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ORIGINAL ARTICLE

Ernst Haeckel and the philosophy of sponges

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Abstract

Nearly 150 years ago, Ernst Haeckel published a three volume monograph on the calcareous sponges. These volumes contained the results of his extensive investigation of the anatomy, reproduction, and development of these marine invertebrate organisms. This paper discusses how Haeckel's contribution to spongiology was so distinct from that of earlier writers on the natural history of sponges, by focusing on his "philosophy of sponges." This included "an analytic" proof of Darwin's theory of descent, an argument for the monophyletic origin of the Metazoa from an ancient sponge-like embryo (the "gastraea theory"), and proof of the philosophy of monism that humans are no different than lowly sponges in their perfectly natural and material origins according to the laws of ontogeny in a universe devoid of supernatural beings or purpose. Haeckel was a philosopher using the methods of natural science. He was also a gifted artist—as his illustrations attest—and like most artists he disliked criticism of his creations, including his theoretical work. His observations and speculations regarding sponges (and certainly his more philosophical conclusions drawn therefrom) were and continue to be criticized, but as a review of the current literature shows, Haeckel's imprint on sponge biology is still very evident.

Keywords Sponges · Gastraea theory · Biogenetic law · Monistic philosophy

Introduction

In 1872, Ernst Haeckel published an extensive three volume monograph on calcareous sponges, a group of marine sponges whose internal skeleton consists of a network of needles (spiculae) composed of calcium carbonate. The first volume, *Biologie der Kalkschwämme*, was devoted to their anatomy, physiology, reproduction, development, and distribution; the second, *System der Kalkschwämme*, attempted a systematic classification or taxonomy of all known species of calcareous sponges; and the third, *Atlas der Kalkschwämme*, contained 60 plates of illustrations depicting exterior gross morphology, internal canal systems, and finer details of the various cell types, spiculae morphology, and their arrangement into a supporting skeleton, all drawn with great artistic talent by Haeckel himself. But perhaps most remarkable about this monograph is the fourth and final section of the first volume, strikingly titled "Philosophie der Kalkschwämme." A philosophy of *sponges*? What on earth could that mean? one wonders. That the phrase sounds odd to our modern ears is probably an anachronism, habituated as we are to associate philosophy with the high-minded contemplation of abstract and ethereal concepts like *beauty*, *truth*, and *justice*, when in fact it is still relatively recent since philosophy and science have grown quite separate as professional disciplines. (One need only to recall that in the nineteenth century science was still commonly known as "natural philosophy.")

Nevertheless, one could still be excused for thinking that a discussion of the "philosophy of sponges" is a bit unusual or out of place in a technical treatise intended for a rather narrow and specialized audience of professional zoologists. Indeed, it is my intention here to explain why Haeckel's discussion of the philosophy of sponges is remarkable, and

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To the natural philosopher there is no natural object unimportant or trifling. From the least of nature's works he may learn the greatest lessons. The fall of an apple to the ground may raise his thoughts to the laws which govern the revolutions of the planets in their orbits. John Herschel section 9 Preliminary Discourse on the Study of Natural Philosophy (1830).

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how it is emblematic of both the genius and the daring (some might say rashness) that made Haeckel simultaneously an inspirational and a controversial figure. It was in *Die Kalkschwämme* that Haeckel first introduced the Gastraea theory, his argument for the monophyletic origin of all multicellular animals or Metazoa–including humans—from a sack-shaped diploblastic ancestor similar to the gastrula stage found in embryos of representatives of all the major animal phyla, and it is here too that the idea that "ontogeny is a short and brief recapitulation of phylogeny" was branded by Haeckel the "fundamental biogenetic law" (*biogenetischen Grundgesetze*) (Olsson et al. 2017, 21). These were important elements in Haeckel's lifelong mission to do science with big philosophical implications, a mission that drove him to write about quite technical matters of embryology, anatomy, and evolution for a much broader audience beyond that of his professional scientific peers.

Haeckel's ability to look at a group of rather small and seemingly unremarkable sponges and see implications of great scientific and philosophical significance evokes the opening line of William Blake's poem *Auguries of Innocence*: "To see the world in a grain of sand." Like Blake's poem, with what Wikipedia describes as its paradoxical juxtaposition of innocence with evil and corruption,[1] Haeckel has become iconic of the fine line separating scientific and artistic genius from over-zealous romanticism. Robert J. Richards in his excellent study of Haeckel's life and work attributes Haeckel's negative reputation to his success as a science popularizer (Richards 2008, 213). Richards has done much to rehabilitate Haeckel's scientific reputation, yet even he concludes that "The sustained hostile reaction to Haeckel over the years has stemmed, I believe, from his passionately driven personality and the reckless abandon with which he pursued his Darwinian modernist convictions" (Richards 2008, 453). Haeckel's study of sponges reveals both his passion and energy for empirical research and his philosophical vision and imaginativeness. It also reveals perhaps a bit of the recklessness mentioned by Richards; for Haeckel's ability to spin an entire philosophy about the nature of humanity and the cosmos from the spongy material of lowly marine organisms is emblematic of his genius. Haeckel was essentially a *philosophical* zoologist or, that is to say, a philosopher using the methods of science to answer the big questions that spurred him to investigate and to write so feverishly. He refused to be bound by narrow professional disciplinary norms in his pursuit of answers to essentially philosophical questions about the nature of humankind and the universe in which we find ourselves. With analogy to his famed ability to see with one eye through the microscope and the other on the page on which he drew his specimen, Haeckel always had one eye focused on the big questions while the other observed a concrete reality before him.

Haeckel was also a talented artist—as both his professional and more popular biological illustrations plainly demonstrate—and like any artist he was protective of his creations, whether they were visual in nature or theoretical. This too, I believe, helps us to understand his complex attitudes toward observational fact and theoretical insight.

Earlier studies of sponges

Historically sponges have been a source of great perplexity for naturalists. Some regarded them as plants, on account of their sessile nature and in some case their plant-like shape. Aristotle noted that some observers claimed they exhibited an animal-like ability to contract in response to external stimuli.[2] Naturalists like Linnaeus, Lamarck, and Cuvier in the eighteenth and early nineteenth centuries grouped them with the corals, sea anemones, and medusae ("jellyfish") among the *Zoophyta*—those polyploid organisms whose natures were somehow midway between the two major kingdoms (Brusca and Brusca 2003, 180). Proper understanding of their animal nature is generally credited to the efforts of Robert Grant, who was a student of Lamarck and a mentor to the young Charles Darwin when he was a medical student in Edinburgh.[3]

Sponges are today generally regarded as multicellular animals, but of a distinct kind, because they lack true specialized tissues and possess no organs, no nervous system, no true musculature, no blood or circulatory system, nor any stomach or digestive system, relying on a unique aquiferous system for obtaining food and disposing of wastes. They are sessile filter feeders found in both fresh water and marine environments.[4] By means of the beating activity of internal flagella-bearing cells called choanocytes, water is drawn through the many small pores (ostia) dotting the outer dermal layer of the sponge into the internal channels and eventually expelled through larger openings called oscula. Digestion of small plankton and other organic particles occurs intracellularly in the choanocytes and other amoebocyte cells that line the canals and chambers internal to the sponge body. Digestion occurs therefore as it does in

[1] "Auguries of Innocence", Wikipedia [https://en.wikipedia.org/wiki/Auguries_of_Innocence] accessed July 18, 2018.

[2] Sponges are in fact able to respond to external stimuli in subtle but observable ways, for instance, by closing their pores upon being touched (Brusca and Brusca 194–196).

[3] See (Stott 2003) for an account of Darwin's initiation into marine invertebrate biology under the tutelage of Grant, the "sponge doctor."

[4] With the exception of members of the family Cladorhizidae, which trap and envelop their prey with tentacle-like structures (Brusca and Brusca 2003, 194–195).

the unicellular amoebae and other protozoans, but may be shared among neighboring cells of the sponge. The sponge body consists of two cell layers: an outer *pinacoderm* and an inner *choanoderm*, between which is a middle *mesohyl* composed of non-cellular collagen fibers, spicules, and a variety of motile cell types responsible for reproduction, digestion, and spicule formation. From a histological perspective, sponges appear similar to a colony of unicellular protozoa consisting of totipotent amoeboid and flagellated forms (Pechenik 1991, 63; Brusca and Brusca 2003, 182–183). Upon mechanical disaggregation, the individual cells of a sponge will crawl about and reaggregate to form smaller sponge bodies (Brusca and Brusca 2003, 191). They are thus said to exhibit a cellular grade of construction as opposed to the Metazoa that develop germ layers during embryogenesis from which specialized tissues and organs are created. It is for this reason that some biologists still classify them as Parazoa (as T. H. Huxley did in 1875), keeping them separate from the tissue-forming animals or Eumetazoa.

