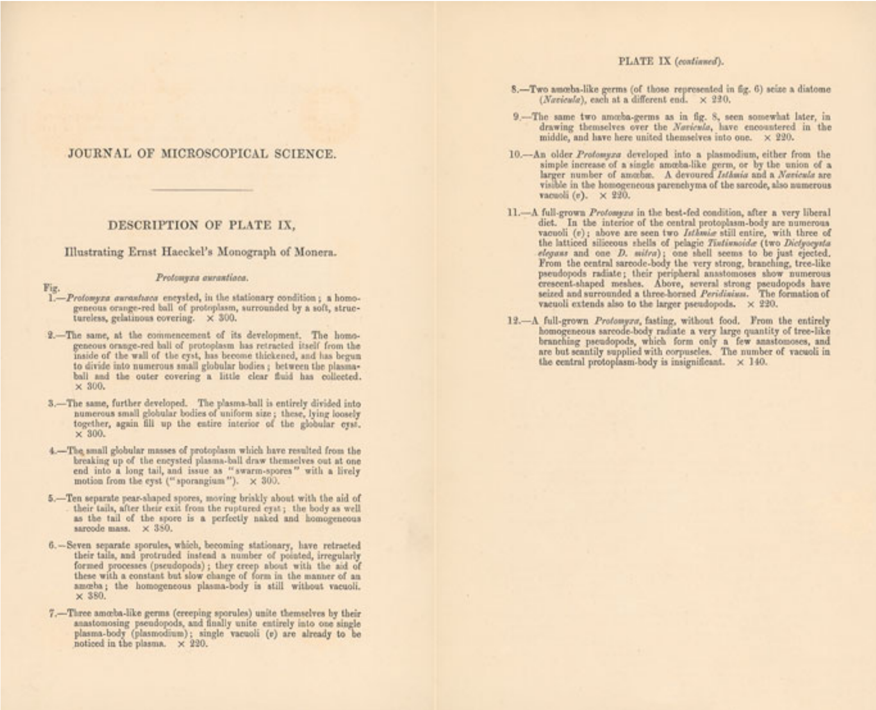


Fig. 2.2 Plate IX from Haeckel's "Monograph of Monera": (Quarterly Journal of Microscopical Science, Vol. IX, 1869). The plate depicts one of the new monera Haeckel found on the coastline of the Canary Island Lanzarote. The orange-colored "Rhizopod-like" organism was found on empty shells of *Spirula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



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DESCRIPTION OF PLATE IX,

Illustrating Ernst Haeckel's Monograph of Monera.

Protomyxa aurantiaca.

Fig.

1.—*Protomyxa aurantiaca* encysted, in the stationary condition; a homogeneous orange-red ball of protoplasm, surrounded by a soft, structureless, gelatinous covering. × 300.

2.—The same, at the commencement of its development. The homogeneous orange-red ball of protoplasm has retracted itself from the inside of the wall of the cyst, has become thickened, and has begun to divide into numerous small globular bodies; between the plasma-ball and the outer covering a little clear fluid has collected. × 300.

3.—The same, further developed. The plasma-ball is entirely divided into numerous small globular bodies of uniform size; these, lying loosely together, again fill up the entire interior of the globular cyst. × 300.

4.—The small globular masses of protoplasm which have resulted from the breaking up of the encysted plasma-ball draw themselves out at one end into a long tail, and issue as "swarm-spores" with a lively motion from the cyst ("sporangium"). × 300.

5.—Ten separate pear-shaped spores, moving briskly about with the aid of their tails, after their exit from the ruptured cyst; the body as well as the tail of the spore is a perfectly naked and homogeneous sarcode mass. × 380.

6.—Seven separate sporules, which, becoming stationary, have retracted their tails, and protruded instead a number of pointed, irregularly formed processes (pseudopods); they creep about with the aid of these with a constant but slow change of form in the manner of an amœba; the homogeneous plasma-body is still without vacuoli. × 380.

7.—Three amœba-like germs (creeping sporules) unite themselves by their anastomosing pseudopods, and finally unite entirely into one single plasma-body (plasmodium); single vacuoli (*v*) are already to be noticed in the plasma. × 220.

PLATE IX (*continued*).

8.—Two amœba-like germs (of those represented in fig. 6) seize a diatome (*Navicula*), each at a different end. × 220.

