could be printed *en masse* in vivid detail. His favourite scientific subjects, radiolarians and jellyfish, feature big also in this visual cornucopia, but he broadened his horizon to a wider range of animals and plants. Haeckel's desire was to showcase 'what is out there' in the realm of the microscopic, the inaccessible or the exotic. As with the Radiolaria, his focus is on elaborate, complex structures to evoke the insight that even seemingly simple, 'lowly' life forms exhibit astounding structural complexity if only looked at carefully. But he also let his artistic vision run free in the way the organisms are enlivened in movement or arranged in baroque displays overflowing with detail, all as though he wanted to illustrate Darwin's famous "grandeur in this view of life".

The *Kunstformen* were immensely popular and remain so to this day. Remarkably, their otherworldly beauty has withstood the onslaught of perfect biological images modern technology has wrought. You can find them printed on T-shirts and coffee mugs. Like the radiolarians before, they inspired the *art nouveau* (*Jugendstil*) movement in which artists and designers were looking to images of the natural world as inspiration for a new language of ornamental form — an effect Haeckel had intended explicitly. Radiolarians, medusae and others of Haeckel's subjects formed the basis for lamps, wallpapers and architecture. Haeckel even implemented some of these bio-inspired designs himself, in his residence, the 'Villa Medusa', and a 'phyletic museum' he opened in Jena.

More than in his taxonomic studies or in his ardent, evolution-infused monistic quasi-religion, Haeckel's legacy lives on in the visual domain. (The opulent tome *The Art and Science of Ernst Haeckel* attests to that.) In some cases, like the phylogenetic trees or some of his embryo pictures, when his theoretical persuasions got the better of him, and influenced what he saw and what he drew, they need to be looked at with caution. But where he applied his extraordinary artistic skill to what was once the primary purpose of art in science, the depiction of the unseeable, his images reveal a beauty that transcends purely technical reproduction.

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Essay

Ernst Haeckel in the history of biology

Georgy S. Levit and Uwe Hossfeld

The German zoologist Ernst Haeckel (1834–1919) was arguably the most influential champion of Darwin's theory of evolution on the European continent and one of the most significant worldwide. As his biographer Robert Richards emphasized: "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" [1]. Furthermore, Darwin himself considered Haeckel a crucial proponent of his theory. How can we explain the mismatch between Haeckel's extraordinary influence among his contemporaries and his relatively modest place in the current historiography of biology? Why are Haeckel-studies nothing like the 'Darwin-industry'? To answer these questions, we outline Haeckel's contribution to evolutionary biology and anthropology and — to a lesser extent — the general history of ideas. We argue that Haeckel is currently underestimated, because history written by the advocates of the modern synthesis focused on neo-Darwinian schools of thought and neglected 'old-school-Darwinism' which Haeckel was part of. Besides, Haeckel's militant anti-clericalism and his exotic philosophy of 'monism' made him an uncomfortable figure in European intellectual history. In contrast to Darwin, Haeckel from the very beginning tried to turn Darwinism into a universal worldview, thus jeopardizing his credibility as a scientist.

Widely regarded at the time as the 'German Darwin', Ernst Haeckel (Figure 1 and Box 1) was influential in Germany, but also in non-German speaking countries [2]. He was a key figure during the first 'Darwinian revolution', a period of rapid acceptance of the theory of evolution following the publication of Darwin's *Origin of Species* in 1859. The triumph of evolutionism in the 19th century is unthinkable without Haeckel. He defended and developed the Darwinian theory with a passion and energy like nobody else on the continent and created a conceptual framework within which the majority of Darwinians worldwide worked over decades. Contemporary

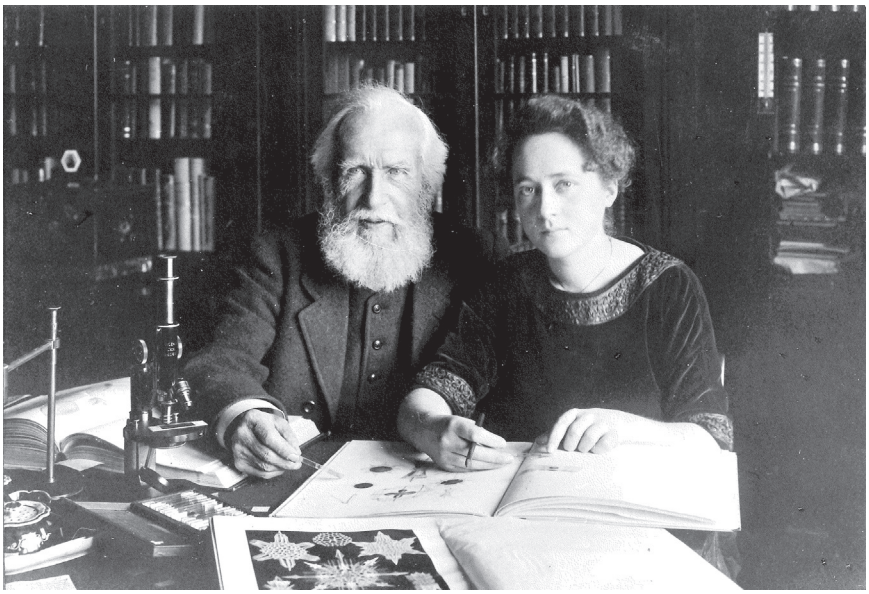

Figure 1. Ernst Haeckel.
Ernst Haeckel and his granddaughter Else Meyer in the workroom of his 'Villa Medusa' in Jena, 1916. (Image from the private archive of Uwe Hossfeld.)

biology is not conceivable without terms coined by Haeckel, such as Metazoa, 'phylogeny', 'ontogeny', 'monophyletic', 'polyphyletic' or 'ecology'. Moreover, his theories were admired by Darwin himself. It was Haeckel who crucially contributed to the visualization of the Darwinian theory by designing multiple phylogenetic trees reflecting evolutionary pathways of various groups of organisms, including humans [3]. In that sense, Haeckel can be regarded as pioneer of Darwinian biological anthropology as well.

