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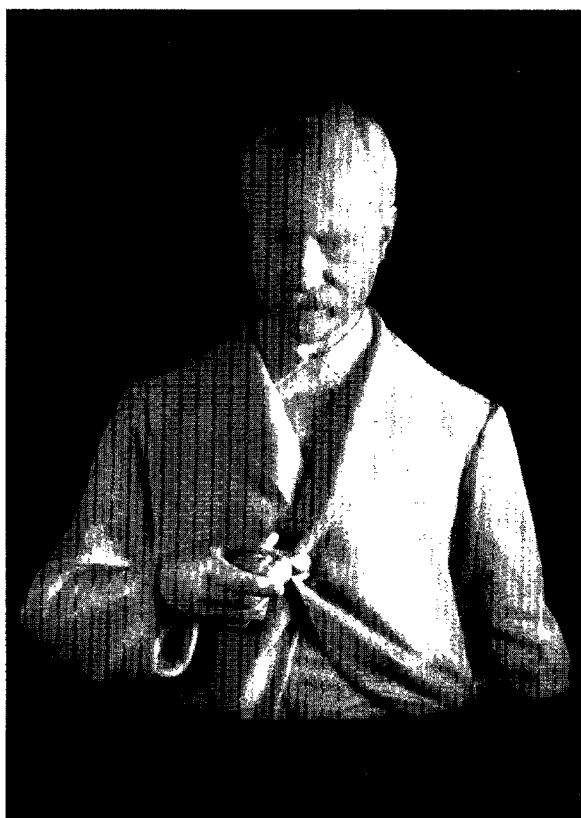
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# “Giving Body” to Embryos

## Modeling, Mechanism, and the Microtome in Late Nineteenth-Century Anatomy

*By Nick Hopwood\**

### ABSTRACT

Reinvestigating the work of the anatomist Wilhelm His (1831–1904) shows how engaging with models in three dimensions can revise our accounts of scientific change. His is known to historians of biology for articulating a mechanical approach to embryology and for inventing a section cutter, or microtome. Focusing on the wax models that he also made in the late 1860s shows how the other two innovations were linked; reconstructing embryos from the sections, His claimed, provided compelling evidence for mechanical views. The next generation of embryologists appropriated His’s work selectively. In the 1880s anatomists took up “plastic reconstruction” to visualize the complex forms of higher vertebrate, especially human, embryos. An increasingly dominant experimental embryology, by contrast, drew on His’s mechanical approach but had little use for the waxes and effaced them from the history of his work. Recovering these models offers a fresh perspective on the transformation of a central science of animal life and enriches our understanding of the relations between representation in two dimensions and three.

**T**HE VISUAL WORLDS OF SCIENCE PAST were not as flat as we often assume. Scientists do usually represent their three-dimensional surroundings in two dimensions,

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learning visual languages to depict objects on paper or inventing instruments to extract a set of numbers from an experiment. This reduction is a key step in mastering messy phenomena: “there is,” says Bruno Latour, “nothing you can dominate as easily as a flat surface.” Two-dimensional inscriptions readily move without change among scientific centers and between laboratories, museums, and the world outside. More complex, bulkier and more fragile, harder to reproduce and recombine, three-dimensional objects make less effective “immutable mobiles.” Yet scientists and technologists in various disciplines have found them indispensable. Eighteenth-century Italian anatomists commissioned wax models to stand in for scarce and perishable corpses. Enlightened rulers prided themselves on collections of miniature machines, and until the 1870s the United States Patent Office required inventors to submit a model with every application. Mathematicians in the decades before World War I grounded abstract mathematics by displaying cabinets of models. Perhaps the icon of the biological sciences in the twentieth century is a photograph of James D. Watson and Francis Crick posing with their double-helical model of DNA. Muscles and machines, mathematical surfaces and molecules, have been modeled, above all, with a view to achieving a vividness and tangibility that no flat picture could match.<sup>1</sup> It is unlikely that such models will ever occupy a more prominent place in the history of science than historians of art have granted to sculpture. But they have played key roles, and we have much to gain by taking them seriously.

Studying the production and uses of scientific models in three dimensions offers two clear benefits. First, it can deepen our appreciation of the variety of representational work in the sciences. Even historians writing primarily about pictures increasingly acknowledge that the interplay in scientific representation between three dimensions and two may be more complex and hence more interesting than reduction.<sup>2</sup> For example, rendering a bio-

<sup>1</sup> Bruno Latour, “Drawing Things Together,” in *Representation in Scientific Practice*, ed. Michael Lynch and Steve Woolgar (Cambridge, Mass.: MIT Press, 1990), pp. 19–68, on p. 45. See also Martin J. S. Rudwick, “The Emergence of a Visual Language for Geological Science, 1760–1840,” *History of Science*, 1976, 14:149–195. On anatomical models see esp. Thomas N. Haviland and Lawrence Charles Parish, “A Brief Account of the Use of Wax Models in the Study of Medicine,” *Journal of the History of Medicine and Allied Sciences*, 1970, 25: 52–75; *La ceroplastica nella scienza e nell’arte: Atti del I Congresso Internazionale, Firenze, 3–7 giugno 1975*, 2 vols. (Florence: Olschki, 1977); Urs Boschung, “Medizinische Lehrmodelle: Geschichte, Techniken, Modelleure,” *Medita*, 1980, 5 (*Geschichte der Medizin und der Medizinischen Technik*, 4): ii–xv; L. J. Jordanova, “Gender, Generation, and Science: William Hunter’s Obstetrical Atlas,” in *William Hunter and the Eighteenth-Century Medical World*, ed. W. F. Bynum and Roy Porter (Cambridge: Cambridge Univ. Press, 1985), pp. 385–412; Michel Lemire, “Representation of the Human Body: The Colored Wax Anatomic Models of the Eighteenth and Nineteenth Centuries in the Revival of Medical Instruction,” *Surgical-Radiologic Anatomy*, 1992, 14:283–291; and Susanne Hahn and Dimitrios Ambatelios, eds., “Wachs—Moulagen und Modelle”: *Internationales Kolloquium 26. und 27. Februar 1993* (Dresden: Deutsches Hygiene-Museum, 1994). On technological models see Eugene S. Ferguson, “The Mind’s Eye: Nonverbal Thought in Technology,” *Science*, 1977, 197:827–836; and Svante Lindquist, *Technology on Trial: The Introduction of Steam Power Technology into Sweden, 1715–1736* (Uppsala: Almqvist & Wiksell, 1984), pp. 23–33. On mathematical models see Gerd Fischer, ed., *Mathematische Modelle: Aus den Sammlungen von Universitäten und Museen*, 2 vols. (Braunschweig: Vieweg, 1986); and Herbert Mehrrens, *Modeme Sprache Mathematik: Eine Geschichte des Streits um die Grundlagen der Disziplin und des Subjekts formaler Systeme* (Frankfurt am Main: Suhrkamp, 1990). On models in chemistry and for a programmatic statement see Eric Francoeur, “The Forgotten Tool: The Design and Use of Molecular Models,” *Social Studies of Science*, 1997, 27:7–40. For one prominent use of the photo of the double-helical model see Merriley Borell, *The Biological Sciences in the Twentieth Century* (Album of Science, 5) (New York: Scribner’s, 1989), frontispiece; further, see Harmke Kamminga and Soraya de Chadarevian, *Representations of the Double Helix* (Cambridge: Wellcome Unit for the History of Medicine, 1995).

