Contributions

Click here for all previous articles in the History of the Ecological Sciences series by F. N. Egerton

History of Ecological Sciences, Part 47: Ernst Haeckel's Ecology

Frank N. Egerton
Department of History, University of Wisconsin-Parkside, Kenosha, Wisconsin 53141
E-mail: frank.egerton@uwp.edu

Ernst Haeckel, one of the world's best-known and most-read zoologists, named and defined a new science, "Oecologie" (1866, II:286). Was he, therefore, an ecologist? Robert Stauffer (my dissertation advisor) said yes (1957), but wrote that what was good in his ecology he got from Darwin, and what was misguided, he got from himself. There is some truth to that, but the story is more complex. (Stauffer was more interested in Darwin than Haeckel.) Haeckel had already absorbed Alexander von Humboldt's ecological perspective long before he read Darwin's *Origin*, though Humboldt's ecology lacked Darwin's concept of competition. If Haeckel is accepted as one founder of ecology, ecologists will want to know why he remains a controversial figure and how to evaluate the controversies. An introduction to these matters follows at the end.

Ernst Heinrich Philipp August Haeckel (1834–1919) wanted to be a botanist—his favorite book as a teenager was Mathias Schleiden's *Die Pflanzen und ihr Leben* (1848), and his hero was Humboldt (Uschmann 1972, Krausse 1987, Hopwood 2000, Di Gregorio 2005, Richards 2008). He was so precise at matching his collected plants with published descriptions that he kept two herbaria, one each for "good and bad species" (translated in Gasman 1971:xv).

> *One, arranged on official lines, offered to the sympathetic observer all the species in "typical" specimens, as radically distinct forms, each decked with its pretty label; the other was a private collection, only shown to one trusted friend, and contained only the rejected kinds that Goethe so happily called "the characterless or disorderly races* [Geschlechter]*, which we hardly dare ascribe to a species, as they lose themselves in infinite varieties,"... In this a large number of specimens arranged in a long series, illustrated the direct transition from one good species to another.*

Ernst's father, a lawyer and government official, thought the career prospects in botany were poor and insisted that he study medicine. Being a patriotic Prussian, with enormous respect for and love of his parents, he did as advised, studying medicine at universities in Berlin and Würzburg. However, the professors who excited him were zoologists, especially Johannes Müller, whom he joined on a field trip at Helgoland Island, North Sea, in August, 1854 (Bulnheim 1990, Lohff 1990). That trip turned Haeckel's interests to invertebrates; if Müller had been a botanist, this pivotal moment might have returned him to botany. Since his parents were nature lovers, he thought they would like to know the details of what he saw (Haeckel 1923:252).

> *...among the seaweed there were to be found many of the dearest little animals, specially charming polyps* (Tubularia, Eudendrium, Actinia), *sea spiders* (Pycnogonum littorale), *and a very strange member of the* tunicata (Amaraecium rubicundum)*... we saw a few seals at no great distance from us ... The strangest thing we caught was a beautiful green garpike* (Belone vulgaris) *with green bones, and I have been sitting all day examining the highly peculiar ova under the microscope; besides that we caught swimming crabs, a few shrimps, which are very scarce here, sea devils* (Cottus scorpius), *sprats, a quantity of different plaice and haddock* (torsk), together *with other fish.*

In 1855 Haeckel published his first article in an important new journal edited by Müller (Richards 2008:40). In summer 1856, he accompanied Professor Albert Kölliker to Nice, France, where he found the marine fauna both rich and remarkable (Haeckel 1923:416). He wrote a doctoral dissertation on histology of river crayfish. He returned home to Potsdam in 1858, with an M.D., to practice medicine, and hated it. He spent 1859–1860 in Italy, studying marine life.

Charles Darwin sent about a dozen copies of the *Origin of Species* (Darwin 1859) to German zoologists and botanists and soon received an appreciative response from paleontologist–zoologist Heinrich Georg Bronn (1800–1862), whom Darwin then authorized to translate the work into German (Hansen 1970, Gliboff 2008:1–3). Bronn's edition (1860) appeared just months after the English edition. Haeckel read it and found it entirely convincing (Breidbach 2006:99–100, Richards 2008:68–72). As a teenager, he had read Darwin's *Journal of Researches*. He became Darwin's most enthusiastic German disciple and wrote to express (9 July 1864, in Darwin 2001:265 [German] and 482 [English, reprinted in Richards 2008:168]).

> *... what high esteem and profound respect I hold the discoverer of the "Struggle for life" and of "Natural selection". Of all the books I have ever read, not a single one has come even close to making such an overpowering and lasting impression on me, as your theory of evolution of species. In your book I found all at once the harmonious solution of all the fundamental problems that I had continually tried to solve ever since I had come to know nature as she really is. Since then your theory—I can say so without exaggeration—has occupied my mind* every day *most pressingly, and whatever I investigate in the life of humans, animals or plants, your theory of descent always offers me a harmonious solution to all problems, however knotty.*

Thus began a warm friendship that lasted the rest of Darwin's life (Gliboff 2008:155–188).

Fig. 1. Ernst Haeckel in 1860. [Wikipedia]

In 1861 Haeckel published part of his research to qualify for appointment to the faculty of Jena University. He owed the position to Carl Gegenbaur (1826–1903), whom he had known at Würzburg. Gegenbaur became his closest friend and collaborator (Nordenskiöld 1928:499–503, Uschmann 1959:27–33, Coleman 1978). Aside from numerous journeys, Haeckel spent the rest of his life at Jena. In 1862, he was promoted to associate professor and Director of the Zoological Museum, and on 18 August he married his cousin, Anna Sethe (1835–1864)—the great love of his life—who died a year and a half later, on Haeckel's 30th birthday. He continued studying specimens collected in Italy, which led to his monograph, *Die Radiolarien* (1862); the impressive illustrations in it, which he drew, undoubtedly helped win a gold medal from the Leopold-Caroline Academy. In this work, he speculated on species relationships and genealogy and continued doing so for the rest of his life (Wilson and Doner 1937:57–58). He sent Darwin a copy. Darwin had already seen Huxley's copy, and Huxley sent Haeckel an enthusiastic letter and some specimens (Di Gregorio 2005:72–73).

After publishing *Die Radiolarien*, Haeckel embarked upon his most ambitious work, *Generelle Morphologie der Organismen* (two volumes, 1866), volume I dedicated to Gegenbaur and volume II to Goethe, Lamarck, and Darwin. He aspired to reorganize zoology along Darwinian lines, and exercised his polemical inclinations in doing so (Smit 1967:236, Breidbach 2006:105–115). Later, he explained