Sponges are generally divided into three (sometimes more) classes on the basis of the composition and morphology of the spicules and/or collagen fibers comprising the internal skeleton: Hexactinellida (glass sponges with skeletons composed of silicate spicules), Demospongiae (skeletons composed of soft spongin fibers, silicate needles, or both), and Calcarea with skeletons composed of calcite, a form of calcium carbonate (Brusca and Brusca 2003, 182). The Calcarea are typically small in size (less than 10 cm in height) and limited to shallow waters (less than 100 meters) in temperate regions (Brusca and Brusca 1990, 202–203).

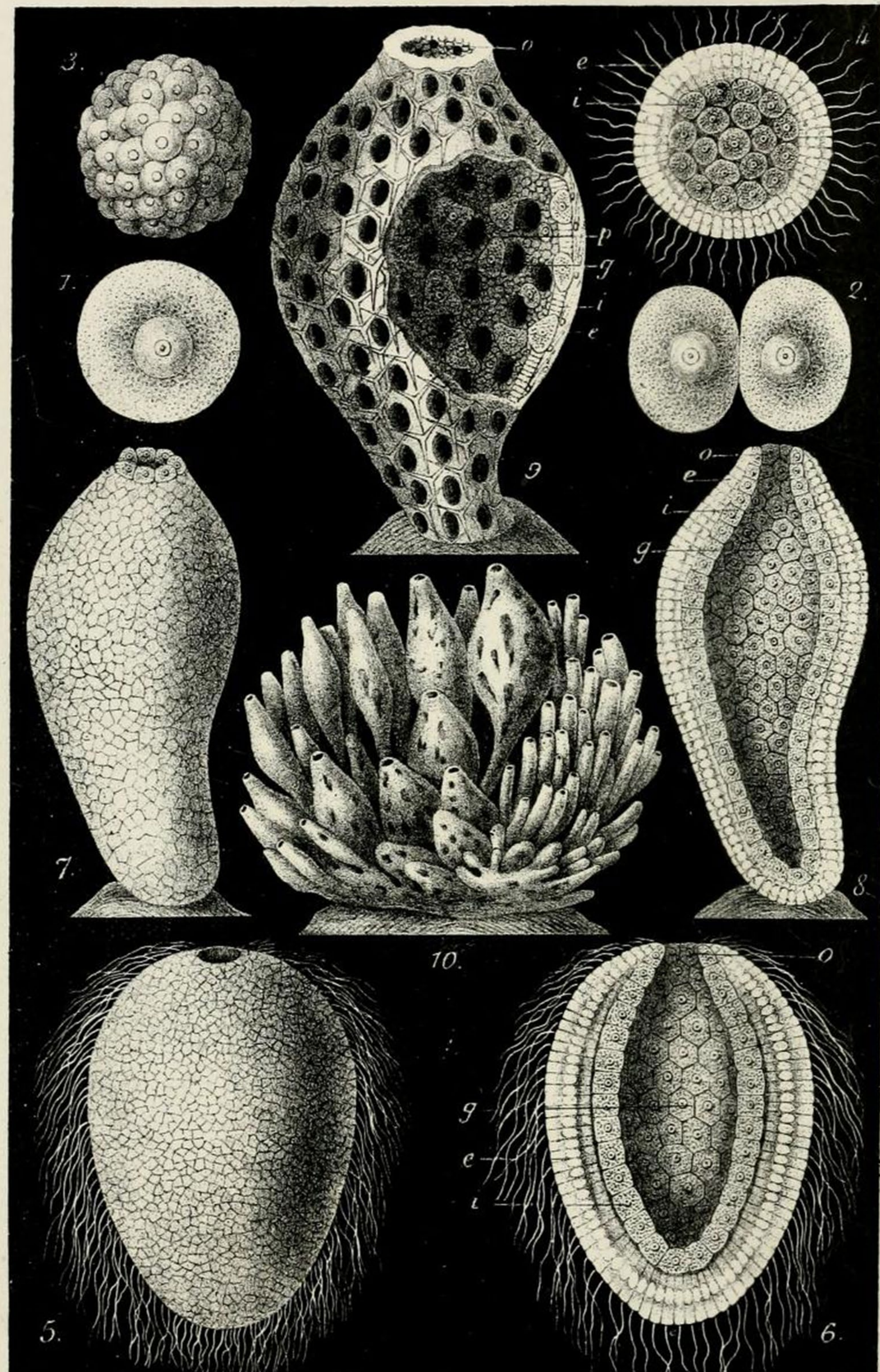
In his historical introduction to the study of the calcareous sponges, Haeckel (1872, I, 3–37) discusses the work of Robert Grant (1793–1874), George Johnston (1797–1855), J. S. Bowerbank (1797–1877), Nathaniel Lieberkühn (1822–1867), Oscar Schmidt (1823–1886), Albert von Kölliker (1817–1905), Henry James-Clark (1826–1873), Henry John Carter (1813–1895), and his own student Nicolaus Miklucho-Maclay (1846–1888). In a series of papers in the 1820s Grant provided solid evidence of the animal nature of sponges (Grant 1825, 1826a, b, c, d, 1827). Using newly improved microscopes, Grant discovered the small pores that dot the sponge body through which they draw water and with it food and oxygen. In reference to these small pores, Grant devised the name Porifera for the group as a whole. He also observed the ova cells and ciliated embryos (planulae) as they emerged through the larger excurrent pores (oscula) to swim about freely in the water. Grant divided the sponges with reference to the composition of the spiculae into three main classes: horny sponges, siliceous sponges, calcareous sponges.

Johnston and Bowerbank (1858, 1862a, b) are chiefly credited by Haeckel with describing the grosser anatomical features of various British sponges and the details of the spiculae of which their skeletons are composed. Lieberkühn described in the 1850s and 1860s the flagellated cells of the internal canals responsible for creating the inward current and the fertilization of the ovum cell by a sperm cell. Haeckel credits Schmidt for being the first to do proper comparative anatomical investigations of sponges and to apply the theory of descent to his investigations carried out in the in 1860s (Schmidt avoided the Calcarea in recognition of Haeckel's own concurrent research). Haeckel approves of Schmidt's identification of a sponge individual with a mass of material surrounding an osculum, so that a sponge exhibiting several oscula would count as a colony (or *corm* in Haeckel's terminology) of sponge individuals. Kölliker paid close attention to the cellular and histological nature of sponges and believed they belonged with the protozoa. Likewise, James-Clark (1867) believed sponges to be colonies of individual choanoflagellate protozoans, each of which possess a single long flagellum surrounded by a collar of protoplasm strongly reminiscent of the flagellated sponge choanocytes. Carter (1848) also considered the sponges to be protozoan colonies, although of rhizopods or amoebae, and therefore not directly related to the multicellular animals.

Miklucho-Maclay accompanied Haeckel in 1867 to the Canary Islands where he discovered a new species of Calcareous sponge that he named *Guancha blanca* (Miklucho-Maclay 1868). This was a colonial form of sponge remarkable for its polymorphosis, i.e., its variability of form spanning what appeared to be distinct species and even, according to Haeckel, distinct genera.[5] [see Fig. 1] Haeckel would rename this species *Ascetta blanca* under his own system of taxonomic nomenclature which he intended to be more logically coherent and precise than previous attempts. Miklucho-Maclay and Haeckel believed that in *G. blanca* water was both drawn in and expelled through the larger osculum, on account of which they referred to it as a "mouth opening" leading into a central "stomach" cavity, in analogy with the Coelenterata (e.g., corals, sea anemones, jellyfish).[6] As a matter of fact, Haeckel would claim this similarity of organization to be homologous and therefore of momentous

[5] Haeckel distinguished *polymorphosis* from *polymorphism* (the occurrence of differentiated and specialized forms of organs and persons within a single individual organism or colony of organisms, e.g., the siphonophorae, which arises through a division of labor among the parts). By *polymorphosis,* Haeckel referred to the great variability of morphology of outer form observed among individuals of one and the same species, or a polymorphism without any division of labor (Haeckel 1872, 480). This is more frequently today called phenotypic plasticity.

