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HISTORY OF BIOLOGY

From Idea to Law: Theory, Concept and Terminological Formation in Ernst Haeckel's Works

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Abstract—Since Charles Darwin (1809–1882) and Ernst Haeckel (1834–1919) published their trailblazing ideas, the scientific community's discussion of evolutionary biology has included the topic of embryological development. The concepts of ontogeny and phylogeny, still current in contemporary biology, together with the now obsolete biogenetic law and his Gastraea theory, which trace back to Haeckel, all underwent an evolution of their own in Haeckel's works. The record of this evolution makes clear how the features of his thinking that proved durable, such as ontogeny and phylogeny, were established as such through a difficult creative process of formation of concepts, theories, and terminology that themselves enjoyed varying fortunes. Beginning with Haeckel's *Generelle Morphologie der Organismen* [*General Morphology of Organisms*] (1866), this paper traces aspects of the conceptual and terminological evolution that takes place both *within* the pages of this highly complex but seminal work and then chronologically in later works. We include the use of text data mining of his works to establish and analyse word frequency patterns. We seek to indicate here some of the challenges Haeckel faced in establishing new concepts and terminology in the *General Morphology* (hereafter *GM*), and we draw attention to his efforts in later works to extend this didactic work.

Keywords: Ernst Haeckel, biogenetic law, Gastraea theory, ontogeny, phylogeny, morphology, zoology

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INTRODUCTION

Ernst Haeckel was arguably the most important continental figure on the frontlines of Darwinism during the latter part of the 19th century and into the 20th century (Fig. 1; Richards, 2008; Hoßfeld, 2010; Rieppel, 2016; Joshi, 2018a; Watts et al., 2019; Kutschera et al., 2019; Hoßfeld et al., 2019). In his first major work, the two-volume *General Morphology of Organisms* (hereafter simply *GM*), appearing in 1866, Haeckel was the first biologist to offer detailed phylogenetic trees (otherwise referred to in current literature as 'genealogical trees') which included humans (Hoßfeld and Levit, 2016; Hoßfeld et al., 2017; Watts et al., 2019). The work was dedicated to his "dear friends and colleagues": volume one to the anatomist Carl Gegenbaur (1826–1903) and volume two to the "founders of the theory of descent", Charles Darwin, Johann Wolfgang von Goethe (1749–1832) and Jean-Baptiste de Lamarck (1744–1829). Goethe was for Haeckel so important because he regarded Goethe, amidst the German speaking world, as the one who "most diligently, in the quiet depths, concerned himself with the analogies and secret relations between creatures, and delved most deeply into the actual being of these relations." (Haeckel, 1866b, p. 157; Levit and Hoßfeld, 2017).

GM, in fact, provides the key to his later work, establishing the boundaries and conceptual content that would define the fields pursued in later works (Ulrich, 1967, p. 201). In it, Haeckel self consciously went far beyond Darwin in pursuing Darwin's theory of evolution into all of biology (Olsson et al., 2017). Already here he also called on evolutionary biology to take on not only the central, transformative role for all the biological sciences, but also more much beyond that as the foundation for a modern worldview oriented toward—and orienting others toward—the betterment of humanity as a whole, on the foundations of the natural sciences. Throughout his life, Haeckel was thus engaged in a kind of didactic mission (Dodel, 1906; Porges et al., 2019). Two years later Haeckel began to express his natural philosophical views in more popular form in his *Natürliche Schöpfungsgeschichte* [*The History of Creation*] (1868), which went through 9 editions and was translated into 12 languages, including English in 1876, and into Russian in 1908

Fig. 1. Ernst Haeckel ca. 1872 (Archive: Uwe Hoßfeld).

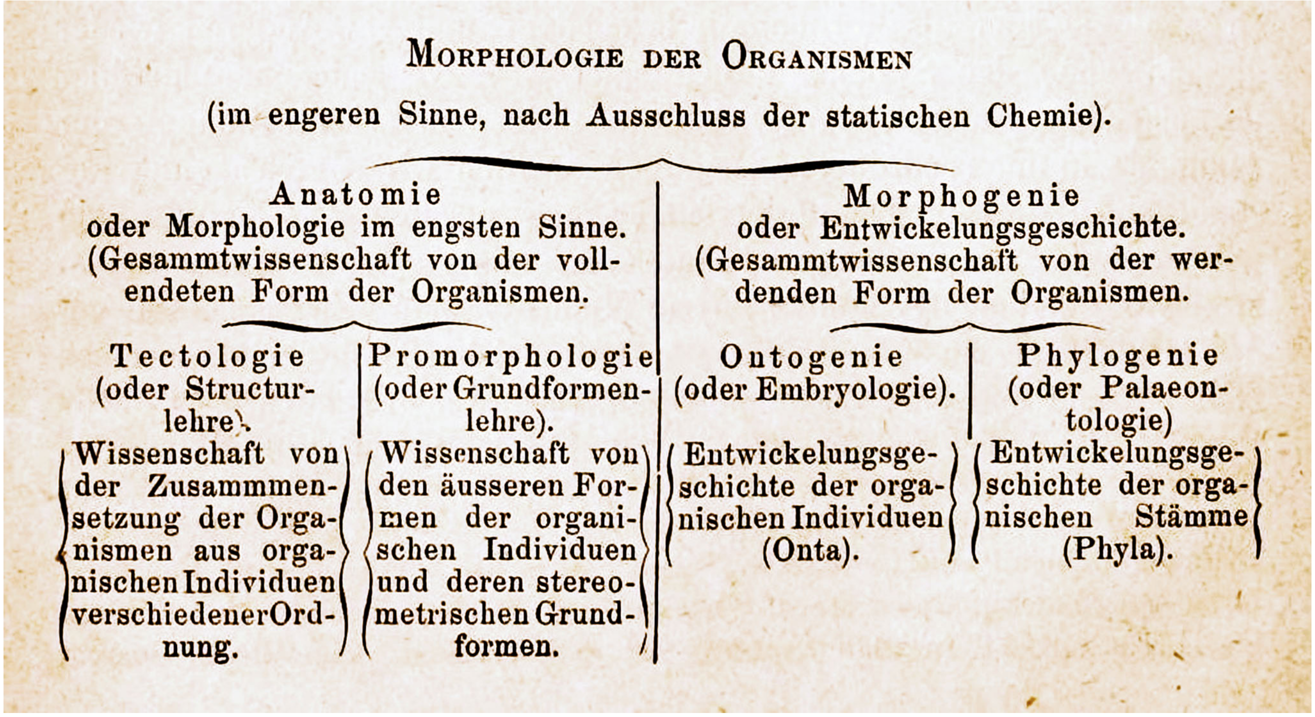
(Kolchinsky and Levit, 2019). This and his *Anthropogenie oder Entwickelungsgeschichte des Menschen* [*Anthropogeny: Or, the Evolutionary History of Man*] (1874), in contrast to *GM,* were successful in terms of extent of readership, and served as amongst the earliest introductions into a wider, indeed international readership of the work of Darwin (Nordenskiöld, 1935). As Robert Richards has emphasised: "More people at the turn of the century learned of evolutionary theory from his pen than from any other source, including Darwin's own writings" (Richards, 2018, p. 35). Although it is the case that after 1859 Darwin's doctrines had gained relative wide acceptance, and Haeckel's works had circulated worldwide, in some countries, including Russia, the works of both authors were also at different times forbidden (Kolchinsky, 2019; Kolchinsky and Levit, 2019). This was only exacerbated by the fact that Haeckel's constant close-coupling of science, monistic worldview, religion, and artistry gave, and still give, Haeckel's works a distinctive character, but also allowed room for controversial interpretations, critiques, and political-ideological appropriations of quite diverse sorts (Kleeberg, 2007; Stewart et al., 2019). The lure of the 'forbidden fruit,' however, served in the schools and academic contexts rather to further their appeal (Hopwood, 2015, p. 189).