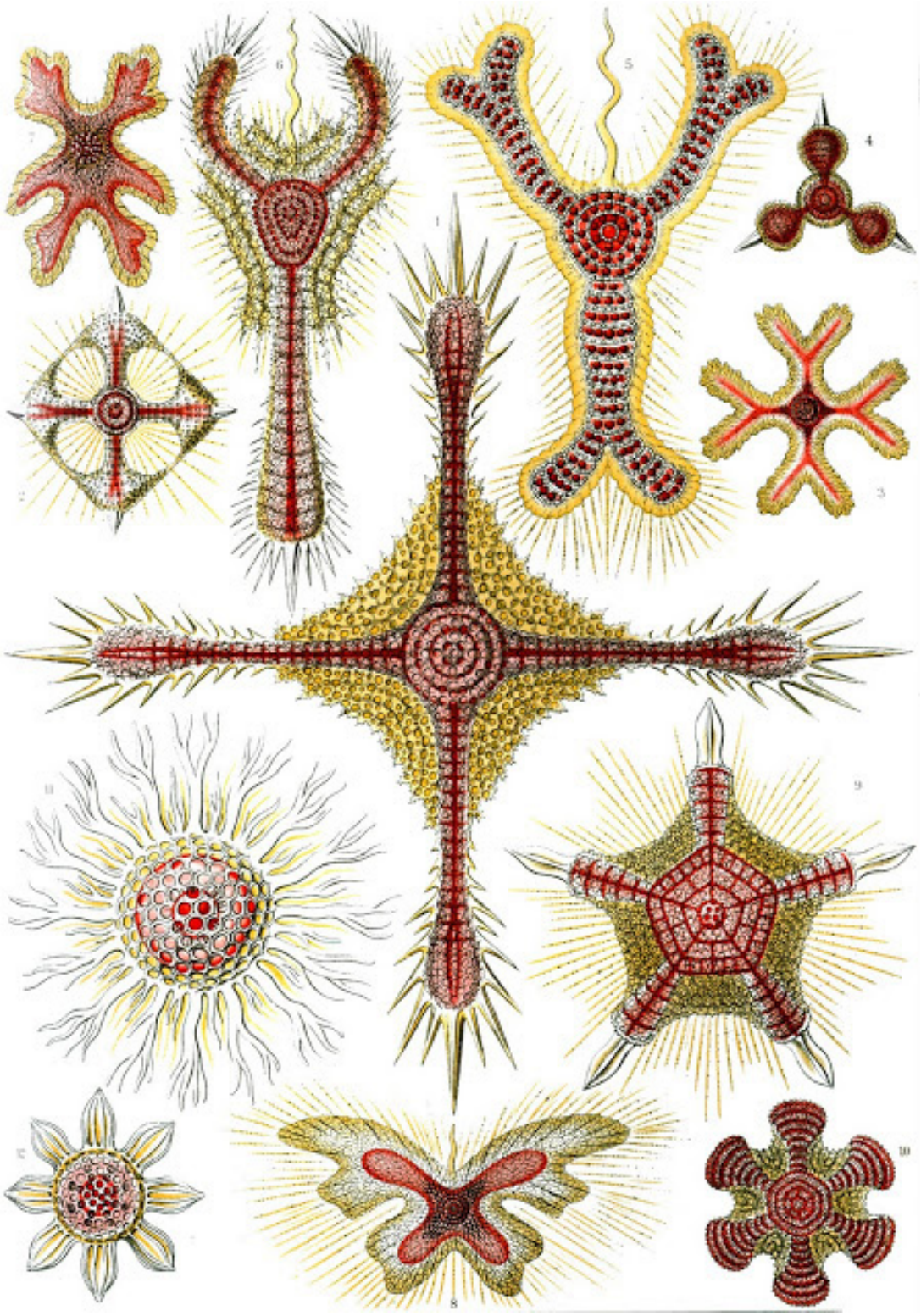

Fig. 2. Radiolaria. Haeckel 1899–1904. Lithographer Adolf Gilitsch transformed Haeckel's sketches into forms with somewhat exaggerated colors.

that this work (Haeckel 1876:xiii)

> *... constituted the first attempt to apply the general doctrine of development to the whole range of organic morphology (Anatomy and Biogenesis), and thus to make use of the vast march onwards which the genius of Charles Darwin has effected in all biological science by his reform of the Descent Theory and its establishment through the doctrine of selection.*

Every group of organisms that Haeckel studied became grist in his theoretical mill: he had a good command of Greek and coined many terms from Greek roots, including oecologie, phylum, ontogeny, phylogeny, and protista. He pioneered the construction of phylogenetic charts that indicated which groups of species were most closely related, and their likely ancestors (Dayrat 2003). He thought radiate rhizopods were the lowest level of animals, and so proper subjects for discussing the relationships between plants and animals. He coined the terms protista for all unicellular organisms. Other zoologists offered other names, but Haeckel's has stuck (Rothschild 1989:282–291). He also formulated a biogenetic law (ontogeny recapitulates phylogeny), which was a useful hypothesis to investigate. However, as a Haeckelian pronouncement it went too far and elicited far more disagreement than agreement (Churchill 1980, Rinard 1981, Rasmussen 1991). He provided a chart showing how to organize zoology, with ecology and animal geography placed under a broader heading of Animal Physiology.

His two volumes expounded upon this chart in great detail. Volume II, chapter 11 is "Oecologie und Chorologie" (Haeckel 1866, II:286–289, reprinted in Acot 1998:II, 703–706). Here is his explanation of ecology (translated by Stauffer 1957:140–141).

> *By ecology, we mean the whole science of the relations of the organism to the environment including, in the broad sense, all the "conditions of existence." These are partly organic, partly inorganic in nature; both, as we have shown, are of the greatest significance for the form of organisms, for they force them to become adapted. Among the inorganic conditions of existence to which every organism must adapt itself belong, first of all, the physical and chemical properties of its habitat, the climate (light, warmth, atmospheric conditions of humidity and electricity), the inorganic nutrients, nature of the water and of the soil, etc.*
>
> *As organic conditions of existence we consider the entire relations of the organism to all other organisms with which it comes into contact, and of which most contribute either to its advantage or its harm. Each organism has among the other organisms its friends and its enemies, those which favor its existence and those which harm it. The organisms which serve as organic foodstuff for others or which live upon them as parasites also belong in this category of organic conditions of existence. In our discussion of the theory of selection we have shown what enormous importance all these relations have for the entire formation of organisms, and specially how the organic conditions of existence exert a much more profound transforming action on organisms than do the inorganic. The extraordinary significance of these relations does not correspond in the least to their scientific treatment, however. So far physiology, to which this* [science] *belongs, has, in the most one sided fashion, almost exclusively investigated the conserving functions of organisms (preservation of the individual and the species, nutrition, and reproduction), and among the functions of relationship* [investigated] *merely those which are produced by the*

relations of single parts of the organism to each other and to the whole. On the other hand, physiology has largely neglected the relations of the organism to the environment, the place each organism takes in the household of nature, in the economy of all nature, and has abandoned the gathering of the relevant facts to an uncritical "natural history," without making an attempt to explain them mechanistically.

We have seen that the struggle for existence did not preclude Darwin from accepting the balance of nature (Egerton 2011:359–360). Haeckel also accepted the balance of nature (Haeckel 1866, II:233, translated in Di Gregorio 2005:159).

This indubitable and highly important fact is revealed most strikingly in the tendency on average for the absolute number of organic individuals populating our world to remain constant, and for only the relative numbers of the individual species to alter continually in relation to each other.

In the zoology chart (Fig. 3: lower right corner), Ecology is placed beside Geography of Animals, but in the chapter 11 title it is beside Chorology. "Chorologie," like "oecologie," is a term Haeckel coined. What did it mean? In *The History of Creation* (English, 1876, I:351) he said that Humboldt and Schouw had discussed plant geography and Berghaus and Schmarda animal geography

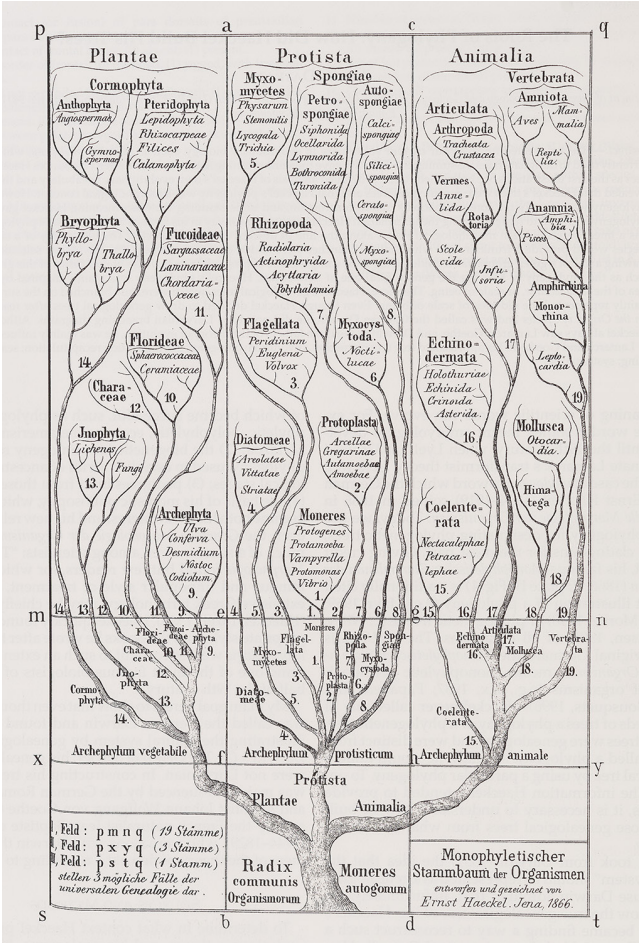

Fig. 3. Monophyletischer Stammbaum der organismen. The first phylogenetic chart for the evolution of life. Haeckel 1866, II: plate 1.