[6] Rudolf Leuckart in 1847 introduced the term *Coelenterata* to denote invertebrate animals with a single opening into the gastrovascular cavity functioning as both mouth and anus. Haeckel preferred the older term *Zoophyta* and for the purposes of this paper the two will be used interchangably.



Development of a Calcareous Sponge (Olynthus)

◂**Fig. 1** Development of a calcareous sponge (Olynthus). From Haeckel (1876) frontispiece. 1 egg cell, 2 egg cell after cleavage, 3 morula, 4 planula, 5–6 gastrula, 7–8 juvenile ascula (Olynthus), 9 adult Olynthus, 10 *Ascometra primordialis* a social corm consisting of several 'artificial' species (cp. *G. blanca* Miklucho-Maclay), the simplest flute-shaped forms on right; more complicated (anastomosed) forms in the middle. Figure 9 is adapted from Haeckel (1872), III, Tafel I, Fig. 1. Figure 10 originally appeared in Haeckel (1872), III, Tafel II as Fig. 17

phylogenetic significance. Other spongiologists, however, disputed this and today there is consensus that in all sponges, water is taken in exclusively through the smaller ostia and expelled through the osculum.[7]

Two senses of "philosophy"

In *Die Kalkschwämme* and other related writings of the same period Haeckel employs the term "philosophy" (*Philosophie* in German) in two distinct senses: i) with respect to the *methodology* to be followed in the empirical study of sponges and the logical interpretation of the results and ii) in reference to the *broader implications* of the results of the study for questions of a more general and theoretical scope, for instance, the nature of species generally, the reconstruction of the phylogenetic tree of genealogical relations among all the members of the animal kingdom, including the origins and nature of the human species itself, and the philosophical implications for understanding humanity's place in the universe.

Philosophy as methodology

In the first of his publications recounting his observations and experiments on the anatomy and physiology of the sponges, Robert Grant wrote,

> the philosophy of the sponge, the immutable foundations on which scientific discriminations of the species ought to rest, the minute investigation of the mechanism, the composition, and the uses of all the parts of this animal, and of the extraordinary phenomena it exhibits in the living state,—its mode of growth,—its kind of food,—its habits and diseases,—the means of cultivating an animal, which has so long rendered important services to mankind,—its mode of propagating the species, and extending them over the globe, and the great purposes which it is destined to fulfil in the universe, have remained where Aristotle left them. (Grant 1825, 99)

In a similar vein Haeckel discussed in the second chapter (the "methodological introduction") of the first volume (*Biologie der Kalkschwämme*) the method of *philosophical investigation*, in addition to the method of *empirical investigation* (with separate sections pertaining to the investigation of both the living and dead condition of specimens), and the method of *systematic classification*.

Haeckel begins his section on the "method of philosophical investigation" with a quote from his former professor and mentor, Johannes Müller (1801–1858).

> The most important truths in science are not found through dissection of philosophical concepts alone, nor through naked or raw experiences, but rather through an intellectual experience, which is essentially distinct from a chance one, and through it fundamental principles are found that lead to many more experiences. This is more than a simple experience, if one wishes, it may be called a philosophical experience.[8] (Haeckel 1872 1, 63)

Haeckel proclaims this recognition of the essential interaction between empirical observation (*Empirie*) and philosophy, between experience (*Erfahrung*) and perception (*Erkenntniss*), between observation (*Beobachtung*) and reflection (*Reflexion*), to be fundamental to all mature scientific investigation. This was intended to be a middle path between the excesses of the speculative *Naturphilosophie* of the eighteenth and early nineteenth centuries and the too restrictively empirical approach limited to simple description by which it had been replaced, (an approach typically described as Baconian inductivism in the English-speaking world). Haeckel railed against what he called the ruling empiricism of his time (*der herrschende Empirismus*), the tendency for researchers to publish mere catalogues of facts and observations without any theoretical or "philosophical" guidance nor any attempt to draw from them broader hypotheses or theoretical framework for further investigation. The mass of facts piled up by zoologists were, he believed, in need of some organization and interpretation in order to attain the proper status of science. This was not only the method of Müller in anatomy and physiology, but also of Karl Ernst von Baer (1792–1876) in embryology and of Darwin on the question of species and of biology more generally (Haeckel

[7] Ironically, *osculum* is Latin for "little mouth."

[8] Translations are my own unless otherwise noted. Haeckel speaks here of experience (*Erfahrung*) rather than observation (*Beobachtung*), but modern philosophical discussions of epistemology in English typically draw the distinction between *observation* and *theory* or *sensation* and *thought*. At first glance Haeckel seems to be making the Kantian claim that there is no perception without conception or that all observation is theory-laden; but in reality, he does not seem to be denying the possibility of pure observations (*blosses Erfahren*) but that science requires the conscious and therefore voluntary intellectual reflection upon pure observations.

1872, I, 65). Science, he insisted, involves the assimilation of empirical analysis and induction (i.e., careful, precise observation) with the intellectual activities of synthesis and deduction (careful reasoning and inference). To quote Goethe, as he often did, "Only the two together, like inhaling and exhaling, makes for the life of Science" (ibid., 66).

Haeckel was making it clear that his monograph on sponges was not going to be a dry descriptive catalogue of facts about the shapes and sizes of the specimens in his collection. He was not interested in doing traditional natural history but natural science or *wissenschaftliche Zoologie*, i.e., he intended to situate the empirical facts within a theoretical framework of causal laws that would provide a scientific explanation of those facts.[9]

Haeckel then went on to explain how this approach had led him to the subject of the fourth section—the "Philosophie der Kalkschwämme"—where he described a new approach to solving "the problem of the origin of species," one he referred to as an "analytical solution" in contrast to all earlier "synthetic" attempts, such as had been offered by Lamarck, Darwin, and Haeckel himself in his earlier *Generelle Morphologie* (1866) and *Natürliche Schöpfungsgeschichte* (1868).

The section on "The Philosophy of the Calcareous Sponges" consists of two separate chapters: chap. 7 "The place of the calcareous sponges in the animal kingdom", and chap. 8 "The calcareous sponges and the theory of descent." In these chapters Haeckel makes two chief theoretical claims of great import for the theory of evolution or "Descendenz-Theorie." One is that the calcareous sponges demonstrate the truth of the species transmutation thesis, that species change over time and as a consequence species that appear to be closely related are in fact related by a history of genealogical descent from some common ancestor. The other is that all the tissue-forming animals or Metazoa share a common descent from a sponge-like ancestor. The first, what Haeckel called his analytic solution to the species problem, is immediately specific to the Calcispongiae; the other, which involves his gastraea theory, has more general significance beyond the taxonomy of the Metazoa, for human origins and as a purported proof of his philosophy of monism.

Haeckel's "analytic" proof of Darwin's theory of species transmutation

Haeckel began the foreword of his sponge monograph by explaining that his objective was to provide an "analytic proof" of the common descent of all the species of an entire group of organisms (Haeckel 1872, I, xi). "One could describe this way of proof," he wrote, "as 'the analytic solution of the problems of the origin of species', in contrast to the synthetic solution, which Lamarck attempted in 1809 in his admirable *Philosophie Zoologique*, and then a half century later was carried out brilliantly by Darwin with his *On the Origin of Species*" (ibid.).

