


The biogenetic law and the Gastraea theory: From Ernst Haeckel's discoveries to contemporary views

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Abstract

More than 150 years ago, in 1866, Ernst Haeckel published a book in two volumes called *Generelle Morphologie der Organismen (General Morphology of Organisms)* in the first volume of which he formulated his biogenetic law, famously stating that ontogeny recapitulates phylogeny. Here, we describe Haeckel's original idea as first formulated in the *Generelle Morphologie der Organismen* and later further developed in other publications until the present situation in which molecular data are used to test the “hourglass model,” which can be seen as a modern version of the biogenetic law. We also tell the story about his discovery, while traveling in Norway, of an unknown organism, *Magosphaera planula*, that was important in that it helped to precipitate his ideas into what was to become the Gastraea theory. We also follow further development and reformulations of the Gastraea theory by other scientists, notably the Russian school. Elias Metchnikoff developed the Phagocytella hypothesis for the origin of metazoans based on studies of a colonial flagellate. Alexey Zakhvatina focused on deducing the ancestral life cycle and the cell types of the last common ancestor of all metazoans, and Kirill V. Mikhailov recently pursued this line of research further.

KEYWORDS

heterochrony, *Magosphaera planula*, ontogeny, phylogeny

1 | INTRODUCTION

The “German Darwin” Ernst Haeckel (1834–1919) published his first major scientific work, *General Morphology of Organisms*, in 1866. Here, he started to formulate his biogenetic law, which was then further elaborated by him in his monograph on calcareous sponges (*Die Kalkschwämme*) in 1872. These books were never translated into other languages, reaching only a limited audience even in German-speaking countries. The popularization of Haeckel's ideas followed in 1868 when a collection of lectures

held at the University of Jena (where he was the first professor of zoology) was published as *Natürliche Schöpfungsgeschichte (Natural History of Creation)* (Hoßfeld & Olsson, 2003). This popular science book became a bestseller and was also translated into many different languages.

The objective of this paper is to exemplify how Haeckel's insights stimulated the growth of what is known today as evolutionary developmental biology. Our perspective is a contemporary one, we are interested in interpreting historical events as viewed with today's eyes rather than focusing on an authentic historical reconstruction.

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In the first section, we describe how Haeckel presented his ideas on ontogeny and phylogeny and an empirical inspiration for the Gastraea theory, his discovery of an unknown organism, the protist *Magospaera planula*.

2 | THE HISTORICAL AND INTELLECTUAL BACKGROUND OF THE BIOGENETIC LAW AND THE GASTRAEA THEORY

Following the publication of Darwin's *On the Origin of Species* (1859), it became important to reconsider existing research fields in light of Darwin's ideas and they were applied from early on to the question of the connection between ontogeny and phylogeny (Gould, 1977). In Germany, Ernst Haeckel used comparative anatomy and embryology as evidence for Darwin's theory of common descent. As Johann Friedrich Meckel (1781–1833) and his school before, Haeckel also put great theoretical emphasis on the parallels between the developmental stages of the embryo and the series from lower to higher animal forms studied in comparative anatomy and systematics. Haeckel used the term “Entwicklung” (development) for both, the development of the individual and the “development” of new forms over evolutionary time (Olsson & Hoßfeld, 2007). To these two parallels, he added a third based on paleontological data. In this “threefold genealogical parallelism” of phyletic (paleontological), biontic (individual), and systematic development, he saw one of the greatest, most wonderful, and important phenomena in organic nature (Haeckel, 1866, II, 371ff). He named his theory “The fundamental law of organic development,” or in short form the “Biogenetic law.” Haeckel wrote about the reciprocal causal relationships in his *Generelle Morphologie der Organismen*:

41. Ontogenesis is the short and fast recapitulation of phylogenesis, controlled through the physiological functions of inheritance (reproduction) and adaptation (nutrition). 42. The organic individual [...] recapitulates through its fast and short individual development the most important of the changes in form, which the ancestors have gone through during the slow and long palaeontological development following the rules of inheritance and adaptation (Haeckel, 1866, II, p. 300).

At the same time, Haeckel realized the problems associated with his theory (Olsson et al., 2017; Ulrich, 1968; Uschmann, 1966). The “complete and faithful recapitulation” becomes “effaced and shortened,” because the “ontogenesis always chooses the straighter road.” In addition, the recapitulation becomes “counterfeited and changed through secondary adaptations” and is, therefore, “better the more similar the conditions of existence were, under which the Bion and its ancestors have developed” (Haeckel, 1866, p. 300). Haeckel uses “Bion” to refer to individual organisms.

In 1875, Haeckel introduced the concepts “Cenogenie” (secondary adaptation leading to non-recapitulation) and “Palingenie” (“real” recapitulation) attempting to accommodate his theory to increasing evidence against his original formulation of the biogenetic law.

He viewed inheritance and adaptation as the driving factors for the occurrence of “Cenogenie” and “Palingenie” during the evolutionary process. Haeckel also wrote in *Natürliche Schöpfungsgeschichte* (1868) that this relationship (the causal connection, or nexus, between biotic and phyletic development) is the most important and irrefutable proof of the theory of common descent. While this parallel was first discussed at length as the biogenetic law in Haeckel's *Monographie der Kalkschwämme* (1872), the most comprehensive use of it can be found in his writings on the Gastraea theory (Hoßfeld et al., 2019). The Gastraea is a hypothetical “Urform” from which all metazoans have evolved, according to Haeckel. It has left no paleontological traces and can, therefore, only be seen as the gastrula stage in the development of many extant animals:

From these identical gastrulae of representatives of the most different animal phyla, from poriferans to vertebrates, I conclude, according to the biogenetic law, that the animal phyla have a common descent from one unique unknown ancestor, which in essence was identical to the gastrula: Gastraea (Haeckel, 1872, 1, p. 467).

With his Gastraea theory, Haeckel thought he had proved the monophyletic origin of all multicellular animals. If the two primary germ layers really are homologous in all metazoans, as Haeckel postulated, then he had given an explanation for the evolutionary origin of germ layer formation (Haeckel, 1874b, 1875; Olsson et al., 2017).

As it will be discussed later, Haeckel's far-reaching generalizations were not generally accepted. However, embryology soon counted as an indispensable tool for recognizing otherwise uncertain homologies.

Fritz Müller made an important contribution to Haeckel's thinking about the biogenetic law with his critical discussion in *Für Darwin* from 1864 (Müller, 1864). Müller (1822–1897), by studying crustaceans, concluded that evolutionary changes take place mostly through “Abirren” (lit. going astray, here to diverge from the original developmental pathway) and “Hinausschreiten” (lit. transgress, here to develop beyond the endpoint of the original developmental pathway). Thus Müller explained phylogenetic changes on the basis of changes in ontogeny. This is contrary to Haeckel who saw phylogeny as the explanation for ontogeny. The goals were also different. While Müller sought causal explanations, Haeckel erected a law based on his observations and preconceived ideas.

The discussions surrounding the biogenetic law exemplify the fertile interaction between embryology and comparative anatomy in the 19th century. They also show that ontogenetic results must be interpreted with caution in evolutionary biology. When the concepts and terminology introduced by Haeckel did not suffice to answer the

questions at hand, several biologists tried to supplement or replace the biogenetic law. These discussions became important milestones in the history of evolutionary developmental biology.

