Mediating Objects.
Scientific and Public Functions of Models in Nineteenth-Century Biology
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Abstract - The aim of this article is to examine the scientific and public functions of two- and three-dimensional models in the context of three episodes from nineteenth-century biology. I argue that these models incorporate both data and theory by presenting theoretical assumptions in the light of concrete data or organizing data through theoretical assumptions. Despite their diverse roles in scientific practice, they all can be characterized as mediators between data and theory. Furthermore, I argue that these different mediating functions often reflect their different audiences that included specialized scientists, students, and the general public. In this sense, models in nineteenth-century biology can be understood as mediators between theory, data, and their diverse audiences.

Keywords - Models as mediators, material models, history of Embryology, Ernst Haeckel, Wilhelm His

Models are ubiquitous in scientific practice and of crucial importance in a large variety of disciplines. Despite their abundance, models are not clearly defined entities and their overwhelming diversity – consider theoretical models in quantum physics compared to anatomical teaching models – undermines the prospects of an all-encompassing definition (Leonelli 2007). One way of reacting to this situation is to distinguish between different kinds models such as theoretical, two-dimensional, or three-dimensional models. Many current debates draw this distinction at least implicitly by focusing solely on theoretical models. Especially philosophers follow Ian Hacking in considering a model “something you hold in your head rather than in your hands” (Hacking 1983, 219). It is clear that theoretical models often differ considerably from two- and threedimensional models and it seems that we can avoid many definitional problems by clearly distinguishing between them.

For discussions of theoretical models in philosophy of science, see Bailer-Jones (2009) as well as Frigg and Hartmann (2006). Discussions of material models are more common in the history of science, see Dirks and Knobloch (2008) and especially Hopwood and de Chadarevian (2004). Natascha Myers proposes an interesting account that combines theoretical and material models “in the embodied imagination of the modeler” (Myers 2007, 63).
However, even if we focus on only one type of models, definitions still have clear limits. In the case of three-dimensional material models, there do not seem to be any physical or abstract features that distinguish material models from other material objects. A scientific model that is made with a toy construction kit (such as some DNA-models) does not have any physical properties that distinguish it from a toy – the very same object could be a toy in a different context. Whether an object is a scientific model or toy crucially depends on how it is used. The same point can be made with respect to other objects such as jars with peas in different colors as they are sometimes found in biological teaching collections. Whether these jars are a model of Mendelian inheritance or just a food stock solely depends on how they are used. Furthermore, they could “turn” into a model of Mendelian inheritance for just an hour by being brought to class by a biology teacher.

If there are no physical or abstract features that distinguish material models from other material objects, material models have to be understood in the context of scientific practice: an object qualifies as a model if and only if it is used in specific ways. This agency-focused approach is consistent with much of the current philosophical literature on models (e.g., Giere 2004; 2010; Myers 2007) but it does not solve the problem that models are far too diverse to allow a substantial and all-encompassing definition. Of course, it is possible to point out some very general functional features of scientific models. For example, models are used as representations of something else such as an object, a process, a fact, or a theory. Furthermore, they are usually non-arbitrary representations in the sense that their representation is not purely conventional. This distinguishes models from arbitrary linguistic representation. The word “embryo” is a representation but it is not a model of an embryo as the connection between the word and its referent is entirely arbitrary.

Unfortunately, general characterizations of material models (or even scientific models in general) such as “physical objects that are used as non-arbitrary representations” will not provide a precise definition with necessary and sufficient conditions. For example, not every non-arbitrary representation is a model. Sculptures and drawings are non-arbitrary
representations but they are not necessarily models. Again, there are no physical or general functional features that distinguish statues or drawings that are models (e.g., a statue of a chimpanzee in a natural history museum or a drawing of chimpanzee in a biology book) and statues or drawings that do not qualify as models (e.g., a statue of a chimpanzee in an art gallery or a drawing of a chimpanzee in a comic book). A satisfying characterization of models will have to go beyond these general features and offer a more fine-grained description of the uses of models in scientific practice.

The goal of this article is to offer a more substantial philosophical characterization of two- and three-dimensional models by describing them in concrete historical and disciplinary contexts. By discussing models in three episodes of nineteenth-century embryology and comparative morphology, I hope to be able to provide an account that is richer than a discussion of models that seeks a general definition of material or scientific models. My account is based on Mary Morgan and Margaret Morrison’s idea that models serve as mediators between theory and data (Morgan and Morrison 1999). According to Morgan and Morrison, scientific models are not simply derived from theory but they are not just data, either. Instead, they incorporate aspects of both theory and data and play an autonomous role as mediators between them. For example, models can be used to explore a theory that is already in place, but they can also serve as instruments for exploring processes for which theories do not give good accounts yet.

Although Morgan and Morrison developed the framework of models as mediators with theoretical models in economics and physics in mind, I will argue that it also works surprisingly well in the context of two- and three-dimensional models in nineteenth-century biology. This extension of the framework of models as mediators should not be confused with a precise and general definition of “scientific model.” On the contrary, Morgan and Morrison’s proposal works so well for different modeling contexts because it is broad enough to encompass a diversity of mediating functions. A generalized concept of models as mediators helps to uncover important similarities between different kinds of models even if
it does not lead to an all-encompassing definition. While the concept of models as mediators between data and theory is helpful in characterizing the different methodological standards of model construction, I also argue that these mediating functions have to be understood in the context of their diverse audiences. While research models were often created with the ambition to present very specific data to an equally specific audience, many popular models embodied general theoretical assumptions through schematized and simplified representations. Furthermore, I argue that even models that were intended for rather specialized audiences often reached a broader public and became of crucial importance in the public engagement with science. I therefore suggest to describe models in nineteenth-century biology as mediators between theory, data, and their diverse audiences.