. . . yet Chorology as a whole remained, as far as their labours were concerned, only a desultory knowledge of a mass of individual facts*. It could not be called a science as long as the* causes *for the explanation of these facts were wanting. These causes were first disclosed by the theory of selection and its doctrine of the* migrations *of animal and vegetable species, and it is only since the works of Darwin and Wallace that we have been able to speak of an independent* science of Chorology.

In other words, animal geography could tell us that Darwin's finches on different Galápagos Islands were different species, but not tell us why. Biologists have accepted his new science of ecology but have

Fig. 4. Ernst Haeckel and Nikolai Miklucho-Maklai, one of three student assistants who joined Haeckel's private expedition to the Canary Islands, 1866. Ernst-Haeckel-Haus, Friedrich-Schiller-Universität, Jena, Germany.

not considered his chorology a new science. Some biologists adopted Haeckel's term, but most simply added Darwin's new explanations to the preexisting science of biogeography.

Having dedicated one volume of *Generelle Morphologie* to Darwin (in part), Haeckel, of course, sent Darwin a set. Darwin thanked him, but did he ever read it? His copy does contain marks and comments,

though not at the definition of oecologie (Di Gregorio and Gill 1990:355–357). Darwin would have been pleased that Haeckel wanted to reorganize zoology along evolutionary lines, but his own interest in the work concerned specific observations that Haeckel cited in support of his arguments. Haeckel became as much a missionary as a scientist, and missionaries repeat their message over and over to have it accepted as gospel. The readership of his ambitious 1866 tomes was not as great as Haeckel had hoped, so he gave a talk on his vision of zoology to the Jena faculty in January 1869, published that year in the university's periodical, reprinted in German in 1879, and translated into English in 1883 (Stauffer 1957:141, 144). This is the translated quotation from it which Allee, Emerson, Park, Park, and Schmidt placed at the beginning of their *Principles of Animal Ecology* (Allee et al. 1949:v).

> *By ecology we mean the body of knowledge concerning the economy of nature—the investigation of the total relations of the animal both to the inorganic and to its organic environment; including, above all, its friendly and inimical relations with those animals and plants with which it comes directly or indirectly into contact—in a word, ecology is the study of all those complex interrelations referred to by Darwin as the conditions of the struggle for existence.*

Still dissatisfied with the progress of his reform, in 1906 he published a one-volume abridgement of *Generelle Morphologie*. Repetition and a clear definition possibly helped establish his term, oecologie, for there were alternative suggestions available (Schurig and Nothacker 2001). In 1907 he established a Phyletisches Museum at the university, partly financed with royalties from his books (Uschmann 1959:165–175, Di Greogorio 2005:526–527). When his successor as director of the museum did not run it as Haeckel had expected, he turned his home into a museum—Ernst Haeckel-Haus (photos of both buildings in Smit 1967 and Richards 2008).

The first general survey of animal ecology was not by Haeckel, but by Würzburg professor of zoology Karl Gottfried Semper (1832–1893), who had been a student there during some of the time that Haeckel was (Mayr 1975). Semper spent the period December 1857–May 1865 exploring the Philippines and Palau, and afterwards published *Reisen im Archipel der Philippinen* (10 volumes, 1868–1905; see Johnson 1969). In 1877 he delivered 12 lectures at Lowell Technological Institute in Boston, then prepared them for publication in both German (1880) and English (1881). His *Animal Life as Affected by the Natural Conditions of Existence* never used Haeckel's term oecologie. He could hardly have been ignorant of Haeckel's *Generelle Morphologie,* which aspired to reorganize zoology. One Haeckel biographer (Di Gregorio 2005:292) characterized Semper as "a dangerous enemy because he saw with remarkable insight which aspects of the Gegenbaur-Haeckel partnership were due to one or the other of the partners and attacked them accordingly." One of Semper's attacks was entitled *Haeckelismus in der Zoologie* (1875, edition 2, 1876). Semper's preface to *Animal Life* dismissed talk about ontogeny and phylogeny as useless—without mentioning Haeckel. He did reprint a Haeckel drawing of a sponge, duly acknowledged (1881:342), and his explicit attack on Haeckel was relegated to a long end-note (1881:461–463). Semper accepted Darwin's theory; his aversion was Haeckel's dogmatic pronouncements (Di Gregorio 2005:293–296).

Haeckel adequately defined the new ecological science; but did he also contribute to the substance of ecology? The explorations of Humboldt and Darwin permanently impressed Haeckel. He never explored on a government expedition (though using government funds), but while at Jena he took some 90 trips,

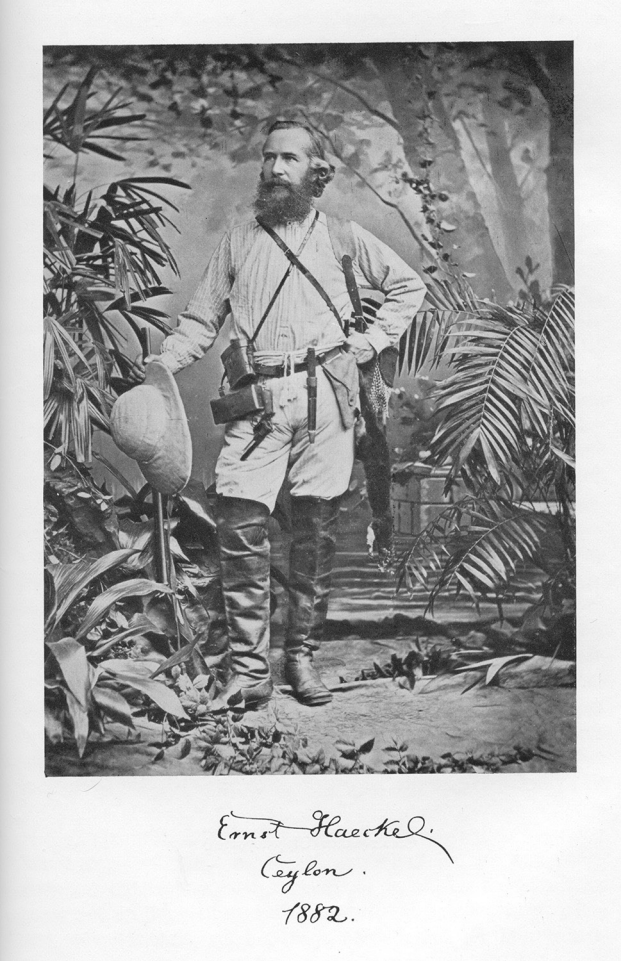

Fig. 5. Haeckel in Ceylon, 1882. Schmidt 1934: facing page 32.

in Europe (24 to Italy) or abroad (Bozzolato and Stolz 1993, Di Gregorio 2005:438, Breidbach 2006:205–209). He published accounts of some foreign journeys, which can be mined for observations comparable to those by his models, Humboldt and Darwin, in their travel books. Haeckel's books, based upon field journals and sometimes letters sent home, include *Arabische Korallen* (1876), *Indische Reisebriefe* (1882), *Aus Insulinde: Malayische Reisebriefe* (1901), *Italienfahrt: Briefe an die Braut, 1859–1860* (1921), *Berg- und Seefahrten: 1857–1883* (1923). Wallace's *Malay Archipelago* (1869, German edition, 1869) was a magnet, drawing both Haeckel, and later two of his students, to Indonesia (Hossfeld 2004). Landscape painting was a lifelong hobby, and Haeckel returned from journeys with numerous scenes of places visited, some of which appeared in his travel books. His only son, Walter, became a landscape painter who lived in Munich.