<sup>2</sup> See, e.g., Maria Trumpler, “Techniques of Intervention and Forms of Representation of Sodium-Channel Proteins in Nerve Cell Membranes,” *Journal of the History of Biology*, 1997, 30:55–89, on p. 82; and David Topper, “Towards an Epistemology of Scientific Illustration,” in *Picturing Knowledge: Historical and Philosophical Problems Concerning the Use of Art in Science*, ed. Brian S. Baigrie (Toronto: Univ. Toronto Press, 1996), pp. 215–249, on p. 243.

logical specimen into "representation devices" may proceed via two-dimensional micrographs, through a three-dimensional diagram,<sup>3</sup> to a three-dimensional object; alternatively, a model may itself be an intermediate stage, such as a means to a better drawing. Whatever its purpose, however, making a solid model is never just another step; its very three-dimensionality brings special advantages and problems, and these offer a rich field of research. Second, investigating three-dimensional representation devices may not just enrich but also revise our accounts of scientific controversy and change. Innovations in producing and using models in three dimensions have been important sources of novelty, but scientists have achieved less consensus on their representational virtues than on those of pictures. Detractors have reluctantly conceded their uses where vividness is at a premium, such as in teaching or communicating with laypeople, while advocates have prized them as the ultimate in representational achievement, scientific documents to be valued even above journal articles or monographs. Precisely because they have been so disputed, bringing models in three dimensions into general histories of the sciences may do more than just fill them out. By studying models that some groups promoted or relied on and others ignored or opposed, we can develop new views of what was at stake in struggles over change.<sup>4</sup>

This essay illustrates these points by highlighting waxes made in the late 1860s by the Basel, later Leipzig, anatomist and embryologist Wilhelm His but systematically excluded from the dominant histories. Historians of biology remember His for two major innovations of those same years: a mechanical approach to embryology and a microtome.<sup>5</sup> In the decades following Darwin's *Origin of Species*, the German zoologist and evangelist of evolution Ernst Haeckel led embryologists in explaining individual development, or ontogeny, in terms of the evolutionary development of the species, or phylogeny. Embryology enjoyed a heyday as a key means of reconstructing the history of life on earth. But His stood against the Darwinist tide, opposing the reduction of the present to the past and instead asking physiologically how one embryonic stage was transformed into the next. *Unsere Körperform und das physiologische Problem ihrer Entstehung* [The Form of Our Body and the Physiological Problem of Its Development] explained the embryogenesis of the chick in terms of the pressures and pulls generated by differential growth. His argued for the relevance of mechanical principles by mimicking the bending and folding of the embryo in simple materials, likening, for example, the developing nervous system to a rubber tube. He initially failed to draw embryologists from evolutionary studies, but in the 1880s anatomists and physiologists began to take up his call to discover the proximate causes of form. The most successful of these initiatives was Wilhelm Roux's *Entwicklungsmechanik* ("developmental mechanics"), the main program of a new experimental

<sup>3</sup> Michael Lynch, "The Externalized Retina: Selection and Mathematization in the Visual Documentation of Objects in the Life Sciences," in *Representation in Scientific Practice*, ed. Lynch and Woolgar (cit. n. 1), pp. 153–186, on pp. 164–168. See this volume for the term "representation device."

<sup>4</sup> For advocacy of models see, e.g., Francoeur, "Forgotten Tool" (cit. n. 1); and the statements of Wilhelm His that I report in this essay. Mehrrens, *Moderne Sprache Mathematik* (cit. n. 1), argues that cabinets of pedagogical models played a special role in "countermodernist" mathematics.

<sup>5</sup> See Erik Nordenskiöld, *The History of Biology: A Survey*, trans. Leonard Bucknall Eyre (London: Kegan Paul, Trench & Trubner, 1929), pp. 405, 518, 531–532; and the most influential recent accounts of His's work: Stephen Jay Gould, *Ontogeny and Phylogeny* (Cambridge, Mass.: Harvard Univ. Press, 1977), pp. 189–193; Jane Maienschein, *Transforming Traditions in American Biology, 1880–1915* (Baltimore: Johns Hopkins Univ. Press, 1991), pp. 89–96; and Maienschein, "The Origins of *Entwicklungsmechanik*," in *A Conceptual History of Modern Embryology*, ed. Scott F. Gilbert (1991; Baltimore: Johns Hopkins Univ. Press, 1994), pp. 43–61, on pp. 43–46.

embryology, one of the key sciences of the modern biology that was created in the decades around 1900. His's second innovation was to pioneer the major change in histological practice of the later nineteenth century. He produced one of the first microtomes for cutting specimens into thin slices, or sections, which he used to visualize the internal development of the chick in unprecedented detail. Systematic sectioning of microscopical specimens became routine among anatomists and zoologists during the 1870s and has for generations been a standard method of morphological research.<sup>6</sup>

A marble bust (see the cover illustration) made by the sculptor Carl Seffner—probably either for His's seventieth birthday in 1901 or to mark his death in 1904—expands our view of the anatomist from that current in the history of biology. The downcast eyes and the crossed folds of his coat lead our gaze to the wax model of a human embryo that he holds in his right hand. The statue forcefully draws our interest to the manual labor of embryology and—itself a product of the plastic arts—specifically to the role of modeling in His's work.<sup>7</sup> It directs us to revisit his investigations of the late 1860s and, instead of looking only at the books and articles, their texts and illustrations, to pay attention also to the wax models of the chick—which, it turns out, he published at the same time. Whereas historians of biology have presented the mechanical embryology and the microtome as a conceptual and a technical contribution, respectively, connected—if at all—in that sectioning provided empirical evidence against Haeckel's generalizations, engaging with the

<sup>6</sup> Wilhelm His, *Unsere Körperform und das physiologische Problem ihrer Entstehung: Briefe an einen befreundeten Naturforscher* (Leipzig, 1874; but the preface is dated Jan. 1875) (hereafter cited as **His, *Unsere Körperform***). For surveys of evolutionary embryology and the rise of *Entwicklungsmechanik* see E. S. Russell, *Form and Function: A Contribution to the History of Animal Morphology* (London: Murray, 1916); Jane M. Oppenheimer, "Analysis of Development: Problems, Concepts, and Their History," in *Essays in the History of Embryology and Biology* (New Haven, Conn.: Yale Univ. Press, 1967), pp. 117–172; Gould, *Ontogeny and Phylogeny*, pp. 69–114, 167–206; Klaus Sander, "Von der Keimplasmatheorie zur synergetischen Musterbildung—Einhundert Jahre entwicklungsbiologischer Ideengeschichte," *Verhandlungen der Deutschen Zoologischen Gesellschaft*, 1990, 83:133–177; Frederick B. Churchill, "The Rise of Classical Descriptive Embryology," in *Conceptual History of Modern Embryology*, ed. Gilbert, pp. 1–29; Maienschein, *Transforming Traditions in American Biology*; Maienschein, "Origins of *Entwicklungsmechanik*"; and Lynn K. Nyhart, *Biology Takes Form: Animal Morphology and the German Universities, 1800–1900* (Chicago: Univ. Chicago Press, 1995) (hereafter cited as **Nyhart, *Biology Takes Form***). On the history of microtechnique see Stefan Apáthy's unfinished *Die Mikrotechnik der tierischen Morphologie: Eine kritische Darstellung der mikroskopischen Untersuchungsmethoden*, 2 parts, Pt. 1 (Braunschweig, 1896), pp. 35–140; J. W. Moll, "Die Fortschritte der mikroskopischen Technik seit 1870," *Progressus rei botanicae*, 1908, 2:227–291; Brian Bracegirdle, *A History of Microtechnique: The Evolution of the Microtome and the Development of Tissue Preparation* (London: Heinemann, 1978); and Bracegirdle, "The Microscopical Tradition," in *Companion Encyclopedia of the History of Medicine*, ed. W. F. Bynum and Roy Porter, 2 vols. (London: Routledge, 1993), Vol. 1, pp. 102–119.