Models on Paper
In 1863, 26-year young Ernst Haeckel held his first major lecture on evolutionary theory at a meeting of the Gesellschaft Deutscher Naturforscher und Ärzte (Assembly of German Naturalists and Physicians) in Stettin, today Szczecin, in western Poland. Four years after the publication of The Origin of Species, the audience was well-aware of the controversies surrounding Darwin's work. However, Haeckel's goal with this lecture was not just to introduce evolutionary theory but to introduce evolutionary theory as the battle ground of two fundamentally opposed world views:

If, despite these and many other difficulties, I try to draw you into the strife that has arisen as result of Darwin's theory of Evolution, it is because of the vast dimensions that this strife has already assumed. Already the whole vast army of zoologists and botanists, of palaeontologists and geologists, of physiologists and philosophers is divided into two widely separated parties. On the standard of the progressive Darwinists are the words “Evolution and Progress.” From the camp of the conservative foes of Darwin sounds the cry: “Creation and Species.” (Haeckel 1924, 4-5, translation, Haeckel 1883, 4)

Haeckel's contribution to this “strife” was meant to be twofold. On the one hand, he wanted to educate the public by presenting evolutionary
theory in a non-technical way. By the end of the nineteenth century, he would become the most influential popular science writer in Germany. Haeckel sold 100,000 copies of his *Welträthsel* in the year of its publication and the book was translated into twenty-four languages (Richards 2005, 2-3). On the other hand, Haeckel also understood himself as a scientist who contributed to the advancement of evolutionary theory – most importantly with his marine biological and embryological research. Embryology was at the very core of Haeckel's evolutionary program and supposed to provide a major source for the understanding of phylogenetic development. Haeckel's basic idea is expressed by the recapitulation theory (or biogenetic law) which he summarized as the idea that "ontogeny recapitulates phylogeny" (e.g., Haeckel 1866, 371; 1872, 276; 1874, 58). Haeckel's starting point was Karl Ernst von Baer's observation that embryos develop from general to more specific forms and only gradually acquire species-specific characteristics (e.g., Baer 1828, 223). In his recapitulation theory, Haeckel offered an evolutionary interpretation of this observation by arguing that the ontogenetic development actually recapitulates the evolutionary history of the species (cf. Churchill 2007). Humans, for example, are phylogenetically more closely related to other mammals than to amphibians, and closer related to amphibians than to fish. This is why a human embryo "at an early stage has essentially the anatomical structure of a fish, later the constitution of amphibian and mammalian forms" (Haeckel 1874, 4). In this sense, recapitulation theory promised the reconstruction of the evolutionary history of species through embryological research.

The general claims of the recapitulation theory were mediated by specific models of the ontogenetic development of vertebrates. Figure 1 shows the initial formation of embryos of a dog, a hen, and a tortoise. They are indistinguishable and therefore seem to support Haeckel's claim that vertebrates share an early stage in ontogenetic development. Figure 2 shows eight vertebrate embryos in different developmental stages. During the first stage, the embryos are almost indistinguishable. The second row shows specific features of fish and amphibian embryos, while the remaining embryos only differ in details. In the last row, all embryos
are clearly distinguishable. Nevertheless, the four mammalian embryos share many morphological features that separate them from the four other vertebrate embryos.

Haeckel’s embryo drawings fit the framework of models as mediators between theory and data well as they present the recapitulation theory in the light of specific anatomical details which are by no means implied by the general theoretical assumptions that Haeckel was promoting. Although Haeckel did not discuss the sources he used for his drawings, he most likely relied on a variety of publications from other scientists such as Kölliker and Bischoff (Hopwood 2006; Richards 2008, 242) as well as his own observations. Haeckel’s eclectic and undisclosed use of different sources would later become a focus of criticism and Haeckel certainly utilized the available sources in an often casual way to make his theoretical points. This is especially evident in his illustration of three vertebrate embryos (Figure 1) that seemed to support the recapitulation theory because of their stunning similarity but were simply printed from the same woodcut. In Figure 2, Haeckel also simplified representations in order to stress similarities as they were predicted by his theory. For example, Haeckel’s drawings neglected size differences and excluded the yolk material from the pictures because they would distract from similarities which were essential for the recapitulation theory (Haeckel 1874, 256).

While all of this illustrates the dominance of theoretical assumptions in Haeckel’s illustrations, he did not ignore the available data and he did not invent details to support his theories. For example, he used the same wo-

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odcut in Figure 1 because his own observations and the available literature had convinced him that there are no morphological differences between vertebrates at this early stage of development (Richards 2009, 153). Haeckel clearly used a top-down approach that was dominated by his recapitulation theory but the drawings served this goal so well because they presented the general theoretical claims in the light of concrete data. Haeckel used accurate data but selected and organized it in a way that made a strong case for his theoretical framework. In this sense, his drawings were
designed to mediate between a general theory and concrete data. Haeckel's drawings may appear innocent if they are understood as simplified models; however, the way he presented them provoked criticism which later developed into a public scandal. The first open challenge to Haeckel's embryo drawings was published by the comparative anatomist Ludwig Rütimeyer in the *Archiv für Anthropologie* (Archive for Anthropology). Rütimeyer was outraged that Haeckel presented his drawings as evidence and not as schematic illustrations, accusing him of