Since Ceylon (Sri Lanka) was a British colony, Haeckel's *Indische Reisebriefe* was translated into English (as *A Visit to Ceylon*, 1883). It will be our sample of his travel books. It would have been greatly enhanced by some of his artwork, and perhaps a map. However, it is buoyed up by his constant enthusiasm for what he found and his enjoyment of the scenery. It was a six-month expedition, although it took a month each for the journeys there and back, funded by the Weimar government, perhaps because he was director of the university zoology museum and would collect specimens and information for it. It was a good choice because Sri Lanka is a biodiversity "hot spot" (Groves and Manamendra-Arachchi 2009). He began planning for this trip at Easter 1881 and spent the summer learning oil painting, photography, use of gun, nets, and traps, and he departed with 16 trunks of equipment, including books and microscope (Haeckel 1883:6). He left Jena on 8 October by train to Trieste, and then by boat from Trieste to Bombay via the new Suez Canal. He had been to the Red Sea in March 1873 to study the marine life (the subject of his 1876 book), but that had not dampened his enthusiasm for "my beloved Medusae, which appeared in the mornings between nine and twelve, at first singly and then in swarms: blue *Rhizostoma*, rose-coloured *Aurelia*, and reddish-brown *Pelagia*" (Haeckel 1883:41). He obtained a bucket of seawater at night to study the phosphorescent creatures, finding that the majority were minute Crustacea, and the remainder were mostly Medusae, Salpae, and Annelidae, though the brightest was *Pyrosoma*. He spent much of the voyage writing descriptions of his treasures. November 8 was "the glorious and memorable

day of my life when I first set foot in a tropical land, admired tropical vegetation, and gazed in astonishment at tropical life in man and beast" (Haeckel 1883:42), and he had only reached Bombay, where he spent a very pleasant week on the estate of a German couple. It helped that both the Europeans and natives wherever he went were warmly welcoming.

Haeckel's enthusiasm for plants had never diminished just because he had become a zoologist, and his book actually devoted more space to describing plants than animals, simply because the plants stayed still while he looked and plucked (he carried a "tin" for them, presumably a vasculum). For 30 years he had dreamed of seeing what his heroes Humboldt and Darwin had written about the tropics, and the reality matched his expectations. He also saw brightly colored birds, butterflies, and lizards, but waited for Ceylon to collect them, as he would have to unpack his equipment. Details of his descriptions seem to indicate he was watching with one eye while writing with the other, and he still found time to paint scenery. Haeckel was as much tourist as Humboldt and Darwin had been on their longer expeditions, but that aspect of his book is omitted here, though his recording of demographic data (as they had) can be noted (Haeckel 1883:85–91). Unlike modern ecologists who write about the Third World, he thought Ceylon's 1250 square miles could support six or seven times its ~2,500,000 people. (Seven times that figure would be 17,500,000; the current population of Sri Lanka is over 21 million.) Ancient chronicles and village remains indicated that the northern half of Ceylon was more heavily populated 2000 years earlier than it was in 1881.

After a week in Bombay he took a boat to Colombo, on the western side of Ceylon, where he spent a month in a suburb, at the mouth of the Colombo River. The mangrove vegetation was very interesting. The term referred to several genera and families—*Rhizophora, Sonneratia, Somnitzera, Avicennia*, etc.—that had more or less spherical bushy crowns six or eight feet high, with thick stems above many-branched roots rising from the water (Haeckel 1883:99–100). The roots retained mud and sand from the river and extended the land. Roots also caught corpses and organic matter, and mangrove thickets were sometimes feared as sources of fevers (before mosquitoes were discovered as the carriers of malarial parasites). Haeckel did not fear fevers

Fig. 6. Ceylon (now Sri Lanka). Map by John P. Wood. National Geographic 129, No. 4 (April 1966):454.

where he stayed, because frequent storms washed away stagnant water. One Colombo host gave Haeckel several bird-catching spiders, *Myale*, which his host had seen chase small birds, *Nectarinia*, and small geckos, *Platyaactylus* (1883:107). Green parrots and large black monkeys eluded Haeckel's gun, but he did shoot a green lizard, *Hydrosaurus salvator*, over six feet long, sunning beside a ditch, which had a strong tail that could inflict wounds on assailants (Haeckel 1883:121–122).

From hot Colombo Haeckel traveled by train to the capital, Kandy, in central Ceylon at 1500 feet elevation, and on to a nearby botanical garden, Peradenia, founded in 1819. Its second superintendent, George Henry Kendrick Thwaites (1812–1882) had spent 30 years compiling *Enumeratio Plantarum Zeylandiae* (1864), describing about 3000 vascular species (Desmond 1977:612). Haeckel's copy had been owned by a German collector, Nietner, who had died in Ceylon, and Nietner's widow had given the copy to Haeckel (1883:147–148). The current superintendent, Henry Trimen (1843–1896), who befriended Haeckel, estimated that Ceylon had at least 5000 vascular species (Desmond 1977:618).

Haeckel had come to Ceylon mainly to study Monera, Radiolaria, Sponges, Corals, Medusae, and Siphonophora (Haeckel 1883:149), for which he wanted a bay to explore. Ceylon had three suitable bays, and he went to the two southwestern ones. He left Colombo for Galle on 9 December and remained there until the 12th, when he moved 15 miles away to Belligam, where he remained six weeks. In 1873, he had studied corals at Tur, in the Red Sea: "I had endeavoured to sketch these wonderful creatures and their communities with various other animals" (Haeckel 1883:184). Now he could compare those with Ceylon's coral communities, and found many genera and species common to both, but a much greater number and variety at Galle and Belligam. The general physiognomy was also different (Haeckel 1883:185).

> *While the reefs at Tur are, for the most part, conspicuous for warm colouring—yellow, orange, red, and brown—in the coral gardens of Ceylon, green predominates in a great variety of shades and tones: yellow-green* Alcyonia*, growing with sea-green* Heteropora*, and malachite-like* Anthophylla *side by side with olive-green* Millepora; Madrepora*, and* Astraea *of emerald hue with brown-green* Montipora *and* Maeandrina*.*

Haeckel had earlier mentioned that "Ransonnet's fine work especially contains much valuable information as to the coral reefs of Galle" (1883:153), and he continued (Haeckel 1883:185): "Ransonnet had already pointed out (Haeckel 1883:134) how singularly and universally green prevails in the colouring of Ceylon." That coloring prevailed on land as well as at sea, with birds, lizards, butterflies and beetles being mostly various shades of green, though the examples Haeckel cited were aquatic. He explained it by natural selection (1883:185–186): "The less the predominant colouring of any creature varies from that of its surroundings, the less will it be seen by its foes, the more easily can it steal upon its prey, and the more it is protected and fitted for the struggle for existence."