3 | THE ORIGIN OF HAECKEL'S BIOGENETIC LAW IN *GENERELLE MORPHOLOGIE*

As previously mentioned, the biogenetic law has been and still is one of the most influential concepts in biology. Therefore, it is interesting to trace the origin and later elaboration not only of the biogenetic law but also of Haeckel's understanding of the key terms ontogeny and phylogeny. Haeckel's first thoughts of what would later be condensed in his biogenetic law was his holistic view of the individual organism. The crucial point here is that the concept of the "individual" for Haeckel, at whatever level, needed to be considered both morphologically and physiologically, as both static and dynamic. The former was the "form-individual" [*Formindividuum*] whose character depended on the simultaneous relation of its elements or parts, and thus which could not be separated. The latter was the "performance-individual" [*Leistungsindividuum*] which was understood in its transient duration in life from birth to death (Haeckel, 1866, pp. 265–268). But crucial for Haeckel was that these two standpoints were related. As Olivier Rieppel puts it, "higher animals without complex life cycles successively realize, through a process of multiplication and differentiation, the lower levels of form individuality during their development, while each of these lower levels of form individuality represents a mature physiological individual at successive levels of plant and animal organization" (Rieppel, 2016, p. 43). This was, in essence, the core concept of what later works will call the biogenetic law, expressly described only later in *Generelle Morphologie* as a "thesis" of recapitulation connecting ontogeny and phylogeny, and which could only become clearer after a fuller discussion of ontogeny and phylogeny in Volume II of *Generelle Morphologie*.

Thus, the opening words of Volume II define ontogeny more expansively than in Volume I: "Ontogeny, or the evolutionary history of organic individuals, is the total science of changes in form that bionts, or physiological individuals, pass through during their lives, from birth to death." The relation of ontogeny to morphology is even further elaborated from that in Volume I:

the task of ontogeny is thus the perception and explanation of the changes in form-individuals, that is, the determination of the natural laws according to which the changes in forms of morphological individuals follow, and through which bionts are represented (Haeckel, 1866, p. 3).

And phylogeny receives expanded treatment in Book VI, which opens with this definition:

Phylogeny, or the evolutionary history of organic phyla [Stämme] is the complete science of the changes in form that phyla pass through during their entire existence, due to the changes of its kinds or species, comprising either successive or coexistent blood-related members of each phylum (Haeckel, 1866, p. 303).

The longest chapter in the entire two volumes (Chapter 19: "The theory of descent and selection") introduces the reader to a brief history and expanded explanation of the central concepts of inheritance and adaptation, each following their own empirically derived laws [*Gesetze*] (Haeckel, 1866, pp. 180–222). It is only in Chapter 20, "Ontogenetic theses" that the key concept of what will in later works be called the biogenetic law is articulated amidst a total of 44 theses (Thesis 40 and 41 are cited above) that themselves surveyed, as from a lookout point along a mountain path, the territory that has been traversed, and with an eye looking forward to paths that yet lay ahead in *Generelle Morphologie*. The use of such revisionary "theses statements" as a didactic technique would influence later texts in biology such as those of his student Richard Hertwig (1850–1937).

In his *Generelle Morphologie*, Haeckel explicitly distinguished his "theses" from "laws" (*Gesetze*), a term he was, as we have seen, happy to use in reference to empirical regularities observed in inheritance and adaptation (Haeckel, 1866, pp. 180–225), and which he regarded as comparable to laws when describing "phylogenetic evolution," which he discusses in Chapter 26 of Volume II. As with his extended discussion in Volume I of "morphological theses" (Haeckel, 1866, p. 364), so here "theses" for Haeckel was the appropriate term for science itself in its evolutionary infancy: "A science such as the morphology of organisms that is still in its cradle [*in primis cunabilis*] must still undergo metamorphoses, before it can dare to claim for its general statements the rank of unmitigated, unqualified laws of nature...Their further "development to laws we must hope for from our followers" (Haeckel, 1866, p. 295, n. 1). Haeckel himself would carry that development further.

4 | THE BIOGENETIC LAW AND THE GASTRAEA THEORY IN LATER TEXTS

The transformations of Haeckel's own terminology within his subsequent writings is one marked by both (1) further attempts at making the key concepts such as the thesis of recapitulation both more epistemically secure and (2) more understandable for a broader readership. In his *Natural History of Creation* (1868), whose popularity and wide dissemination we have already noted, the causal nexus between the biontic development and phyletic evolution was treated as the most important and irrefutable proof of Darwin's theory of descent (Haeckel, 1868, pp. 227–258). It was in 1872 in the first volume of his three-volume monograph on calcareous sponges, that the term

biogenetic law first appears for this nexus: sponges expressed in their whole being “the profound meaning of this biogenetic fundamental law. For the entire organization of these animals only becomes clear to us through their ontogeny, through which we are led directly to their phylogeny” (Haeckel, 1872, I, p. 215). What has been a humble “thesis” in the *Generelle Morphologie* has now, received, Haeckel argued, an empirical foundation through this text (Porges et al., 2019; R. Reynolds 2019). In the same work, he cites himself, clarifying his concepts and locating in a single, central expression the theses on recapitulation that he had developed in the *Generelle Morphologie*. As he put it, he placed the “foundational law of organic evolution” at the pinnacle of the “theory of the causal nexus of ontogeny and phylogeny,” on which the whole of evolutionary history is founded (Haeckel, 1872, I, p. 471). In the same first volume, Haeckel devoted a whole chapter to the “phylogeny of sponges,” employing synonymously the terms “phylogeny,” “history of the phylum” (or stem history) [*Stammesgeschichte*] and “paleontological evolutionary history” (Haeckel, 1872, I, p. 340). A separate chapter on ontogeny introduces the term “Germ history” [*Keimesgeschichte*] and “individual evolutionary history” [*individuelle Entwicklungsgeschichte*] as synonyms (Haeckel, 1872, I, p. 328). In the third volume of his monograph on calcareous sponges, Haeckel then made his results more accessible to the general readership by pictorial means (Figure 1; Haeckel, 1872).

In general, Haeckel's popular works strengthened the currency of the German terms *Keimesgeschichte* and *Stammesgeschichte*, especially in his later *Anthropogeny: Or, the Evolutionary History of Man* [*Anthropogenie oder Entwicklungsgeschichte des Menschen*] and in his *Riddle of the Universe* [*Welträthsel*]. The term “biogenetic fundamental law” [*biogenetisches Grundgesetz*] appears after 1872 with increasing frequency in the popular books, which contributed substantially to the term's resilience in the subsequent decades of Haeckel's varied reception (Ulrich, 1968). For example, in his *Anthropogeny* (1874), which by 1910 had reached six editions, Haeckel sought to show to what extent it was possible to recognize in a single organism the whole historically connected series of its ancestors. There, he outlined the animal ancestral lineage of humans that he established through the developmental history of individual organs by means of the biogenetic law. It was in the same work that he unveiled the images of embryos, which quickly became (and still are today) iconic of Haeckel. His use of embryo images began, however, already in 1868 in his *Natural History of Creation*, in a chapter revealingly entitled “Evolutionary laws [*Entwicklungsgesetze*] of organic phyla [*Stämme*] and individuals: phylogeny and ontogeny” (Figure 2; Haeckel, 1868, pp. 227–258). Notably, the pairs of embryo illustrations for dogs and humans, and chicken and turtles, respectively, were gradually developed in later editions (1868–1909). In the same work, the biogenetic law as developed in Volume II of *Generelle Morphologie* is restated, with reference to the key chapters in the same book such as the “Evolutionary history of morphological individuals” and the “ontogenetic theses” (Haeckel, 1868, pp. 253).