In an earlier letter to Darwin (dated Dec. 21, 1871) Haeckel wrote: "I have now attempted to treat the whole question not synthetically—as earlier—but rather analytically, and to prove through a single immensity of facts the common origin of a whole group of species."[10] By describing the approach as "analytic" Haeckel meant a concentrated empirical investigation of a specific group rather than the more abstractly theoretical and general discussion he had provided in his *Generelle Morphologie*, *Natürliche Schöpfungsgeschichte*, or Darwin had in the *Origin of Species*.[11]

The Calcareous sponge monograph would therefore provide a precise and concentrated empirical analysis of one particular group, supporting the inference that all the members of that group are descended from one original stem-form ancestor. This it seems was intended by Haeckel to provide a definitive response to Heinrich Bronn's criticism that Darwin had in the *Origin* only shown his theory of descent with modification to be a possibility, but had failed to demonstrate it as a positive fact (Richards 2008, 256).[12]

As Haeckel explained in a later edition of the *Natürliche Schöpfungsgeschichte*: "They [the critics and opponents to Darwin] demand…that the descent of species from common ancestral forms shall be proved in a particular case; that, in contradistinction to the *synthetic* proofs adduced for the Descent Theory, the *analytic* proof of the genealogical continuity of the several species shall be brought forward" (Haeckel 1876, xv). Later Haeckel wrote of the monograph on the *Kalkschwämme*:

> Here, I think, I have given an *analytic* solution of the problem of the origin of species, and so met the demand of certain opponents of evolution for an actual instance of descent from a stem-form. Those who are

[9] Nyhart (1995) and Gliboff (2008) discuss the emphasis on *wissenschaftliche Zoologie* in the German context of the 18th and 19th centuries, indicated in part by the move of instruction in zoology out of the medical faculties into the philosophical faculty and its gradual recognition as an autonomous *Wissenschaft* in its own right. Haeckel was himself appointed the first full professor of zoology, and in the philosophical faculty, at the University of Jena in 1865.

[10] Darwin Correspondence Project, "Letter no. 8114," accessed on 8 April 2018, http://www.darwinproject.ac.uk/DCP-LETT-8114.

[11] I draw out this point because 'analytic' means something quite different in the context of Kantian philosophy.

[12] Bronn (1800–1862) had made this criticism in the final chapter of his translation of *The Origin of Species*, see Bronn (1860).

> not satisfied with the *synthetic* proofs of the theory of evolution which are provided by comparative anatomy, embryology, paleontology, dysteleology, chorology [biogeography], and classification may try to refute the analytic proof given in my treatise on the sponge, the outcome of five years of assiduous study. I repeat: It is now impossible to oppose evolution on the ground that we have no convincing example of the descent of all the species of a group from a common ancestor. (Haeckel 1906, 34) (italics mine)

Haeckel's approach for providing this analytic proof included the inspection of the morphology of adult sponges and the ontogeny of embryonal and larval morphology.

Haeckel explained that he chose the calcareous sponges as the subject matter for this analytic approach to the species problem for the following four reasons: (1) The sponges possess a relatively simple organization compared to the other animal phyla (the worms, echinoderms, molluscs, and vertebrates all possess a body cavity and organ systems), and the calcareous of all the sponges include some of the very simplest forms; (2) the relationship between the morphological and physiological relations (form and function) is not so complicated that they are not adequately described; (3) they exhibit a remarkable variability of form (*polymorphosis*) that demonstrates how fluid and inconstant the notion of a species is among them; (4) they comprise a relatively small group in number of species and would therefore allow him—with assistance from the worldwide scientific community of sponge collectors—to investigate the entire group as a whole (Haeckel 1872, I, xii–xiii). The calcareous sponges would also turn out to have been a fortuitous choice because they provided the clearest and simplest example of development from what he insisted were two primary germ layers analogous and homologous to those in the other major animal phyla, and this made them ideal for tracing the stem history of the whole group of sponges and the Metazoa.

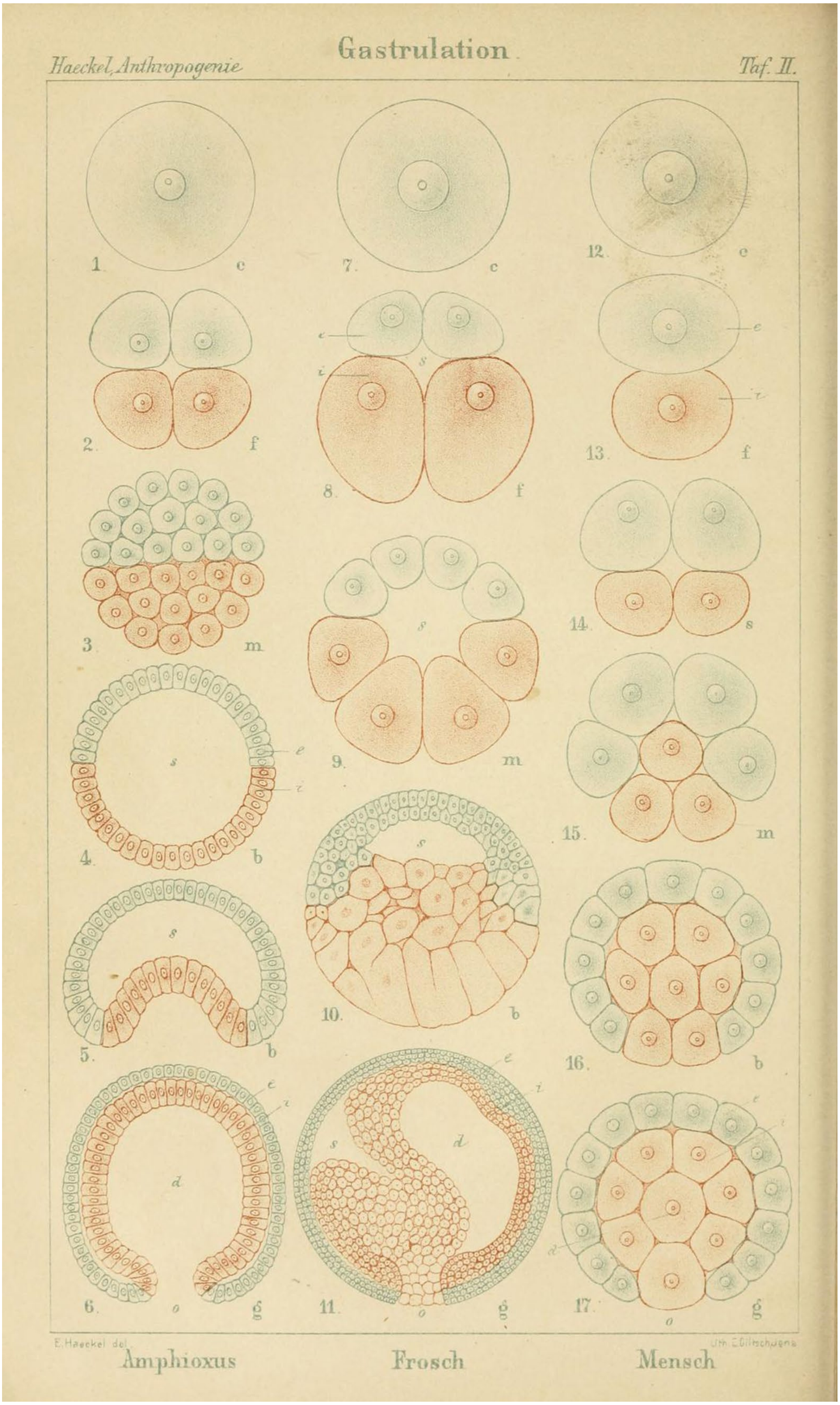
On account of the extreme variability of form in the sponges Haeckel announced that there are in the group no "bona species" or truly sharply delimited species as understood by traditional systematists (Haeckel 1872, I, xii, 354). The sponges he insisted were so highly plastic and adaptable to their local environments that it was impossible to draw rigid and clearly defined boundaries around various groups, one could at best devise a multitude of artificial systems premised upon different choices about which characters to use as species definitive, and even then the polymorphism (i.e., phenotypic plasticity) within those characters frustrated efforts to definitively place each and every specimen in one species box rather than another. One could identify 21 genera with 111 species, 39 genera with 289 species; 43 genera with 381 species; 113 genera and 590 species; or 3 genera and 21 species, or even 1 genus and 1 species according to how one wished to mark characters (ibid., 477). Because there were no "good species" within these sponges, there was no one uniquely correct taxonomy for them. This he argued could only be explained by the descendence theory, and therefore, the only natural system was a genealogical one that attempted to identify as best as possible the correct relations of descent among the apparent "bad" species.

Of special importance in this regard was Miklucho-Maclay's colonial or "social" sponge, *Guancha blanca* (renamed *Ascetta blanca* by Haeckel), because it seemed to reveal distinct species and even genera all growing together from one common root or point of attachment to the substrate.[13] It revealed he said species "in statu nascenti," in the process of being born (Haeckel 1872, I, 36). The simplest form of calcareous sponge Haeckel dubbed the *Olynthus*, a cylindrical tube with a single large osculum ("mouth") leading into a "stomach cavity" (ibid., 34) [see Fig. 1, fig. 9].