Haeckel also explicitly tried to turn Darwinism into a universal worldview by introducing an exotic philosophical doctrine of monism. Monism and evolutionary theory were for Haeckel parts of the same research program labelled the 'monistic doctrine of evolution' (*monistische Entwickelungslehre*). At the core of the monistic worldview was the unity of God and nature, where God is understood as a 'general causal law' recognizable by the means of science. Methodologically, monism meant that everything that can be approached scientifically will be explored in the framework of a united natural science. All sciences exploring humans and their soul (including humanities) must be seen as natural sciences as well. Trying to establish a such a universal scientific worldview brought Haeckel into conflict with traditional religions. He definitely transcended the domain of natural science by turning Darwinism into a religion-like doctrine, but, at the same time, he took a step towards unifying science and humanities.

Below, we summarize Haeckel's achievements and formulate a hypothesis explaining Haeckel's relative fringe position in the history of science, especially if compared to his major inspiration Charles Darwin.

"The most magnificent eulogium" to the *Origin of Species*

Darwin was already excited about Haeckel's monograph *Radiolaria*, which explicitly advocated the theory of evolution as applied to these single-celled aquatic animals [4]: "It is one of the most magnificent works which I have ever seen, & I am proud to possess a copy from the author" [5]. Haeckel's student Heinrich Schmidt (1874–1935) regarded *Radiolaria* as his first pro-Darwinian book "at a time when Darwin's work was met with great general distrust even among his later champions" [6]. Yet, *Radiolaria* did not offer a systematic review of evolutionary theory. The revolution within Darwinism came with Haeckel's *Generelle Morphologie der Organismen* (*General Morphology of Organisms*) [7]. This two-volume book, which appeared in 1866, was Haeckel's first major work in evolutionary biology and included almost all the ideas that made him famous (Box 2). In *Generelle Morphologie*, Haeckel coined the terms ontogeny and phylogeny and showed detailed Darwinian phylogenetic trees reflecting hypothetical pathways of evolution. This time Haeckel did not focus on the visible beauty of nature and description of new species, but rather on the driving forces of evolution, which he laid out in a transparent and holistic theory. In *Generelle Morphologie*, Haeckel offered a complete theory of evolution in a Darwinian sense, comprising both a detailed discussion of evolutionary mechanisms and overwhelming evidence for the very fact of evolution. Between 1859 and the turn of the century, evolutionary biologists concentrated mainly on establishing evidence for evolution as a fact, such as phylogenetic reconstructions. This was because exact causal relations of evolutionary events (the issues of direct and indirect inheritance, the role of mutation, geographic isolation, selection or questions concerning evolutionary progress) could be formulated in only a preliminary and

Box 1. Biography of Ernst Haeckel.

Ernst Heinrich Philipp August Haeckel (1834–1919) was born on 16th February 1834 in Potsdam (Germany) to wealthy parents. After graduation from a cathedral gymnasium (secondary school) in Merseburg, Haeckel studied medicine and allied sciences at the Universities of Berlin, Würzburg and Vienna (with Johannes Müller, Albert Kölliker and Rudolf Virchow). At 23, Haeckel earned his Medical Doctor's degree and started to work as a physician. However, after being confronted with real patients, he gave up practical medicine and decided to move to Italy to study radiolarians. In 1860, back from Italy, Haeckel read the German translation of Darwin's *On the Origin of Species*. Haeckel's work on the systematics of Radiolaria resulted in his promotion as a lecturer at the University of Jena, which was encouraged by the famous comparative anatomist Carl Gegenbaur. In 1863 Haeckel, at the Meeting of the German Association of Naturalists and Physicians held in the city of Stettin, held his seminal talk *Über die Entwickelungstheorie Darwins* (*On Darwin's Evolutionary Theory*) known as the 'Stettin Speech'. The speech marks Haeckel's Darwinian turn and delighted Darwin himself. Since that time and through his whole life, Haeckel became known as one of the most influential advocates and popularizers of evolutionism.

In 1865 Haeckel earned his second doctorate, in zoology, and was appointed Chair of Zoology at the University of Jena, the position he held until 1909. In his nearly 50 years in office, Haeckel turned Jena into a stronghold of Darwinism. As well as his British counterparts Charles Darwin and Alfred Russel Wallace, Haeckel gained much field experience in various parts of the world. The specificity of Haeckel's approach to Darwinism was in his aspiration to make it into a universal worldview opposing major religious doctrines. He tried to harmonically combine science, philosophy and art as mutually strengthening instruments.

Already in his lifetime Haeckel was seen as a key figure of evolutionary theory both in Germany and abroad. He was awarded a Darwin-Wallace Medal of the Linnean Society of London and in his Laudatio on 1st July 1908, the President of the Society rightly called Haeckel "the great Apostle of the Darwin-Wallace theory in Germany" [2].

Haeckel died on 9th August 1919 in Jena, aged 85, in his home called 'Villa Medusa', which reflected in its design his both scientific and artistic aspirations.

Box 2. Haeckel's major works.

1866: *Generelle Morphologie der Organismen. Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanisch begründet durch die von Charles Darwin reformierte Descendenztheorie* (General Morphology of Organisms. Main Features of the Science of Organic Forms, Mechanically Accounted for by Charles Darwin's Reformed Theory of Descent).