4.1 | The perception of the biogenetic law from Haeckel to modern times

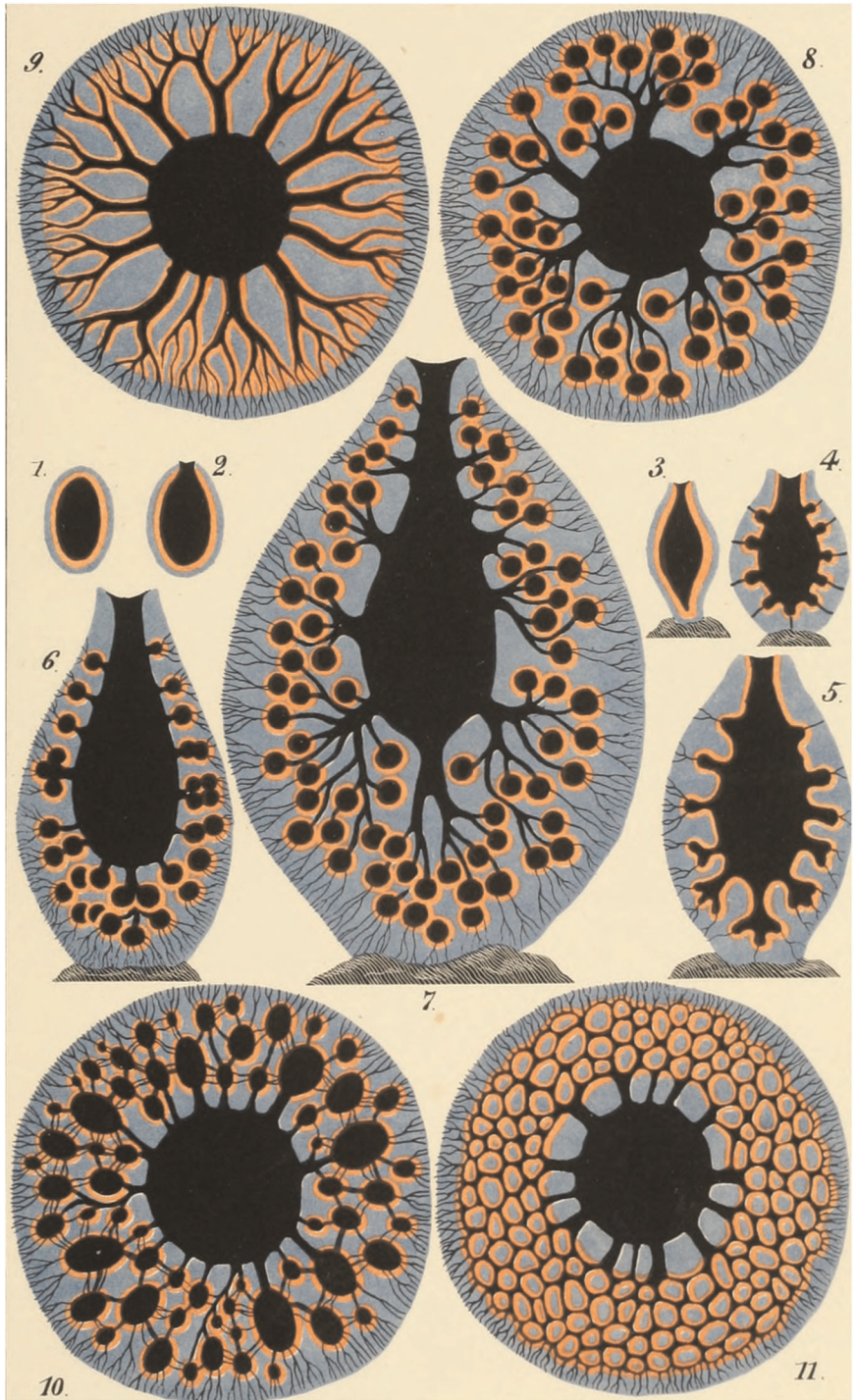
The observation that embryos of different species share some morphological similarities is not exclusive to Haeckel (Junker & Hoßfeld, 2009; Levit et al., 2015). In 1828, the Baltic-German embryologist Karl von Bear wrote:

I have two small embryos preserved in alcohol, that I forgot to label. At present I am unable to determine the genus to which they belong. They may be lizards, small birds, or even mammals.

Baer proposed four laws of animal development applicable across the animal kingdom (Baer, 1828): (1) General characters appear before specialized characters; (2) More general characters form first, followed by less general characters until most specialized characters develop last; (3) Embryos diverge from embryos of other groups with progressive development; (4) Embryos of higher species resemble embryos of lower species. In brief, early embryonic stages show the most morphological similarities between different species. For example, all vertebrates develop a vertebral column early in embryonic development. It is, sometimes, supposed that von Baer's insights best correlate with the “early conservation model” predicting that the highest developmental constraints occur at the beginning of embryogenesis (Pieasecka et al., 2013). Von Baer's law, however, is compatible with the “hourglass model” as well. The idea that modern vertebrate embryos pass through a certain stage characterized by the highest morphological similarity may be compatible with both “early conservation” and “hourglass” models. Brauckmann pointed out that the recent interest in von Baer's law of individual development, and especially its third proposition (embryos of different species progressively diverge from one another during ontogeny) is connected with the appearance of the concepts of the phylotypic stage and the hourglass model (Brauckmann, 2012).

Haeckel promoted in his law that all, or at least most vertebrates pass through an identical stage and differ from each other at later stages (Haeckel, 1866). Unlike von Baer, he stated that embryonic development recapitulates the replaced adult ancestral features: “v. Baer's law shows us the order in which the characters which are present today in adult animals were established; the law of recapitulation shows us, on the contrary, the order in which the ancestral characters, which once were present in the adults of the ancestors of the discussed forms, but have been replaced by other characters in the recent adult animal, develop” (Sewertzoff, 1931, pp. 278–279). Haeckel observed the highest conservation at the earliest stages of embryonic development. In later stages, differences increase gradually until the adult stage of development is reached (Figure 3a). His recapitulation of phylogeny during ontogeny was highly discussed and revived in the context of developmental mechanisms for more than a century. Especially, the search for highly conserved embryonic stages, which reflect a whole phylum and its basic body plan, challenged Haeckel's biogenetic law. Even if the

FIGURE 1 Schematic presentation of the gastrocanal system in different leucon-type sponges (Haeckel, 1872, Plate 40) [Color figure can be viewed at wileyonlinelibrary.com]



biogenetic law per se is no longer accepted in recent embryological works (Gould, 1977), some aspects are retained and can be partially found in the so-called funnel model of development (Rasmussen, 1987; Riedl, 1978). This model predicts that the earliest stages of ontogeny show the most ancestral features. Subsequently, development becomes less conserved and the amount of ancestral features decreases (Figure 3a). This process increases the differences between phyla. The causal basis of the funnel model is called developmental burden, a concept stating that all ongoing

developmental processes depend on the previous ones. Such dependence between late and early developmental processes leads to the assumption that highly conserved patterns should be found in the earliest stages of development. This assumption is shared by the generative entrenchment concept (Wimsatt, 1986). This concept implies a strict hierarchical order of developmental programs in which the most important developmental functions are the most ancient ones. This is explained by proposing that upstream programs are strictly responsible for the successful initiation and execution of