Haeckel identified three families of calcispongia based on main types of adult morphology: asconoid (a simple sack or tube shape with one major osculum, the *Olynthus* form), syconoid (body folded into distinct pouches each containing a chamber of choanocytes), and leuconoid (a more complicated subdivision of the interior into multiple choanocyte chambers connected by a system of internal canals). The occurrence of the ascon or Olynthus form in the juvenile stage of all three classes of calcareous sponge Haeckel interpreted as evidence that it is the original ancestral form from which all the others have evolved. Haeckel proposed a series of evolutionary forms, beginning with the Prosycum—a simple sack-shaped sponge consisting simply of a "stomach" and "mouth" lacking pores or spiculae, followed by the Olynthus—a simple sponge with mouth and stomach but whose body wall is perforated with small pores and with spiculae in the exoderm (Haeckel 1872, II, 216).

Previous to completion of the *Kalkschwämme* monograph, Haeckel published an article (Haeckel 1870a; English translation Haeckel 1870b) in which he discussed the evidence for a close genealogical relationship between the sponges and the corals (and other acalephs or zoophytes). Despite the obvious difference that sponges lack the tentacles and stinging cells (*cnidocysts*) characteristic of corals and other cnidaria, Haeckel pointed to the following evidence of their close relationship: (1) the morphological and physiological analogy between simple sponges like the flute-shaped *G. blanca* and the body of a coral, namely that both, according to Haeckel, possess a mouth leading into and out of a digestive cavity (this was why Miklucho-Maclay and

[13] Haeckel (1872, II, 38). *G. blanca* is now accepted as *Clathrina Gray*, 1867 according to the World Porifera database. http://www.marinespecies.org/porifera/porifera.php?p=taxdetails&id=192734#sources. Accessed Aug. 10 2018.



Haeckel, Anthropogenie
Gastrulation
Taf. II.
E. Haeckel del.
Amphioxus
Frosch
Mensch

◂**Fig. 2** Three distinct means of gastrulation in holoblastic eggs with total cell cleavage. Tafel II from Haeckel (1877b). 1–6 gastrulation by invagination in Amphioxus, resulting in an archigastrula (the original palingenetic form according to Haeckel). 7–11 gastrulation by involution in a frog resulting in a cenogenetic amphigastrula. 12–17 gastrulation by epiboly (or unequal cell growth) in a mammal (human) resulting in an amphigastrula

Haeckel's claim that the apical osculum of this particular sponge had both an incurrent and excurrent function was so significant); (2) sponges and corals are both composed of two layers (exoderm and endoderm) each a single cell thick, while the "higher" animal phyla all have a third middle cell layer or mesoderm; (3) a similarity of embryogenic events in both groups, in particular the events leading to the formation of what Haeckel called the gastrula stage.

The *gastrula* denoted a stage in the development of the free-swimming sponge larva, at which point the cleavage cells derived from a fertilized ova arrange themselves into a tiny egg-shaped body consisting of two cell layers (an outer ciliated layer and an inner non-ciliated) enclosing an internal cavity with an opening at one end. Haeckel initially believed the gastrula was created from the earlier morula stage when a central fluid-filled cavity eventually burst through at one end to create the mouth-osculum opening (Haeckel 1872, I, 336). Later he would identify invagination of the single-layered blastula at one end as the primary and original form of gastrulation. [see Fig. 2] The simplest sponges he suggested retained the basic gastrula form throughout their adult lives only adding the features of incurrent pores (ostia) and spicule formation. This was the *Olynthus* form. [see Fig. 1]

By claiming that the process of gastrulation in sponge larvae was homologous with similar events in the embryogenesis of the other animal phyla, Haeckel created a wide-sweeping argument for the monophyletic origin of all the metazoa. In accordance with the biogenetic principle ("ontogeny recapitulates phylogeny"), he would argue that the gastrula stage in animal embryogenesis was a conserved recapitulation of the earliest and most primitive multicellular animal, a stem-ancestor which he called the *gastraea* (Haeckel 1872, I, 345, 347, 466–467).

The Gastraea theory—an empirical-philosophical argument for the monophyletic origin of the Metazoa

Key to Haeckel's gastraea theory was the supposition that the internal cavity of the sponge gastrula was analogous (and homologous) in rudimentary form to the gastrovascular cavity of the coral polyp and other zoophytes. Indeed, Haeckel derived the term "gastrula" from the Greek *gastrin*, meaning belly or gut. Haeckel interpreted the creation of the gastrula cavity in the sponges to be a primordial stomach (*Urdarm* in German, *progaster* in Latin), and the opening created by the invagination hole to be the rudiment of a mouth (*Urmund*, *prostoma*), as it is in the coelenterates or zoophytes. This again explains the significance of the claim made by Miklucho-Maclay and Haeckel that the sponge *G. blanca* (in its simplest Olynthus form) used its apical osculum as both inhalant and exhalant cavity (as a mouth and anus) in homology with the corals, jellies, and freshwater hydra (zoophyta).[14]

Another important element in the gastraea theory was the assumption that the two cell layers in the sponge larva created by gastrulation were equivalent to the two primary germ layers known in other animal embryos to be responsible for the development of all the differentiated tissues and organs.[15] "[T]hese tissues," he wrote, "always arise from the two primary germ-lamellae only which have been transferred as an inheritance of the Gastraea of all the Metazoa, from the simplest sponge up to the man" (Haeckel 1874a, 150). Insisting on this homology was further evidence in Haeckel's mind for associating the sponges with the other two-layered or diploblastic animals.

Haeckel initially believed that in sponges the gastrula formed when a solid morula (or *planula* in the case of the free-swimming sponge larva) developed a fluid-filled internal cavity (the primordial gut) that eventually broke through at one end to form a primordial mouth that would eventually become an osculum in the adult sponge. Later he would insist gastrulation via invagination of the blastula at one end is the original and most significant form (Haeckel 1875, 159). Pressed in part by divergent observations made by others on sponges and other animals (e.g., Metschnikoff 1875; Schmidt 1876; Schulze 1875), Haeckel (Haeckel 1877a, 78ff) came to recognize four distinct forms of gastrula resulting from distinct processes of gastrulation: the archigastrula, amphigastrula, discogastrula, and perigastrula. Yet still he insisted the first (the archigastrula formed by invagination) to be the original Ur-form, while the others represented *cenogenetic* "falsifications" or alterations of the original and simplest *palingenetic* form that resulted from adaptations in the larval or embryonal stage. [See Fig. 2]

The basis for claiming any one gastrula form and process of gastrulation to be the original from which the others

[14] Grant (1825a) had similarly spoken of the osculum as a 'fecal pore' and a 'mouth,' without however claiming that the water current ever entered through the osculum.

[15] The other animal phyla are all triploblastic, having a middle germ layer (mesoderm) derived from either or both the endoderm and exoderm. Haeckel was building here on the earlier work of T. H. Huxley, Fritz Mueller, Nicolai Kleinenberg, and Alexander Kowalevsky who had identified the presence of the germ layers (first described in vertebrates) in jellyfish, crustaceans, hydra and, the amphioxus, respectively. See Hall (1998).

had evolved, however, was highly subjective and subject to much criticism (Nyhart 1995, 191-193). Still, the gastraea theory represented the sort of intellectual work that Haeckel believed necessary to move research beyond natural history to a properly scientific (*wissenschaftliche*) zoology. As he would later explain:

> I must lay claim to that liberty of natural philosophical speculation (or in other words, intelligent comparison of empirical results), without which, in my opinion, general biology cannot advance a step forwards. I have fully explained my ideas of the right of necessarily combining the empirical and philosophical methods in my "critical and systematic introduction to the general morphology of organisms," as well as in my systematic introduction to the monograph of calcareous sponges. (Haeckel 1874b, 153)

In the *Generelle Morphologie,* he had proclaimed that "All natural science is philosophy, and all true philosophy is natural science. All true science is natural philosophy" (Haeckel 1866, II, 447).[16] In the first instance, Haeckel meant by philosophy the search for general causal laws—and mechanical laws most importantly, those appealing solely to the properties of material bodies and processes. This was the very basis for his philosophy of monism (about which more below). Philosophy for Haeckel also meant the employment of theoretical speculation and of hypotheses to interpret empirical facts. His gastraea theory involved several other key theories and hypotheses, for instance: the theory of the germ layers, the biogenetic law and the theory of recapitulation, and of course Darwin's theory of descent or evolution by means of natural selection. But Haeckel was not content to stop there. His monism was a direct challenge to the traditional philosophy of dualism, which was premised on the belief that aside from material bodies and material processes (to which the natural sciences must be restricted), there also exist immaterial minds, souls, a Deity (and his miraculous acts), which could only be comprehended through religious practice and its system of superstitious beliefs.