1868: *Natürliche Schöpfungsgeschichte* (Natural History of Creation).

1872: *Die Kalkschwämme* (Calcareous Sponges).

1874: *Anthropogenie oder Entwickelungsgeschichte des Menschen* (Anthropogeny or Evolutionary History of Humans).

1894/1896: *Systematische Phylogenie* (Systematic Phylogeny).

1899: *Die Welträthsel* (The Riddle of the Universe).

1899/1904: *Kunstformen der Natur* (Art Forms in Nature).

hypothetical manner [8]. Haeckel was one of the most prominent figures in this movement.

The *Generelle Morphologie* consists of two parts. The first part is entitled *General Anatomy of Organisms* and dedicated to his teacher, the well-known vertebrate comparative morphologist Carl Gegenbaur (1826–1903) whereas the second part is called *General Evolutionary History of Organisms* and was dedicated to Darwin, Goethe and Lamarck as "three founders of the theory of descent" [7]. (Haeckel used the term '*Entwicklung*' (development) for both the development of the individual and development over evolutionary time; we translate here Haeckel's '*Entwickelung*' as 'evolution' to avoid misunderstanding.) The full subtitle to *Generelle Morphologie* is "Critical foundations of a mechanical science of evolving forms of organisms substantiated by the theory of descent". 'Mechanical' in this context meant 'causal' and so already in the title Haeckel emphasized that he had written a natural history of creation without any appeal to supranatural forces. Although the title of the first volume (*General Anatomy*) does not presuppose a scientific revolution, it wasn't anatomy in the traditional pre-Darwinian sense. The first part of the first volume was devoted to the methodology of general morphology. Haeckel saw the major task of morphology not in a mere description of organic forms, but in discovering "the laws of nature" [7].

Haeckel put forward a whole series of 'natural laws' as he ultimately intended to contribute to a "general science of living and inert natural bodies on Earth" [7]. This general natural science was to be divided into physics (in a very broad sense) or 'dynamics' on one hand, and morphology (in a very broad sense) or 'statics', on the other. Morphology (in the narrow, biological sense) was conceived as a science of external and internal forms of living bodies and the laws that determine the relationships among these forms. Haeckel attributed morphology to 'statics', as he believed that every natural body is either in the state of equilibrium or in a state of change or movement. Morphology is thus the study of equilibria, whereas "physics in the narrow sense" or physiology in Haeckel's mind was concerned with the study of change of moving forces. That is why Haeckel regarded physiology as 'dynamic zoology'. According to this concept, Haeckel's newly coined notions of ontogeny and phylogeny were also nested within 'zoostatics', whereas 'zoodynamics' concentrated on Haeckel's ideas of physiology (Figure 2) [39]. This example shows a crucial difference between Haeckel and Darwin. Haeckel envisaged evolutionary theory in a very broad theoretical context within the whole pantheon of natural sciences. Haeckel viewed evolution as a universal phenomenon, affecting everything from inorganic matter to man [9]. He believed in the ultimate unity of nature and therefore in the unity of spirit and matter. This monist doctrine continued to guide Haeckel's work from the *Generelle Morphologie* to his last book on '*Crystal Souls*' [10]. Developing this monistic creed Haeckel claimed: "All true natural science is philosophy, and all true philosophy is natural science. All true science, however, is natural philosophy" [7].

In the second volume of *Generelle Morphologie*, Haeckel delivered an immense amount of evidence for the very existence of organic evolution and described mechanisms of evolutionary change, including natural selection [7]. Haeckel, like Darwin, was convinced that natural selection is crucial but not the only evolutionary mechanism and advocated a multitude of evolutionary factors, including inheritance of acquired characters by means of use or disuse, a direct effect of the environment on evolutionary change and some saltatory, large-effect mutations leading to the appearance of new species in a single step.

Furthermore, in the *Generelle Morphologie* Haeckel coined his influential concept of the "threefold parallelism". He put great theoretical emphasis on the parallel between the stages of development of the embryo and the series from 'lower' to 'higher' forms of animals studied in comparative anatomy and systematics. To these two parallels he added a third, based on palaeontological data. In the threefold parallelism of the phyletic (palaeontological), biontic (individual), and systematic developments, he saw one of the most important phenomena in organic nature [11]. Although the very term was coined later, Haeckel began formulating the biogenetic law in the *Generelle Morphologie*: "The organic individual […] recapitulates through its fast and short individual development the most important of the changes in form, which the ancestors have gone through during the slow and long palaeontological development following the rules of inheritance and adaptation" [8]. In his 1872 monograph on calcareous sponges (*Die Kalkschwämme*) [12], he pushed the biogenetic law to the extreme and formulated the so-called 'Gastraea theory' of animal origin [13]. The term 'gastraea' refers to a hypothetical primordial organism from which all metazoans have originated. According to Haeckel, Gastraea left no paleontological traces and can only be recognized as the gastrula stage through which most extant animals pass during development.

CellPress

In *Generelle Morphologie,* Haeckel also approached a topic ignored in Darwin's *Origin of Species*, but essential for a complete picture of evolution: the origin of life. Haeckel postulated that life on Earth originated by way of 'archegonia' — spontaneous generation of most primitive structureless organisms (monera) from inorganic matter. Thus, according to Haeckel, the very initial appearance of all life was polyphyletic [8], and living matter occurred directly from inorganic chemical substances and not from previously generated organic substances. Haeckel repeated the idea that various monera were generated independently from inorganic substance also in later publications [14,15].