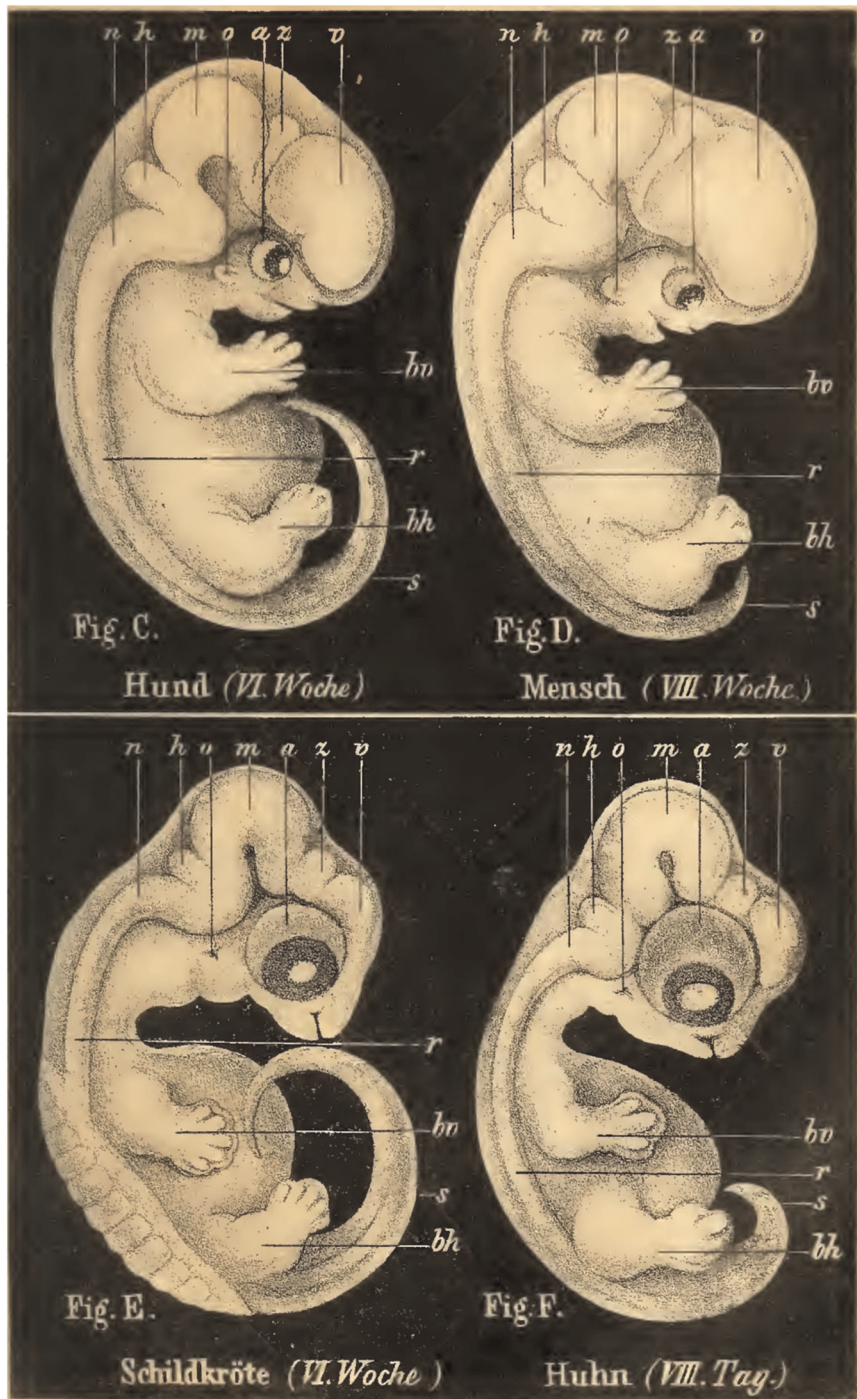


FIGURE 2 Vertebrate embryos in *Natural History of Creation* (1868, 240c) [Color figure can be viewed at wileyonlinelibrary.com]

downstream programs, resulting in a strong dependence of the downstream programs on the successful work of the upstream ones. It was proposed that even small changes in the upstream programs inevitably lead to very large downstream alterations that an organism cannot survive. Because of this high risk of lethality, these upstream programs are unlikely to be changed during evolution. This leads to the question if development follows a strict hierarchical order from ancient upstream programs to evolutionary younger downstream programs, how is it possible that within the animal kingdom, a huge variety of different cleavage and gastrulation modes

exists? Especially, the last question is not sufficiently addressed by the funnel model.

An alternative model was proposed in the early 1990s, incorporating some ideas of the fourth law of von Baer. This model includes these diverse early embryonic processes and combines them with the recently discovered highly conserved Hox cluster gene expression. Duboule (1994) presented a phylotypic egg-timer, which will later be known as the so-called hourglass model (Figure 3b) of development. It states that early embryogenesis is characterized by simple and few molecular networks. The intermediate stage of

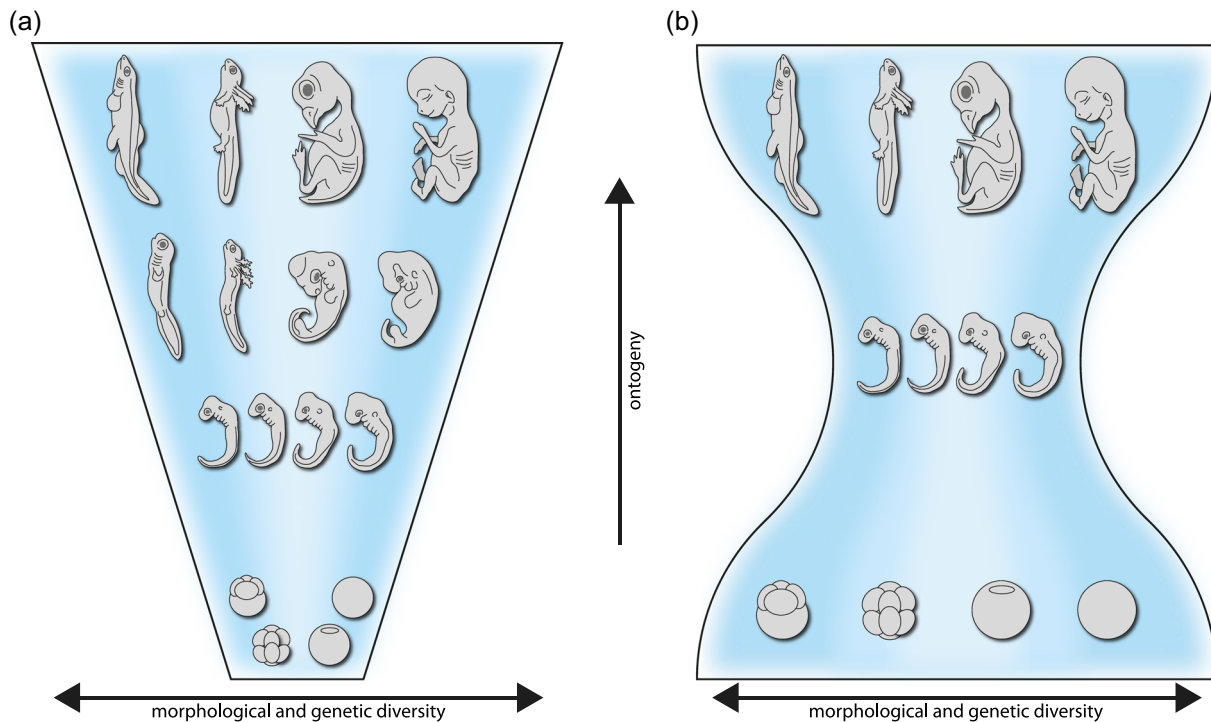


FIGURE 3 (a) Funnel and (b) hourglass models [Color figure can be viewed at wileyonlinelibrary.com]

embryogenesis instead consists of multiple molecular networks in every organ system which are highly dependent on each other. The late embryogenesis consists of multiple molecular networks too, but they are mostly independent. Therefore, this model explains the highly diverse stages of early and late embryogenesis and a highly conserved intermediate stage, the phylotypic stage (Duboule, 1994; Raff, 1996). It is a physical link between the highly diverged early and late stages of embryogenesis, but the question remains why it even exists. Duboule proposed that the establishment of the Hox-cluster gene expression is fundamental for development and the anterior–posterior axis of the animal and leads to its conservation (Duboule, 1994). Raff instead emphasized that the highly interlinked molecular networks of the developing organs constraint overall embryonic development during the phylotypic period (Raff, 1996). Both have in common, that this conservation induced and reinforced itself because of the high risk of lethality after small changes at this period.

4.2 | The biogenetic law challenged by genomics and transcriptomics

The proposal of the hourglass model revitalized the task of finding the causal link between development and evolution. Different approaches were employed to uncover this crucial link (Bininda-Emonds et al., 2003; Hall, 1997; Poe, 2006; Poe & Wake, 2004; Richardson et al., 1997, 1998). However, it remained unclear if the hourglass model is appropriate to explain the observations. Alternative models were proposed, for example, the ontogenetic

adjacency model (Poe & Wake, 2004) or the adaptive penetrance model (Richardson et al., 1997). Newly developed tools for sequence-based analysis of genomic or transcriptomic data provided new insights into the conservation of specific embryonic stages. Expression profile studies from single species and later from multiple species challenged once again the hourglass model of development (Hazkani-Covo et al., 2005; Kalinka et al., 2010; Levin et al., 2012; Schep & Adryan, 2013; Wang et al., 2013; Yanai et al., 2011). But there are also studies that give evidence for the existence of a conserved phylotypic period as well as for the hourglass model itself. A useful tool for the comparison of transcriptomic data is the so-called transcriptomic age index (Domazet-Lošo & Tautz, 2010). This index revealed that the oldest transcriptomes are expressed during the phylotypic stage, the bottleneck of the hourglass model, and that younger transcriptomes are expressed during late and early embryogenesis. Additionally, they claimed that the older (in the sense of later developmental stages) the specimen becomes, the older the transcriptomes are. They add that the mid-embryonic, phylotypic stage bears the oldest transcriptome because of strong constraints which are acting on developmental regulation and gene interaction during this phase (Domazet-Lošo & Tautz, 2010). A highly constrained mid-embryonic stage similar to the phylotypic stage was described in mice (Irie & Sehara-Fujisawa, 2007) and further vertebrate embryos (Irie & Kuratani, 2011). Even in plants, there is evidence for morphological and molecular patterns of a hourglass model-like development (Quint et al., 2012). Nevertheless, the hourglass model remains controversial as some studies find no evidence for the presence of hourglass-like development (e.g., Wu et al., 2019).