Within evolutionary biology itself, Haeckel developed Darwin's thought into further directions, including into the domain of embryology. Although the embryological regularities were known to many researchers before Haeckel, including his friend Gegenbaur, alongside Fritz Müller (1821–1897) he was among the first to formulate the 'fundamental law of biogenetics' (biogenetic law) [*Biogenetisches Grundgesetz*] (Junker and Hoßfeld, 2009; Hoßfeld et al., 2016; Hoßfeld et al., 2019). The 'Gastraea theory' as well as still current concepts such as ontogeny and phylogeny, trace back to Haeckel. Darwin and Haeckel inspired and influenced each other reciprocally; although Darwin had adopted early on the theory of recapitulation, he was encouraged by Haeckel's approval (Richards, 2018).

In overview one can conclude that although Haeckel's far-reaching generalizations were not generally accepted, his influence meant, for example, that embryology soon would count as an indispensable tool for recognizing otherwise uncertain homologies between organisms. Further, one can say that the scientific debate surrounding the biogenetic law exemplifies the fertile interaction that developed between embryology and comparative anatomy in the late 19th century (Hoßfeld et al., 2003; Hoßfeld and Olsson 2003a, 2003b; Hoßfeld et al., 2019). When the concepts and terminology introduced by Haeckel did not suffice to answer the questions at hand, or were contradicted by further anatomical research and reflection, several biologists tried to supplement or replace the biogenetic law. It was in the context of such critical discussion that later important milestones in the history of evolutionary developmental biology emerged. Ultimately the biogenetic law served as a creative object of critique; ideas in biology, such as ontogeny and phylogeny still current today, were articulated in relation to it, as was the very idea of a causal nexus between ontogeny and phylogeny that is implicit in that law (Levit et al., 2015; Joshi, 2018b; Watts et al., 2019).

MORPHOLOGY'S MAIN DIVISIONS: TECTOLOGY, PROMORPHOLOGY, ONTOGENY, AND PHYLOGENY

Haeckel followed didactic principles in his works; he argued from general to specific, and framed concrete questions, always concerned to win over his readers to his thought processes, concepts and theories (Ulrich, 1967, p. 205; Levit et al., 2004, 2014; Olsson et al., 2006). In speaking of Haeckel's 'didactic' efforts, it should be made clear that Haeckel himself, and his early readers, recognized that the massive two-volume *GM*, his first foray into transforming the language and concepts of biology as a whole, was not his finest didactic effort (Haeckel, 1906, IV). Even his staunchest supporters made this point, seeking an explanation for its rhetorical failings in the personal



Morphologie der Organismen

(im engeren Sinne, nach Ausschluss der statischen Chemie).

Anatomie oder Morphologie im engsten Sinne. (Gesammtwissenschaft von der vollendeten Form der Organismen.		Morphogenie oder Entwickelungsgeschichte. (Gesammtwissenschaft von der werdenden Form der Organismen.	
Tectologie (oder Structurlehre).	Promorphologie (oder Grundformenlehre).	Ontogenie (oder Embryologie).	Phylogenie (oder Palaeontologie)
Wissenschaft von der Zusammmensetzung der Organismen aus organischen Individuen verschiedener Ordnung.	Wissenschaft von den äusseren Formen der organischen Individuen und deren stereometrischen Grundformen.	Entwickelungsgeschichte der organischen Individuen (Onta).	Entwickelungsgeschichte der organischen Stämme (Phyla).

Fig. 2. Overview of the morphology of organisms (from: Haeckel, 1866a, p. 30).

context in which the work was written at fever-pitch within a single year (Schmidt, 1924, I: XXII; Ulrich, 1967). Nevertheless, as these same readers also noted, Haeckel was seeking a monumental re-formation of thinking in the whole field of biology. As is evident in various transformative moments in the history of science, challenges of Haeckel's reformulations carried with them unavoidably formidable challenges of mixing old and new concepts and language (Levit et al., 2014). Some of these we highlight below.