Haeckel's general evolutionism, his novel research in ontogeny and phylogeny, and his hypothesis on the origin of life stimulated the growth of biological sciences. At the same time, trying to establish Darwinism as a worldview competing with religious doctrines of the late 19th century, Haeckel evidently (even for his contemporaries) transcended the framework of natural science. *Generelle Morphologie* documented Haeckel's attempts to turn Darwinism into a universal philosophy. His later publications only strengthened this tendency.

Making anthropology Darwinian

When Darwin introduced his theory of evolution, the most heated controversies concerned the origin of humans. From an early time, Haeckel was convinced that Darwinian principles apply to human evolution. Having only two hominid fossils at his disposal throughout his career — the Neanderthal was discovered in 1856 and *Pithecanthropus* (now known as *Homo erectus*) in 1891 — Haeckel tried to reconstruct human phylogeny as well as the migration of ancient humans. In contrast to Darwin, who had placed human origins in Africa, Haeckel postulated the existence of an ancient continent called 'Lemuria' in the Indian Ocean, from where humans had spread around the globe. Darwin reacted very favorably to Haeckel's anthropological publications. In the introduction to the *Descent of Man* (1870) he wrote referring to Haeckel's

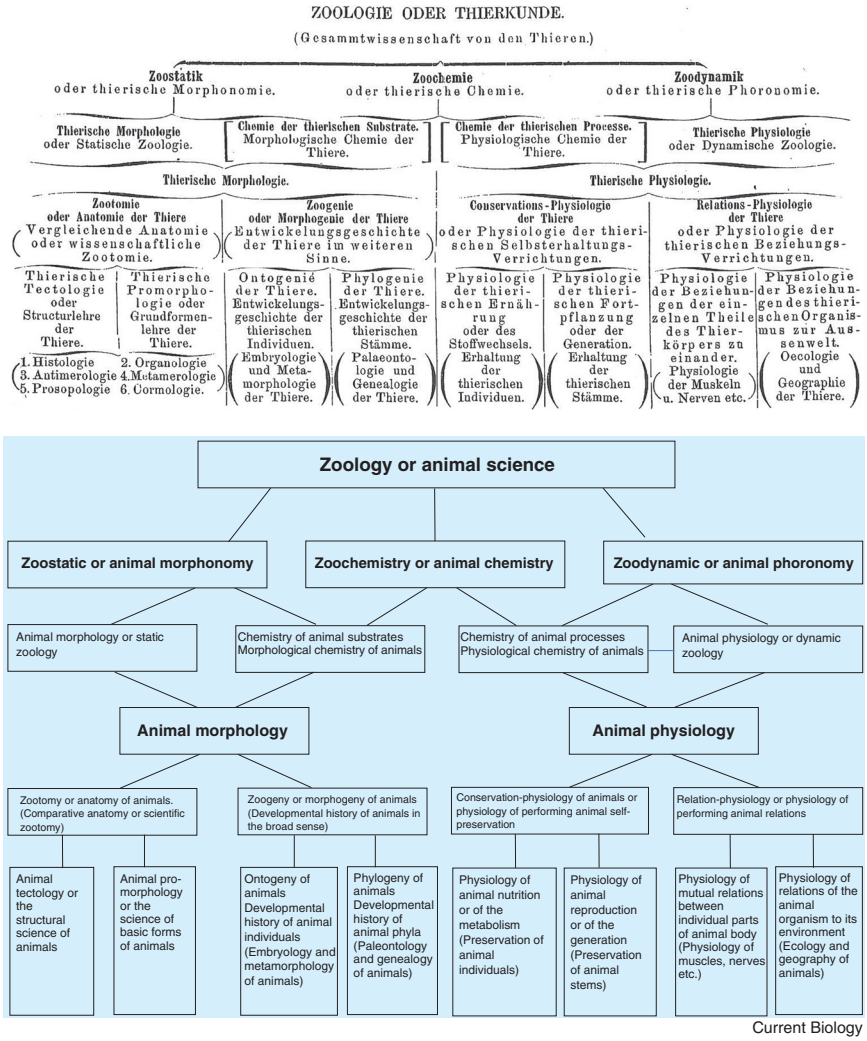

Figure 2. Haeckel's 'Animal Science'.
Haeckel's overview of zoology, where he introduced his famous concepts of ontogeny, phylogeny and ecology. The scheme incorporates both the 'static', and 'dynamic' aspects of animal life, where 'static' is used to describe structures and forms (morphology), and 'dynamic' deals with a state of change. Translated by and reproduced by the authors with slight changes from the original scheme in: Haeckel (1866), vol. 1, p. 11, p. 238.

History of Creation that almost all the conclusions he had arrived at were already confirmed by Haeckel [16].

Haeckel was occupied with human evolution for 45 years, beginning with the *Stettiner Vortrag* (*Speech in the City of Stettin*) in 1863 and ending in 1908 with *Unsere Ahnenreihe* (*Our Ancestry*) [17]. In contrast to Darwin, who merely postulated the descent of humans from an ape-like ancestor, Haeckel tried to reconstruct and visualize the exact pathways of human evolution. For him, it was a task of a very special mission: "Of all the individual questions answered by the Theory of Descent, of all the special inferences drawn from it, there is none of such importance as the application of this doctrine to Man himself" [18]. These efforts made Haeckel a highly controversial figure. Putting forward the hypothesis widely accepted today that several human species simultaneously co-existed on Earth, Haeckel suggested that this was still the case and proposed phylogenetic (genealogical) trees encapsulating this idea. The latter made Haeckel vulnerable to accusations of theorizing racism as he placed various human 'species' higher or lower on the tree.