A causal explanation for the hourglass shape of development was that the phylotypic period is highly prone to lethality and even small changes lead to negative selection. Nevertheless, recent works have shown that the period before the phylotypic period suffers from the highest lethality rates. This means that lethality itself is not sufficient to explain the hourglass-like conservation of development (Uchida et al., 2018). Thus, the old question of the conservation of a particular developmental stage and the reasons for this conservation remain a very active area of research, as shown by the other papers in this special issue.

4.3 | The Gastraea theory and its birth from the biogenetic law

The most comprehensive use of the biogenetic law can be found in Haeckel's writings on the Gastraea theory. According to Haeckel, the Gastraea is a hypothetical *Urform* from which all metazoans have evolved. It has left no paleontological traces and can, therefore, only be seen as the gastrula stage in the development of many extant animals:

From these identical gastrulae of representatives of the most different animal phyla, from poriferans to vertebrates, I conclude, according to the biogenetic law, that the animal phyla have a common descent from one unique unknown ancestor, which in essence was identical to the gastrula: Gastraea (Haeckel, 1872, p. 467).

In his Gastraea theory, Haeckel postulated that the two primary germ layers are homologous in all metazoans. This would prove the monophyletic origin of all animals and would provide an evolutionary explanation of the origin of germ layers (Haeckel, 1874a, 1875).

The first volume of the monograph on calcareous sponges (1872) was, thus, important not only for its express formulation of the biogenetic law. In the same work, Haeckel wrote a short (four pages long) chapter named "The germ layer theory and the animal phylogenetic tree" (Haeckel, 1872, pp. 464–467). Here, he claimed for the first time the homology of the germ layers among all metazoans. In Volume II of the *Generelle Morphologie*, Haeckel had already assumed the common ancestry of the whole animal kingdom [*Thierreich*] from a single phylogenetic form (Haeckel, 1866, pp. 408–17). Moreover, Haeckel was emboldened by the fact that the phylogenetic theses of *Generelle Morphologie* were in line with the work of the outstanding Russian embryologist Alexander O. Kowalevsky (1840–1901) (Haeckel, 1872, p. 466; Kowalevsky, 1866). In successive editions, he clarified his view on embryos, for example, in the third edition of *Natural History of Creation* (Haeckel, 1872, Plate III, p. 499). In the later editions, he integrated drawings to visualize the Gastraea theory (Figure 4). He also integrated images of germ layers of different organisms into his works (Figure 5).

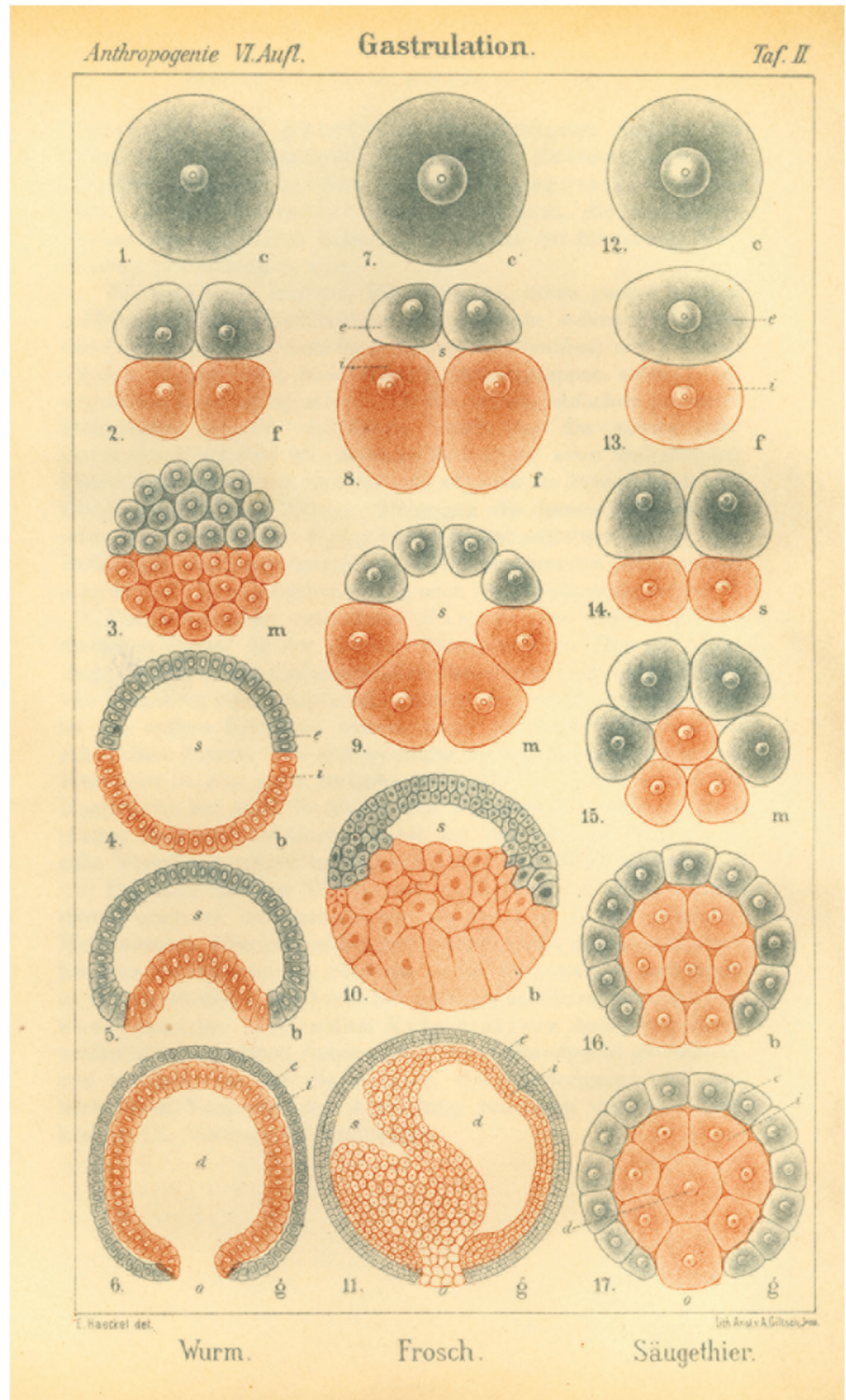
4.4 | The enigmatic *M. planula* and its influence on the Gastraea theory