Haeckel employed four boatmen whom he paid 5 rupees a day, and paying more when they dived with a crowbar for coral chunks weighing 50–80 pounds. He had not attempted his own dives at the Red Sea, but did in Ceylon, and found it very rewarding to see marine life as it lived. However, "Never in my life have I been so gashed and mangled as after a few days of diving and coral fishing at Galle, and I suffered from the consequences for several weeks after" (Haeckel 1883:190), although he thought the experience was worth the pain. At Belligam he had available a government rest-house with four

Fig. 7. Waterfall at Pangerango, Tjiburrum, Java. By Haeckel.
Krausse 1984: inside front cover.

servants (in addition to his boatmen), and set up a satisfactory zoological laboratory, though there were no screens on the windows (Haeckel 1883:206–209). His surface net revealed many pelagic species similar to those of the Straits of Messina, Italy, but also new species. The *Challenger* Expedition had shown that oceanic species are more widespread than continental species (Haeckel 1883:220). Ceylon's heavy daily rains were great for land vegetation, but they also washed "large quantities of red earth into the sea, which clouds its waters on most parts of the coast; its saltiness is reduced, and that pure and transparent condition of the sea–water is destroyed, which is the first and indispensable condition

of life for many marine creatures, especially those of the coast" (Haeckel 1883:221). The 20 cases of specimens collected at Galle and 30 cases at Belligam were a rich reward for all his troubles in obtaining them (Haeckel 1883:225), and he still had time for an expedition into the wild high country with Trimen, who made all the arrangements.

Ceylon's tallest central mountains reached 7000–8000 feet elevation, and uplands covered about a quarter of the island. In 1817, much of it was home to elephants, bears, tigers, boars, elk, and primitive Veddah people, but in 1825 Governor Edward Barnes established a successful coffee plantation there, and in less than 20 years coffee planters cut and burned the forests and built more plantations. Soon, came "greedy" Golunda rats (*Golunda elliotti*), "mischievous" coffee-bugs (*Lecanium coffeae*), and parasitic fungus (*Hemileja vastatrix*). The response had been a switch to growing tea and *Cinchona* for quinine (Haeckel 1883:275–277). After touring plantations, Haeckel met Trimen at the resort Newera Ellia and they traveled south into wild country where primeval forest alternated with dry or marshy meadows, patenas. These grew so densely that mountain myrtle (*Careya arborea*) was the only tree that could occasionally find places to grow (Haeckel 1883:302–303). High plateaus had Nilloo shrubs (*Strobilanthus* sp.), which was the favorite haunt of the elephants that ate them. The forest contained climbing bamboo (*Arundinaria debilis*) that crept up the tallest trees and had long stems that hung down from tree branches (Haeckel 1883:309). Their explorations concluded at World's End, where the plateau ended at a 5000-foot cliff, and where Haeckel saw 10–12 wild elephants. He and Trimen then descended a steep, winding trail for five hours to the Black River, the second largest in Ceylon. Crocodiles had once been common, but had declined due to heavy river traffic (Haeckel 1883:324). There were still large lizards and turtles, abundant fish, and large butterflies. Gnats and mosquitoes were often a problem, but not in March. On the steamship back to Egypt, Haeckel arranged and completed his notes and sketches. In Egypt he realized that Egypt depended heavily on the date palm and Ceylon on the coconut palm, and he found the coconut palm more picturesque (Haeckel 1883:334). (Sometimes his comments were more Humboldtian than Darwinian.)

Modern oceanography was given a magnificent boost by the British *Challenger* expedition, 1873–1876 (Linklater 1972, Corfield 2003). After the voyage, specialists were invited to describe collected specimens within their expertise, and Haeckel wrote three of the reports, on *Deep-sea Medusae* (1882), *Radiolaria* (1887), and *Keratozoa* (1889). Since there were several years between the return of the expedition and publication of reports, some authors chose to include specimens from subsequent expeditions, duly identified, along with *Challenger* material. For Radiolaria, Haeckel decided to include a survey of all known species, worldwide: about 600 species were already known and 3508 were new (Breidbach 2006:210–227, Richards 2008:77–78). His introductory discussions are always interesting, and the introduction to *Radiolaria* included this discussion (Haeckel 1887:cxxxi).

> *205.* Symbiosis.—*Very many Radiolaria, but by no means all members of this class, live in a definite commensal relation with yellow unicellular Algae of the group Xanthellae. In the Acantharia they live within the central capsule* (Zooxanthella intracapsularis, ¶ *76*), *in the Spumellaria and Nassellaria, on the other hand, within the calymma but outside the central capsule* (Zooxanthella extracapsularis, ¶ *90*); *in the Phaeodaria a special form of these symbiotic unicellular Algae appears to inhabit the phaeodium in the extracapsulum, and to compose a considerable portion of the phaeodellae* (Zooxanthella phaeodaris, ¶ *90, or better perhaps*

Fig. 8. Haeckel, Report on the Radiolaria collected by H.M.S. *Challenger* during the years 1873–1876. Volume 18, 1887, plate 99, drawn by Haeckel. [Linklater 1972:169]

Zoochlorella phaeodaris, ¶ *89*). *Undoubtedly this commensal life is in very many cases of the greatest physiological significance for both the symbionts, for the animal Radiolarian cells furnish the inquiline Xanthellae not only with shelter and protection, but also with carbon dioxide and other products of decomposition for their nutriment; whilst on the other hand the vegetable cells*

> *of the Xanthellae yield the Radiolarian host its most important supply of nutriment, protoplasm and starch, as well as oxygen for respiration. Hence it is not only theoretically possible, but has been experimentally proved, that for a long period in closed vessels of filtered sea-water, kept exposed to the sunlight; the two symbionts furnish each other mutually with nourishment, and are physiologically supplementary to each other by reason of the opposite nature of their metastasis. This symbiosis is not necessary, however, for the existence of the Radiolaria; for in many species the number of Xanthellae is very variable and in many others they are entirely wanting.*

He then compared this symbiosis with that of lichens. Karl Brandt (1881), in Berlin, wrote on the algae that lived within invertebrates, and he named and discussed the genera *Zooxanthella* and *Zoochlorella* (Sapp 1994:11). The symbiosis concept originated in the work of Simon Schwendener (1869) on the relationship between algae and fungi in lichens, but it was botanist Albert Bernhard Frank who coined the term "Symbiotismus" in 1877, and botanist Anton de Bary used the term "Symbiose" in 1878 (Sapp 1994:4–7, Mitchell 2002).

While Haeckel was writing his reports for the *Challenger* Expedition, a fellow German, Victor Hensen (1835–1924), a year younger than Haeckel, who had been at Würzburg partly while Haeckel was there, began pioneering quantitative studies of plankton (Hensen's term, 1887) near his university at Kiel (Porep 1970, Rothschuh 1972). He had been in the Prussian Lantag (parliament) for four months, 1867–1868, long enough to establish a government research institute at Kiel to study fluctuations in fish populations. He thought phytoplankton might provide the food for animals in the sea that land plants provided for animals on land (Schlee 1973:229–238, Lussenhop 1974, Mills 1989:10–14, Breidbach 1990, Jahn 2000). If so, fluctuations in phytoplankton abundance could affect fish abundance. He began testing sampling methods around Kiel in 1887, and in 1889 he led a trans-Atlantic plankton expedition. An unexpected discovery was that cold northern waters were more productive than tropical waters—opposite to what exists on land. Northern waters were richer in nutrients than tropical waters. Hensen published his methods and findings from the start and continued doing so until 1893. His sampling method assumed that a sample represented a uniform density of plankton over a broad area (Mills 1989:15–28). Haeckel was an authority on plankton species and anatomy, and he assumed this made him competent to evaluate Hensen's work. He might have responded: interesting if accurate, but more research is needed to verify it. Instead, he was convinced (Haeckel 1890, translation Haeckel 1891:572)

> *...that the whole method employed by Hensen for determining the plankton is utterly worthless, and that the general results obtained thereby are not only false, but also throw a very incorrect light on the most important problems of pelagic biology.*

Hensen replied that Haeckel was ideologically motivated and scientifically backward (Breidbach 1990:109–110, Di Gregorio 2005:448), and four historians of biology have condemned Haeckel's response (Stauffer 1957:141–143, Damkaer and Mrozek-Dahl 1980:465–466, Taylor 1980:516). Haeckel's skepticism motivated Hensen and other marine biologists to spend more time testing sampling methods than they might have without such skepticism (Porep 1972, Lussenhop 1974:331–337, Mills 1989:29–42, Breidbach 1990, Jahn 2000). Determining oceanic plankton abundance remained a difficult challenge well into the 1900s (Herman and Platt 1980).