"playing with the public and science" (Rütimeyer 1868, 302). An even more momentous attack came from the Swiss embryologist Wilhelm His who did not just discuss Haeckel's embryos in detail but also questioned his scientific integrity: “I grew up believing that of all qualifications of a naturalist, reliability and the unconditional respect for the truth are the only ones which cannot be spared. [...] Let therefore others worship Haeckel as the active and ruthless leader, in my opinion he has lost the right to count as an equal among serious researchers” (His 1875, 171).
In a series of influential publications, Lorraine Daston and Peter Galison have argued that the feud between His and Haeckel has to be understood in the context of a broader conflict of different epistemic traditions. According to Daston and Galison, His’s work was influenced by the ideal of a “mechanical objectivity”, while Haeckel was part of an older morphological tradition which took idealizations as an important and necessary precondition of a true understanding of nature. “When Haeckel followed the older usage in using his drawings to extract “the essential,” or what he believed to be the true idea hidden beneath the false appearances, His indicted him for sinning against objectivity” (Daston 2001, 20; see also Daston and Galison, 1992; 2008, chapter 4).

Daston’s and Galison’s assessment of the His-Haeckel controversy has been criticized for presenting Haeckel as a naïve proponent of an outdated epistemic tradition. According to Robert Richards, the contrast between two concepts of objectivity obscures that “the epistemological situations for His and Haeckel were […] exactly the same: on the basis of individual examples, they produced through judgment and experience a standard organism; each reproduced what he thought and not what he immediately perceived” (Richards 2008, 311, emphasis in the original).

Richards argues that the epistemological disagreement between His and Haeckel is better understood as a disagreement about the relation between data and theory. While His subscribed to a “paleo-positivist” and inductivist methodology, Haeckel considered data and theories to be inextricably entangled. According to Richard’s view, Haeckel was convinced that theories are not only derived from facts but that they can play an active and important role in the discovery of new facts.

I think that the concept of models as mediators can help to clarify the situation. Models are mediators in the sense that they incorporate aspects of both data and theory. However, models can be mediators in different ways and the controversy between His and Haeckel illustrates the diversity of these mediating functions. As I will discuss in more detail in the next section, His developed an explicit theory of material models as research publications. According to His, material models are important because they allow a precise presentation of anatomical details. As
His put it in his short opinion piece *Ueber die wissenschaftliche Wertung veröffentlichter Modelle* (On the Scientific Evaluation of Published Models):

“I regard complicated spatial relationships as only fully understood when they are available as plastic representations and I consider the model, even more than the written word, the decisive record of the understanding of form” (His 1895, 359). His’s ideal of models as research publications is closely connected to the technological innovation of the microtome that fundamentally changed the practice of anatomists and radically altered embryological modelling (Hopwood 1999). The microtome provided thin-cut sections that not only revealed anatomical features more precisely but provided a new kind mechanically retrieved data as a basis of His’s highly systematic drawings as well as three-dimensional reconstruction of embryos with wax models.

His considered models an opportunity for research as they allowed for a precise representation of anatomical relations. This ideal of precise research models seems to be consistent with Daston’s and Galison’s interpretation of “mechanical objectivity” as well as Richardson’s presentation of His as an inductivist “paleo-positivist.” However, it is important to note His’s own qualifications. In the beginning of his *Anatomie menschlicher Embryonen* (Anatomy of Human Embryos, 1880), His discusses different modes of representation: descriptions, photographs, drawings, and three-dimensional models. In his discussion of drawings, His explicitly acknowledges the importance of interpretation. Every drawing – no matter how precise – has to focus on aspects the author considers essential and has to neglect aspects the author does not consider important (His 1880, 6). Given His’s awareness of the complexity of different modes of representation and the irreducibility of subjective elements, neither Daston’s and Galison’s “mechanical objectivity” nor Richardson’s “paleopositivism” seem to offer an entirely balanced account of His’s stance.

However, even if we take His’s sophisticated discussion of two- and three-dimensional models into account, there can be no doubt that he advocated modeling as a research strategy that allows a precise representation of anatomical forms. This process might be interpretative to some degree because it requires the selection of important aspects but
His’ ideal still clearly contrasts with Haeckel’s use of drawings as tools for the presentation of general arguments about evolution and embryology. While His’ account of modeling can be described as data-driven in the sense that it presented models as a medium for a more precise representation of anatomical details, many of Haeckel’s drawings are clearly theory-driven in the sense that they utilized eclectic sources with the goal of making theoretical points. It is certainly no coincidence that the controversy focused on one of Haeckel’s most iconic illustrations of his recapitulation theory: where Haeckel saw an opportunity to illustrate his theoretical framework in the light of embryological data, His saw a violation of the standards of scientific modeling.

Reframing the controversy between His and Haeckel as a debate between different accounts of modeling has the advantage of allowing a balanced account that does neither simplify His’ nor Haeckel’s position. The contrast between data- and theory-driven modeling is not absolute but gradual. His acknowledged that every model requires interpretation while Haeckel’s illustrations do not only present a theory but a theory in the light of concrete data. His and Haeckel do not subscribe to two fundamentally opposed epistemologies but they stand at two opposing ends of the gradual spectrum of different modeling functions.

My presentation of the controversy between Haeckel and His presupposes that Haeckel’s drawings qualify as models. Any characterization of two-dimensional representations as models, however, implies an awkward conceptual situation as there are countless drawings and illustrations that we do not want to consider models. The characterization of drawings as models, therefore, appears to inflate the discussion of models in an unacceptable way unless there is some clear distinction between drawings that qualify as models and drawings that do not qualify as models.