In volume I of the *GM* (titled the 'General anatomy of organisms') Haeckel first discusses in systematic overview the subject of morphology, or the "the doctrine of forms in the developing organism" [*Formenlehre des werdenden Organismus*]. In his first pass over new terminology, Haeckel used older terms, ostensibly to make himself clear. As can be seen in Fig. 2, Haeckel divided morphology into the two fundamental fields: anatomy and morphogeny. Morphology "in the narrowest sense" [*im engsten Sinne*] was called anatomy in an effort to connect his new conceptions to older pre-evolutionary notions of anatomy that had tended to capture the temporally 'permanent' forms found in individual organisms. Fundamental for Haeckel is that forms were never permanently static in the older pre-Darwinian sense, but could be *considered* as such from a certain point of view, namely an individual "which at this moment is considered as if an unalterable being" (Haeckel, 1866a, p. 265).

Within that, anatomy was divided into tectology and promorphology, the former being the analysis of organisms on the basis of their structural components, the latter being the study of 'invariable,' underlying stereometric properties of the forms (*Grundformen*) that themselves combine to form the organism as a whole (Haeckel, 1866a, pp. 46–49; Rieppel, 2016, p. 22). The second main division of morphogeny introduced the new terms of ontogeny and phylogeny to introduce a dynamic aspect of organisms as evolving, both within their individual life process as "becoming" [*werdende*] form (ontogeny) and the evolving history of the phylum or 'stem' [*Stamm*] (a term of Greek origins Haeckel coined), of which they were a member: phylogeny (Haeckel, 1866a, pp. 29–30). As can be seen above, 'ontogeny' in Fig. 2 is identified with 'embryology' and 'phylogeny' with 'palaeontology.'

CONCEPTS AND WORDS, OLD AND NEW

Haeckel's creative use of old and new vocabulary is distinguished by a self-conscious attempt to deal with the problem of new concepts clothed in old language, and new language requiring explanation, which unavoidably uses also old vocabulary. It is a stunning feature of Haeckel's creative genius at work in the *GM* that he was not only creating neologisms but also constantly adapting terminology from established disciplines in order articulate the deep connections between areas of inquiry. For example, the aforementioned definition of morphology in terms of an epistemic perspective, namely treating individuals "as if" they were unalterable, what Olivier Rieppel calls a "time slice" definition of morphology (Rieppel, 2016, p. 42), has its roots in an ontological principle that emerges from Haeckel's more fundamental concepts of nature and how it should be known. In the earliest pages of *GM* Haeckel sought to situate morphology in relation, *inter alia,* to the science of physics, understood as the science of forces [*Kräfte*]. From the most universal perspective, all of nature is "nothing other than a system of moving forces, from which follows that there is no such thing as actual rest anywhere, so that where rest appears to exist in regions of matter this is only the result of counter-balancing forces..." (Haeckel, 1866a, p. 11). Insofar as morphology is the study of form discovered in organisms, every form thus considered is "nothing other than the result of a balance of moving forces at a given moment. The science of forms or morphology of natural bodies is thus, in the broadest possible sense, the statics of matter" (Haeckel, 1866a, p. 11), or to use more modern formulation, a study of equilibria (Watts et al., 2019).

Another example is the case of "embryology." In Fig. 2, the term ostensibly served to connect the new term "ontogeny" to popular distinctions of temporal development within a certain stage of life of a growing, individual being. But he immediately stressed that embryology was "far too narrow a field, applicable only for the higher orders of animals" (Haeckel, 1866a, p. 30), and that terminology for evolution both inside and outside the embryonal membrane was lacking (Haeckel, 1866a, p. 55). Haeckel would go on to define ontogeny variously as the "evolutionary history of individuals", "evolutionary history of the genealogical individual of the first order" and "evolutionary history of the egg product", in an effort to address this lack (Haeckel, 1866a, p. 55). The *onta* of ontogeny, he will also call "bionts" [*Bionten*] (Haeckel, 1866a, p. 266) to avoid, as he says later in volume I, "the sluggish [*schleppend*] and the polysyllabic term 'physiological individual'" (Haeckel, 1866a, p. 367). Whichever term he used (and he used them interchangeably) these he understood to be concrete bodies, distinguished as over against abstractions or conceptual bodies: "concrete individuals (as spatially delimited unities of the form), which at a given time are the object of consideration and investigation." As we shall see below, the very notion of "individual" was itself in evolution during this period, to which Haeckel contributed.

Similarly, the *onta* or living individuals in this sense stand over against the *phyla* or genealogy of individuals [*Individuen-Stämmen*] under which term we understand the abstract totality of all *onta* related by blood" (Haeckel, 1866a, p. 55). In the same way, ostensibly 'palaeontology' was used here in Fig. 2, as a first approximation to phylogeny. The older term indicated that this was a study of whole collections of species related over vast periods of evolutionary time scales that would be central to Haeckel's new terminology of *phylon* (and its variants in Latin, *phylum, phyla*) or *Stamm* in German, and its study: phylogeny. But palaeontology was quickly qualified by Haeckel as a term loaded with what were, for Haeckel's new study of phylogeny, distracting associations with static, indeed "sluggish" [*schleppend*] pre-Darwinian periods, and with the relative lack of interest, as he saw it, on the part of geologists in organic history (Haeckel, 1866a, pp. 59–60). Although the word will be used repeatedly later in *GM*, as we'll see, as a synonym for 'phylogeny', its meaning in the text of *GM* (and indeed the whole field, in Haeckel's eyes), would be transformed, as the new terms and their definitions govern the entire work: "Phylogeny and ontogeny should thus serve as mutually coordinated branches of morphogeny. Phylogeny is the evolutionary history of the abstract genealogical individual; ontogeny is the evolutionary history of the concrete morphological individual" (Haeckel, 1866a, p. 60).