Fig. 9. A collection of sea anemones. Haeckel 1899–1904.

In 1898 Haeckel began a somewhat Platonic affair with Frida von Uslar-Gleichen, who was 34 years younger than he. She visited him after reading his popular *Natürliche Schöpfungsgeschichte* (History of Creation). In a following letter (Werner 1930:98) he told Frida about his invalid second wife, Agnes Huschke Haeckel (1842–1915), who was unhappy about his loss of faith, and about their depressed daughter. He trusted Frida's judgment, and she helped him select 100 illustrations for his *Kunstformen der Natur* (1899–1904), which was intended to show how nature could inspire artists (Di Gregorio 2005:515–518, Breidbach 2006:228–243, Richards 2008:405–406). Frida died on 11 November 1903 from a drug overdose (Richards 2008:413–419), and he wrote in a 1904 installment of *Kunstformen* concerning the illustration of a new species of jellyfish which he named *Rhopilema Frida (*quoted from a translation in Richards 2008:411).

> *This magnificent new species of the genus* Rhopilema*, one of the most beautiful of the medusae, was captured on 10 March 1901 under the equator in the Malaccan Straits. It bears its name as a remembrance of Fräulein Frida von Uslar-Gleichen, the artistic friend of nature, who has advanced the "Kunstformen der Natur" in numerous ways by her exquisite judgment.*

Since neither was willing to end his marriage because of their mutual love, their relationship was mainly conducted through the mail—over 900 letters written between them (Elsner 2000). Less than a third of them were first published without either author's name (Werner 1927), and translated into English with his name listed and a pseudonym for her (Werner 1930).

A recent biographer dated Gegenbaur's ending his friendship with Haeckel to 1899 (Di Gregorio 2005:545–546). A letter in Werner's edition of Haeckel and Frida's correspondence indicates the break occurred the following year (Haeckel to Frida, 18 February 1900, Werner 1927:149, 1930:165–166).

> *You asked recently what my friend Gegenbaur had said about the book* [Die Welträtsel (1899, Riddle of the Universe)]. *Up to now, not a word! He shares my views from first to last, but has always been of the opinion that these are esoteric mysteries to which the great public has no right; he too has always censured the sharp aggressiveness of my phraseology.*

By "he too has always censured…" Haeckel meant in addition to Frida's own complaints. Haeckel's son lent the correspondence with Frida to Werner to edit. This letter and the one quoted below are not in the Ernst-Haeckel-Haus archives today (Thomas Bach e-mail 19 July 2010); all of their existing correspondence is in the Elstner edition (2000). Either these two letters were lost after Werner edited them, or he filled in gaps with what he imagined Haeckel thought. Apparently, *Die Welträtsel* was the last straw for Gegenbaur, who was not the only professor unhappy with it (Di Gregorio 2005:512–513, Richards 2008:7). Haeckel never recovered from the loss of Gegenbaur's friendship.

When Haeckel was an undergraduate at Würzburg, his letters home show that he was a sincere Protestant, but he met skeptics there who made him feel uneasy (Haeckel 1923). He wrote to Frida about his loss of faith (22 February 1898, Werner 1927:31, 1930:29).

> *Both my beloved parents remained pious Christians in the best sense of the word to their death; and even I as a student up to my 21st year, clung ardently to the Church—faith that I*

loved—despite all the assaults of science. It was only when I had penetrated farther and farther into the mysteries of life and its evolution, when as a practicing physician I grew thoroughly familiar with all the misery of mankind, and as a student with all the grandeur of "godless" nature, that I became after the most desperate spiritual conflicts a freethinker and a pantheist.

The death of his first wife had also been a blow to his faith (Richards 2008:107). Many scientists have outgrown a childhood religion without attacking it as an adult, but Haeckel did attack Christianity in *Die Welträtsel*, which was a best-seller and translated into several languages (Richards 2008:398–403). He replaced Christianity with a secular religious philosophy, monism (DeGrood 1965). He may not have heard or not appreciated the adage that one can attract more flies with honey than vinegar, but he might have noticed that Darwin was conciliatory and thereby persuaded Protestants, including Asa Gray, to accept evolution (Richards 2008:385). Haeckel wanted to replace godly religions with a secular monistic religion (Holt 1971).

He may have expected Christians to counterattack, but he may not have anticipated that questioning his scientific honesty would be one weapon they used. Haeckel was adept at illustrating his own publications, and he illustrated his biogenetic law with illustrations of embryos of unrelated vertebrate species at early and later stages, showing strong similarities in an early stage and progressive differences in later stages (Breidbach 2006:117–147). While this progressive differentiation does occur, contemporary zoologists accused him of exaggerating the similarities of the early stages, and recent studies show that he did (Richardson et al. 1998, Richardson and Keuck 2001, Di Gregorio 2005:229–230, Hopwood 2006, Richards 2008:301–311). Religious opponents were glad to take up this complaint to not only discredit Haeckel, but also to discredit evolutionary theory. Some of his scientist critics were also Christians, and it turned out that his own choice as his successor as head of his Phyletic Museum, his former student, Ludwig Plate (1862–1937), was one of them. Plate gradually pushed him out of rooms that were to remain his for his work, and in 1921 Plate explained why (translation quoted from Richards 2008:423).

Haeckel was a crass materialist and atheist and had ridiculed Christianity in numerous ways. For that reason he was celebrated by the Social Democrats and the Jews as the world-famous light of true science. I, on the other hand, am an idealist, freethinking Christian, German populist, and anti-Semite.

We have reviewed three areas of Haeckel's controversies: quantitative plankton studies, anti-Christianity, and falsified embryo illustrations. Even worse, he has been accused of founding an ideology and organization that led to Nazi ideology (Gasman 1971, 1998). Haeckel's monism seemed to be abstract philosophy (Haeckel 1877:495).

The unity in the conception of the universe (or "monism") to which the new doctrine of evolution thus leads us, annuls the opposition which hitherto existed between the different world systems. It avoids the one-sidedness of materialism as well as that of spiritualism, it unites the practical idealism with the theoretical realism, it combines natural science with mental science to form an all-comprising uniform general or total science.

In 1906 Haeckel organized the Monistenbund (Monist League). An American member, Paul Carus,

founded the periodical, *Monist*, and the Open Court Press. He opposed Haeckel's attacks and felt Monists should stick to positive messages (Richards 2008:371–373). The German Monistenbund, however, was heavily influenced by Haeckel's ideas.

We want unblemished heroes and can be thankful for Darwin, Lyell, Wallace, Hooker, Bates, Asa Gray, and many others who lived in stable, strong nations. Haeckel grew up in Germany in turmoil. A failed 1848 revolution left many Germans deeply frustrated by a lack of German unity. A similar struggle occurred in Italy, which achieved unification in several steps in 1860–1861. Haeckel was in Italy around that time, and when he returned to Germany, he wrote to a friend that if the degenerate Italians could unify, so could the superior Germans (partly quoted in translation in Gasman 1971:3–4). Haeckel believed some human races were superior to others, and in 1868 he published a chart of human evolution with Germans, Jews, and two other groups at the top (reproduced in Richards 2008:245). In the early 1890s, he responded to an inquiry about Jews: he deplored ignorant Russian Jews, but highly respected educated German Jews (translated in Richards 2008:504, note 15).