<sup>7</sup> This brief analysis by no means exhausts the sculpture's challenges to the dominant historiography of embryology. We may, for example, interpret it in gendered terms as a male embryologist displaying, cradled in his hand as the fruit of his body, the embryo he might appear to have generated alone. On His's human embryology see Ronan O'Rahilly, "One Hundred Years of Human Embryology," *Issues and Reviews in Teratology*, 1988, 4:81–128; and Nick Hopwood, "Producing Development: The Anatomy of Human Embryos and the Norms of Wilhelm His," *Bulletin of the History of Medicine*, 2000, 74, in press. On portraits of scientists with their models see Francoeur, "Forgotten Tool" (cit. n. 1), p. 33. Professor Carl Ludwig Seffner (1861–1932) of Leipzig specialized in portraits in marble; see *Deutsches Biographisches Archiv: Eine Kumulation aus 264 der wichtigsten biographischen Nachschlagewerke für den deutschen Bereich bis zum Ausgang des neunzehnten Jahrhunderts*, ed. Bernhard Fabian (Munich: Saur, 1982), microfiche, fiche 1170, 50; and *Deutsches Biographisches Archiv: Neue Folge bis zur Mitte des 20. Jahrhunderts*, ed. Will Gorzny (Munich: Saur, 1989–1993), microfiche, fiche 1211, 316–317. The His bust, which stands today in the Anatomisches Institut Basel, is believed to date from 1900 or shortly thereafter (H. Kurz, personal communication). It could be the "present in the form of a work of graphic or plastic art" given to His on his seventieth birthday in July 1901; for his Leipzig colleagues' call to contribute toward this gift see Ingrid Kästner and Achim Thom, eds., *575 Jahre Medizinische Fakultät der Universität Leipzig* (Leipzig: Barth, 1990), p. 80. Alternatively, Seffner may have made the inscription reported by His's son, "Wilhelm His. Professor der Anatomie. 1831–1904," at the same time as the work itself, which then must have been made posthumously; see Wilhelm His [Jr.], *Wilhelm His der Anatom: Ein Lebensbild* (Berlin/Vienna: Urban & Schwarzenberg, 1931), p. 56.

modeling allows us to appreciate how the other two innovations were more deeply linked.<sup>8</sup>

His's rubber nervous systems are well known but have not been taken sufficiently seriously. We may regard what he called "simple experiments" as "analogue models" for bringing the resources of analytical mechanics into embryology. They exemplify a kind of model that historians and philosophers of science have shown scientists using to construct links between domains or between the generation of phenomena and the framing of theories. But in the course of introducing the microtome into embryology, His also developed a form of scale modeling. He claimed as the principal advantage of the new instrument that it allowed him to collect every section and so use them to build three-dimensional wax models from the fragmented images. This "plastic reconstruction," he argued, let him recover the more direct bodily apprehension of form that his predecessors had enjoyed. So for His, "the form of our body" was not a self-evident problem awaiting physiological explanation. In a complex interplay between two and three dimensions he had first to *make* his problem, to use his fingers, as he put it, "to *give* body" to his views.<sup>9</sup> But wax modeling was still more intimately related to mechanical reasoning. His actually developed plastic reconstruction continuously with the rubber nervous systems and leather embryos, and the experience of modeling from sections was, he claimed, the most compelling evidence of the importance of mechanical principles in development.

The first three sections of this essay substantiate and develop these arguments, introducing the "simple experiments" and then plastic reconstruction before exploring the relationship between them. In the fourth section I go on to analyze how modeling became so prominent that at the turn of the twentieth century perhaps the most distinguished embryologist of the age was depicted holding a wax model. Seffner sculpted His with a model he had published in the early 1880s as part of the founding work of modern human embryology, which applied the methods developed on the chick to the much scarcer human material.<sup>10</sup> Embryologists welcomed the commercially available reproductions of his models into their lectures, where for decades they remained ubiquitous teaching aids. During the 1880s His's anatomical colleagues were also persuaded to follow him into reconstructive modeling; they were won over by a new method tailored to the demands of younger scientists for ease, speed, and objectivity. Instead of hiring modelers to give wax form to

<sup>8</sup> Most history of embryology has taken the visual world of the science for granted, but for studies focusing on embryological pictures see Reinhard Gursch, *Die Illustrationen Ernst Haeckels zur Abstammungs- und Entwicklungsgeschichte: Diskussion im wissenschaftlichen und nichtwissenschaftlichen Schrifttum* (Frankfurt am Main: Lang, 1981); Scott F. Gilbert, "Epigenetic Landscaping: Waddington's Use of Cell Fate Bifurcation Diagrams," *Biology and Philosophy*, 1991, 6:135–154; and Jane Maienschein, "From Presentation to Representation in E. B. Wilson's *The Cell*," *ibid.*, pp. 227–254. From the large body of work on images of the human embryo and fetus see Jordanova, "Gender, Generation, and Science" (cit. n. 1); and Barbara Duden, *Disembodying Women: Perspectives on Pregnancy and the Unborn*, trans. Lee Hoinacki (Cambridge, Mass.: Harvard Univ. Press, 1993). For the received view of His's two "contributions" see the works cited in note 5, above.

<sup>9</sup> Wilhelm His, "Beschreibung eines Mikrotoms," *Archiv für Mikroskopische Anatomie*, 1870, 6:229–232, on p. 231 (emphasis added) (here and throughout, translations are my own unless otherwise indicated). For work on models see Timothy Lenoir, "Models and Instruments in the Development of Electrophysiology, 1845–1912," *Historical Studies in the Physical and Biological Sciences*, 1987, 17:1–54; and Lenoir, "Helmholtz and the Materialities of Communication," *Osiris*, N.S., 1994, 9:185–207. "Model" is a "heterogeneous concept," which philosophers of science have attempted to taxonomize in various ways; see James R. Griesemer, "Modeling in the Museum: On the Role of Remnant Models in the Work of Joseph Grinnell," *Biol. Phil.*, 1990, 5:3–36, on p. 6. On scale models, which "bring the remote and the unknown to our own level of middle-sized existence," see Max Black, *Models and Metaphors: Studies in Language and Philosophy* (Ithaca, N.Y.: Cornell Univ. Press, 1962) pp. 219–221, on p. 221.

<sup>10</sup> On His's human embryology see O'Rahilly, "One Hundred Years of Human Embryology," (cit. n. 7); and Hopwood, "Producing Development" (cit. n. 7).

their drawings, photographs, or specimens, they now made original models themselves. By 1890 plastic reconstruction was anatomists' main means of visualizing the complex structures of higher vertebrate embryos, and dozens of waxes were among the most important products of leading embryologists' research.

The final section of the essay asks how, if modeling was so central, it later became invisible. His's interest in the proximate causes of form inspired Roux, who with some reservations also took up the "simple experiments." But experimentalists tended to use the wax models only for teaching and to disparage the work that produced them as "merely descriptive." Historians of biology, interested in the transformation of embryology around 1900 as a paradigm of the making of modern biology, have reinforced this dismissal. Although they have worked against experimentalist condescension, the very agenda of searching for the origins of the new *biology* has obscured continuing embryological activity in the *medical* science of anatomy. The major exclusions were productive lines of work in the descriptive embryology of the higher vertebrates, especially humans, in which plastic reconstruction played a constitutive role well into the twentieth century.<sup>11</sup>

The different embryological traditions not only appropriated His's modeling practices in opposing ways; they also produced correspondingly divergent histories of his work. Human embryologists honor him as the founder of their science and the inventor of plastic reconstruction—very much the figure of Seffner's bust. By contrast, experimental embryologists and historians of biology produced the dominant image of, on the one hand, a precursor of *Entwicklungsmechanik* and, on the other, an inventor of the microtome. Biographical accounts, most of them written by anatomists, include all of these innovations, but without bringing out their connections.<sup>12</sup> By taking His's wax models seriously, this essay shows how modeling, mechanism, and the microtome were once united in his studies of the chick; how different successor traditions, including one that the models can help us recover, appropriated them selectively; and how as a result they produced different partial images of the embryologist. More generally, it argues that heeding scientists' production and uses of models in three dimensions can transform our accounts of scientific change.

<sup>11</sup> On the transformation see Garland E. Allen, *Life Science in the Twentieth Century* (1975; Cambridge: Cambridge Univ. Press, 1978), pp. 21–39, 114–126; Gould, *Ontogeny and Phylogeny* (cit. n. 5), pp. 186–202; special section on "American Morphology at the Turn of the Century," *J. Hist. Biol.*, 1981, 14:83–191; Maienschein, *Transforming Traditions in American Biology* (cit. n. 5); Maienschein, "Origins of *Entwicklungsmechanik*" (cit. n. 5); Adele E. Clarke, "Embryology and the Rise of American Reproductive Sciences, circa 1910–1940," in *The Expansion of American Biology*, ed. Keith R. Benson, Jane Maienschein, and Ronald Rainger (New Brunswick, N.J.: Rutgers Univ. Press, 1991), pp. 107–132; and Nyhart, *Biology Takes Form*. On the problems of experimentalist history more generally see John V. Pickstone, "Museological Science? The Place of the Analytical/Comparative in Nineteenth-Century Science, Technology, and Medicine," *Hist. Sci.*, 1994, 32:111–138. For a view of the changes in embryology around 1900 that builds on this essay and stresses the variety of embryological activities in the twentieth century see Nick Hopwood, "Embryology," in *The Cambridge History of Science*, Vol. 6: *Life and Earth Sciences since 1800*, ed. Peter J. Bowler and Pickstone (New York: Cambridge Univ. Press, in press).