THE PROBLEM OF THE INDIVIDUAL

In each of these four main divisions, Haeckel tackled the question of individuation, which had challenged both morphologists and physiologists in botany as in zoology throughout preceding decades (Rieppel, 2016, pp. 41–43; Rieppel, 2019). The "problem," simultaneously logical and systematic, had only become more challenging in the context of evolutionary development, since not only was the individual, understood as mature reproducing organism, made up of parts (introducing a new dimension to the classical parts/whole distinction), but each of these parts, depending on which organisms were in question, need to be considered over varying time-scales in their *relation* to one another and their relations to homologous parts within species and phyla (Rieppel, 2019). In chapter 8 of book 3 of the first volume, Haeckel canvases the bewildering array of precedent approaches to the problem of individuation (Haeckel, 1866a, pp. 241–268). He sought to capture his solution in his concept of "relative individuality" (Haeckel, 1866a, p. 264), which involved "abandoning" the very notion of an "absolute individual", vestiges of which had persisted in the debate of preceding decades. Haeckel organized that relativity by proposing six "orders" of individuality that were analogous amongst protists, plants and animals, using terms themselves borrowed from the considerable discussion amongst botanists and zoologists in preceding decades (Rieppel, 2019): *Plastiden* or cells, as either unicellular individuals or nested within multi-cellular organisms; *Werkstücke* or organs and systems of organs composed of cells; antimeres (*Antimeren*) or morphological structures corresponding across a symmetry plane, such organs with right and left parts, or organ systems in bilaterally symmetrical organisms; metameres (*Metameren*), or the corresponding parts along an axis, such as the internodes of vegetative stems, segments in worms or somites in vertebrates; persons (*Personen*); sixth and last are col-

Table 1. Terminological frequency according to Haeckel's texts (excluding Tables of Contents and Indexes). The overall digital sources of all texts used were either https://archive.org or http://caliban.mpipz.mpg.de. In each case, we have used the search engine within that software to carry out the word search. Grey rows indicate Haeckel's intentionally more popular works. (a)–(k)—specific URLs for each text

Titles	Terms											
	Bion	Embryologie	Onta	Ontogenie	Keimesgeschichte	Paläontologie	Phylogenie	Stammesgeschichte	Gastraea	Gastraea-Theorie	Keimblätter-Theorie	Biogenetisches Grundgesetz
(a) Generelle Morphologie, Bd. 1 (1866)	109	23	5	33	0	21	23	0	0	0	0	0
(b) Generelle Morphologie, Bd. 2 (1866)	84	32	0	146	0	67	146	0	0	0	0	0
(c) Natürliche Schöpfungsgeschichte (1868)	0	17	0	61	0	21	34	5	0	0	0	0
(d) Kalkschwämme, Bd. 1 (1872)	22	4	0	53	3	2	49	4	12	0	4	17
(e) Kalkschwämme, Bd. 2 (1872)	0	0	0	1	0	0	0	0	0	0	0	1
(f) Kalkschwämme, Bd. 3 (1872)	0	0	0	4	0	0	0	0	0	0	0	0
(g) Anthropogenie (1874)	0	11	0	109	87	16	56	73	46	15	8	47
(h) Systematische Phylogenie, Bd. 1 (1894)	0	4	0	71	9	38	83	54	3	0	0	25
(i) Systematische Phylogenie, Bd. 2 (1896)	0	2	0	146	9	40	53	62	36	14	2	26
(j) Systematische Phylogenie, Bd. 3 (1895)	0	6	0	101	10	33	46	55	7	1	0	21
(k) Die Welträtsel (1899, Volksausgabe)	1	9	0	39	30	15	24	42	1	8	0	26

(a) https://archive.org/details/generellemorphol01haec.
(b) https://archive.org/details/generellemorphol02haec.
(c) http://caliban.mpipz.mpg.de/haeckel/natuerliche/natuerliche.html.
(d) https://archive.org/details/diekalkschwmme01haec.
(e) https://archive.org/details/diekalkschwmme02haec.
(f) https://archive.org/details/diekalkschwmme03haec.
(g) https://archive.org/details/anthropogenieod05haecgoog.
(h) https://archive.org/details/systematischephy01haec.
(i) https://archive.org/details/systematischephy02haec.
(j) https://archive.org/details/systematischephy03haec.
(k) http://caliban.mpipz.mpg.de/haeckel/weltraethsel/weltraethsel.html.

onies or corms (*Cormen oder Tierstöcke*) (Haeckel, 1866a, pp. 241–268).

Each of these six "orders" of individuals is considered on both "sides" of the "anatomy/morphogeny" division of Fig. 2 above. Thus in chapter 9, book III of the first volume of *GM* he discusses the "morphological individuality of organisms" from the point of view of their tectology by moving upward from cells (1st order) to colonies (6th order), and then again as "physiological individuals" in chapter 10 (Haeckel, 1866a, pp. 269–363). The terms of "relative individuality" help structure the discussion of *Grundformen* (promorphology) in book IV (Haeckel, 1866a, pp. 377–399, 528–539), while in chapter 18 of book V of the second volume he considers the "evolutionary history of morphological individuals" along the same six orders, in the context of book V's discussion of "General ontogeny," which included both embryology and metamorphology (Haeckel, 1866b, pp. 110–147). The concept of the individual would be further developed by Haeckel in volume II to include a three-fold concept of the genealogical individual, also crucial for his biogenetic law, but which will not be discussed here (Haeckel, 1866b, pp. 26–31, 421–422; Rinard, 1981; Rieppel, 2019).

THE BIOGENETIC "LAW" AND ITS ORIGINS IN THE *GM*

The key 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 (Olsson et al., 2010; Hoßfeld et al., 2017). 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, 1866a, 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 represent 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 *GM* as a 'thesis' of recapitulation connecting ontogeny and phylogeny, and which could only become more evident after a fuller discussion of ontogeny and phylogeny in volume II of *GM*.