A convenient reaction to this situation seems to be the exclusion of two-dimensional representations from a discussion of models. If we accept both theoretical and three-dimensional models, however, this exclusion remains ad hoc and systematically unsatisfying. For example, why should a three-dimensional representation of an embryo qualify as a model of an embryo while a two-dimensional representation of the same
embryo with the same anatomical details does not qualify as a model? Furthermore, an exclusion of two-dimensional representations does not solve the conceptual problem as it reappears in the case of three-dimensional models: there are also countless three-dimensional representations – from religious statues to animal-shaped candy – that we usually do not want to consider models.

The framework of models as mediators can help to clarify this situation by ignoring abstract and physical properties such as overall similarity and focusing on the uses of models in scientific practice: a two or three-dimensional representation is a model if it is used as a mediator between theory and data.² We do not need to inflate a discussion of two- and three-dimensional models if we restrict it to objects that play a mediating role in scientific practice. This is why Haeckel’s embryo drawings qualify as models while, for example, illustrations in children’s books or paintings usually do not qualify as models.

So far, the reconceptualization of two- and three-dimensional models as mediators between theory and data has proven helpful in at least two crucial ways. On the one hand, it offers a framework for understanding the controversy between His and Haeckel as being based on a methodological disagreement about the diversity of modeling functions. On the other hand, the characterization of models as mediators has also proven helpful in distinguishing models and other representations that we do not want to consider models. Two-dimensional models, for example, may not look different from other illustrations, but they are used in a different way.

Despite these explanatory benefits, I also think that a discussion of two- and three-dimensional models requires an extension of Morgan and Morrison’s framework. Any comprehensive account of two- and three-dimensional models in eighteenth-century biology will have to move beyond their internal scientific functions and consider their role in communicating with diverse audiences and especially the general public. Haeckel’s embryo drawings provide an excellent example for this necessity.

²A similar point is made by Nickelsen (2006) who describes eighteenth-century botanical illustrations as models.
The rage of Haeckel’s critics would not be understandable if the controversy would have been only about the epistemology of modeling and it can seem bizarre that German biologists of the 1860s and 1870s focused on a few illustrations instead of debating the core issues of evolutionary theory.

However, Haeckel’s models were more than “a few illustrations,” they were powerful tools in the public presentation of his evolutionary program. This popularizing function of Haeckel’s illustrations is not independent from their epistemic function as mediators between theory and data. Haeckel’s illustrations were so successful in public because they presented general theoretical claims such as the biogenetic law through nontechnical and vivid illustrations. As I will discuss in the next sections, models in nineteenth-century biology had diverse audiences that included scientists, students, and the general public. Furthermore, the methodological differences in the construction of models often reflected different intended audiences and therefore cannot be understood independently of them.

Models in Wax

Haeckel only created models on paper. Two-dimensional drawings were easy to include in his popular publications and also met his artistic interests. However, the second half of the nineteenth century also saw an increased interest in three-dimensional scientific models, mostly driven by the demand of scientific university collections (Ludwig and Weber, forthcoming). Although wax was already a popular material during the eighteenth century and utilized by model makers such as Clemente Susini and Josef Benedikt Kuriger, the outstanding importance of wax models within nineteenth-century embryology is most closely connected to the work of Adolf Ziegler and his second son Friedrich Ziegler. Wilhelm His invited Adolf Ziegler in 1867 to Basel in order to learn the creation of wax models (Hopwood 2004, 186). The collaboration between His and Ziegler turned out beneficial for both sides. Ziegler’s advanced methods

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3On Susini see Cattaneo (1970); on Kuriger see Suter (1986); on anatomical models in the eighteenth century in general, see also Maerker (2006).
of modeling gave His the opportunity of presenting scientific models as serious research publications. In the case of three-dimensional objects such as embryos, material models promised more detailed and more precise representations than two-dimensional drawings. The collaboration was equally fruitful for the Zieglers. Material models in embryology were not an immediate commercial success as they required more time and resources than two-dimensional drawings. However, His’s ongoing campaign for the use of material models in embryology was an important aspect of the later success of the Zieglers and by the early 1880’s most embryologists accepted modeling as a crucial part of their scientific practice. The Ziegler Studio for Scientific Modeling largely benefited from this development and was able to establish itself as the almost unchallenged marked leader in the production of embryological wax models.

Given the controversy about Haeckel’s embryo drawings, a collaboration between Haeckel and the Zieglers might seem unlikely. The Zieglers worked closely with His, whose bitter feud with Haeckel was wellknown. Adolf Ziegler had not only taught His how to model in wax, the Ziegler studio also produced embryological models based on His’s research on several occasions between 1869 and 1892. Still, Adolf Ziegler produced a model series “authored” by Haeckel in 1876. The simultaneous collaboration with both His and Haeckel was possible because Ziegler kept out of their feud. A letter from Ziegler to Haeckel during the peak of the controversy illustrates that Ziegler maintained a friendly but cautious correspondence. Haeckel had sent Ziegler a copy of his Ziele und Wege der heutigen Entwicklungsgeschichte (Aims and Approaches of Contemporary Developmental History), a book full of insults against His, who was described as incompetent and insincere (Haeckel 1875). Ziegler’s response was polite but he refrained from taking sides. Instead of waging in on the embryological issues, Ziegler stressed his insufficient understanding of scientific matters.