9.—The same two amœba-germs as in fig. 8, seen somewhat later, in drawing themselves over the *Navicula*, have encountered in the middle, and have here united themselves into one. × 220.

10.—An older *Protomyxa* developed into a plasmodium, either from the simple increase of a single amœba-like germ, or by the union of a larger number of amœbæ. A devoured *Isthmia* and a *Navicula* are visible in the homogeneous parenchyma of the sarcode, also numerous vacuoli (*v*). × 220.

11.—A full-grown *Protomyxa* in the best-fed condition, after a very liberal diet. In the interior of the central protoplasm-body are numerous vacuoli (*v*); above are seen two *Isthmiæ* still entire, with three of the latticed siliceous shells of pelagic *Tintinnoidæ* (two *Dictyocysta elegans* and one *D. mitra*); one shell seems to be just ejected. From the central sarcode-body the very strong, branching, tree-like pseudopods radiate; their peripheral anastomoses show numerous crescent-shaped meshes. Above, several strong pseudopods have seized and surrounded a three-horned *Peridinium*. The formation of vacuoli extends also to the larger pseudopods. × 220.

12.—A full-grown *Protomyxa*, fasting, without food. From the entirely homogeneous sarcode-body radiate a very large quantity of tree-like branching pseudopods, which form only a few anastomoses, and are but scantily supplied with corpuscles. The number of vacuoli in the central protoplasm-body is insignificant. × 140.

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*),[5] 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,[6] 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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[5] 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*.

[6] "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)