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 already now further evolved 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, 1866b, 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, 1866b, 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 the explanation of the central concepts of inheritance and adaptation, each following their own empirically derived laws [*Gesetze*] (Haeckel, 1866b, 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 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 *GM*. 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) (Ulrich, 1967, p. 206).

The last five theses (40–44) concern "The causal nexus of biontic and phyletic evolution", and the 'law' is best expressed in his own words: "Ontogenesis...is indirectly conditioned [*bedingt*] through the phylogenesis... of the phylum to which it belongs" (40); it is "the brief and rapid recapitulation of phylogenesis, conditioned through the physiological functions of inheritance (reproduction) and adaptation (nutrition)" (41); and "the organic individual repeats [*wiederholt*] during the rapid and brief course of its development the most important of those alterations of form which its ancestors passed through during their long and slow paleontological evolution, according to the laws of inheritance and adaption" (42) (Haeckel, 1866b, p. 300).

The first three theses (40–42) were crucially modified by the last two (43, 44), which take into account complexities Haeckel recognized in the evolutionary evidence: the "complete and faithful recapitulation" is "effaced and shortened" [*verwischt und abgekürzt*] because "ontogenesis always chooses the straighter road" (43); and recapitulation itself becomes "counterfeited and changed through secondary adaptations" [*gefälscht und abgeändert durch secundäre Anpassung*] and thus the recapitulation "is, therefore, the more faithful, the more similar were the conditions of existence under which the Bion and its ancestors developed" (44) (Haeckel, 1866b, p. 300).

Haeckel explicitly in the *GM* distinguished his "theses" from "laws" (*Gesezte*), a term he was, as we've seen, happy to use in reference to empirical regularities observed in inheritance and adaptation (Haeckel, 1866b, pp. 180–225), and which he regarded as applicable *qua* laws to his later discussion of "phylogenetic evolution" discussed in chapter 26 of volume II. As with his extended discussion in volume I on "morphological theses" (Haeckel, 1866a, p. 364), so here "theses" for Haeckel was the appropriate term for a 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, 1866b, p. 295). Haeckel himself would carry that development further.

BIOGENETIC LAW AND GASTRAEA THEORY IN LATER TEXTS

The transformations of Haeckel's own terminology within his subsequent writings is one marked by both further attempts at making the key concepts such as the thesis of recapitulation both more epistemically secure and more understandable by a broader readership (Olsson and Hoßfeld, 2007; Hoßfeld and Olsson, 2008; Hoßfeld et al., 2011). 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 the theory of descent (Fig. 3; 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 [*biogenetischen Grundgesetzes*]. 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 was in the *GM* a "thesis" was now, Haeckel argued, given empirical foundation through this text (Reynolds and Hülsmann, 2008; Reynolds, 2019). In the same work, he cites himself (from the *GM*), clarifying his concepts and locating in a single, central expression the theses on recapitulation that he had developed in the *GM*. 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 'palaeontological 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 (Fig. 4; Haeckel, 1872b).

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 Entwickelungsgeschichte des Menschen*) and in his *Riddle of the Universe* (*Welträthsel*). As can be seen in Table 1 below, in these three books far fewer specialist terms appear, and in some cases (eg. "Bion" and "Onta") not at all. And conversely, 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; Joshi, 2018b). 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 sought to explicate 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 (Hopwood, 2015). 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" (Fig. 3; Haeckel, 1868, pp. 227–258). Notably, the pairs of embryo illustrations for dogs and humans, and chickens and turtles, respectively, were gradually developed in later editions (1868–1909) (Hopwood, 2015). And in the same work, the biogenetic "law" as developed in volume II of GM is restated, with reference to the key chapters in *GM* such as the "Evolutionary history of morphological individuals" and the "ontogenetic theses" (Haeckel, 1868, p. 253).

But the most comprehensive use of the biogenetic law can be found in Haeckel's writings on the *Gastraea*-theory. The Gastraea is a hypothetical *Urform* from which all metazoans have evolved, according to Haeckel. It has left no palaeontological 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). With his Gastraea-theory, Haeckel thought he had proved the monophyletic origin of all multicellular animals. Were the two primary germ layers homologous in all metazoans, as Haeckel postulated, then this would have been an evolutionary explanation of this early and important embryological process, the origin of germ layers (Haeckel, 1874a, 1875; Grell, 1979).

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 (4-page) 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 between the germ layers of all metazoans. In volume II of the *GM* Haeckel had already assumed the common ancestry of the whole animal kingdom (*Thierreich*) from a single phylogenetic form (Haeckel, 1866b, pp. 408–417). Moreover, Haeckel was emboldened by the fact that the phylogenetic theses of *GM* were later confirmed by the work of Alexander O. Kowalevsky (1840–1901) (Haeckel, 1872, p. 466). In successive editions, he clarified his views on embryos, for example, in the third edition of *Natural History of Creation* (Haeckel, 1872, Plate III, p. 499). In later editions he integrated drawings to visualize the Gastraea theory (Fig. 5). He also integrated images of germ layers of different organisms into his works (Fig. 6).

In later works he further developed his Gastraea theory, such as in his *Morphology of Infusoria* (*Zur Morphologie der Infusorien*) (Haeckel, 1883) and in his *Studies on the Gastraea Theory* (*Studien zur Gastraea-Theorie*) (Haeckel, 1873–1877) and in other shorter pieces such as his article in 1874 for the *Jena Journal of*