<sup>12</sup> For the human embryologists' view see O'Rahilly, "One Hundred Years of Human Embryology" (cit. n. 7). The main biographical studies are Wilhelm His, *Lebenserinnerungen* (Leipzig, 1903), rpt. in *Wilhelm His der Aeltere: Lebenserinnerungen und ausgewählte Schriften*, ed. Eugen Ludwig (Bern: Huber, 1965); Rudolf Fick, "Wilhelm His †," *Anatomischer Anzeiger*, 1904, 25:161–208 ("†" signifies an obituary); Wilhelm Waldeyer, "Wilhelm His: Sein Leben und Wirken," *Deutsche Medizinische Wochenschrift*, 1904, 30:1438–1441, 1469–1471, 1509–1511; His [Jr.], *Wilhelm His* (cit. n. 7); Hans Querner, "Wilhelm His," in *Dictionary of Scientific Biography*, ed. Charles Coulston Gillispie, 16 vols. (New York: Scribner's, 1970–1980), Vol. 6 (1972), pp. 434–436; Hugo Kurz, *Wilhelm His (Basel und Leipzig): Seine Beiträge zur Weltgeltung der Anatomie im 19. Jahrhundert* (Basel: Anatomisches Museum, 1992); and Gottfried Zirnstein, "Wilhelm His (1831–1904)," in *Sächsische Lebensbilder*, Vol. 4, ed. Reiner Groß and Gerald Wiemers (Leipzig: Sächsische Akademie der Wissenschaften; Stuttgart: Steiner, 1999), pp. 157–173. His is sometimes confused with his son of the same name, who discovered the bundle of His in the heart.

## "SIMPLE EXPERIMENTS" IN DEVELOPMENT

In a speech at the University of Basel in 1869, His gave an account of the relations of his recent research to the major tendencies that were competing for control of his field. He described how morphological and physiological approaches to the organization of living beings had become estranged since the articulation in the late 1840s of a physicalist physiology that denied the scientificity of the morphologists' comparative method. Twenty years later the "modern" physiologists—Hermann Helmholtz, Carl Ludwig, Emil du Bois-Reymond, and Ernst Brücke—prided themselves on having made physiology a field of applied physics, but morphologists accused them of giving up on animal organization. Embryology, the science on which His was focusing his efforts, was a case in point. The new physiologists could gain no causal understanding of development from the morphologists' series of forms and deemed the whole problem recalcitrant to physical analysis, at least in the short term. They abandoned it to anatomists and zoologists, many of whom found a rich field of investigation in the development of tissues and cells. The rise of Darwinism in the 1860s, His explained, had temporarily eclipsed this dispute by appearing to give developmental series a genealogical explanation, derived ultimately from the physiological principles of inheritance and adaptation. Haeckel, the Jena zoologist and champion of *Darwinismus*, claimed that he could explain individual development according to the "biogenetic law" as the accelerated recapitulation of the evolutionary development of the species. His accepted the fact of evolution but doubted this simple parallelism; above all, he rejected Haeckel's claim to have provided a physiological explanation of the facts of embryology. Against it, he promoted the other major new approach to studying development, his own recent application of the new physiology to embryos. Rejecting ultimate phylogenetic explanations of ontogeny, he instead sought the proximate causes by which one stage of development transformed itself into the next, and he found them in the forces set up by differential growth. His's speech was an early shot in a key battle over how to study embryos that by the mid 1870s had escalated into an acrimonious controversy. The basic conflict over approaches to embryology was exacerbated by His's accusation that his enemy forged pictures of embryos to suit his theories and complicated by the wider implications of Haeckel's propagandizing for the relationships between scientists, their publics, and the state. I focus here on enriching our understanding of His's enterprise. How, in the face of the rising popularity of Haeckel's phylogenetic embryology, did he use mechanical demonstrations to persuade life scientists to back his alternative?<sup>13</sup>

The son of a silk merchant from an old Basel family, in the early to mid 1850s His had studied in Berlin with Johannes Müller and Robert Remak and in Würzburg with Albert Kölliker and Rudolf Virchow. Appointed in 1857 to the chair of anatomy and physiology in his hometown, he initially continued exploring the histological questions in which Virchow, especially, had stimulated an interest. In the mid 1860s he was studying the development of the chick with a view to removing the exceptions to Remak's germ-layer doc-

<sup>13</sup> Wilhelm His, *Ueber die Bedeutung der Entwicklungsgeschichte für die Auffassung der organischen Natur: Rectoratsrede, gehalten den 4. November 1869* (Leipzig, 1870). For an analysis of these changes see Nyhart, *Biology Takes Form*. On Haeckel's controversies with His and others see Dietrich von Engelhardt, "Polemik und Kontroversen um Haeckel," *Medizinhistorisches Journal*, 1980, 15:284–304; Gursch, *Illustrationen Ernst Haeckels* (cit. n. 8); Keith M. Anderton, "The Limits of Science: A Social, Political, and Moral Agenda for Epistemology in Nineteenth-Century Germany" (Ph.D. diss., Harvard Univ., 1993); and Martina Staub, "Wilhelm His: 'Unsere Körperform und das physiologische Problem ihrer Entstehung'—Eine Kontroverse zwischen Wilhelm His und Ernst Haeckel" (Staatsexamensarbeit, Fach Biologie, Albert-Ludwigs-Univ. Freiburg im Breisgau, 1995).



trine that remained obstacles to a comprehensive linking of embryology and histology; instead, he was led to revise it completely. I will not examine his daring and controversial “parablast” theory but focus on the second of the two major claims he made in a series of publications between 1866 and 1875: that the development of form could be traced back to mechanical principles governed by a general law of growth.<sup>14</sup> His presented the case at length in an 1868 monograph on the early development of the chick in the egg. It was enough for Ludwig to bring him to a chair of anatomy in Leipzig in 1872, but too dry and expensive to compete with Haeckel’s bestsellers. So in the winter of 1874–1875 His targeted a brilliant polemic at his Jena neighbor’s most recent embryological popularization. Dedicated to Ludwig and written as a series of letters to His’s nephew, the physiologist Friedrich Miescher, *Unsere Körperform und das physiologische Problem ihrer Entstehung* is a critique of embryological phylogenizing and a sustained argument that the development of the “form of our body” is a physiological problem.<sup>15</sup>

Years later His would deploy geological analogies to support his mechanical approach, but he began by modeling the germinal disc of embryology on the imperfectly elastic plate of analytical mechanics. Different regions of the germ grew at unequal rates, he noted, and the resulting pressures forced changes in shape. The slower-growing periphery resisted the expansion of the faster-growing central region, causing the surplus material to be thrown up into the system of crisscrossing folds that divided the embryo into the major anatomical regions. The distribution of growth for each species, even each individual, was described by a law that could in principle be expressed as a function dependent on space, time, and other variables, such as temperature and the chemical composition of the medium. His had the Basel mathematician Eduard Hagenbach derive an equation for “the change in form of an imperfectly elastic plate, of which the different parts grow unequally.” Though His recognized that he was far from solving the growth equations that he insisted must express the development of a chick or a human being, he judged not just that they would turn out to be simple but that “the formulae of the growth laws for all beings of the living creation stand in wonderfully simple relation to each other.” He declared that “the higher the growth maximum, the smaller the initial temporal and the larger the middle spatial gradient, the more perfectly must the organism develop.” He supposed that the female body was more juvenile than the male because the temporal gradient of the law of growth was steeper; if one of two individuals had a higher maximum and thus a steeper

<sup>14</sup> Already in 1865 His had reflected on the role of mechanical forces in directing the formation of tissues, especially fibrous connective tissues, of different structures. A growing striated muscle generated different mechanical forces from a growing eye; and the formation, respectively, of a tendon and a concentric capsule could, he argued, be accounted for in terms of the different pressures to which the associated connective tissues had been subjected. See Wilhelm His, *Die Häute und Höhlen des Körpers* (Basel, 1865), rpt. in *Archiv für Anatomie und Physiologie (Anatomische Abteilung)*, 1903, pp. 368–404. His first outlined the growth law in “Ueber die erste Anlage des Wirbelthierleibes (Fortsetzung),” *Verhandlungen der Naturforschenden Gesellschaft in Basel*, 1868, 4:617–639. Biographical information is taken from the works cited in note 12, above.