4 Other model makers who produced anatomical wax models include Rudolf Weisker and Paul Loth, see Hackethal (2008, 22-23).
5 For a list of Ziegler models, see the documentation in (Hopwood 2002, 164–166).
Haeckel had developed his gastraea theory in series of publications during the 1870s, most importantly his *Kalkschwämme* (*Calcareous sponges*, 1872) and *Die Gastraea-Theorie, die phylogenetische Classification des Thierreichs und die Homologie der Keimblätter* (*The Gastraea-Theory, the Phylogenetic Classification of the Animal Kingdom and the Homology of the Germ Layers*, 1875). The starting point for Haeckel's theory was the discovery of germ layers which had been described by Christian Pander in 1817 and Karl Ernst von Baer in 1828. Dividing all animals into organisms with germ layers (metazoa) and without germ layers (protozoa), Haeckel assumed that the similarities in the early ontogenetic stages of metazoa proved not only their common descent but were also explainable within the framework of the recapitulation theory. More specifically, Haeckel assumed that all metazoa would form the twolayered, cup-like gastrula early in their development (see Figure 3). Applying the recapitulation theory to the process of gastrulation, Haeckel concluded that all multicellular animals have a common ancestor in a gastrula-like species. Haeckel later summarized this theory in his bestseller *Die Welträthsel*: “in all the metazoa only two primary layers appear at first, and these have always the same essential significance […] I called the germ, which always arises first from the impregnated ovum, and which consists of these two primary layers, the ‘gut-larva’ or the gastrula; its cup-shaped body with the two layers encloses originally a simple digestive cavity, the primitive gut […]. From this similarity, or homology, of the gastrula in all classes of compound animals I drew the conclusion, in virtue of the biogenetic law, that all the metazoa come originally from one simple ancestral form, the gastraea, and that this ancient (Laurentian), long-extinct form had the structure and composition of the actual gastrula, in which it is preserved by heredity” (Haeckel 1899a 37; translation Haeckel 1905, 61). One can easily imagine that the possibility to produce a model of the gastrulation process put Adolf Ziegler in an ambivalent position. On the
one hand, the collaboration with Haeckel promised additional attention and increasing sales. On the other hand, it also created the danger of becoming involved into bitter debates as the gastraea theory was a crucial part of Haeckel’s phylogenetic approach to embryology. Although Ziegler finally agreed to produce the models (see Figure 4), his commercial expectations were not met. In fact, the sales were a huge disappointment. The failure of the Haeckel-enterprise did not stop the Ziegler Studio from becoming extremely successful from the 1880s on. On the one hand, this development can be partly explained by general technical innovations in wax modeling, especially Gustav Jacob Born’s plate reconstructions, which made embryological modeling cheaper, quicker, and more exact (Hopewood 1999; Wellner 2009). On the other hand, the Zieglers were restless in advertising their products, presenting them at conferences and exhibitions, and keeping contact to established scientists.

Understanding the role of the Ziegler models in scientific practice requires a more careful evaluation of their audiences. My discussion so far suggests a rather simple dichotomy. By following His’ ideal of models as
research publications, the Zieglers targeted a scientific audience while Haeckel's popular illustrations provide examples of models that were targeted at the general public. Given this contrast, the Ziegler models of

![Ziegler wax models of the process of gastrulation “authored” by Haeckel, 1875 or later; Museum anatomicum Jenense - Anatomical Collection of Friedrich-Schiller-University Jena. Photo: Rosemarie Fröber.](image)

Haeckel's gastraea theory appear as a rather odd exception. While there is certainly some truth to this characterization, it also oversimplifies the complex interactions between these models and their audiences. An adequate account will require a more complex picture than the simple contrast between a scientific and a public audience. Ludwik Fleck's (1935) account of thought collectives offers such a picture as it distinguishes between a diversity of audiences along an esoteric-exoteric spectrum. The most esoteric circle is a highly specialized thought collective of scientists such as the group of physiologically oriented embryologists in the case of His. Highly specialized thought collectives are part more inclusive groups such as embryologists in general which are again part of the group of biologists. Furthermore, Fleck does not limit this esoteric-exoteric spectrum to scientists but explicitly includes students and finally also non-academic audiences to his analysis. Fleck (1936, 107) stresses that publications are often targeted at specific
audiences in this esoteric-extoric spectrum. For example, highly specialized research publications are intended for an equally specialized esoteric circle, textbooks are intended for students, and popular science books are intended for an exoteric audience beyond academia. There appears to be an analogous structure in the case of models as His’ models were conceived as research publications of highly specific anatomical details that are only of interest for an esoteric circle while Haeckel’s models served as illustrations of general theoretical assumptions of relevance of a much more exoteric circle. This observation suggests that the His’ and Haeckel’s different ideals of modeling are at least partly the result of their intentions to reach different audiences.

However, even models that had an esoteric target audience often reached a broader public. Although the Ziegler models were materializations of His’ ideal of models as research publications, they were not only of interest for embryologists who were concerned with highly specific anatomical details. Instead, much of the Ziegler’s success was based on the use of their models in academic education and even today countless German university collections still hold Ziegler embryo models. Nick Hopwood even argues that “[t]eaching became unimaginable without their publications, and involvement in new microscopical methods ensured the press a near monopoly in active fields of research” (Hopwood 2004, 170).