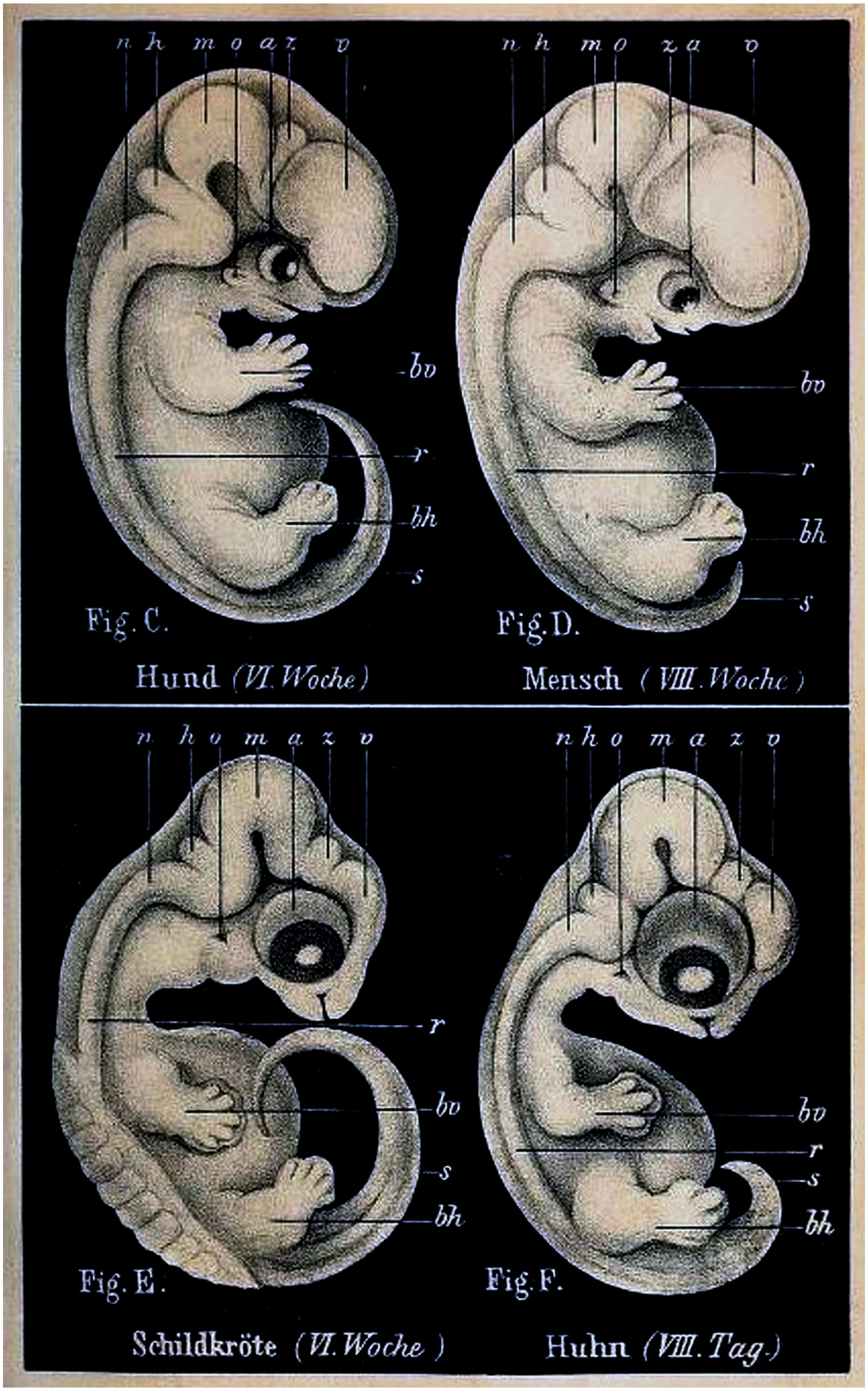


Fig. 3. Vertebrate embryos in *Natural History of Creation* (from: Haeckel, 1868, p. 240).