<sup>15</sup> Wilhelm His, *Untersuchungen über die erste Anlage des Wirbelthierleibes: Die erste Entwicklung des Hühnchens im Ei* (Leipzig, 1868) (hereafter cited as **His, Erste Anlage des Wirbelthierleibes**); and His, *Unsere Körperform*. Praising His to the ministry, the medical faculty followed Ludwig’s lead and wrote that “the drawings and models through which he represents the contents of his anatomical investigations attest as much to a keenly mechanical conception as they show his desire for artistic perfection.” See undated copy of letter [Feb./Mar. 1872] in Universitätsarchiv Leipzig: Personalakte 1405 (Wilhelm His), Bl. 2; and Zirnstein, “Wilhelm His” (cit. n. 12). A small group of anatomists in the 1850s and 1860s was closely aligned with the new physiologists, especially Ludwig, and applied mechanics to the forms of bodily structures, particularly the human locomotor apparatus and the circulation of the blood; see Nyhart, *Biology Takes Form*, pp. 80–84. His was part of this network: in Basel, Christoph Theodor Aeby had been his prosector; in Leipzig, he succeeded E. H. Weber and became the close colleague of the other full professor of anatomy, Wilhelm Braune.

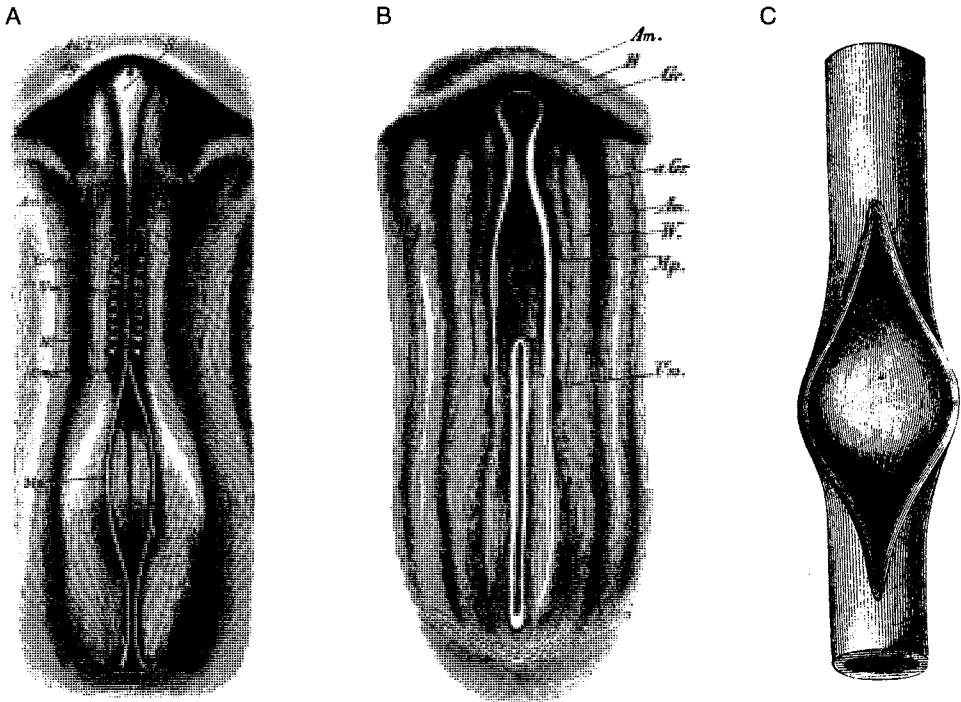
decline of the function, then, he reckoned, it would have more nervous system and be cleverer but weak, while the other would have more musculature and be less intelligent but strong.<sup>16</sup>

In its sweeping vision of the organization of the animal kingdom and bourgeois society, His's law of growth (*Grundgesetz des Wachstums*) was quite as ambitious as Haeckel's biogenetic law (*biogenetisches Grundgesetz*). But the elastic plate and the growth law remained abstractions. To make the approach a convincing alternative, His would have to use the rather limited resources at his disposal to demonstrate concretely the relevance of mechanics to embryology. The physicalist physiologists investigated just those activities of living organisms that were central to the burgeoning industrial economy; Ludwig and his comrades in arms had modeled processes in living organisms in terms of the mechanical engineering devices they had learned about at the Berlin Physical Society in the 1840s. Helmholtz represented the nervous system as a telegraph, the eye as a photometer, and the ear as a tuning-fork interrupter with attached resonators.<sup>17</sup> The distance between muscles working instruments in physiological laboratories and muscles working machines in factories was routinely traversed, but in the 1860s the gap between the factory and the embryological laboratory was still huge. His could, then, have no reasonable expectation of finding machines that would allow him to do for the development of form what the physiologists were doing for muscle contraction and nervous conduction. At best he might make a mechanical approach to embryology credible by overturning the prejudices among anatomists that mechanical methods were hopelessly crude and among physiologists that development was hopelessly complex.

His taught his readers to see the formation of the chick embryo mechanically, inviting them to imagine that they were bending and folding layers of embryonic tissue. In *Unsere Körperform* he introduced successively younger stages, showing how readers might run development backward by grasping the edges of the germ and pulling them apart; the embryo, he argued, developed by the same movements in reverse. He described the formation of the central nervous system as the production of a tube from a plate of tissue. More rapid growth in the central region of the embryo and in the upper germ layer caused it to fold. Two longitudinal folds approached each other in the dorsal midline so as to enclose a tube between them. The tube separated off, and the continuity of the plate that now covered it was restored. To reverse the process—to go from a two-day-old to a one-day-old embryo—the tube had to be slit open along its whole length, the walls spread out

<sup>16</sup> His, *Erste Anlage des Wirbelthierleibes*, pp. 183–224, on pp. 194, 212, 218; on individual differences see His, "Anlage des Wirbelthierleibes" (cit. n. 14), p. 634. It is certainly possible that His was inspired by geology—as a student he attended Bernhard Studer's lectures in Bern—but beyond reference to "mountain and valley folds" there are no geological analogies in the works I discuss in this section. For an early comment on geology see "On the Principles of Animal Morphology, by Professor Wilhelm His of Leipzig: Letter to Mr John Murray, V.P.R.S. Ed.," *Proceedings of the Royal Society of Edinburgh*, 1887–1888, 15:287–298, on p. 294, rpt. in *The Interpretation of Animal Form: Essays by Jeffries Wyman, Carl Gegenbaur, E. Ray Lankester, Henri Lacaze Duthiers, Wilhelm His, and H. Newell Martin, 1868–1888*, ed. and trans. William Coleman (New York: Johnson, 1967), pp. 167–178. His's only extended discussion of parallels to geology, the late article "Ueber mechanische Grundvorgänge thierischer Formenbildung," *Arch. Anat. Physiol.*, 1894, pp. 1–80, draws mostly on geological work, especially of the Zurich professor Albert Heim, that was not published until the late 1870s. Interestingly, His not only discussed similarities in patterns of bending and folding but also mentioned the models produced by Heim's students; see Wilhelm His, *Anatomie menschlicher Embryonen*, 3 vols., Vol. 3: *Zur Geschichte der Organe* (Leipzig, 1885), p. 5. On geological modeling see Mott T. Greene, *Geology in the Nineteenth Century: Changing Views of a Changing World* (Ithaca, N.Y.: Cornell Univ. Press, 1982).

<sup>17</sup> Lenoir, "Models and Instruments" (cit. n. 9); Lenoir, "Helmholtz and the Materialities of Communication" (cit. n. 9); and Robert M. Brain, "The Graphic Method: Inscription, Visualization, and Measurement in Nineteenth-Century Science and Culture" (Ph.D. diss., UCLA, 1996), Ch. 2.