Figure 3. Haeckel's hypothetical 'speechless man'.
Reconstruction of '*Pithecanthropus alalus'* of the Upper Pliocene by the German artist Gabriel von Max (1840–1915). Ernst-Haeckel-Haus in Jena (EHH-Archive, Jena). (Photo taken by Uwe Hossfeld and used with permission.)

He was even regarded complicit in Nazi biology later on [19], but in fact, despite of isolated attempts to exploit Haeckel's fame to support Nazi ideology, "the official guardians of party doctrine quashed any suggestion of consilience between Haeckel's Darwinism and the kind of biology advanced by their members" as noted by Robert Richards [20].

From the contemporary perspective, Haeckel's "speculations" (his own words) are definitely racist, as he admitted that the Earth is populated by several human races so different that they may even be considered different species and represented in a hierarchy. But Haeckel's racial diagrams are mere speculations, hypotheses as he never became tired repeating. Haeckel's intention was not to create a ready-made discriminatory scheme of hierarchical relations between human races but to suggest hypotheses with the aim of moving biological anthropology toward an exact Darwinian science based on comparative anatomy and ontogenetic research [17,21]. It is this intention that was so highly appreciated by Darwin. Haeckel's works of that period mark the strengthening of his philosophical aspirations and of his anti-clerical views.

Haeckel made a systematic effort to establish a Darwinian anthropology in his *Generelle Morphologie*. Here, he clearly stated that anthropology becomes a science only in the light of evolutionary biology. He defined anthropology as a general biological science of humans and a branch of zoology subdivided into human morphology and human physiology. Two years later, in the *Natural History of Creation* (1868), Haeckel clearly stated that the origin of humans can be ultimately traced back to monera and specifically that "Man has developed gradually, and step by step, out of the lower Vertebrata, and more immediately out of ape-like mammals" [18]. He also introduced the idea of a hypothetical pre-human species *Pithecanthropus alalus* (speechless man) originating from Asian man-like apes (Catarrhini) as a hypothetical link between 'Anthropoides' and the actual 'speaking- or genuine man" (Homines) (Figure 3) [18]. Human origin from Catarrhini was supported by the argument that the anatomical differences between humans and the most human-like apes (orangutan, gorilla, chimpanzee) are less than the differences between the latter and the lowest stages of Catarrhini, such as baboons [18]. Altogether Haeckel's hierarchy of animal and human ancestors consisted of 22 steps with *Pithecanthropus* in 21st place and 'genuine humans' on top. As language is the major distinguishing feature of humans, and philologists suggested that there was no primeval common language, Haeckel proposed a "polyphyletic transition from speechless ape-like men to genuine men" [18], that means that transitions to 'genuine humans' took place several times. That is why Haeckel supported the view that

humans appeared monophyletically in a wide sense (they all come from *Pithecanthropus*), but polyphyletic in a narrow sense (the different human 'species' had originated independently of one another). Australians and Papuans were categorized by Haeckel as nearest living relatives of the ancestral stages.

In Haeckel's view, extant humanity consisted of 12 species, subdivided into 36 races. The human 'species' were presented in their pedigree hierarchically from "lower" (more ape-like) to "higher" (higher mental development) [18] with Indo-Germans and Americans (he meant native Americans) on the highest level and Hottentots, Papuans and Australians in the lowest portion of the pedigree. Haeckel's genuine motivation for arranging human races in such a way was the idea to employ human genealogy as a proof for the animal origin of man. He looked for a resemblance "between the lowest woolly-haired men, and the highest man-like apes" [18] as evidence of human evolution. The latter led to a controversy between Haeckel and his Russian student Nikolai Miklucho-Maclay (1846–1888), who, by way of empirical ethnographic studies in New Guinea, demonstrated the absence of significant differences between various human races and the unity of all humans. Miklucho-Maclay spent several years among Papuans and came to conclusion that both Haeckel's morphological descriptions (for example, the character of their hair) and his estimations of their intellectual abilities were wrong. At the same time, Haeckel did not believe in the separate creation of human races, advocating ultimate monophyletic evolution from a common ancestor. In that sense, he remained a fully Darwinian anthropologist. The major question for Haeckel, Darwin and other early anthropologists was not the monophyletic origin. The question was in how far back they would place the last common ancestor of all human races or species and therefore 'how human' this hypothetic ancestor was [22]. Haeckel tended to give human species more time to diverge (definitely more than Darwin), but in his view they nevertheless diverged already at the stage of humans with a speaking ability. This position, along with the disregard of widespread racial prejudices (he placed dark-skinned Berbers and Jews on the same level as white Europeans), hints at the idea that Haeckel's genuine motivation was not to establish discriminatory schemes, but to prove human evolution. His genealogical trees were unsuitable for discriminatory practices, because he often changed them and always stressed emphatically that they were only hypotheses.

Haeckel's other significant anthropological work was *Anthropogenie oder Entwickelungsgeschichte des Menschen* (*Anthropogeny or The Genesis of Man*), a series of lectures to general audiences [23]. Contemporaries saw it as a great contribution to Darwinian theory. As palaeontologist Lester Frank Ward claimed: "Both in his History of Creation and in his Anthropogeny, Haeckel has done a service to the cause of evolution by reviewing, in a fair and disinterested manner, the history of the origin and progress of those ideas which have culminated in the Darwinian theory" [24]. The major objective of the book was to make explicit the causal relations between human ontogeny and phylogeny [23]. In *Anthropogeny*, Haeckel provided powerful arguments in favour of human evolution, for example comparing human ontogeny with that of invertebrates. He listed the most important homologies between lower and higher vertebrates and investigated sexual selection. Furthermore, Haeckel demonstrated homologies in human sexual organs and used linguistic methods for phylogenetic reconstructions.