The philosophy of sponges: philosophy as interpretation of the science's broader implications (proof of the philosophy of monism)

If "philosophy" is taken literally, as "the love of wisdom", or more specifically as contemplation of the questions "What is man?," "Why are we here,?" "What is the meaning of life?," then one might naturally wonder what one can learn about these profound and deeply cosmic questions from reflection on a simple sponge–"This humble and apparently insignificant being," as Robert Grant described it (Grant 1825, 97). Most people's familiarity with sponges extends little further than what was once a common household item—a bath sponge—and what could such a mundane and lowly object possibly teach us about the question of "Man's place in Nature"?[17] A scientific route to answering this question became possible after Darwin provided his solution to what the astronomer John Herschel had called "that mystery of mysteries, the replacement of extinct species by others." Darwin's suggestion that new species gradually arise from existing ones by means of a natural selection of favorable subspecies variants as they adapt to changes in local environments removed the need to appeal to acts of special creation on the part of a supernatural being. *On the Origin of Species* (1859) presented a serious challenge to the traditional Biblical account of "man's creation," even though Darwin himself would not directly address the implications for humans until 1871 with his *The Descent of Man, and Selection in Relation to Sex*. But in the opinion of many of his critics, such as the somewhat sympathetic German paleontologist Heinrich G. Bronn, while Darwin had made the case for saying that it was a *possibility* that species could change over time and diversify into a branching tree of related types, he had not positively shown that they had *in fact* done so. Haeckel, we noted earlier, chose the calcareous sponges specifically for this purpose. But additionally, by revealing that humans, like all other animals, developed by purely natural (i.e., mechanical) means from primitive cells (the male and female gametes), in recapitulation of the events that produced our ancient *Gastraea* ancestor, Haeckel also sought to prove the purely natural origin of the human species without intervention from any supernatural deity. In his words: "But as the body of the Calcispongiae in the developmental stage of the *Gastrula* already consist of the same two germ-lamellae which compose the body of man and all the higher animals at an early period of embryonic development, we must consistently assume the same mechanical development for man also" (Haeckel 1873, 430). Haeckel would make an extensive case for the wholly natural origin of humankind in his popular *Anthropogenie* (Haeckel 1874c).

So it was, as Mario di Gregorio noted, that the "calcareous sponges…became a real piece of cosmic philosophy, in which these apparently insignificant creatures acquired

[16] It is not at all clear that this syllogism is valid (assuming Haeckel intended the third line to be a conclusion drawn from the first two), but it would seem to follow from this set of statements that 'All philosophy is science'!.

[17] "Die Frage aller Fragen fuer die Menschheit, die Frage von der Stellung des Menschen in der Natur" (Haeckel 1872, I, 67). Bath sponges are in fact the dead remains of a demosponge, whose skeletons consist of a fibrous and "spongy" network of collagen proteins, quite unlike that of the sharp flinty spicules of calcareous or siliceous sponges.

universal meaning" (Di Gregorio, 203).[18] Haeckel himself summarized the significance of his study of the calcareous sponges thus: "The most general results furnished by the present monograph of the Calcispongiae are of a purely philosophical nature, and may be summed up in the statement that *the biogeny of the Calcispongiae is a coherent proof of the truth of monism"* (Haeckel 1873, 430).[19]

Reaction to Haeckel's sponge work

Haeckel believed that sponges like *Ascetta blanca* and *Ascometra primordialis* form colonies including forms characteristic of distinct species and even distinct genera of sponge. This led him to the conclusion that "*The entire natural history of the sponges is a coherent and striking argument 'For Darwin'*" (Haeckel 1870b, 118), and that "*In these extremely remarkable and important sponges the organic species is to be observed as it were 'in statu nascenti'*" (ibid., 119). Sponges are in fact notoriously variable and difficult to classify (Brusca and Brusca 2003, 180), but it is the opinion of modern spongiologists that the specimens of *G. blanca* and *A. primordialis* that so impressed Haeckel were in fact mixed colonies of separate species grown one on the other (Borojevic et al. 2002; Rapp 2006).

Haeckel's observations and interpretations of sponge development were also strongly contested by his contemporaries. William Saville Kent's remarks were not unusual, except perhaps in the effort to be charitable, when he wrote that,

> not only has it been shown that errors do exist [in Haeckel's observations and depictions of the sponge's so-called gastrula], but that these are of such a radical and fundamental nature that the inference is most reluctantly arrived at that Haeckel, carried away in his ardent pursuit of the Metazoic archetype, has lost for the time his power of discrimination between matters of fact and hypothesis, and so evolved from his own inner consciousness those details that are wanting to complete and perfect his theory. (Kent, 1880-81, I 158)

Kent disputed that the ciliated larva of the sponges ever possesses two distinct cell layers comparable to the exoderm and endoderm of other animal planulae or embryos, that there is a distinct gastric cavity or oral-apical opening, and thirdly, he claimed Haeckel had reversed the true anterior and posterior poles of the larvae as they are found in nature so as to conform to his theory that the opening into the gastrula–larva became the mouth–osculum of the adult sponge. "Taken altogether," Kent concluded, "it is clearly evident that the so-called sponge-gastrulae, described and figured over and over again in Haeckel's 'Monograph,' are an entire myth, and that the superstructure of the gastraea theory, so far as it rests upon this basis, is entirely worthless" (Kent 1880–1881, I, 158). Metschnikoff (1875) doled out similar (and even more strident) criticism.

But not all reviewers were so unkind. The British geologist and spongiologist William Johnson Sollas (1849–1936) wrote in the *Encyclopedia Britannica* (9th edition) article on sponges that,

> However erroneous in detail, Haeckel's views are confirmed in their broad outlines, and it was with true insight that he pronounced the *Calcarea* to offer one of the most luminous expositions of the evolutional theory. In this single group the development in general of the canal system of the sponges is revealed from its starting point in the simple Ascon to its almost completed stage in the Leucon, with a completeness that leaves little further to be hoped for, unless it be the requisite physiological explanation. (Sollas 1878, 422).

It is also worth mentioning that Haeckel's work on sponges was valued highly enough by the coordinators of the massive scientific project on marine organisms resulting from the Challenger Expedition (1872–1876) that he was one of six naturalists asked to write a report on one of the major sponge groups, Haeckel being assigned the deep-sea keratosa (Haeckel 1889). Haeckel also wrote the reports on the deep-sea medusae (1882), radiolaria (1887), and siphonophorae (1888). It is hard to imagine that he would have been asked to make such significant contributions to the project if there were serious doubts about the quality of his research.

With respect to his interpretation of the events of embryo development, critics have, however, suggested the two primary germ layers may be an adaptation leading to greater physiological efficiency and that the distinct modes of gastrulation are instances of convergent evolution, not modifications of one original hereditary form, thereby weakening Haeckel's case for a monophyletic origin of the Metazoa on the basis of the occurrence of the gastrula stage in representatives of all the major animal phyla (Ereskovsky and Dondua 2006). Some dispute that gastrulation, if properly understood to mean the formation of the two primary germ

[18] Gliboff (2008, 181) also discusses the broader significance of the empirical study of the calcareous sponges for what he called Haeckel's "sponge philosophy", i.e. his mechanistic monism.