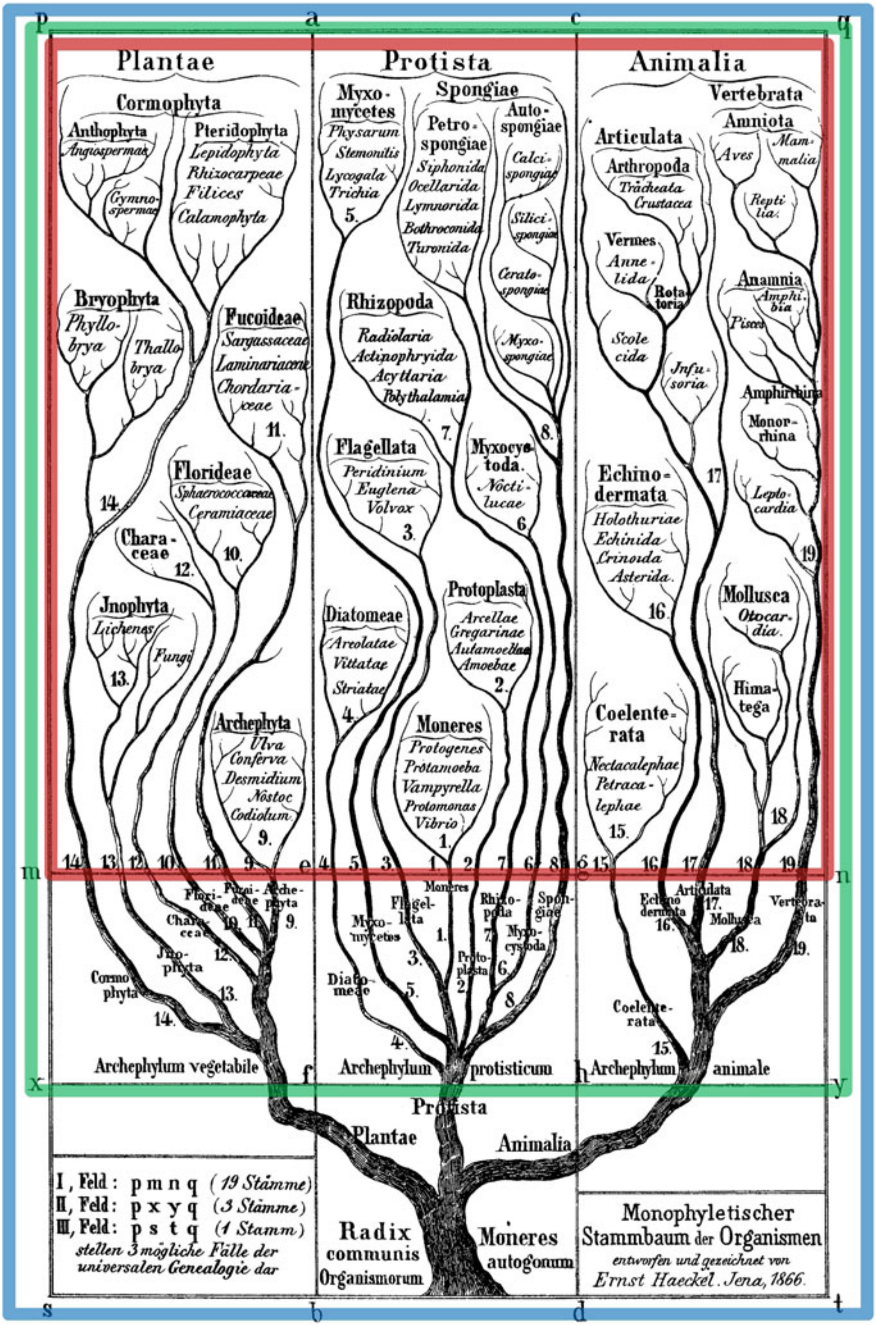

Fig. 2.4 Monophyletic stem tree from *General Morphology* [Generelle Morphologie] (Haeckel 1866, Vol. II, Table I). Color lines are added by us. Although entitled by Haeckel "Monophyletic Stem-Tree of Organisms," this stem tree, in fact, includes three different diagrams illustrating three hypothetical "universal genealogies." I. Rectangle "pmnq" represents 19-stem model (red line). II. Rectangle "pxyq" represents 3-stem model (green line). III. Rectangle "pstq" 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 proto-forms themselves, which form roots of the single stems, arose completely independently of each other via spontaneous generations [. . .]” (1866, Vol. II, p. 394).[7]

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

[7] 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 naben.”

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)