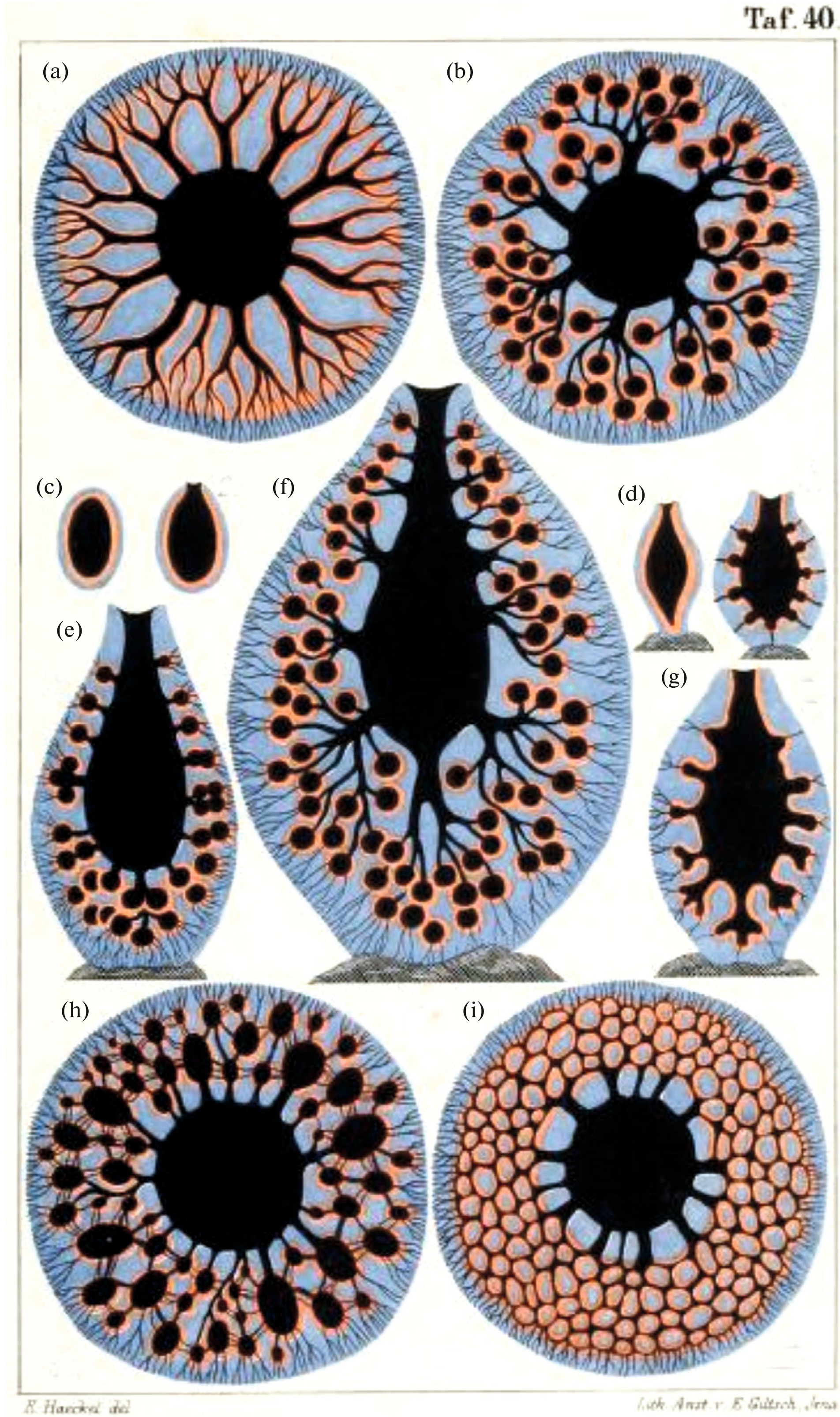


Fig. 4. Schematic presentation of water-current system in different sponges with the leuconoid body plan: (a, b, h, i) longitudinal sections along the sponge apical-basal axis; (c–g) cross sections through the sponge apical-basal axis at the different developmental stages (from Haeckel, 1872b, Plate 40, with modifications).

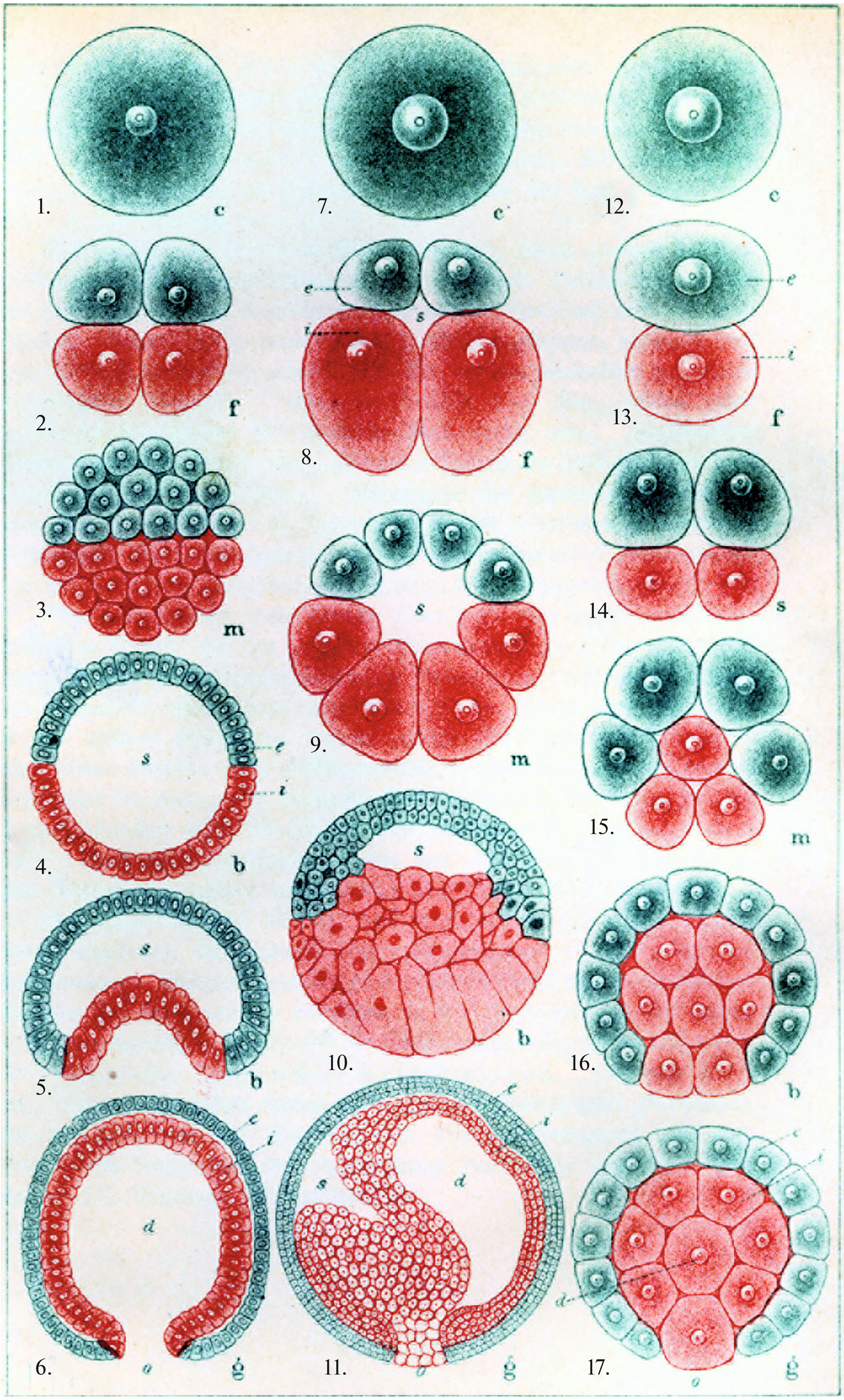


Fig. 5. Gastrula formation in worm (1–6), frog (7–11), and mammal (12–17) (from Haeckel, 1910, Plate 2).