"On what he calls phylogeny" — Haeckel's trees

Darwin was the first to formulate the very idea of a phylogenetic tree in the sense of newly established theory of evolution in a well-known sketch in 1837 and published his 'diagram' more than 20 years later in the *Origin of Species* [25]. Yet, Darwin's diagram was just an abstract scheme reflecting the very principle of evolution without visualizing its actual course of events. Haeckel was the first who conceived a detailed Darwinian phylogenetic tree as a diagram visualizing the hypothetic course of evolution as it could really have proceeded [26]. Although there were plenty of other 'trees of life' before Darwin and Haeckel, only the Haeckelian tree imbodied the spirit of Darwinian doctrine and thus founded Darwinian phylogenetic systematics [27].

Darwin himself was excited by Haeckel's visualizations and somewhat critical of overemphasis on his use of ontogenetic analysis as the primary method of phylogenetic reconstruction. Haeckel's simplistic recapitulationism (ontogeny recapitulating phylogeny) was met very critically by many of his contemporaries, and Haeckel himself seemed to be aware as well that complete and faithful recapitulation is never observed in nature. Nevertheless, Darwin approved Haeckel's tree-like diagrams as the way forward: "Professor Haeckel in his '*Generelle Morphologie*' and in other works, has recently brought his great knowledge and abilities to bear on what he calls phylogeny, or the lines of descent of all organic beings. In drawing up the several series, he trusts chiefly to embryological characters, but receives aid from homologous and rudimentary organs, as well as from the successive periods at which the various forms of life are believed to have first appeared in our geological formations. He has thus boldly made a great beginning, and shows us how classification will in the future be treated" [28].

Darwin's major point above is the idea that Haeckel's trees open the door to a research programme that will determine the future of phylogenetic reconstruction. And Darwin was right: by placing great theoretical emphasis on the parallelism between the stages of individual development of the embryo to an adult and the serial development of lower forms of animals to higher forms, Haeckel used comparative anatomy, palaeontology and embryology as a means of substantiating Darwin's theory of descent. Generations of biologists would do the same and even the introduction of molecular analysis into phylogenetics would not contradict Haeckel's basic idea but only contribute to its development. Haeckel's trees were not mere illustrations of Darwin's insights. As in many other cases, Haeckel broadened Darwin's theory and made it more inclusive. For example, while Darwin referred to the Linnaeus' two-kingdom system

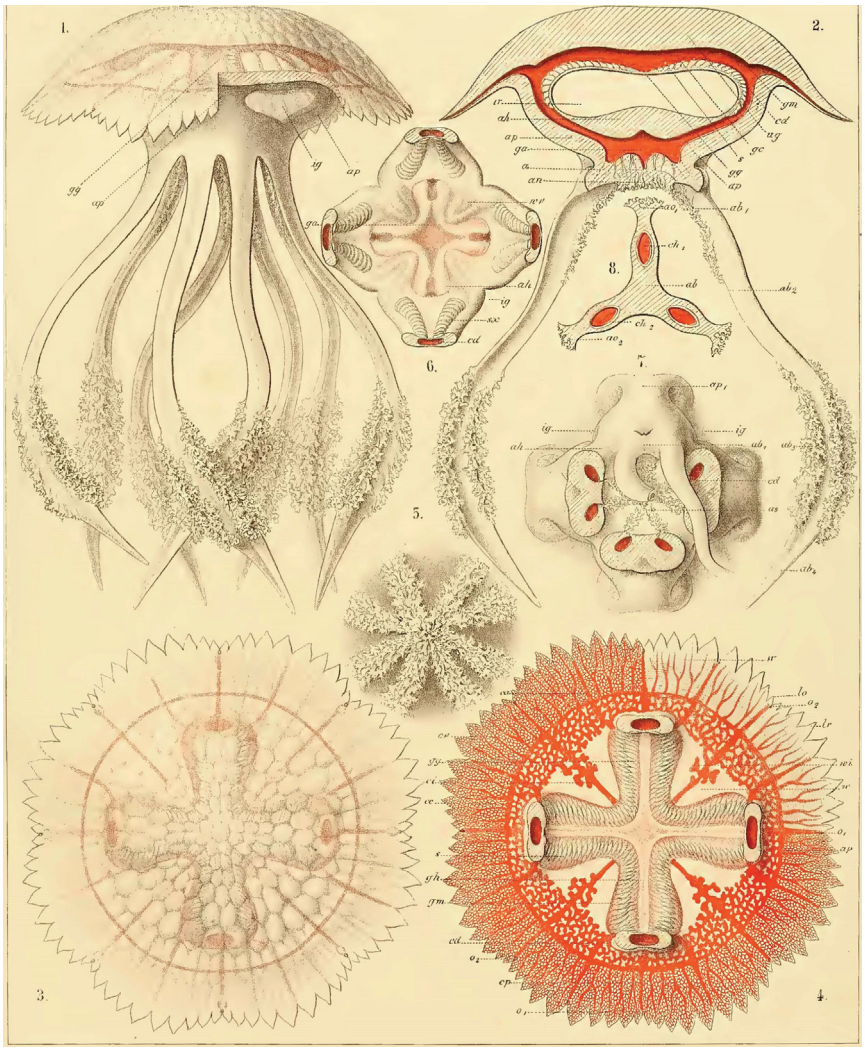

Figure 4. Haeckel's drawing of a medusa.
Deep sea medusae *Leonura terminalis*. From R*eport of the Challenger Expedition*: Pl. 32. E. Haeckel, *Die Tiefsee-Medusen der Challenger Reise.* Atlas. Jena: Gustav Fischer (1881).

of Animalia and Vegetabilia, Haeckel introduced "the first three-kingdom tree of life that included microorganisms" [15], thus ushering in another revolution within Darwinism.