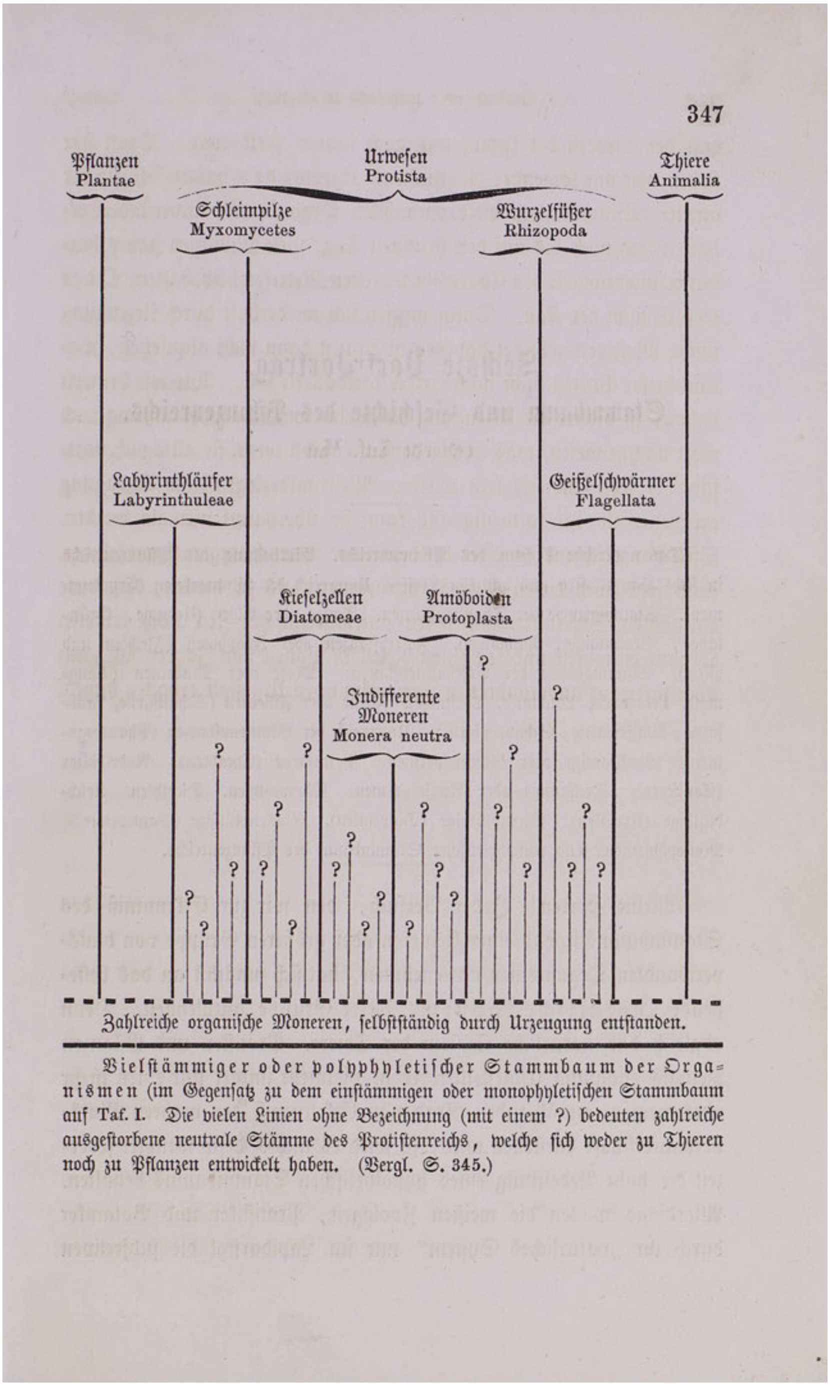

Fig. 2.5 Polyphyletic stem tree from the first German edition of the *History of Creation*; it illustrates the idea of multiple independent spontaneous generation of monera and their evolution

polyphyletic origin of life (Haeckel 1879a, p. 401; Reynolds and Hülsmann 2008) (Fig. 2.6). At the same time, he introduced the concept of "archigone monera," which could have been giving rise to all other kinds of monera (Haeckel 1879a, p. 400) and presented a diagram illustrating the hypothesis of the monophyletic origin of life (Fig. 2.7). In a comment on these diagrams, Haeckel explained that a "well-founded decision between monophyletic and polyphyletic hypotheses is completely impossible [ganz unmöglich] considering our present imperfect phylogenetic knowledge" (Ibid. 1879a, p. 399). The same idea was repeated in the English edition of the *History of Creation* published in 1887, where he stated that a safe means of deciding between the monophyletic and polyphyletic hypotheses is "as yet quite impossible" (Haeckel 1887, p. 73). At the same time, Haeckel, again, clearly expressed his bias toward the concept of spontaneous generation as a repetitive process and toward the independent origin of the three kingdoms:

> But the more deeply we penetrate into the genealogical secrets of this obscure domain of inquiry, the more probable appears the idea that the *vegetable kingdom and the animal kingdom are each of independent origin*, and that midway between these two great pedigrees a number of other independent small groups of organisms have arisen, *by repeated acts of spontaneous generation*, which on account of their indifferent neutral character, and in consequence of their mixture of animal and vegetable properties, may lay claim to the designation of independent Protista" [our italics—*auth*.] (Haeckel 1887, p. 73).

Of these two issues—repetitive spontaneous generations and the polyphyly controversy—Haeckel considered the latter as a minor issue as the whole body of a moneron consists anyway only of a formless mass "made up of a single albuminous combination of carbon," and therefore, primary monera were quite uniform, morphologically identical, differing only by their "chemical nature" (Haeckel 1887, p. 45). In other words, in Haeckel's typological approach to phylogeny, even major organismic groups originating from different acts of spontaneous generation (kingdoms) could be depicted as elements of the same monophyletic stem tree.

In the first volume of his very last technical (i.e., strictly scientific, as opposed to popular) work, the three-volume *Systematische Phylogenie* (Systematic Phylogeny), Haeckel devoted several paragraphs to the discussion of polyphyly vs. monophyly (Haeckel 1894, pp. 31–32; pp. 88–89) and formulated a general principle determining the relations between these two concepts. In §69 of the chapter "The Unity of the Organic World" (vol. I), Haeckel, again, explained that monism, "the doctrine of the perfect unity of the organic world," is the true foundation of his understanding of evolution. This unity can be observed everywhere; for example, he observes that "the same protein-like substance, called plasma, is the common material foundation of the organic life" (Haeckel 1894, p. 88). He posed the question of how the "perfect morphological and physiological unity of the world" relates to the concept of phylogeny: "May we conclude from this that all different organic forms originally