[19] This line is from an English translation of an excerpt of *Die Kalkschwämme*. In the original Haeckel wrote "The biogeny of the calcareous sponges is a coherent proof for the truth of Monism" (Haeckel 1872 I, 483). The final line of the first volume (*Biologie der Kalkschwämme*) says, in reference to the development of the calcareous sponges, that "This explains most clearly the high significance of the calcispongiae for the monistic philosophy" (Haeckel 1872, 484).

layers from which the other specialized animal tissues and organs eventually develop, occurs in the sponges at all. The morphogenetic movements of cells in sponge larvae they claim do not result in the formation of true germ layers, and sponges do not develop a true gut or differentiated and specialized digestive organ. Sponges, according to this interpretation, have inherited the capacity for these cell movements from earlier unicellular ancestors and true gastrulation in the metazoa has not been inherited from any sponge ancestor.[20]

It has, however, recently been argued "that the present interpretation of early metazoan evolution implies that all eumetazoans, including man, are descendants of derived sponge larva or, more specifically, a larva of a homoscleromorph-like ancestor" (Nielsen 2008, 254).[21] And similarly, the evolutionary developmental biologist Brian Hall has written, "Whether Haeckel's Gastraea theory was right or wrong, it represented a brilliant synthesis of recapitulation, Darwin's theory of evolution, comparative morphology, homology of structures, comparative embryology (which had revealed the common embryological plan shared by many animals) and subsequently in the discovery that these organisms were all constructed on the basis of similar (equivalent) germ layers…" (Hall 1992, 61).[22]

As for Haeckel's attempt to establish a natural phylogeny of the Calcispongiae, one modern reviewer concludes that it is "particularly demonstrative of an ideal conception of the classification reflecting a biological thinking dominated by the pre-eminence of universal laws and logic" (Manuel 2006, 231).[23] Haeckel attempted to devise an entirely logical system for naming the sponges that would reflect key characteristics, e.g., the prefixes 'Asc-', 'Syc-', and 'Leuc-' referred to the asconoid, syconoid, and leuconoid organization, and similarly suffixes, such as '-etta', '-illa', '-yssa' indicated combinations of the three spicule morphologies (diactine, triactine, tetractine). While this was intended to bring clarity and precision to the task of classification it has been largely abandoned for a number of reasons (Manuel et al. 2002, 1107-1108). "Although coherent and aesthetic, Haeckel's 'natural system' of the calcareous sponges was soon regarded as unsatisfactory and artificial by other specialists because it split into remote genera many species whose body and skeleton architecture were very similar" (Manuel 2006, 231). Klautau et al. (2013), on the other hand, report that their molecular analysis largely vindicates Haeckel's phylogeny of the Calcarea.[24]

In summary, despite there being some difference of opinion about his ideas (which is not at all surprising or uncommon for science nearly a century and a half old), Haeckel's imprint is still clearly visible on modern sponge biology, as evidenced by the continued use of his classification of the aquiferous system into the asconoid, syconoid, and leuconoid varieties, continued discussion of his interpretation of sponge embryology, and the number of species named either by him or eponymously for him.[25]

Conclusions

Haeckel's efforts to forge a research program around his gastraea theory illustrate that a clearly articulated statement of a hypothesis can be quite valuable for the progress of scientific investigation, especially in times when a glut of empirical data exists, needing interpretation and guidance with the prioritizing of which experiments to tackle next. Nyhart (1995, 183) writes that "The basic elements of the theory had the kind of simplicity Haeckel found appealing" and as Di Gregorio (2005, 208) observed Haeckel adopted the unhealthy practice of looking for evidence that confirmed his theories and dismissing evidence that refuted them. "All this embodied the whole spirit of Haeckel's search for perfection, featuring as it did empirical research and theoretical biology finally united through the humble calcareous sponges" (ibid., 212).

Haeckel was never interested in merely doing descriptive empirical science; but neither was he content to be a theoretical biologist alone. Haeckel was also—and perhaps primarily—concerned to sketch out his monistic philosophy. Bob Richards (2008, 454) has suggested that the tragedy of Haeckel's legacy is the result of his having contained two souls: "a deeply feeling spirit and the aggressively rational mind." But I would like to propose a slight variation on this

[20] Ereskovsky and Dondua (2006), Ereskovsky (2007) and Nakanishi et al. (2014). Leys and Eerkes-Medrano (2005) offer a contrary opinion partially vindicating Haeckel's account of sponge development. Comparative analysis of a draft sequencing of the genome of the demosponge *Amphimedon queenslandica* suggests that sponges evolved from an earlier animal ancestor of much greater genetic complexity than previously suspected (Srivastava et al (2010)). See Breidbach (2006) for a historical and critical review of Haeckel's gastraea theory in light of modern scientific evidence.

[21] Nielsen proposes that the first step toward eumetazoans occurred when the larval stage of a sponge ancestor achieved sexual maturity in a process called dissogony, thereby abandoning the sessile lifestyle of the adult sponge form (Nielsen 2008), 248–249.

[22] For more historical and scientific analysis of the gastraea theory and the theory of recapitulation see Hoßfeld and Olsson (2003), Laubichler and Maienschein (2007) and Levit et al. (2015).

[23] See Rieppel (2016) for an extensive evaluation of Haeckel's approach to taxonomy as well as the broader philosophical issues (e.g., his monism) treated in this paper.

[24] Haeckel failed, however, to recognize the widely accepted division of the Calcarea into the subclasses Calcinea and Calcoronea, as suggested by Minchin (1896).

[25] Klautau et al (2013) introduce the new genus of sponge in the order Clathrinida, named *Ernstia*. For explanation see Collins (2013).

thesis: that the two souls struggling within Haeckel's breast were scientific and artistic. As a theoretical biologist Haeckel was guided by a creative vision that he sought to make tangible or real (e.g., the reconstruction of the phylogenetic tree of life on the basis of the fundamental biogenetic law and the gastraea theory), and just like the striking illustrations he created for which he is both famous and infamous, he sought not to capture the exact details of the material specimens before him but the more abstract and general truth or idea to which they pointed.[26] But whereas it is acceptable for the artist to shield his creation from criticism until it is completed and to wish for it eternal appreciation, this is not acceptable for a scientist; and it was that struggle within Haeckel's persona that invoked the most severe criticism of his scientific work from his peers. And yet even now, one hundred years after his passing, it remains difficult to ignore his many contributions to science and culture.

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References

Borojevic R, Bory-Esnault N, Manuel M, Vacelet J (2002) Order Clathrinida, Hartman 1958. In: Hooper JNA, Van Soest RWM (eds) Systema porifera: a guide to the classification of sponges. Kluwer Academic, New York, pp 1141–1152

Bowerbank JS (1858) On the anatomy and physiology of the Spongiadae. Part 1. Philos Trans R Soc Lond 148:279–332

Bowerbank JS (1862a) On the anatomy and physiology of the Spongiadae. Part 2. Philos Trans R Soc Lond. 152:747–836

Bowerbank JS (1862b) On the anatomy and physiology of the Spongiadae. Part 1. Philos Trans R Soc Lond. 152:1087–1135

Breidbach O (2006) The conceptual framework of evolutionary morphology in the studies of Ernst Haeckel and Fritz Müller. Theory Biosci 124:265–280

Bronn HG (1860) Schlusswort des Übersetzers. In Darwin C (ed) Über die Enstehung der Arten im Their-und-Pflanzen-Reich durch natürliche Züchtung; oder, Erhaltung der vervollkollmenten rassen im Kampfe um's Daseyn, 2nd. edn. Trans. H.G. Bronn. Schweizerbart'sche, Stuttgart, pp 525–551

Brusca RC, Brusca GJ (1990) Invertebrates. Sinauer, Sunderland

Brusca RC, Brusca GJ (2003) Invertebrates, 2nd edn. Sinauer, Sunderland

Carter HJ (1848) Notes on the species, structure, and animality of the freshwater sponges in the tanks of Bombay. Ann Mag Nat Hist 1(4):303–311 **[Originally published in 1847 in Trans. Bomb. Med. and Phys. Soc.]**

Collins A (2013) Once again going back to Haeckel, with Calcarean sponges. Web post on the Smithonian National Museum of Natural History, Department of Invertebrate Zoology News—No Bones web site. http://nmnh.typepad.com/no_bones/2013/05/once-again-going-back-to-haeckel-with-calcarean-sponges.html. Accessed 17 Aug 2018

Darwin C (1859) On the origin of species. Charles Murray, London

Di Gregorio MA (2005) From here to eternity: Ernst Haeckel and scientific faith. Vandenhoeck & Ruprecht, Göttingen

Ereskovsky AV (2007) Sponge embryology: the past, the present and the future. In Lobo-Hajdu G, Custódio MR, Hajdu E, Muricy G (eds). Porifera research: biodiversity, innovation and sustainability. Museu Nacional 28, Rio de Janerio, pp 41–52