Finally, Ziegler models also became popular objects and reached nonacademic audiences. For the general public, embryology had become an outstandingly interesting science. In nineteenth-century Germany, public schools barely taught anything about biology and certainly nothing about topics related to sex. From the 1860s on, however, popular science books such as Haeckel’s *Natürliche Schöpfungsgeschichte* and the *Anthropogenie* started to fill the gap and by the end of the century countless popular books, sexual education lectures, hygiene exhibitions and shows brought embryology to the public and made them even an often used

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7 For examples, see the digital database of models in German University Collections: [http://www.universitaetssammlungen.de/modelle/suche/krp/30](http://www.universitaetssammlungen.de/modelle/suche/krp/30)
motif in *fin de siècle* art. Although the Ziegler models were conceived as academic objects and the relationship between academic embryology and public sex education was complicated, their success with the general audience is obvious. The most impressive document is a picture of Friedrich Ziegler’s contribution to 1893 World’s Fair in Chicago. Ziegler’s display was two-and-a-half meters high, four-and-a-half meters wide, and showed embryos of humans, vertebrates, invertebrates as well as the development of several body parts. The display even won the Fair’s highest prize (Hopwood 2004, 192).

In the last section, I argued that models can be understood as mediators between theory and data in different ways. His proposed an account of models as research publications that starkly contrasts with Haeckel’s use of models as illustrations of general theoretical assumptions. While I have interpreted this as a methodological contrast of different roles of theory and data in the construction of models, this section adds a further dimension to this conflict by focusing on different audiences. Ziegler models had at least two distinct target audiences: scientists who would be able to “read” the models as research publications and students who would benefit from precise models in the initiation to the esoteric circle. These target audiences clearly contrast with the far more exoteric circle that was reached by Haeckel’s publications and at least partly explain differences in methodological standards of model construction.

Furthermore, the tendency of models to reach beyond esoteric circles was recognized by the Zieglers and made the collaboration with Haeckel an interesting enterprise. It was also recognized by both Haeckel and His, although they reached opposing conclusions. For Haeckel, the potential of models to communicate to broader audiences made them a important tool in the popularization of evolutionary theory. For His, this potential came with a responsibility that was violated by Haeckel to a degree that he “lost the right to count as an equal among serious researchers” (His 1875, 171). Although I have argued that we should follow Morgan and

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8For embryos as a *fin de siècle* art, see Menon (2004). For the Haeckel’s influence on early sexology in Germany, see Iwan Bloch’s and Magnus Hirschfeld’s contributions to the second volume of the festschrift *Was wir Ernst Haeckel verdanken* (What we owe to Ernst Haeckel; Schmitt-Jena 1914).
Morrison in describing models as mediating between theory and data, these issues suggest that an exclusive focus on the methodology of modeling will not adequately capture the role two- and three-dimensional models in nineteenth-century biology. Instead, it seems more adequate to describe these models as mediating between theory, data, and diverse audiences that often reached beyond esoteric circles and made biological issues accessible to a broader public.

Models in Glass
Contrary to wax, glass does not seem to be a likely material for biological models. Glass is not only a highly fragile material, it is also tremendously difficult to create realistic glass models of living organisms. Still, two of the most celebrated model makers of the nineteenth century were Leopold and his son Rudolf Blaschka who established themselves with magnificent glass models of invertebrates. While Leopold’s early glass animals were solely based on Philip Henry Gosse’s beautifully illustrated *Actinologia Britannica,* later models drew from a wide variety of publications as well as conserved and even living sea creatures. Ernst Haeckel’s influence on the Blaschka’s later work is obvious, although there are not enough sources to give a complete account of their personal and professional relationship. Haeckel was of outstanding importance for marine biology of the nineteenth century and many of Haeckel’s 4,000 newly described species were cast in glass by Leopold and Rudolf Blaschka. Furthermore, we know that the Blaschkas borrowed biology books from Haeckel’s private collection. During the nineteenth century, it was common for scientists as well as model makers to use each other’s illustrations and models as templates, so that it is often not possible to determine the original source of a specific Blaschka model. In some cases, however, the influence of Ernst Haeckel is obvious. Most importantly, the Blaschka models of radiolarians, a group of unicellular marine organisms, were based on Haeckel’s groundbreaking

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9 On the Blaschkas, see Reiling’s groundbreaking publications (1998; 2000; 2009).
10 On Gosse, see Thwaite (2002) and Gosse (1907).
11 The Ernst-Haeckel-Archive in Jena contains several letters from Leopold and Rudolf Blaschka to Ernst Haeckel (see Hößfeld and Breidbach 2005).
monograph *Die Radiolarien (Rhizopoda radiata)*, published in 1862. The previously almost unknown radiolarians did not only provide the topic for Haeckel’s habilitation thesis but also for his first major contribution to evolutionary theory. Under the microscope, the radiolarians revealed a stunning symmetry and Haeckel arranged them into a “natural system” along two criteria: the relation of the skeleton to the central capsule and the overall form of the skeleton.

According to Haeckel, radiolarians support evolutionary theory, because the transitional character of many morphological characteristics can only be explained by a common *Urform* (primordial form): “Through the whole long series of these figures runs a continuous red thread so that I am able to make the attempt to portray the relationship and the mutual relations of all types in a genealogical relationship chart and even to seek a *Urform*, from which all others forms may possibly be derived” (Haeckel 1862, 233). Haeckel did not only conclude that an Ur-radiolarian must have existed, he rather offered a specific model of the primordial form. Haeckel postulated *Heliosphaera actinota* (Figure 5 and Figure 6) as the Ur-radiolarian by arguing that the diversity of radiolarians must have developed through a deformation of simple and symmetrical forms as they are found in *Heliosphaera actinota*.