Fig. 2.5 (continued) to higher organisms by means of natural selection (Haeckel 1868, Nat. Schöpfungsgeschichte, 1. Auflage, S. 347)

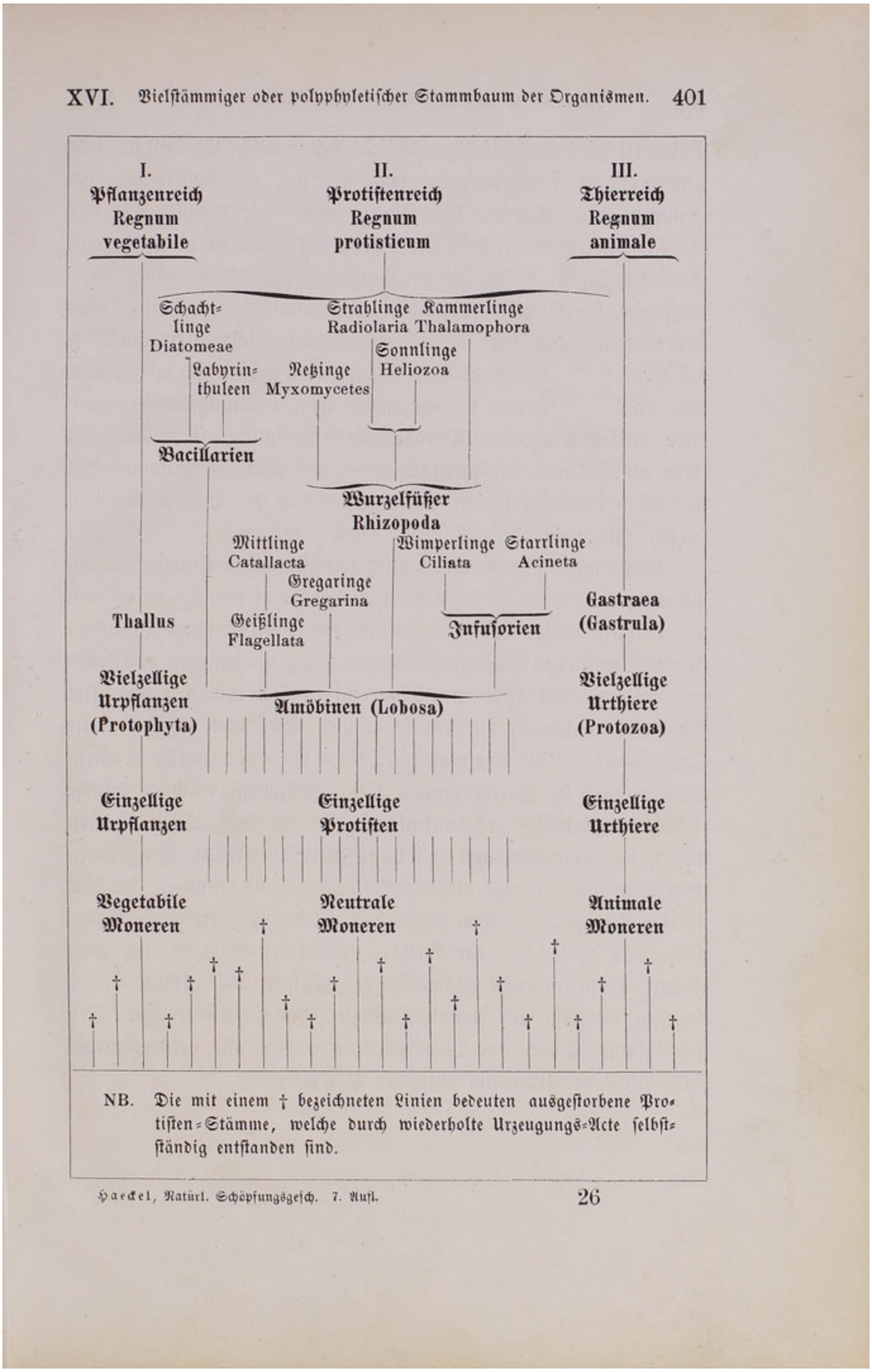

Fig. 2.6 Polyphyletic stem tree published in the 7th German edition of the *History of Creation* (Haeckel 1879a, Nat. Schöpfungsgeschichte, 7. Auflage, S. 401). †† symbolizes extinct independent stems