The Gastraea theory was created by Haeckel within the conceptual context of his biogenetic law and aimed to explain the origin of metazoan germ layers and ontogeny based on idealistic morphology. However, as pointed out by A. Reynolds and Hülsmann (2008), there has been a second, organismic source of inspiration that became an important clue in his understanding of the evolutionary origin of the Metazoa. In 1869, Haeckel, studying calcareous sponges off the coast of Norway, observed a curious little ball-shaped organism (A. Reynolds & Hülsmann, 2008). Assuming that he had collected eggs or ciliated larvae (planulae) of a marine invertebrate he brought the organism to the laboratory and studied them over several days. To his surprise, he recognized that he collected an unknown colonial protist with a complex life cycle. Haeckel named it *M. planula* (Haeckel, 1870a), "the magician's ball," and assigned it to a new major protist taxon, the *Catallacta* (Haeckel, 1870b). The life history of *Magosphaera* as described by Haeckel is illustrated in Figure 6 (Haeckel, 1870a; pp. 139–160). In Figure 6a, we see Haeckel's own illustration of different stages, in Figure 6b, a schematic illustration of the life cycle. Haeckel himself admitted that some of his descriptions of this life history are more assumptions than direct observations. Since then, *Magosphaera* was never collected again by Haeckel or another scientist (A. Reynolds & Hülsmann, 2008). During the first years after his discovery of *Magosphaera*, he was uncertain whether to group it to, what he called, neutral protists or Protozoa (Figure 7a). As outlined in detail by A. Reynolds and Hülsmann (2008), regardless of its phylogenetic position, thinking in the frame of the *scala naturae* and under the doctrine of his biogenetic law, Haeckel assigned *Magosphaera* the "Formwerth" (significance or organizational level) of a planaea or blastosphaera/blastula (Figure 7b). This "Formwerth" marked the fourth stage, between uniform amoebae (third stage) and primitive worms and sponges (fifth stage), of his 22 typological stages of the evolution of complex organisms (A. Reynolds & Hülsmann, 2008). In later years (1894), Haeckel interpreted *Magosphaera* as a modern progeny of a common ancestor of the *Catallacta* and Metazoa that has preserved the "primitive" morphological type of the blastula as an adult stage (Figure 7c) (A. Reynolds & Hülsmann, 2008). *Magosphaera*, as a living example for an adult pre-gastrula stage (blastula), therefore became an important piece of evidence in his argumentation for the correctness of his Gastraea theory.

4.5 | The Gastraea, faux friends, and true foes

After the first mentioning of the Gastraea in his monograph *Die Kalkschwämme* (1872), Haeckel further elaborated this theory through a series of papers and books (Haeckel, 1874a, 1874b, 1875, 1877a, 1877b). He based his theory on the homology of the two primary germ layers. Subsequently, he proposed that the common ancestor of the Metazoa, the Gastraea, was composed

FIGURE 4 Gastrula formation in worm, frog, and mammal (Plate II)
[Color figure can be viewed at wileyonlinelibrary.com]



of a ciliated outer cell layer (ectoderm, serving for locomotion) and an inner cell layer (endoderm, serving as a primitive gut). Both layers were connected through an opening serving as both mouth and anus. The formation of the endoderm is often illustrated as an invagination of the ectoderm forming the gut and mouth opening (Haeckel, 1879, 1909). Haeckel deployed invagination as the ancestral mode of endoderm formation in metazoans during the elaboration phase of the Gastraea theory.

However, in his first version published in *Die Kalkschwämme* (1872), he described that single blastomeres separate from the surface epithelium and gather in the center of the blastula. Some of these cells degrade and some will form a secondary epithelium that surrounds a primitive gut. This hypothetical organism is called a Planogastraea (or its corresponding developmental stage, a planogastrula) and was already built from two germ layers. Subsequently, a mouth opening formed by connecting the

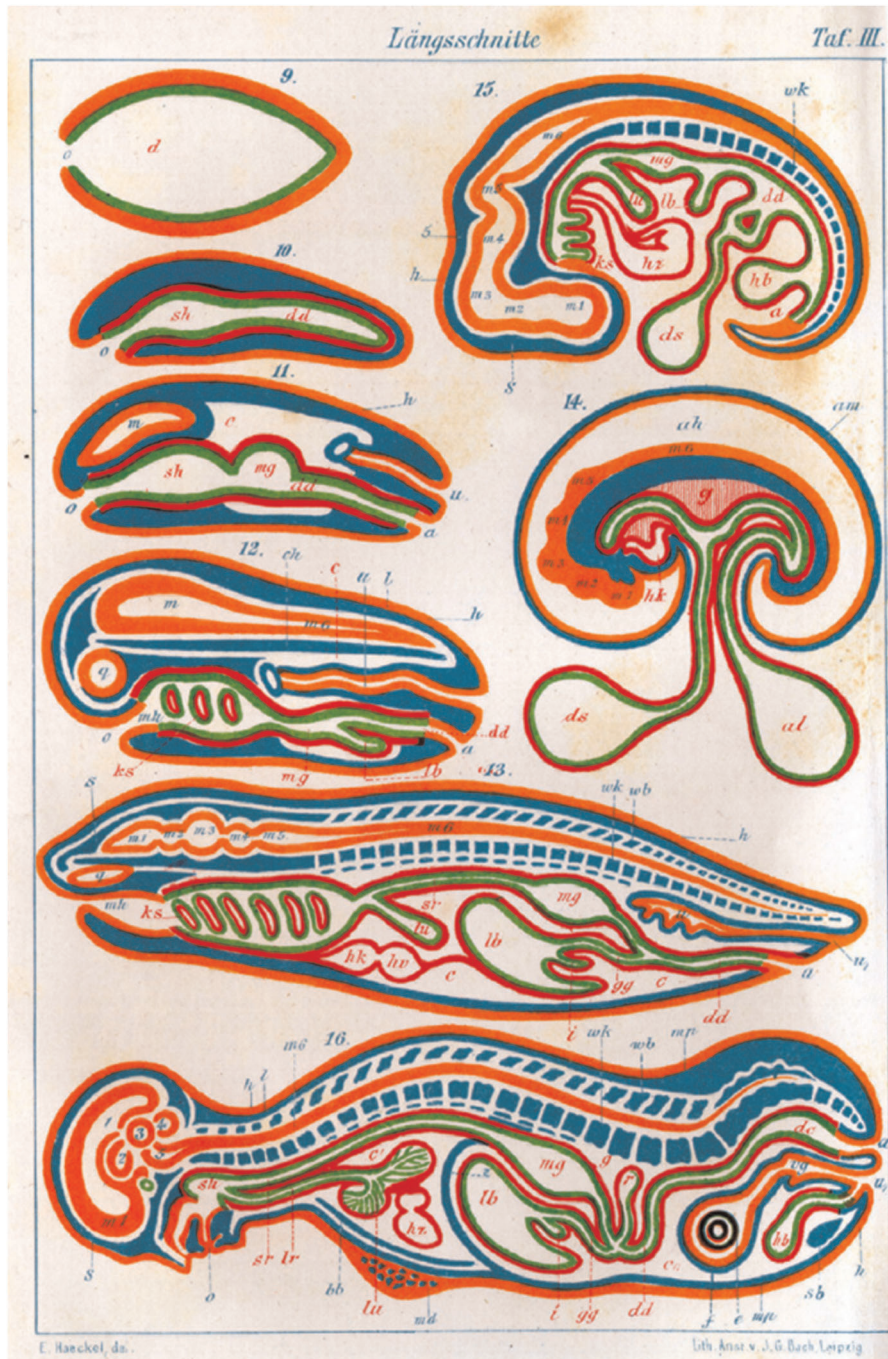


FIGURE 5 Germ layers of different organisms (Haeckel, 1874a, Plate III) [Color figure can be viewed at wileyonlinelibrary.com]

outer epithelium to the primitive gut resulted in the actual Gastraea (or gastrula, respectively). In contrast to his later view of invagination as the primary gastrulation mode, this early version of the Gastraea theory proposed ingression or immigration as the primary mode of gastrulation (Figure 8). This early scenario might have been influenced by his studies on sponge development during the first years and is much more consistent with the views of contemporary zoologists studying the development of marine invertebrates. Haeckel's Gastraea theory inspired many other zoologists to develop and elaborate alternative hypotheses on the origin of the Metazoa (for a detailed review, see Mikhailov et al., 2009). One of the most

promising was the Phagocytella hypothesis proposed by the Russian zoologist Ilya Metchnikov (1845–1916) in 1886 (Figure 8). Studying organismal defense properties, Metchnikov in 1883–1892, demonstrated that in triploblastic animals alien bodies are destroyed by parenchymal cells which he named *phagocytes* (Kolchinsky & Levit, 2019). This discovery ultimately led to the Nobel Prize in 1908. In 1882, he began to develop the aforementioned theory of *phagocytella*. Metchnikov's Phagocytella theory was opposed to Haeckel's *Gastraea* theory, which Metchnikov, as already mentioned, regarded as too speculative. Studying the development of cnidarians and sponges Metchnikov argued that the endoderm evolved into a blastula-like colonial