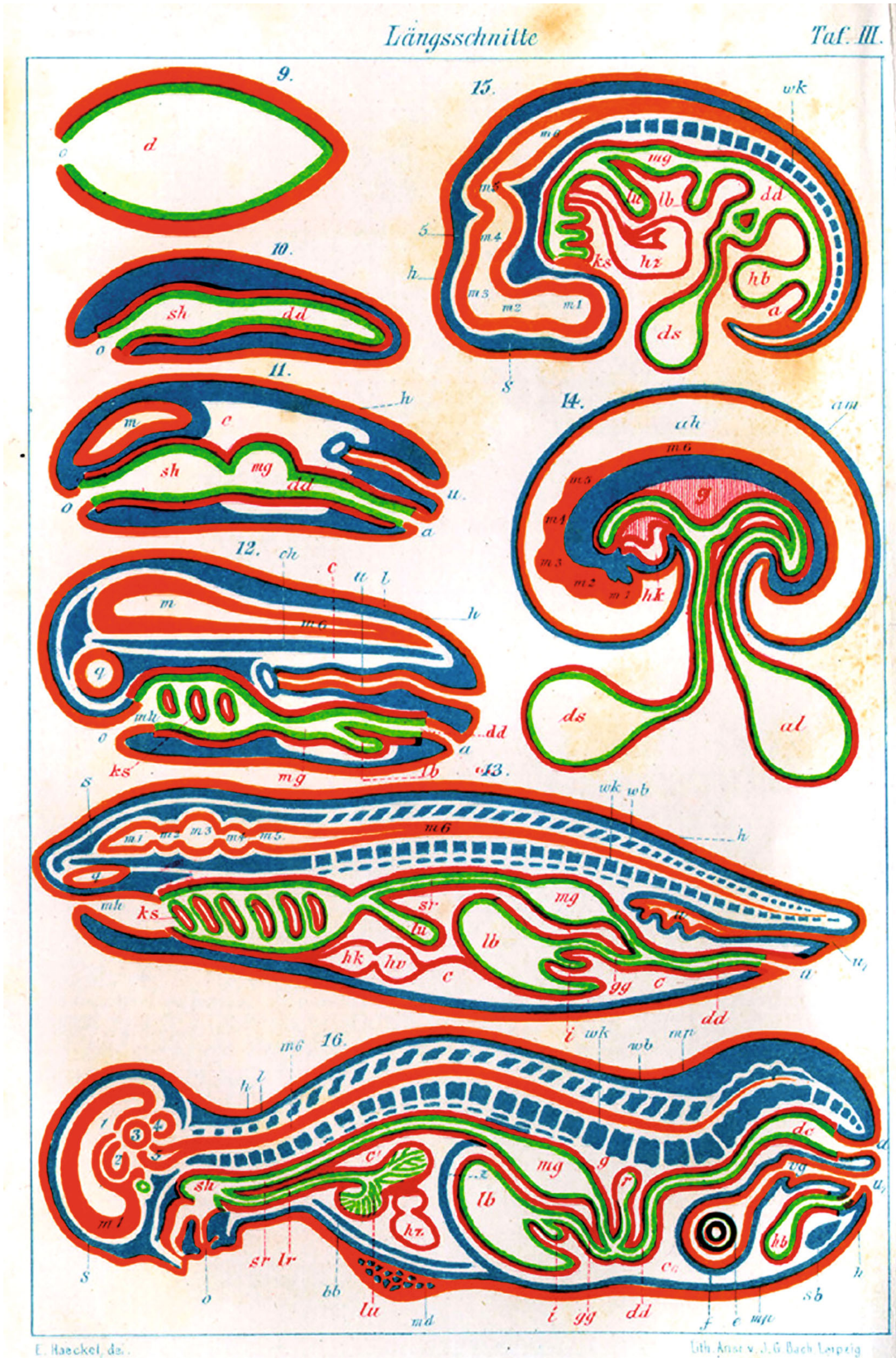


Fig. 6. Formation of germ layers in different organisms (from: Haeckel, 1874a, Plate 3).

Natural Sciences (*Jenaische Zeitschrift für Naturwissenschaft*) (Haeckel, 1874b). In the same year, he published his highly popular *Anthropogeny*, in which he employed the concept of the Gastraea theory, thus making it accessible to a far wider readership (Table 1).

In order to make this more clear, we have done the following. We used text mining methods to extract information from digital sources across a range of Haeckel's more scientific and more popular works. Our results are summarized in the Table 1. The table allows one to view three things at once. First, it provides a summary of which words corresponding to which concepts are found in which works; second it indicates the spread of popularized German expressions for terminology rooted in Greek in Latin originally in GM; and third, more generally, it allows one to perceive a kind of terminological evolution, indicating which terms persisted across his works and which went, so to speak, extinct (Table 1).

CONCLUSIONS

Haeckel embraced the necessity of defining and introducing into scientific and public discourse new terms and concepts. This was one of the main achievements of the initial efforts of his astonishing *GM*. In retrospect, Haeckel himself recognized the limitations of that first effort (Ulrich, 1967). He was conscious of their sheer number and complexity of terminological innovations, and he found ways to reduce the use of 'specialist' terms in his subsequent more popular works. The terminology of ontology and phylogeny, still current today, were central innovations in his *GM*. He soon began to utilize other synonyms and German terminology, especially in his more popular works. The elements of his most influential concepts, namely the biogenetic law and the Gastraea theory, can be found already in his early and most creative period, which saw the production within a single year of the massive two volumes of the *GM*. Neither it, nor the *Monograph on Sponges* were ever translated from the German and reached only limited audiences in the German-speaking world (Ulrich, 1967; Olsson et al., 2017). Undeterred by this, Haeckel applied and made more accessible his new concepts in his later works, using both linguistic and pictorial means. Even during his lifetime, Haeckel's astonishing capacity for mixing concept, language, and graphic presentation was commented on by students and admirers (Dodel, 1906; Porges et al., 2019). The biogenetic law and its application also in the Gastraea theory as causal nexus between ontogeny and phylogeny would play thus the role of *leitmotif* in what was also for Haeckel a didactic mission. That mission, inseparable from his scientific research, was central to his life's focus.

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