> *I hold these refined and noble Jews to be important elements in German culture. One should not forget that they have always stood bravely for enlightenment and freedom against the forces of reaction, inexhaustible opponents, as often as needed, against the obscurantists.*

On the other hand, he had no more sympathy for Judaism than for Christianity, and he thought Jews should be assimilated into German culture. Haeckel was clearly a nationalistic chauvinist, and that influenced his German Monistenbund. However, the Nazis banned his books (De Rooy 1990, Mocek 1991). Gasman's response to attacks on his 1971 blame of Haeckelism for Nazism was to publish a longer book with the same argument (1998). Stephen Jay Gould (1977:77–78) accepted the argument in Gasman's 1971 book, without further elaboration. Bramwell (1989:49–52) and Richards (2008:500–505), however, provide strong arguments against Gasman's thesis. Yet Gasman remained unconvinced, defending his thesis again in 2010 (Gasman and Hopwood 2010). Ecologists who view Haeckel as a founder of their science can recognize that Washington, Jefferson, and other American founding fathers have not lost standing because they owned slaves, deplorable as that now appears. However one judges Haeckel's faults, he remains also an important founder of ecology.

Literature cited

Acot, P., editor. The European origins of scientific ecology (1800–1901). B. P. Hamm, translator. Two volumes. Éditions des Archives Contemporaines and Gordon and Breach, Amsterdam, The Netherlands.

Allee, W. C., A. E. Emerson, O. Park, T. Park, and K. P. Schmidt. 1949. Principles of animal ecology. W. B. Saunders, Philadelphia, Pennsylvania, USA.

Bary, H. A. de. 1878. Ueber symbiose. Tagblatt für Versammlung Deutscher Naturforscher und Aertze 121–126. Cited from M. E. Mitchell. 2002. "Such a strange theory": Anglophone attitudes to the discovery that lichens are composite organisms, 1871–1890. Huntia 11:193–207.

Bary, H. A. de. 1879. Die Erscheinung der Symbiose. Trübner, Strassburg, Germany [now France]. Cited from M. E. Mitchell. 2002. "Such a strange theory": Anglophone attitudes to the discovery that lichens are composite organisms, 1871–1890. Huntia 11:193–207.

Bozzolato, G., and R. Stolz. 1993. Haeckel e l'Italia: la vita come scienza e come storia. Edizioni Centro Internazionale di Storia dello Spazio del Tempo, Brugine, Italy.
Bramwell, A. 1989. Ecology in the 20th century: a history. [Despite title, primarily a history of ecologism.] Yale University Press, New Haven, Connecticut, USA.
Brandt, K. 1881, Über das zusammenleben von Algen und Tieren. Biologisches Centralblatt 1:524–527.
Breidbach, O. 1990. Über die Geburtswehen einer quantifizierenden Ökologie—der Streit im Kieler Plankton-Expedition, 1889. Berichte zur Wissenschaftsgeschichte 13:101–114.
Breidbach, O. 2006. Visions of nature: the art and science of Ernst Haeckel. Prestel, Munich, Germany.
Bulnheim, H.-P. 1990. A century of marine zoological and ecological research around Helgoland Island. Pages 84–93 *in* Ocean sciences: their history and relation to man. Bundesamt für Seeschiffahrt und Hydrographie, Hamburg, Germany.
Churchill, F. B. 1980. The modern evolutionary synthesis and the biogenetic law. Pages 112–122 *in* E. Mayr and W. B. Provine, editors. The evolutionary synthesis. Harvard University Press, Cambridge, Massachusetts, USA.
Coleman, W. 1978. Carl Gegenbaur (1826–1903), comparative anatomy and morphology, zoology. Dictionary of Scientific Biography 15:165–171.
Corfield, R. M. The silent landscape: the scientific voyage of HMS *Challenger*. Joseph Henry Press, Washington, D.C., USA.
Damkaer, D. M., and T. Mrozek-Dahl. 1980. The plankton expedition and the copepod studies of Friedrich and Maria Dahl. Pages 462–473 *in* M. Sears and D. Merriman, editors. Oceanography: the past. Springer-Verlag, New York, New York, USA.
Darwin, C. R. 2001. The correspondence. Volume 12: 1864. F. Burkhardt and six other editors. Cambridge University Press, Cambridge, UK.
Dayrat, B. 2003. The roots of phylogeny: how did Haeckel build his trees? Systematic Biology 52:515–527.
DeGrood, D. H. 1965. Haeckel's theory of the unity of nature: a monograph in the history of philosophy. Christopher, Boston, Massachusetts, USA.
De Rooy, P. 1990. Of monkeys, blacks, and proles: Ernst Haeckell's theory of recapitulation. Pages 7–34 *in* J. Breman, editor. Imperial monkey business: racial supremacy in social Darwinist theory and colonial practice. VU University Press, Amsterdam, The Netherlands.
Desmond, R. 1977. Dictionary of British and Irish botanists and horticulturists, including plant collectors and botanical artists. Edition 2, 1994. Taylor and Francis, London, UK.
Di Gregorio, A. M. 2005. From here to eternity: Ernst Haeckel and scientific faith. Vandenhoeck and Ruprecht, Göttingen, Germany.
Di Gregorio, A. M., and N. W. Gill, editors. 1990. Charles Darwin's marginalia. Volume 1. Garland, New York, New York, USA.
Egerton, F. N. 2011. History of ecological sciences, part 40: Darwin's evolutionary ecology. ESA Bulletin 92:351–374.
Elsner, N., editor. 2000. Das ungelöste Welträtsel: Frida von Uslar-Gleichen und Ernst Haeckel, Briefe und Tagebücher. Three volumes: I. 1898–1900; II. 1900–1903; III. Briefe der Familie, Dokumente und Anhang. Wallstein, Göttingen, Germany.
Gasman, D. 1971. The scientific origins of national socialism: social Darwinism in Ernst Haeckel and the German Monist League. American Elsevier, New York, New York, USA.

Gasman, D. 1998. Haeckel's monism and the birth of fascist ideology. Peter Lang, New York, New York, USA.
Gasman, D., and N. Hopwood. 2010. Letters to the editor. Isis 101:838.
Gliboff, S. 2008. H. G. Bronn, Ernst Haeckel, and the origins of German Darwinism: a study in translation and transformation. MIT Press, Cambridge, Massachusetts, USA.
Gould, S. J. 1977. Ontogeny and phylogeny. Harvard University Press, Cambridge, Massachusetts, USA.
Groves, C., and K. Manamendra-Arachchi. 2009. Sri Lanka. Pages 866–870 *in* Encyclopedia of islands. University of California Press, Berkeley, California, USA.
Haeckel, E. H. P. A. 1862. Die Radiolarien (*Rhizopoda radiaria*). Reimer, Berlin, Germany.
Haeckel, E. H. P. A. 1866. Generelle Morphologie der Organismen. Allgemeine Grundzüge der organischen Formen-Wissenschaft, mechanische Begründet durch die von Charles Darwin reformirte Descendenz-Theorie. Volume I: Allgemeine Anatomie der Organismen. 32 + 574 pages; volume II: Alllgemeine Entwickelungsgeschichte der Organismen. 140 + 462 pages. Georg Reimer, Berlin, Germany.
Haeckel, E. H. P. A. 1876. The history of creation: or the development of the earth and its inhabitants by the action of natural causes. Two volumes. E. R. Lankester, revised translation. H. S. King and Son, London, UK. D. Appleton, New York, New York, USA.
Haeckel, E. H. P. A. 1877. On the evolution theory at the present time. Nature 16:492–496.
Haeckel, E. H. P. A. 1882. Ways of life in Ceylon: Professor Haeckel's record of his own experiences there. New York Times 30 September:2. From London Daily News.
Haeckel, E. H. P. A. 1883. A visit to Ceylon. C. Bell, translator. Kegan Paul, Trench, London, UK.
Haeckel, E. H. P. A. 1887. Report on the Radiolaria collected by H.M.S. *Challenger* during the years 1873–1876. Volume 18 in two parts *in* Report on the scientific results of the voyage of H.M.S. *Challenger* during the years 1873–1876. J. Murray, editor. Eyre and Spottiswoode, London, UK.
Haeckel, E. H. P. A. 1890. Plankton-Studien: Vergleichende Untersuchungen über die Bedeutung und Zussammensetzung der pelagischen Fauna und Flora. Gustav Fischer, Jena, Germany.
Haeckel, E. H. P. A. 1891. Planktonic studies: a comparative investigation of the importance and constitution of the pelagic fauna and flora. G. W. Field, translator. Report of U.S. Commission of Fish and Fisheries 565–641.
Haeckel, E. H. P. A. 1899–1904. Kunstformen der Natur. Bibliographisches Instituts, Leipzig, Germany.
Haeckel, E. H. P. A. 1900. The riddle of the universe, at the close of the nineteenth century. J. McCabe, translator. Harper and Brothers, New York, New York, USA.
Haeckel, E. H. P. A. 1923. The story of the development of a youth, by Ernst Haeckel: letters to his parents, 1852-1856. G. B. Gifford, translator. Harper and Brothers, New York, New York, USA.
Hansen, B. 1970. Heinrich Georg Bronn (1800–1862), paleontology, zoology. Dictionary of Scientific Biography 2:497–498.
Herman, A., and T. Platt. 1980. Meso-scale spatial distribution of plankton: co-evolution of concepts and instrumentation. Pages 204-225 *in* Oceanography: the past. Springer-Verlag, New York, New York, USA.
Holt, N. 1971. Ernst Haeckel's monistic religion. Journal of the History of Ideas 32:265–280.
Hopwood, N. 2000. Ernst Haeckel, 1834–1919, German zoologist. Pages 317–318 *in* A. Hessenbruch,