Haeckel’s drawings of radiolarians seem to offer a further example of his theory-driven approach to biological modeling: Haeckel’s “Urradiolarian” was a highly speculative construct and his presentation of *Heliosphaera actinota* as an Ur-radiolarian was clearly driven by his ambition to provide a unified evolutionary theory of radiolarians. Despite these theoretical ambitions, it would be a mistake to present Haeckel’s work on radiolarians as detached from data. On the contrary, Haeckel based his evolutionary account of radiolarians on extensive research and painstakingly detailed observation. In fact, Haeckel’s work on radiolarians was groundbreaking because it was unique in its empirical depth and breadth.

Haeckel’s work on radiolarians again illustrates how the framework of models as mediators between theory and data can be helpful for understanding modeling in nineteenth-century biology. Haeckel’s illustrations of
radiolarians were based on uniquely detailed and comprehensive data. At the same time, these data were presented as evidence for a speculative phylogenetic account of development of radiolarians through deformation. Furthermore, Haeckel's discussion of radiolarian forms needs to be understood in the context of the German morphological tradition which made the striking and often almost perfectly symmetrical forms of the radiolarians more than just a curious observation. For Haeckel, morphology provided the essential guide to taxonomy, physiology, and phylogeny (Daston 2006, 63). The morphological perspective also allowed a connection between scientific and artistic interests as the work of Haeckel as well as the Blaschkas illustrates. On the one hand, Haeckel and the Blaschkas considered their models scientific objects and exact representations of na-

Fig. 5 - Haeckel's illustration of the radiolarian Heliosphaera actinota which he took
to be comparable to the “Ur-radiolarian.” Ernst Haeckel, *Die Radiolarien (Rhizopoda radiaria)*, Berlin: Reimer, 1862, Plate IX.

ture. Haeckel based his radiolarian work on extensive research and the Blaschkas’ work became famous because of its stunning naturalism. The Blaschka models were created with the ambition to mimic nature in an as detailed and accurate manner as possible. On the other hand, the models were also artistic objects and materializations of a morphological perspective that focused on the stunning forms of radiolarians as evidence of highest importance. Haeckel’s monographs were often generously illustrated and his *Kunstformen der Natur* (Art Forms of Nature) even explicitly tried to bring art and science together. In the foreword of the *Kunstformen*, Haeckel stated he “was not only trying to recognize the laws of design and development [of organisms], but also to penetrate deeper into the mystery of their beauty” (Haeckel 1899b, *Vorwort*).

The ambiguous role of the radiolarian models between science and art is equally striking in the case of the Blaschka glass models. At first glance, the Blaschka models seem to be artistic rather than scientific objects as they combine outlandish forms with an unlikely material. However, the Blaschkas did not produce their models as artistic interpretations but as exact representations of nature. Their goal to produce precise scien-

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tific models becomes especially evident in their late botanical models. In 1890, the Blaschkas signed an exclusive contract with the botanist George Lincoln Goodale to produce glass models for a collection at Harvard University (Parke 1983, 116–122). For fifty years, the Blaschkas worked to produce a collection of about 4000 models of plants, flowers, and botanical details. Goodale saw the commissioned models as scientific objects which were used to teach phylogenetic botanical classification. The glass models were not idealized representations with conventionalized characteristics but mimicked nature by representing individual plants as realistically as possible. The Blaschka models even showed individual peculiarities and included aspects such as shrivelled or pitted leaves. The stunning accuracy of the glass models allowed Harvard students to train botanical classification without field research and the laborious search for appropriate living species.

While radiolarian models offer another example of models as mediators between theory and data, their mediating functions again cannot be understood independently of their audiences. The ambition to mimic nature through accurate and vivid models clearly reflects their intended use as teaching models. As students did not have access to living specimens of many aquatic invertebrates and plants, the Blaschka models had a well-defined role in academic teaching. At the same time, they also embodied a morphological and aesthetic perspective on nature which allowed them to reach a broader public. A selection of glass flowers was presented at the Parisian World Fair and Goodale actively utilized the breathtaking appearance of his scientific collection. Even after the glass models ceased to serve as teaching tools, the “Ware collection of glass models” remained a public spectacle, attracting almost 200,000 visitors a year (McNally and Buschini 1993) by combining accurate botanical details with an artistic presentation of nature.

The case of the Blaschka models provides a further example of how models can have a variety of audiences as described by Fleck through his esoteric-exoteric spectrum. Models fit Fleck’s rough distinction of three types of audiences (Fleck 1936, 105–07) as they were intended to reach specialized scientists (e.g., His’s ideal of models as research publications),
students (e.g., Blaschka teaching models), and the general audience (e.g., Haeckel’s illustrations). However, models in nineteenth-century biology also can be described as having an “exoteric bias” in the sense that they often reached a broad audience even if they were originally intended for a more esoteric circle. This is not only the case with Haeckel’s intentionally popular models but also with Blaschka as well as Ziegler models. An account of models as mediators in the context of nineteenth-century biology therefore has to take their public functions into account. None of the discussed models simply mediated between theory and data in an isolated scientific context but they also mediated between esoteric scientific issues and an exoteric audience.

My discussion suggests that this “exoteric bias” of models can be partly understood through their theoretical component which made them more relevant to the general public than other objects and illustrations. This is especially evident in the case of Haeckel’s illustrations that became the center of a public scandal because they transported a far-reaching theoretical context. Similar points can be made about the Blaschka models that did not only represent botanical details but also a highly aesthetic morphological view on nature. Finally, even the Ziegler models became relevant for a larger audience because they presented developmental processes that may have been well-established and uncontroversial among specialized scientists but provided a novel and fascinating perspective for more exoteric audiences.