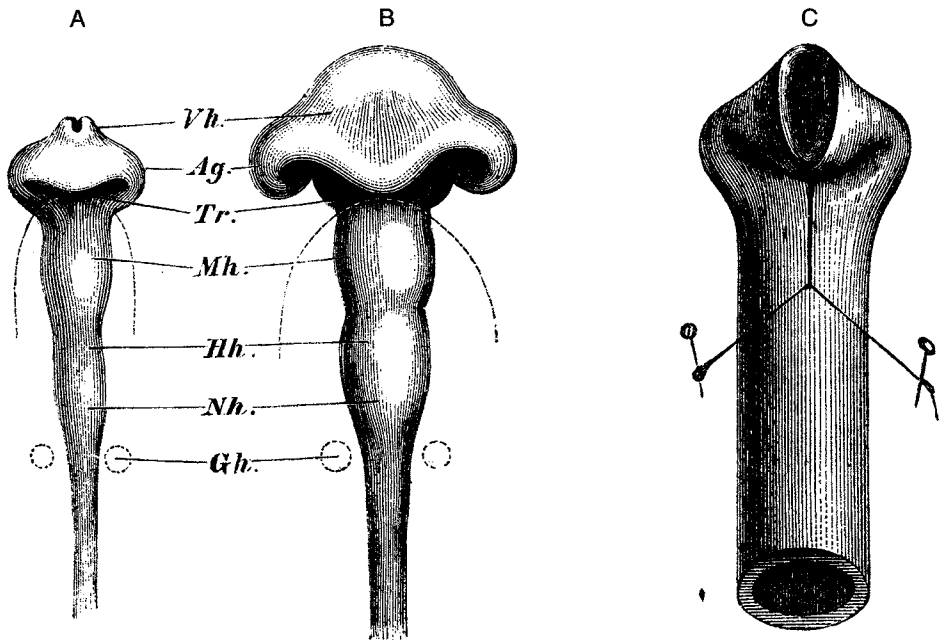


**Figure 1.** Surface (dorsal) views of (A) two-day and (B) end-of-first-day chick embryos; (C) slit rubber tube with convex bend. From Wilhelm His, *Unsere Körperform und das physiologische Problem ihrer Entstehung: Briefe an einen befreundeten Naturforscher* (Leipzig, 1874; but the preface is dated Jan. 1875), Figures 10, 14, and 88. (Courtesy of the Wellcome Institute Library, London.)

flat, and the pockets at the ends evened up (Figures 1A and 1B). Similar bending and folding movements accounted for the formation of the basic plan of the embryonic body and the major organs. The same small set of “paradigms” recurred again and again.<sup>18</sup>

To establish the plausibility of explaining embryogenesis on mechanical principles, His suggested a series of “simple experiments,” physical models in everyday materials such as paper, rubber, leather, and lead plate that mimicked the shape changes of the developing germ layers and organs. For example, he explained the development of the central nervous system by modeling it using a rubber tube with moderately elastic walls and a relatively wide bore. The characteristic spindle-shaped gaping of the developing medullary (neural) tube (Figure 1A) was just what one obtained by slitting a rubber tube along part of its length and applying a convex bend (Figure 1C). More elaborately, His used the same rubber tube model to explain the formation, by folding perpendicular to the axis, of the major divisions of the brain. The most anterior fold was produced by longitudinal growth of the medullary tube while it was attached to the foregut; this could be imitated exactly by pulling back the open end of a rubber tube with a twill thread. The “ears” that the fold produced in the tube corresponded to the optic vesicles (Figures 2A through 2C). He further modeled the future ventral parts folding under the central region, and so closing the em-

<sup>18</sup> His, *Unsere Körperform*, pp. 1–17; for “paradigms” see p. 83.

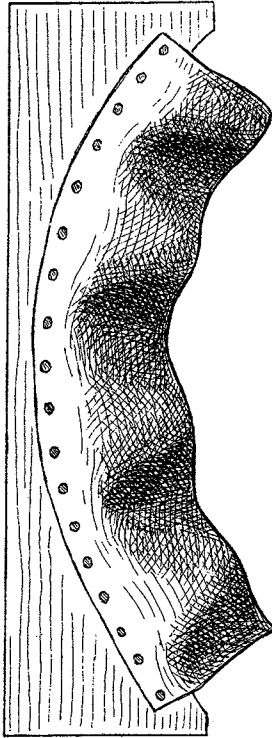


**Figure 2.** Brains of (A) two-day and (B) two- to three-day chick embryos; (C) rubber tube, the open end of which is pulled back by a twill thread. From Wilhelm His, *Unsere Körperform und das physiologische Problem ihrer Entstehung: Briefe an einen befreundeten Naturforscher* (Leipzig, 1874; but the preface is dated Jan. 1875), Figures 82, 83, and 86. (Courtesy of the Wellcome Institute Library, London.)

bryonic body, by folding a letter. The impossibility of closing it completely was like that of trying to fold a letter around a larger piece of stiff card or—better—could be demonstrated on a leather embryo containing a wire frame. Upper and lower germ layers separated like two pieces of paper loosely stuck by their flat surfaces when light pressure was exerted on the edges. His modeled the interdependence of the formation of the anterior embryonic fold and increasing longitudinal folding in lead plate. To model the segmentation into blocks (somites) of the bands of mesoderm on either side of the embryonic backbone (notochord), he fixed one edge of a band of leather or cloth along a concave line so that the free edge crinkled into a zigzag; crinkling made the less elastic somitic plate break up into the individual somites (Figure 3). Pressing a lump of wax or clay together with four fingers showed how the secondary succeed the primary facial structures.<sup>19</sup>

His claimed that, though crude, the forms he produced in rubber, leather, paper, lead, and clay were sufficiently similar to the developing embryo that the same basic mechanical processes must be involved. Beyond demonstrating that the germinal disc, in spite of a texture like wet paper, had some elasticity, he did no experiments to test his growth law on the embryo itself. The Zurich physiologist Adolf Fick suggested some that he might

<sup>19</sup> His, *Erste Anlage des Wirbelthierleibes*, pp. 46, 154, 61, 78, 82, 138. For the term "simple experiments" see *ibid.*, pp. 52, 72, 87; and His, *Unsere Körperform*, p. 48. For the rubber tube model of the nervous system see His, *Erste Anlage des Wirbelthierleibes*, pp. 87, 105; and His, *Unsere Körperform*, pp. 93–104.



**Figure 3.** Leather strip nailed to a board along a convex line; the free concavely bending edge of the strip forms crinkled folds. From Wilhelm His, "Ueber mechanische Grundvorgänge thierischer Formenbildung," *Archiv für Anatomie und Physiologie (Anatomische Abtheilung)*, 1894, pages 1–80, Figure 17. (By permission of the Syndics of Cambridge University Library.)

try—cutting into the edge of the germ or local heating with electric wires to change the rate of growth—but His did not take them up. He raised no objection in principle, but it is unlikely that such experiments would have succeeded; chick embryos would later be found rather intolerant of mechanical intervention. He was more concerned to finish his descriptive work, or perhaps he was waiting for a more positive reception before he took the mechanical investigations further.<sup>20</sup>

The notoriously hostile response His received from Haeckel has tended to overshadow quieter voices of qualified support. The physiologists Fick, Ludwig, and Miescher were actually enthusiastic about his work, as was the anonymous reviewer in the British *Journal of Anatomy*. Several anatomists and physiologists praised the mechanical approach, but most considered that His overestimated the importance of larger mechanical forces at the expense of those specific activities of the cells that were determined by the poorly understood laws of development. In an early review the sympathetic Kiel physiologist Victor Hensen could "perceive in these mechanical relationships only the wheel on the machine

<sup>20</sup> For the elasticity test see His, *Unsere Körperform*, pp. 48–49. The correspondence with Adolf Fick, which began in Feb. 1867, is quoted in Rudolf Fick, "Wilhelm His" (cit. n. 12), pp. 190–191.