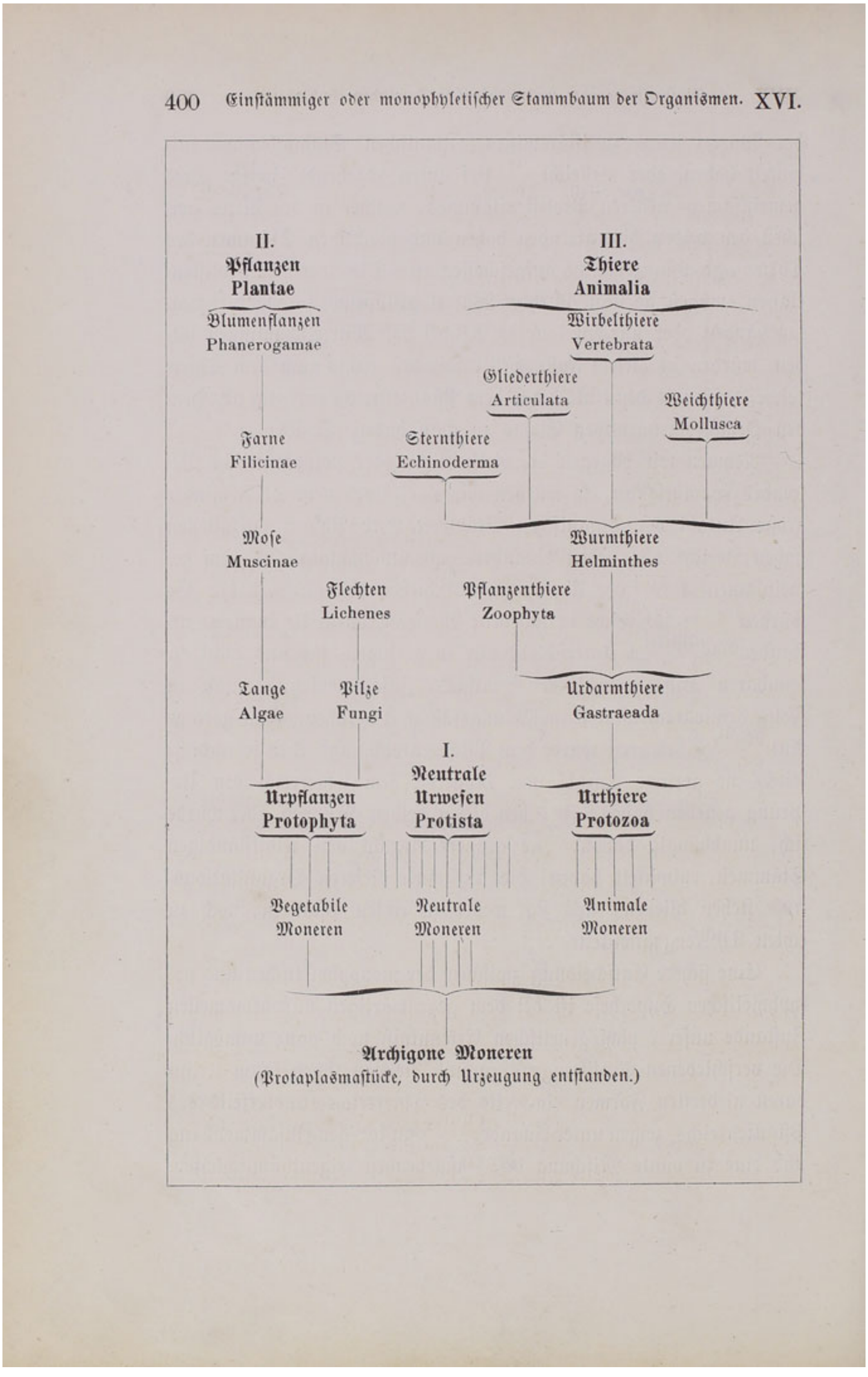

Fig. 2.7 Monophyletic stem tree from the 7th German edition of the *History of Creation* and published next to the polyphyletic tree (Haeckel 1879a, S. 400). The single lines at the very bottom of the tree symbolize multiple monera produced by spontaneous generation