While this theoretical component is an important factor in the public success of models in nineteenth-century biology, it does not explain their appeal to larger audiences compared to other forms of theory presentation. An explanation of their public success therefore cannot be limited to a discussion of the theory component but also has to consider how these models presented theory in the light of concrete morphological and anatomical details. Again, Haeckel’s illustrations provide the most obvious examples. Even readers who had never read a specialized academic text about recapitulation theory and only had basic knowledge of evolutionary biology were able to “see” the relation between humans and other vertebrates in Haeckel’s illustrations. A similar point can be made with respect
to the Blaschka models. Visitors of Harvard’s Glass Flowers Collection did not need detailed background-knowledge about German morphology and the ideal of a unified aesthetic and scientific perspective on nature in order to see the “artforms of nature” in the Blaschka models. What made models often more attractive for a general audience than other forms of theory presentation was their presentation of theory through accessible and vivid representations of morphological and anatomical forms.

To sum up, I have suggested that the methodological issues of mediation between theory and data are closely entangled with their intended and unintended audiences. On the one hand, I have argued that different methodological standards in the construction of models reflect their different intended audiences as illustrated in the contrast between His research models for an esoteric circle and Haeckel’s popularizing models for an exoteric circle. On the other hand, I have argued that models often reached broader audiences because they incorporated both farreaching theoretical assumptions as well as concrete morphological and anatomical details that ensured their accessibility. In this sense, models are paradigmatic examples of the ideal of Anschaulichkeit that played a crucial role in the increasing presence of material models and scientific collections in German academia of the nineteenth-century (Ludwig and Weber, forthcoming).

Understanding the Plurality of Modeling Functions

This article has presented models in nineteenth-century biology as mediators between theory, data, and diverse audiences. It has also been argued that the slogan “models as mediators” refers to a diversity of modeling functions. For example, mediation between data and theory can occur in very different ways. His’ models were conceived as research publications that provide a precise presentation of anatomical details. Although His acknowledged that models are inevitable interpretative in the sense that they require the evaluation of aspects as important or insignificant for the model, he still tried to establish material models as exact representations of anatomical structures. Haeckel’s drawings contrast with His’ “research models” in the sense that they often serve as illustrations of general theoretical
frameworks. For Haeckel, nothing less than everything was always at stake. For example, his models of the gastrulation process were not only meant to be illustrations of microscopic observations but they served as evidence for the general gastraea theory. And Haeckel did not stop there. The gastraea theory was understood as evidence for the recapitulation theory which was again understood as a major pillar of evolutionary theory. Finally, evolutionary theory was presented as the foundation for a general monist philosophy. Haeckel's work exhibits a clear line from the most specific topics such as the ontogenetic development of a specific species to the most general principles of his monistic worldview. However, it would be wrong to claim that Haeckel's models are "nothing but theory." All of his illustrations – no matter whether they presented vertebrate embryos, the process of gastrulation, or different radiolarian forms – were based on the data that was available for Haeckel and presented his theoretical framework in the light of this data.

In the introduction of this article, I discussed the overwhelming diversity of scientific models that makes any attempt to offer a precise and all-encompassing definition of "model" appear hopeless. Although my characterization of models as mediators between theory, data, and the public does not lead to a definition with necessary and sufficient conditions, I hope that it has proven to be of analytical value by offering a framework for understanding the role of models as mediating tools in scientific practice. More specifically, I think that this characterization is helpful in understanding at least three aspects of two- and three-dimensional models in nineteenth-century biology.

First, the framework of models as mediators allows to understand the controversy between His and Haeckel as being based on different ideals of modeling that may be described as data- and theory-driven. For His, models were useful as research publications that provided a more precise representational strategy than traditional print publications. For Haeckel, models provided an opportunity of presenting his general theoretical assumptions in the light of concrete data.

Second, I have argued that the framework of models as mediators offers a better understanding of the distinction of models and other representations
that do not qualify as models. This is especially evident in the case of Haeckel’s drawings as any discussion of two-dimensional models faces the problem that there are countless illustrations that we usually do not want to consider models. I have argued that we can understand Haeckel’s drawings as models because he used them as mediators between theory and data. Haeckel’s illustrations of embryological development, the process of gastrulation, and of Heliosphaera actinota qualify as models not because the look different than other illustrations but because they were used in a specific way.

Third, I have argued that models in nineteenth-century biology did only mediate between theory and data but also between a diversity of audiences that include specialized scientists, students, and the general public. It is important to consider these audiences in the mediation between theory and data because different methodological standards of model construction often reflect these different target audiences. Furthermore, I have argued that models in nineteenth-century biology often reached larger audiences because they incorporated theoretical assumptions of general importance in the light of accessible morphological and anatomical details.

Models remain elusive entities in the history and philosophy of science that are of undisputed importance but resist attempts to offer an allencompassing definition. A discussion of models within specific historic and disciplinary contexts does not solve this definitional problem, but it can provide a framework for an understanding of the roles of models in scientific practice. Of course, such a framework will always reflect the specifics of the involved case studies. For example, I have barely talked about the use of materials models in experimentation and theory construction although this function is clearly of utmost importance in different scientific contexts (see, e.g., Weisberg 2007 or the literature on model organisms such as Leonelli and Ankeny 2008). At the same time, the characterization of models as mediators appears to be helpful as it is applicable in very heterogeneous scientific contexts. While Morgan and Morrison proposed this framework in the context of theoretical models in economy and physics, I have argued that it also proves helpful in a discussion of two- and three-dimensional models in nineteenth-century
biology. It remains to be seen to what degree this framework will also prove helpful in further contexts such as the use of material models in experiments and theory construction.

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