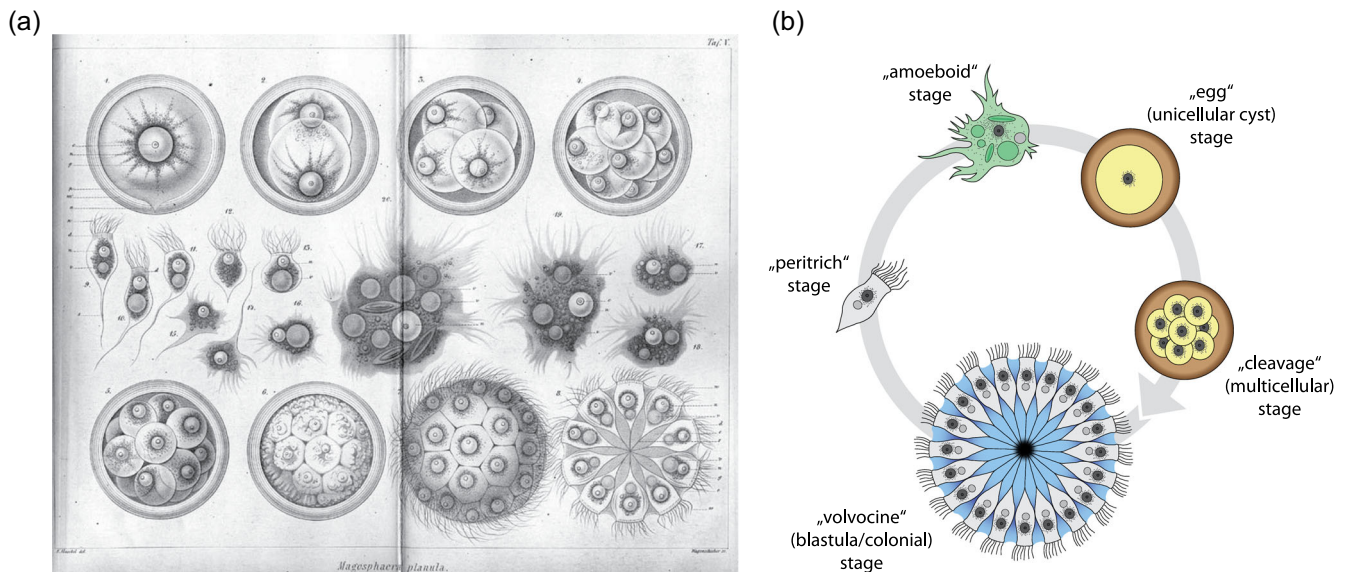


FIGURE 6 (a) Original illustration of *Magosphaera planula*. Plate V from *Biologische Studien. Erstes Heft: Studien über Moneren und Protisten* (Haeckel, 1870a, Plate V; taken from A. Reynolds and Hülsmann, 2008). (b) Schematic illustration of the life history of *Magosphaera* as described by Haeckel in the same study. Development starts as a unicellular encysted “egg.” Within the cyst, the cell divides (cleavage stage) until free-swimming, colonial “volvocine” organisms hatch. After a few hours, these colonies dissociate into single “peritrich” cells. These free-swimming cells transform into a benthic feeding “amoeboid” cell that later encysts into a new “egg” cell [Color figure can be viewed at wileyonlinelibrary.com]

ancestor by the transient ingression of cells that had phagocytized large amounts of food. Through evolution, these cells formed a central digestive (endodermal) parenchyme that subsequently was connected to the ectoderm via a mouth opening forming a *Gastrea*-like organism (Zakhvatkin, 1949). From today's view, the Phagocytella hypothesis was a fruitful elaboration of the *Gastrea* hypothesis which was still biased by the views of idealistic morphology (Hall, 2012). In search of an extant organism supporting his hypothesis, Metchnikov's attention was drawn to a colonial choanoflagellate, *Proterospongia haeckeli*. He considered it as living evidence for the Phagocytella hypothesis (Zakhvatkin, 1949). *Proterospongia* was illustrated as colonial choanoflagellates with several cell types within the colony. A similar observation has been made by Leadbeater (1983) in the species *Proterospongia choanojuncta*. However, it can be seen as a humorous incident but like *Magosphaera*, *Proterospongia haeckeli* was only collected once and described by Kent, calling its actual existence into question (Leadbeater, 2015).

While the *Gastrea* and Phagocytella hypotheses aimed to explain the evolutionary origin of germ layers and the basic metazoan body plan, other researchers focused on the ancestral life history and cell types present in the last common ancestor of the Metazoa. One of these scientists was the Russian entomologist Alexey Zakhvatkin (1905–1950). On the basis of protistology and embryology, Zakhvatkin proposed that metazoans evolved from a unicellular ancestor exhibiting a complex life cycle involving different temporal cell types. In his Synzoospore hypothesis, Zakhvatkin (1949) proposed the presence of three life-history phases corresponding to three different temporal cell types—(I) monotomy, the alteration

between cell growth and division (typical for somatic cells), (II) hypertrophy, the feeding and growth of cells without division (typical for the metazoan oocyte), and (III) palintomy, a series of successive cell divisions without cell growth (typical for cleaving blastomeres). These temporal cell types were then incorporated all together into a colonial life-history phase that evolved in the metazoan stem lineage. Mikhailov et al. (2009) further stressed this Synzoospore hypothesis by elaborating that “the pre-existence of temporal differentiation in complex life cycles of unicellular and colonial pre-metazoans was a platform for the origin of cell differentiation during the emergence of early animals—in contrast to the *Gastrea* hypothesis, which postulates cell differentiation *de novo*.”

The Phagocytella and Synzoospore hypotheses and their later elaboration by Mikhailov. et al. (2009) seem to be the more realistic scenario for the evolution of the Metazoa compared with Haeckel's *Gastrea* theory. However, based on the description of the life history of *Magosphaera* and its placement in the evolutionary lineage leading to the Metazoa, we argue that Haeckel was aware that temporal cell differentiation preceded spatial cell differentiation. The same three life-history phases postulated by Zakhvatkin (1949) were also described by Haeckel for the life history of *Magosphaera*. The blastula and unicellular swimmer stage resemble a monotomic phase, the amoeboid stage is the main feeding stage and might represent a hypertrophic stage while the cyst or egg stage resembles Zakhvatkin's description of a palintomic phase. The major differences are that Zakhvatkin (1949) described the monotomic phase as sedentary and the palintomic phase as pelagic (swarmer phase) while Haeckel (1870) described the (monotomic) blastula stage of *Magosphaera* as pelagic and the (palintomic) egg/cyst stage as sedentary. Maybe it