evolved [historisch entwickelt] from one and the same common proto-form [Urform]?" (Ibid., p. 89). The answer to this question, Haeckel comments, is simultaneously "yes" and "no." One can apply the polyphyletic hypothesis to the origin of "organic stems" (phyla) as in the initial period of "biogenesis" (Haeckel meant abiogenesis, in modern terms), whereby monera spawned from lifeless matter by means of *archigonia* multiple times. However, this process can *also* be described as monophyletic, whereby *archigonia* took place everywhere in the same manner. Haeckel illustrated this typological vision of early phylogeny with a monophyletic-looking diagram (Fig. 2.8).

Elsewhere in the same volume, Haeckel argued that the application of the polyphyletic or monophyletic hypotheses to a certain evolutionary episode must be decided individually for each case (Haeckel 1894, Vol. I, pp. 31–32), although in general monophyly becomes more plausible the higher one climbs in a given phylogenic tree. For example, it is indubitable that all vertebrates evolved in a strictly monophyletic mode, but the polyphyletic hypothesis may be applicable to the low protists.

Haeckel tended to narrow the scope of the polyphyletic hypothesis to early evolution in the latest writings. Yet, he still maintained that abiogenesis was not a unique event, but took place multiple times giving rise to various organismic kingdoms—and in that sense, early evolution was polyphyletic. At the same time, he believed that various kingdoms could have their ultimate roots in monera of the same kind—and in that sense, early evolution was monophyletic.

2.5 Conclusions

Haeckel's theory of abiogenesis, consisting of the hypothesis of spontaneous generation "and the allied carbon theory," was central to his monistic worldview as it allowed him to overcome both ontological dualism and teleology in favor of a purely causal (mechanistic, in his terms) interpretation of natural phenomena (Haeckel 1900, p. 264). For Haeckel, abiogenesis was a necessary logical consequence of his monistic "substance theory," which asserted the fundamental unity of organic and inorganic matter. Being a universal evolutionist, he also saw abiogenesis as a concept linking the Kant–Laplace nebular hypothesis with Darwin's theory of evolution. All events leading from inorganic to organic evolution are law-governed, proceed without external or supranatural influences, and can therefore be thought of as self-organizing (although Haeckel himself did not employ this term, his concept of *autogonia* [linguistically consisting of two parts, *auto* = self and *gonia* (gonos) = creation] suggests he was thinking along these lines). The immediate product of *autogonia* was the simplest living creatures, monera, which gave rise to all other forms of life on earth. In his very late works, Haeckel tended to describe the occurrence of monera as a two-step process: first, the rise of the simplest organic substances, and second, the appearance of monera out of these substances (Haeckel 1900, p. 263).