which is used now this way, and now another." In the second edition of his standard textbook, Kölliker warmly agreed with His's general premises but objected that he highlighted "mechanical moments" in the blastoderm as a whole while neglecting the more important growth, shape-changing, and secretory activities of its elementary parts. More specifically, Kölliker was led by His's "comparisons with rubber tubes, etc.," and "his vivid descriptions of the effects of mechanical moments in early development" to observe "that there is doubtless in the whole animal kingdom hardly a tissue to which less elasticity could be ascribed than the germinal membrane of the chick egg."<sup>21</sup>

While the mild critics declared their solidarity with His's aims but found his methods inadequate, zoologists and comparative anatomists who based their work on the theory of descent attacked him as wrong in principle. Haeckel led his colleagues in the Jena bastion of Darwinism, other scientific friends at home and abroad, and sympathetic journalists into battle. The most polemical of many attacks was *Ziele und Wege der heutigen Entwicklungsgeschichte* [Aims and Approaches in Embryology Today], Haeckel's riposte to *Unsere Körperform*. He satirically contrasted the crudity of his opponent's theories with "the infinitely fine and complex nature of the mechanical problem." While phylogeny saw in rudimentary organs the atrophied remains of parts of the body that evolution had taken out of service, His had described them as "'embryological residues, comparable to the waste which in cutting out a dress cannot be completely avoided however economically the material is used'! . . . Hell's rags then, which the cunning dressmaker 'nature' puts on one side and throws behind the oven, into the 'chimney-corner' [*Hölle*, also 'hell']!"<sup>22</sup>

The "envelope theory" was no less funny, the "rubber tube theory" if possible still cruder. Playing on the concerns even of more conciliatory critics, and appealing to their snobbery, Haeckel's jibes derided His's simple experiments as reducing nature to the level of an artisan. But Haeckel's deeper argument was that, without phylogeny, even the most sophisticated account of ontogeny would be powerless to explain where the bendings and foldings came from. His had tried to trick out his growth law in evolutionary costume, Haeckel said, but he insisted that embryologists had to take sides. Behind him, and mostly behind the scenes, stood his anatomist colleague in Jena, Carl Gegenbaur.<sup>23</sup> For example,

<sup>21</sup> F. M. [Friedrich Miescher?], *Correspondenz-Blatt der Schweizer Aerzte*, 1875, 5:199–202; Anon., *Journal of Anatomy*, 1869, 3:183–186; Anon., *Journal of Anatomy and Physiology*, 1875, 9:387; [Victor] Hensen, "Generationslehre und Embryologie," *Jahresbericht über die Leistungen und Fortschritte in der gesamten Medicin*, 1869, 3:56–65, on pp. 62–63; and Albert Kölliker, *Entwicklungsgeschichte des Menschen und der höheren Thiere*, 2nd ed. (Leipzig, 1876), pp. 396–397. See also Kölliker, *Grundriss der Entwicklungsgeschichte des Menschen und der höheren Tiere*, 2nd ed. (Leipzig, 1884), p. 8; and, for His's response, in which he denied neglecting the cells, "Mechanische Grundvorgänge thierischer Formenbildung" (cit. n. 16), pp. 50–51.

<sup>22</sup> Ernst Haeckel, *Ziele und Wege der heutigen Entwicklungsgeschichte* (Jena, 1875), p. 27; he is quoting His, *Erste Anlage des Wirbelthierleibes*, p. 56.

<sup>23</sup> Carl Gegenbaur, "Die Stellung und Bedeutung der Morphologie," *Morphologisches Jahrbuch*, 1875, 1:1–19. In private Gegenbaur sharply criticized Haeckel for polemical excesses against inappropriate targets in *Ziele und Wege*, but he welcomed his friend's treatment of His: "The polemic against His . . . is . . . splendid, even brilliant, and I believe completely successful." See Carl Gegenbaur to Ernst Haeckel, 25 Nov. 1875, Best, A, Abt. 1, Ernst-Haeckel-Haus, Jena. On the relationship between the two men see Erika Kraube, "Zum Verhältnis von Carl Gegenbaur (1826–1903) und Ernst Haeckel (1834–1919): Generelle und spezielle Morphologie," in *Miscellen zur Geschichte der Biologie: Ilse Jahn und Hans Querner zum 70. Geburtstag*, ed. Armin Geus, Wolfgang Friedrich Gutmann, and Michael Weingarten (Aufsätze und Reden der Senckenbergischen Naturforschenden Gesellschaft, 41) (Frankfurt am Main: Kramer, 1994), pp. 83–99; and Mario A. Di Gregorio, "A Wolf in Sheep's Clothing: Carl Gegenbaur, Ernst Haeckel, the Vertebral Theory of the Skull, and the Survival of Richard Owen," *J. Hist. Biol.*, 1995, 28:247–280. Their Jena botanical colleague Eduard Strasburger signaled his loyalty by attacking His in his inaugural lecture, "Ueber die Bedeutung phylogenetischer Methoden für die Erforschung lebender Wesen: Rede gehalten beim Eintritt in die philosophische Facultät der Universität Jena am 2. August 1873," *Jenaische Zeitschrift für Naturwissenschaft*, 1874, 8:56–80, on pp. 77–78.

he took the Swiss zoologist, veteran materialist, and convert to Darwinism Carl Vogt to task for highlighting points of agreement with His in the *Frankfurter Zeitung*, a prominent liberal newspaper. Giving Haeckel qualified support were the likes of the British comparative embryologist Francis Balfour; amplifying Haeckel's polemics for a wide readership were popularizers such as the zoologist-journalist Otto Zacharias, who derided "His's nonsense" in the Darwinist family magazine *Ausland*.<sup>24</sup>

The power of Haeckel and Gegenbaur over German zoology and anatomy in the decades after Darwin has often been exaggerated. Haeckel's highly controversial popular success did not win the general approval of his peers—nor did it ultimately translate into many chairs for his students. Yet during the 1870s phylogenizing was nevertheless all the rage; his theories appealed especially to younger zoologists competing in a suddenly crowded job market because they could give relatively narrow studies, often employing the new microtomes, wider significance.<sup>25</sup> It is to the microtome that I now turn, asking why His opposed not only Haeckel-style theorizing but also the way the youngsters used an instrument he was himself famous for applying to embryos.

#### RECONSTRUCTING THE WHOLE

The most striking difference between Karl Ernst von Baer's classic treatise on the development of the chick in the egg of 1828 and the monograph on the same topic that His dedicated to the old master forty years later was the revolution in tissue preparation that His's book exemplified and promoted. Von Baer had opened the eggs, macerated the tissues a little in water, and pulled them apart with needles while observing under a simple magnifying glass. His marveled at what his illustrious predecessor had seen but sought by the first systematic use of serial sections to make new discoveries on this classical material.<sup>26</sup> So at the resolutions in which he was interested he no longer confronted an embryo that could be manipulated under a magnifying glass but dozens of tissue slices. To visualize vividly the bending and folding of embryonic tissues that his simple experiments set out

<sup>24</sup> Carl Vogt, "Wissenschaftliche und unwissenschaftliche Bücherei," *Frankfurter Zeitung*, 31 Mar. 1875, pp. 1–2. Gegenbaur reported to Haeckel that he had tackled Vogt, who had recently visited him, about his article in the *Frankfurter Zeitung* and elicited a storm of protest. I assume that it was especially the treatment of His in this review that was at issue. See Gegenbaur to Haeckel, 5 Apr. 1875, Ernst-Haeckel-Haus. F. M. Balfour, *A Monograph on the Development of the Elasmobranch Fishes* (London, 1878), pp. iv–v. M. F. [Balfour's teacher Michael Foster?], "His on Morphological Causation," *Nature*, 1875, 12:328, made a similar objection to Hensen, but much more negatively. Defending His's work on the power of differential growth to generate form, D'Arcy Wentworth Thompson could "well remember the harsh criticism, and even contempt, which His's doctrine met with, not merely on the ground that it was inadequate, but because such explanation was deemed wholly inappropriate, and was utterly disavowed"; see D'Arcy Wentworth Thompson, *On Growth and Form* (Cambridge: Cambridge Univ. Press, 1917), p. 56. Otto Zacharias, "Ziele und Wege der heutigen Entwicklungsgeschichte," *Ausland*, 1876, 49:29–32, on p. 30.