Ereskovsky AV, Dondua AK (2006) The problem of the germ layers in sponges (Porifera) and some issues concerning early metazoan evolution. Zool Anz 245:65–76

Gliboff S (2008) H.G. Bronn, Ernst Haeckel, and the origins of German Darwinism. MIT Press, Cambridge

Grant RE (1825) Observations and experiments on the structure and functions of the sponge. Edinb Philos J 13:94–107, 333–346

Grant RE (1826a) Observations and experiments on the structure and functions of the sponge. Edinb Philos J 14:113–24, 336–341

Grant RE (1826b) Observations on the structure of some siliceous sponges. Edinb Philos J 1:341–351

Grant RE (1826c) On the structure and nature of the Spongilla friabilis. Edinb Philos J 14:270–284

Grant RE (1826d) Remarks on the structure of some calcareous sponges. Edinb Philos J 1:166–170

Grant RE (1827) Observations and experiments on the structure and functions of the sponge. Edinb Philos J 2:121–141

Haeckel E (1866) Generelle Morphologie, vol 2. Georg Reimer, Berlin

Haeckel E (1870a) Ueber der Organismus der Schwämme und ihre Verwandschaft mit den Korallen. Jenaische Zeitschrift für Naturwissenschaft und Medicin V: 207–235

Haeckel E (1870b) On the organization of sponges, and their relationship to the corals. Translated by WS Dallas. Ann Mag Nat Hist Soc 5(25):1–13, 107–120

Haeckel E (1872) Die Kalkschwämme. Eine Monographie, vol 3. Georg Reimer, Berlin

Haeckel E (1873) On the Calcispongiae, their position in the animal kingdom, and their relation to the theory of descendance. Translated by W.S. Dallas. Ann Mag Nat Hist Zool Bot Geol 4(64):241–262, 421–430

Haeckel E (1874a) Die Gastraea-Theorie, die phylogenetische Classification des Thierreichs und die Homologie der Keimblaetter. Jen Zeitschr f Naturwiss 8:1–55

Haeckel E (1874b) The Gastraea-Theory, the phylogenetic classification of the animal kingdom and the homology of the germ-lamellae. Translated by E Percival Wright. Quart J Micro Sci 14:142–165, 223–247

Haeckel E (1874c) Anthropogenie oder Entwickelungsgeschichte des Menschen. Wilhelm Engelmann, Leipzig

Haeckel E (1875) Die Gastrula und die Eifurchung der Thiere. Jenaische Z für Naturwissenschaft 9:402–508 **[Reprinted in Haeckel 1877a]**

Haeckel E (1876) The history of creation, or the development of the earth and its inhabitants by the action of natural causes. A popular exposition of the doctrine of evolution in general, and of that of Darwin, Goethe, and Lamarck in particular, vol 2. Translation revised by E. Ray Lankester. Henry S. King and Co., London

Haeckel E (1877a) Biologische studien: Studien zur Gastraea-theorie. Hermann Dufft, Jena

Haeckel E (1877b) Anthropogenie oder Entwickelungsgeschichte des Menschen. Dritte umgearbeitete auflage. Wilhelm Engelmann, Leipzig

Haeckel E (1889) Report on the deep-sea keratosa collected by H.M.S. Challenger during the years 1873–1876. Prepared under the supervision of the late Sir C. Wyville Thomson. Edinburgh, Her Majesty's Stationery Office

[26] Others have made this point, e.g., Junker and Hoßfeld (2001), 124; Richards (2008), 303–312, 331–341; and Hopwood (2015).

Haeckel E (1906) The evolution of man: a popular scientific study. Translated from the fifth (enlarged edition [of Die Anthropogenie] by J McCabe). Peter Eckler, New York

Hall BK (1992) Evolutionary developmental biology. Chapman & Hall, New York

Hall BK (1998) Germ layers and the germ-layer theory revisited: primary and secondary germ layers, neural crest as a fourth germ layer, homology, and demise of the germ-layer theory. Evol Biol 30:121–186

Hopwood N (2015) Haeckel's embryos: images, evolution, and fraud. University of Chicago Press, Chicago and London

Hoßfeld U, Olsson L (2003) The road from Haeckel. The Jena tradition in evolutionary morphology and the origin of "Evo-Devo". Biol Philos 18(2):285–307

James-Clark H (1867) On the spongiae ciliatae as infusoria flagellate; or observations on the structure, animality and relationship of *Leucoselenia botryoides*. Bowerbank. Mem Boston Soc Nat Hist 1:305–340

Junker T, Hoßfeld U (2001) Die Entdecking der evolution: Eine revolutionäre Theorie und ihre Geschichte. Wissenschaftliche Buchgesellschaft, Darmstadt

Kent WS (1880–1881) A Manual of the Infusoria, vol 3. David Bogue, London

Klautau M, Azevedo F, Cóndor-Luján B, Rapp H, Collins A, de Moraes-Russo C (2013) A molecular phylogeny for the Order Clathrinida rekindles and refines Haeckel's taxonomic proposal for Calcareous Sponges. Integr Comp Biol 53(3):447–461

Laubichler MD, Maienschein J (2007) From embryology to evo-devo: a history of developmental evolution. MIT Press, Cambridge

Levit G, Hoßfeld U, Olsson L (2015) Alexei Sewertzoff and Adolf Naef: revising Haeckel's biogenetic law. Hist Philos Life Sci 36(3):357–370

Leys SP, Eerkes-Medrano D (2005) Gastrulation in calcarous sponges: in search of Haeckel's gastraea. Integr Comp Biol 45:342–351

Manuel M (2006) Phylogeny and evolution of calcareous sponges. Can J Zool 84:225–241

Manuel M, Borojevic R, Bory-Esnault N, Vacelet J (2002) Class Calcarea Bowerbank. In: Hooper JNA, van Soest RWM (eds) Systema Porifera: a guide to the classification of sponges, vol 2. Kluwer, New York, pp 1103–1110

Metschnikoff E (1875) On the development of the Calcispongiae. Translated by W.S. Dallas. Ann Mag Nat Hist Zool Bot Geol 16(91):41–53

Miklucho-Maclay N (1868) Beiträge zur Kenntnis der Spongien I. Jenaische Zeitung Med Nat 4:221–240

Minchin EA (1896) Suggestions for a natural classification of the Asconidae. Ann Mag Nat Hist 18:349–362

Nakanishi N, Sogabe S, Degnan BM (2014) Evolutionary origin of gastrulation: insights from sponge development. BMC Biol 12:26

Nielsen C (2008) Six major steps in animal evolution: are we derived sponge larvae? Evol Dev 10(2):241–257

Nyhart LK (1995) Biology takes form: animal morphology and the german universities, 1800–1900. University of Chicago Press, Chicago

Olsson L, Levit G, Hossfeld U (2017) The "biogenetic law" in zoology: from Ernst Haeckel's formulation to current approaches. Theory Biosci 136:19–29

Pechenik J (1991) Biology of the invertebrates, 2nd edn. Wm. C. Brown, Dubuque

Rapp HT (2006) Calcareous sponges of the order *Clathrina* and *Guancha* (Calcinea, Calcarea, Porifera) of Norway (north-east Atlantic) with the description of five new species. Zool J Linn Soc 147(3):331–365

Richards RJ (2008) The Tragic sense of life: Ernst Haeckel and the struggle over evolutionary thought. University of Chicago Press, Chicago

Rieppel O (2016) Phylogenetic systematics: from Haeckel to Hennig. CRC Press, Boca Raton

Schmidt O (1876) Nochmals die gastrula der Kalkschwämme. Arch für mikroskopische Anat 12(1):551–556

Schulze FE (1875) Ueber den bau und die Entwicklung von Sycandra raphanus Haeckel. Zeitschr f wiss zool 25:247–250

Sollas WJ (1878) Sponges. Encyclopedia Britannica, 9th edn, vol XXII. Scribner's Sons, New York, pp 412–429

Srivastava M, Simakov O, Chapman J et al (2010) The *Amphimedon queenslandica* genome and the evolution of animal complexity. Nature 466:720–726

Stott R (2003) Darwin and the barnacle: the story of one tiny creature and history's most spectacular scientific breakthrough. W.W. Norton & Company, New York, London