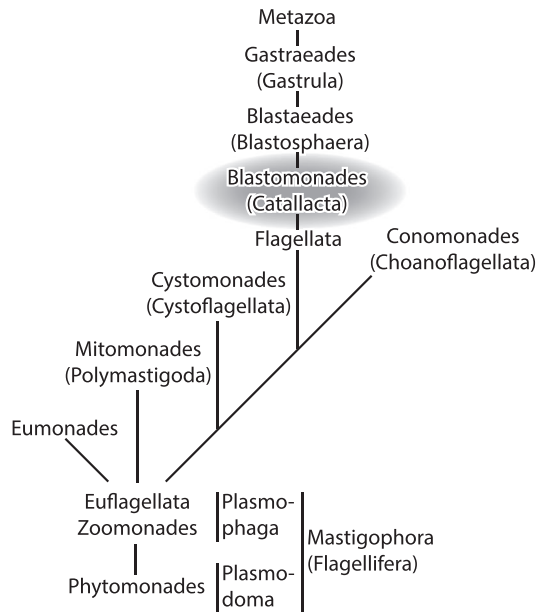
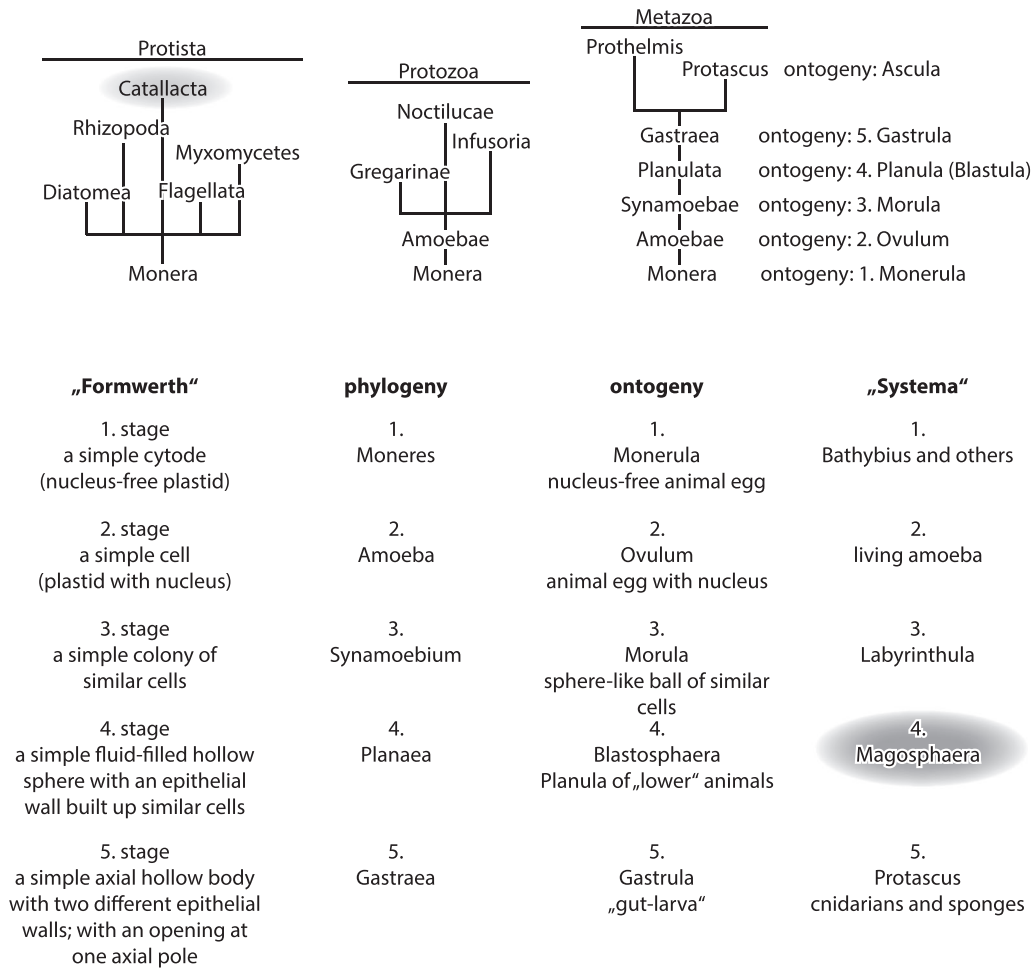
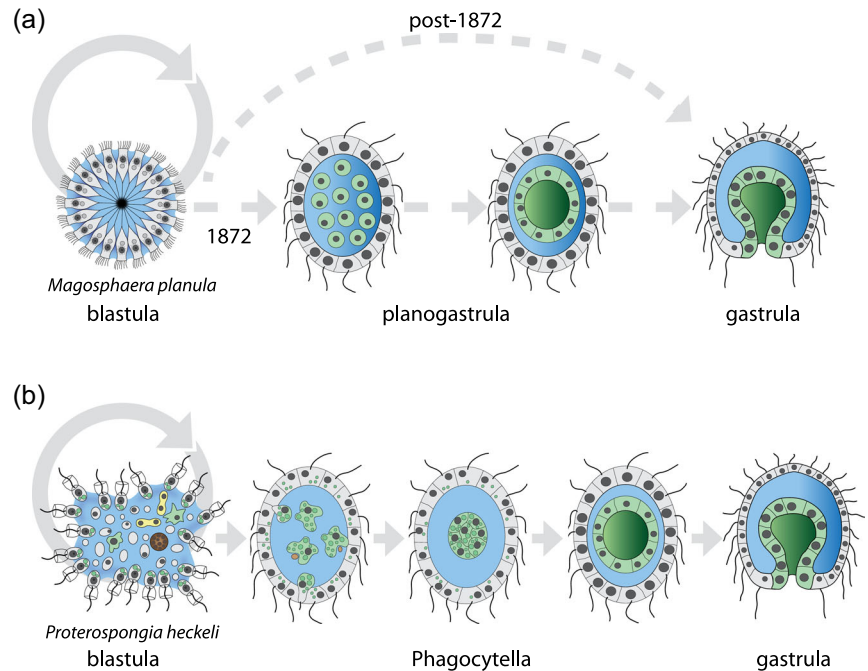


FIGURE 7 Different ideas of Haeckel on the phylogenetic relationship and evolutionary context of *Magosphaera* (Catallacta). The schemes are modified from the original illustrations in the corresponding books. (a) Phylogeny from Haeckel (1872) *Die Kalkschwämme (Calcispongiae)*. (b) Table from Haeckel (1874) *Anthropogenie oder die Entwicklung des Menschen*. (c) Phylogeny from Haeckel (1894) *Systematische Phylogenie*

FIGURE 8 Schematic illustrations of (a) Haeckel's *Gastraea* and (b) Metschnikov's *Phagocytella* theory. In (a), the lower line shows Haeckel's first idea of an immigration/ingression-based endoderm formation in the *Gastraea* (in *Die Kalkschwämme*, 1872) while the upper line shows his invagination-based version from subsequent publications [Color figure can be viewed at wileyonlinelibrary.com]



was his strong adherence to the dogma of idealistic morphology that detained him from incorporating a complex life history into the center of his thoughts about the evolution of the Metazoa.

4.6 | From *Magosphaera* to choanoflagellates

During the times of the *Gastraea* and *Phagocytella* hypotheses, the monophyly and phylogenetic relationship of the Metazoa were highly debated, which complicated the reconstruction of the biology of their last common ancestor. However, without certain knowledge on the sister-group of the Metazoa, the reconstruction of their evolutionary origin seems to be an impossible venture. Nowadays, molecular studies have added profound arguments that choanoflagellates are the closest living unicellular relatives of the Metazoa (Fairclough et al., 2013; King et al., 2008; Richter, 2013). Extensive choanoflagellate research identified many "metazoan-typical" features that actually pre-date the origin of the Metazoa. Some choanoflagellates exhibit a complex life history involving different temporal single cell types and colonial phases (Dayel et al., 2011; Leadbeater, 2015). This has been proposed as one of the most important pre-requisites for the evolution of metazoan multicellularity by zoologists such as, Zakhvatkin (1949), and Mikhailov et al. (2009). Additionally, some choanoflagellates have been shown to be capable of sexual recombination (Woznica et al., 2017) and express many proteins previously thought to be restricted to specialized metazoan cell types such as neurons (Burkhardt et al., 2011; Göhde et al., 2020). Collective cellular contraction, another feature crucial for Haeckel's invaginary *Gastraea* hypothesis and gastrulation, in general, has previously also only been described in Metazoan taxa. However, the recently discovered choanoflagellate *Choanoeca flexa* exhibits collective actinomyosin-mediated apical constriction resulting in a switch from a sphere-like to a sheet-like colony morphology (Brunet et al., 2019).

Furthermore, another recent study shows that the general three-dimensional morphology of choanoflagellate colonies is determined by the amount and stiffness of the secreted extracellular matrix and the form and size of colonial cells (Larson et al., 2020). Therefore, choanoflagellates are valuable models to investigate the evolutionary origin of basic morphogenetic processes involved in metazoan development and for sure will help to further elaborate the intellectual heritage of Haeckel, Metschnikov, Zakhvatkin, and many other outstanding researchers of the late 19th and 20th century.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

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