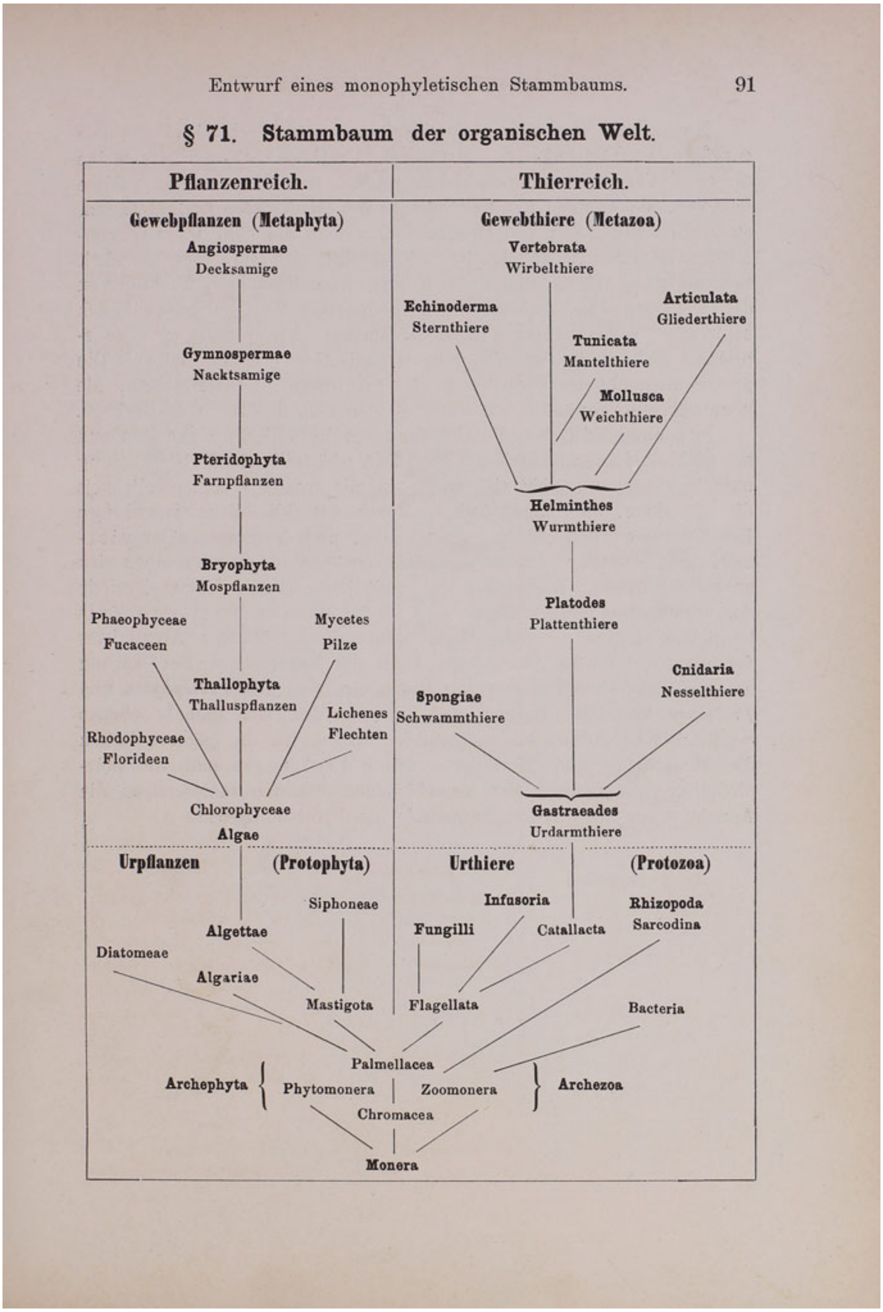

Fig. 2.8 Monophyletic stem tree of the entire organic world published in the *Phylogenetic Systematics* (Haeckel 1894, S. 91). Note that the three lines at the very bottom of the scheme, symbolizing the early evolution of monera, remain separated and do not unite to a single line as on the monophyletic stem tree from the *History of Creation* (1879)

He distinguished three organismic kingdoms (Animalia, Plantae, and Protista) and speculated about their polyphyletic origin—about the possibility that different kinds of monera brought about each kingdom. He even admitted that there could be many (more than three) primitive parent forms, as was reflected in his diagrams of extremely polyphyletic early evolution (Figs. 2.5 and 2.6). Although his monism and the Darwinian paradigm he championed urged him to accept strict monophyly, Haeckel remained biased toward the polyphyletic model of life's origins throughout his life. In his latest works, he narrowed down his application of polyphyly to the early evolution and abandoned the hypothesis of extreme polyphyly he admitted for a long period of time. He elaborated a general principle unifying both concepts (polyphyly and monophyly), which declared that the higher one climbs the phylogenetic trees the more strictly monophyletic they appear. On a purely empirical level, Haeckel's theory was lacking experimental data or direct observations proving the hypothesis of continuing spontaneous generations in fresh or ocean waters. At the same time, Haeckel's monera hypothesis was hardly compatible with strict monophyly, because it favored the idea that multiple and continuing spontaneous generations of various kinds of monera occur repetitively throughout the early history or even throughout the whole history of earth. In accord with the "carbon theory," monera were so easy to generate that it would be difficult to explain why they should not spawn multiple times after the early earth cooled down. In other words, the theory of the origin of life was the terrain, where Haeckel's monistic epistemology came into conflict with his monistic ontology as the former required secure empirical foundation for the abiogenesis theory—which was absent—while the latter required abiogenesis as a necessary logical link in his theoretical system.

Acknowledgments The authors would like to thank Cameron Yetman (Canada) for valuable suggestions.

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