Haeckel's legacy — from old-school- and neo-Darwinism to synthetic Darwinism

After publishing *Generelle Morphologie*, Haeckel spent plenty of intellectual effort to popularize Darwinism and turn it into a universal doctrine. However, he continued to publish voluminous empirical studies, such as *Das System der Medusen* (*The System of Medusae*) [29]. His fundamental three-volume *Systematische Phylogenie* (*Systematic Phylogeny*) [30] reconstructing the whole phylogenetic history was arguably the most pervasive evidence of evolution at the time, as Haeckel's intention was to reconstruct with precision evolutionary pathways of various organismic groups by charting their 'phyletic history'. His special merit was the critical analysis of the very method of phylogenetic systematics and pointing out the gaps in empirical data, for example, in the palaeontological record. These unprecedented studies continued to be the 'eulogium' to Darwinism, substantiating the idea of evolution.

Haeckel's particular interest in marine organisms was linked to their suitability to provide evidence of evolutionary adaptation by natural selection (Figure 4). He referred to jellyfish and other transparent marine fauna, like Ctenophora or Pyrosomatida, as 'crystal animals' or 'glass-animals'. He proceeded from the assumption that, in the past, 'crystal animals' had existed in varieties of different transparency and colorlessness. The more transparent and colorless of these animals had an advantage in the struggle for existence. Over many generations, these individually advantageous features had been strengthened and secured so that, in the end, completely transparent (glass-like) structures came into being. There could be no doubt, Haeckel argued, that these glass-like structures appeared as a result of natural selection, as their close non-pelagic relatives dwelling on the seabed or on the coast are opaque and colored. Besides, as pointed out by Richards [1], Haeckel "not only drew upon his systematic observations of marine life and his ability to conceive of that life as branches of a living evolutionary tree, but he accomplished what virtually no other evolutionary scientist of the nineteenth century was able to do — namely, he introduced experimental procedures into his discipline". Experimenting with siphonophores [31], Haeckel was able to directly demonstrate the connection between development and evolution, thus anticipating evolutionary developmental biology, or evo-devo, as a science infusing evolutionary biology with developmental perspectives.

Unfortunately, none of Haeckel's ground-breaking scientific books (*Generelle Morphologie*, *Systematische Phylogenie*, *Die Kalkschwämme*) was translated into English, and their reception was hindered by English becoming the international language of science after the second World War. This is perhaps the most pertinent reason for the imbalance between Haeckel's influence in his time and his present shadow existence. The second reason is Haeckel's understanding of evolutionary mechanisms. At the end of the 19th century, the psychologist George John Romanes (1848–1894) opposed Darwin, who thought that natural selection had been assisted by 'subordinate principles', such as inheritance of acquired characters and a direct effect of the environment.

Likewise, Alfred Russel Wallace (1823–1913) along with August Weismann (1834–1914) maintained that natural selection should be regarded as the only cause of evolution. To denote "the pure theory of natural selection to the exclusion of any supplementary theory", Romanes coined the term 'neo-Darwinism' as opposed to Darwin's original teaching [32]. Haeckel legitimately insisted that he followed the initial ideas of Darwin, who assumed some roles for non-selectionist mechanisms. Haeckel's successor in Jena, Ludwig Plate (1862–1937), followed Haeckel and Darwin in this respect and coined the term 'old-school-Darwinism' to emphasise their difference from neo-Darwinians and adherence to 'genuine' Darwinism admitting the multiplicity of evolutionary mechanisms [33,34]. At the turn of the century, nobody knew how the battle between neo- and old-Darwinian schools would end. The two most influential German-speaking architects of the Modern Synthesis, Bernhard Rensch (1900–1990) and Ernst Mayr (1904–2005), championed views close to that of the old-school early in their careers. Yet, after the establishment of the Modern Synthesis with its strict focus on natural selection and denial of any neo-Lamarckian hypotheses, the old-Darwinian school was downplayed and Haeckel fell victim to a history written by the 'winners'. Haeckel was thrown out with the old Darwinian idea of a multiplicity of evolutionary mechanisms. The proponents of the Modern Synthesis instead saw a direct line proposed from Darwin via Weismann to the modern view of evolution [35].

There is another reason for Haeckel's shadow existence, which was remarked on by Ernst Mayr. Mayr emphasised that "as a young man Haeckel was brilliant, but one becomes nauseated when reading his letters and polemics of the latter period because of his arrogance, vanity and intolerance" [36]. In other words, Haeckel's attempt to turn Darwinism and natural science in general into a radical and universal worldview alienated many outstanding scientists, including Mayr. Haeckel's "intolerance" stood in sharp contrast to the modest and cautious position of Darwin. At the same time, even Mayr admitted that, as a schoolboy, he was "excited by reading his *The Riddle of the Universe* and especially by Haeckel's attacks on the Church and the Bible".