editor. Reader's guide to the history of science. Fitzroy Dearborn, London, UK.
Hopwood, N. 2006. Pictures of evolution and charges of fraud: Ernst Haeckel's embryological illustrations. Isis 97:260–301.
Hossfeld, U. 2004. The travels of Jena zoologists in the Indo-Malayan region. California Academy of Sciences Proceedings 55, Supplement 2:77–105.
Jahn, I. 2000. Die Humboldt-Stipendien für Planktonforschung und die Haeckel-Hensen Kontroverse. Pages 47–60 *in* E. Höxtermann, J. Kaasch, and R. Kinzelbach, editors. Berichte zur Geschichte der Hydro- und Meeresbiologie und weitere Beiträge zur 8. Jahrestagung der GGGTB in Rostock, 1999. VWB, Berlin, Germany.
Johnson, R. I. 1969. Semper's *Reisen im Archipel der Philippenen, Wissenshaftliche Resultate*, 1867–1916. Society for the Bibliography of Natural History Journal 5:144–147.
Krausse, E. 1987. Ernst Haeckel. B. G. Teubner, Leipzig, Germany.
Linklater, E. 1972. The voyage of the *Challenger*. Doubleday, Garden City, New York, USA.
Lohff, B. 1990. The unknown wonders of the sea: Johannes Müller's research in marine biology. Pages 141–148 *in* Ocean sciences: their history and their relation to man. Bundesamt für Seeschiffahrt und Hydrograpie, Hamburg, Germany.
Lussenhop, J. 1974. Victor Hensen and the development of sampling methods in ecology. Journal of the History of Biology 7:319–337.
Mayr, E. 1975. Carl Gottfried Semper (1832–93), zoology, ecology. Dictionary of Scientific Biography 12:299.
Mills, E. L. 1989. Biological oceanography: an early history, 1870–1960. Cornell University Press, Ithaca, New York, USA.
Mitchell, M. E. 2002. "Such a strange theory": Anglophone attitudes to the discovery that lichens are composite organisms, 1871–1890. Huntia 11:193–207.
Mocek, R. 1991. Two faces of biologism: some reflections on a difficult period in the history of biology in Germany. Pages 279–291 *in* W. Woodward and R. S. Cohen, editors. World views and scientific discipline formation. Kluwer Academic Publishers, London, UK.
Nyhart, L. K. 1995. Biology takes form: animal morphology and the German universities, 1800–1900. University of Chicago Press, Chicago, Illinois, USA.
Porep, R. 1970. Der Physiologie und Planktonforscher Victor Hensen (1835–1924): sein Leben und sein Werk. Kieler Beiträge zur Geschichte der Medizin und der Pharmazie 9:1–147.
Porep, R. 1972. Methodenstreit in der Planktonologie: Haeackel contra Hensen. Medizinhistorisches Journal 7:72–83.
Richards, R. J. 2008. The tragic sense of life: Ernst Haeckel and the struggle over evolutionary thought. University of Chicago Press, Chicago, Illinois, USA.
Richardson, M. K., J. Hanken, L. Selwood, G. M. Wright, R. J. Richards, C. Pieau and A. Raynaud. 1998. Haeckel, embryos, and evolution. Science 280:983–985.
Richardson, M. K., and G. Keuck. 2001. A question of intent: when is a 'schematic' illustration a fraud? Nature 410:144.
Rinard, R. G. 1981. The problem of the organic individual: Ernst Haeckel and the development of the biogenetic law. Journal of the History of Biology 14:249–275.
Rothschild, L. J. 1989. Protozoa, Protista, Protoctista: what's in a name? Journal of the History of Biology 22:277–306.

Sapp, J. 1994. Evolution by association: a history of symbiosis. Oxford University Press, New York, New York, USA.
Schlee, S. 1973. The edge of an unfamiliar world: a history of oceanography. E. P. Dutton, New York, New York, USA.
Schmidt, H. 1934. Ernst Haeckel: Denkmal eines grossen Lebens. Walter Biedermann, Jena, Germany.
Schurig, V., and R. Nothacker 2001. Von der "Oeconomia naturae" zur "Oecologie"; historische Begrüngsversuche einer biologischen Umweltlehre vor 1866. Verhandlungen zur Geschichte und Theorie der Biologie 7:221–235.
Schwendener, S. 1869. Die Algentypen der Flechtengonidien. Basel. Cited from M. E. Mitchell. 2002. "Such a strange theory": Anglophone attitudes to the discovery that lichens are composite organisms, 1871–1890. Huntia 11:193–207.
Smit, P. 1967. Ernst Haeckel and his "Generelle Morphologie": an evaluation. Janus 54:236–252 + 2 plates.
Semper, K. G. 1881. Animal life as affected by the natural conditions of existence. D. Appleton, New York, New York, USA. 1977. Arno Press, New York, New York, USA.
Stauffer, R. C. 1957. Haeckel, Darwin, and ecology. Quarterly Review of Biology 32:138–144.
Taylor, F. J. R. 1980. Phytoplankton ecology before 1900: supplementary notes to the "Depths of the Ocean." Pages 509–521 *in* M. Sears and D. Merriman, editors. Oceanography: the past. Springer-Verlag, New York, New York, USA.
Uschmann, G. 1959. Geschichte der Zoologie und der zoologischen Anstalten im Jena, 1779–1919. Gustav Fischer, Jena, Germany.
Uschmann, G. 1972. Ernst Heinrich Philipp August Haeckel (1834–1919), zoology. Dictionary of Scientific Biography 6:6–11.
Werner, J., editor. 1927. Franziska von Altenhausen: ein Roman aus dem Leben eines berühmten Mannes in Briefen aus den Jahren 1898/1903. Köhler und Amelang, Leipzig, Germany.
Werner, J., editor. 1930. The love letters of Ernst Haeckel, written between 1898 and 1903. I. Zeitlin, translator. Harper and Brothers, New York, New York, USA.
Wilson, H. F., and M. H. Doner. 1937. The historical development of insect classification. John S. Swift, St. Louis, Missouri, USA.

Acknowledgments

I thank Dr. Thomas Bach and Dr. Thomas Potthast, Institut für Geschichte der Medizin, Naturwissenschaft und Technik, Ernst-Haeckel-Haus, Friedrich-Schiller-Universität, Jena, Germany for their assistance, and for the illustration of Haeckel and Miklucho.