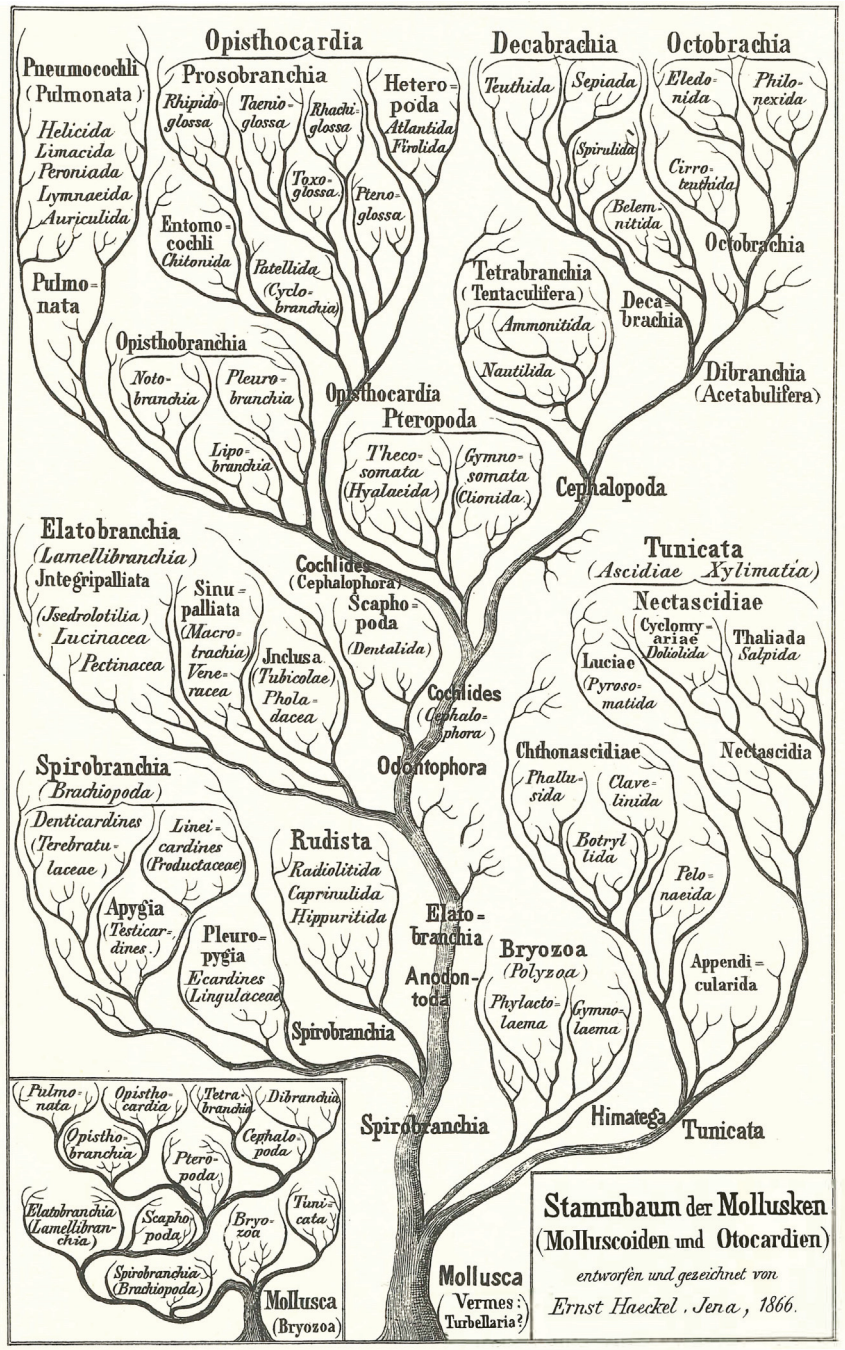

Figure 5. One of Haeckel's phylogenetic trees.
The phylogeny of mollusks. *Stammbaum der Mollusken* from *Generelle Morphologie* (1866), Vol. 2, Tafel VI.

Conclusions

Haeckel contributed significantly to the deepening, widening and establishing of Darwinian theory. Beginning in 1866 and until the turn of the century, he was one of the most popular, if not the most popular of Darwin's supporters worldwide. Haeckel articulated many Darwinian concepts that had only been implicit in Darwin's own writings until he

stepped on the stage. Phylogeny, ontogeny and ecology are the best examples (Figure 5). Furthermore, he developed research programmes that turned out to be very fruitful. Darwin himself appreciated Haeckel's contribution to evolutionary biology very much. Haeckel's somewhat obscure position in contemporary biology and in the history of science can be explained by several factors: the Modern Synthesis [37] arose from a conflict between neo-Darwinism and old-school Darwinism. Haeckel's and Plate's attempts to push the genuine Darwinian agenda of multiple evolutionary mechanisms led to a controversy with neo-Darwinians. Both old-Darwinism and neo-Darwinism ultimately failed in their original form, but the old-school with its neo-Lamarckian agenda looked much more archaic from the viewpoint of the Modern Synthesis.

Another major reason for neglecting Haeckel was his attempt to turn Darwinism into an all-embracing worldview (monism) opposed to world religions. Both philosophy of science in the 20th century and the growing social tolerance in the Western world after the Second World War made Haeckel look like an archaic intolerant radical. The fact that Haeckel's major goal was to establish Darwinian science as a worldview is often ignored. In addition, Haeckel's pioneering efforts to create a Darwinian biological anthropology had a dual effect. On the one hand, Haeckel established theoretical tools, such as comparative anatomy, ontogeny and phylogeny, which made anthropology Darwinian and truly scientific. On the other hand, his tendency to give definitive answers to all major questions of biological anthropology made him look racist. The description of races as 'higher' and 'lower' were characteristic for both Darwin and Haeckel, but Haeckel applied it in a much more radical way.

All of the above was strengthened by the fact that outside of the German-speaking countries Haeckel was available only in the 'light' version, exclusively in form of popular writings, because of the lack of translations of his scientific works. And Haeckel-light is expectedly much more radical and superficial then Haeckel in the hard-core version.

And yet, current biology shows many traces of Haeckel's influence, if only implicitly. The new synthetic science of 'eco-evo-devo' [38], which integrates developmental biology and ecology into evolutionary science is quite in line with Haeckel's initial intention of bringing together these fields within a single conceptual space [39].

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