<sup>25</sup> Nyhart, *Biology Takes Form*, pp. 193–204.

<sup>26</sup> His described Baer's technique in *Erste Anlage des Wirbelthierleibes*, p. 180. For an excellent survey of embryology between Baer and His see Churchill, "Rise of Classical Descriptive Embryology" (cit. n. 6); on earlier investigations of the chick embryo see Anne Bäumer-Schleinkofer, *Die Geschichte der beobachtenden Embryologie: Die Hühnchenentwicklung als Studienobjekt über zwei Jahrtausende* (Frankfurt am Main: Lang, 1993). One of the discoveries with which His's monograph has been credited is of the neural crest; see Sven Hörstadius, *The Neural Crest: Its Properties and Derivatives in the Light of Experimental Research* (London: Oxford Univ. Press, 1950), p. 3, rpt. in Brian K. Hall, *The Neural Crest: Including a Facsimile Reprint of The Neural Crest by Sven Hörstadius* (London: Oxford Univ. Press, 1988). A notebook documenting His's analyses, embryo by embryo, for about a year from the summer of 1866 promises to shed new light on the making of his monograph on the chick, but it came into my hands too late to be used here; see Nick Hopwood and Jaroslav Slička, "'Embryologica 1866': Discovery of Wilhelm His's Notebook on the Development of the Chick in the Egg," *Physiological Society Magazine*, Summer 1998, no. 31, pp. 13–14.

to mimic, he invented a method of reconstructing whole embryos from the sections. Plastic reconstruction, he argued, would recover the immediate apprehension of form that he supposed von Baer to have enjoyed and allow his successors once again to "give body" to their views.

Scientists had cut sections—even with section cutters—before, but new microtomes and associated improvements in methods of specimen preparation broke down skepticism toward the instruments and made sectioning much more complete and routine. His's own machine, though briefly the most effective, was never widely used and rapidly lost out to other designs that exploded onto the market. From the 1870s sections were regularly produced by a long and tedious sequence of operations that might include hardening, fixing, staining, embedding, sectioning, arrangement on a slide, and inclusion in Canada balsam. Within fifteen years the American zoologist Charles Otis Whitman could claim for the microtome "a place in the zoological laboratory second in importance only to the microscope itself." The microtome symbolizes a transformation in the practice of microscopy, a sea change in the experience of laboratory work in the life sciences, and a reorientation of the objects of research from living organisms in their environments to the internal topography of fixed and sectioned specimens. It was credited with making possible an extraordinary accumulation of embryological knowledge. But the wealth of detail revealed by the new histology appeared to many contemporaries and subsequent historians to have been bought at an exorbitant price. E. S. Russell noted that "the tyro" could "confirm in a day what von Baer . . . had taken weeks of painful endeavour to discover" but voiced an elitist lament that the consequent "democratisation of morphology" had produced such "an evil heritage of detailed and unintelligent work." Contemporary protests from older zoologists and anatomists are legion: through mindless sectioning their students were alienating themselves from life. These critics identified two distinct dimensions of impoverishment: loss of the capacity to visualize whole organisms, and loss of an appreciation for how they functioned in environments. Both are instantiated in Haeckel's complaint that "the next generation of 'scientific zoologists' will know only *cross-sections* and *stained* tissues, but neither *whole* animals nor their mode of life!"<sup>27</sup>

Exploring the variety of zoological work carried out in Germany in the 1880s and 1890s, Lynn Nyhart has shown that although "slice-and-stain" problems remained popular training exercises, plenty of zoologists continued to investigate animals' relations to their environments. I wish to draw attention to an attempt to make good the other main loss experienced by anatomists and zoologists: visual alienation from the form of whole animals. The septuagenarian Munich zoologist Carl Theodor von Siebold complained in the early 1880s to the Freiburg anatomist Alexander Ecker that young zoologists could imagine a worm only in the form of series of sections, that they had utterly lost the picture of the whole animal. Though it at first appears paradoxical, His—the man who invented a machine capable of generating scores of sections a week—agreed wholeheartedly with Siebold about the danger of losing the capacity to visualize the whole. Indeed, in the very paper in which he described the microtome, His claimed that its principal advantage over cutting with a knife was that it made serial sectioning possible and that this permitted the three-dimensional reconstruction of whole embryos from the sections. I quote the passage in full. First

<sup>27</sup> C. O. Whitman, *Methods of Research in Microscopical Anatomy and Embryology* (Boston, 1885), p. 2; Russell, *Form and Function* (cit. n. 6), p. 268; and Haeckel to Carl Theodor von Siebold, 5 Mar. 1881, in Georg Uschmann, *Ernst Haeckel: Biographie in Briefen* (Leipzig: Urania, 1983), p. 158. On the microtome see also the works cited in note 6, above.



comes the well-known advertisement for the rapidity of the instrument: "I have been using it since 1866, and have in this time probably prepared with it over 5,000 sections. Without the apparatus I would, like others, have doubtless been able to prepare some nice sections, only certainly not this great number. I have thus gained time and besides that also material." His then explains that being able to make complete series of sections is worth more than speed: "Only higher than this, in itself very important advantage, I rate the consideration that the apparatus has allowed me a precision in working that would never have been possible in sectioning by hand. That is to say, it has made it possible for me to gain uninterrupted series of sections of the investigated objects." Only in the early 1880s did it become possible to cut sections in long ribbons; to produce serial sections His had to collect each slide and arrange them all in order, one at a time. Why was this so desirable?

Gaining plastic views through synthetic combinations of sectional images is indisputably a long and tiring detour, but it is not to be avoided whenever the objects are too fine to reveal their relief to us directly. Anyone who takes the trouble to give body to his views [*seinen Anschauungen . . . Körper zu geben*] in a malleable material [such as] in wax or in clay will soon discover how important the uninterruptedness of the sections is for such reconstructions of plastic views and sectional images.<sup>28</sup>

The greatest advantage of the microtome was that it produced sections suitable for making models.

His promoted plastic reconstruction with a nostalgic rhetoric. The early embryologists, Caspar Friedrich Wolff in the mid-eighteenth century and von Baer in the early nineteenth, "saw bodily [*körperlich*; also 'materially,' 'corporeally'] and dissected bodily," and in this respect they had had the advantage over his own generation. Things changed with the rise of the microscope and of sectioning. The pathbreaking works of the early 1850s—especially of His's own embryology teacher, Remak—had marked the start of "a period in which people often lost contact with bodily perception [*körperlichen Anschauung*]" and allowed the description of sections to take the place of bodily representations of form. His later acknowledged that the microtome had encouraged this "temptation."<sup>29</sup> But sectioning, he would repeatedly remind anatomists and zoologists, was necessary only because the smallness of the objects of interest made physical dissection impracticable, and yet they were too large and opaque for direct microscopical observation of their interiors. The methods of plastic reconstruction that he had developed would allow scientists to "give body" to visual understanding and so return—in richer detail—to the lost world of the pioneers.

In the 1868 monograph His presented cross- and longitudinal sections as well as surface views (Figure 4). But just looking through sections, he argued, did not enable one to build three-dimensional images in the mind. Rather, the preparation of the sections should be regarded as but the first step in an elaborate process of three-dimensional representation.<sup>30</sup> He imagined himself as an architect visualizing the shape of a building from a plan view

<sup>28</sup> Nyhart, *Biology Takes Form*, pp. 202–203, 315; Alexander Ecker, *Hundert Jahre einer Freiburger Professorenfamilie: Biographische Aufzeichnungen* (Freiburg in Baden, 1886), p. 142; and His, "Beschreibung eines Mikrotoms" (cit. n. 9), p. 231.

<sup>29</sup> Wilhelm His, "Über die Methoden der plastischen Rekonstruktion und über deren Bedeutung für Anatomie u. Entwicklungsgeschichte," *Anat. Anz.*, 1887, 2:382–394, on pp. 382–383; see also His, *Erste Anlage des Wirbelthierleibes*, p. 180.

<sup>30</sup> His, *Erste Anlage des Wirbelthierleibes*, pp. 180–182, describes the procedure.

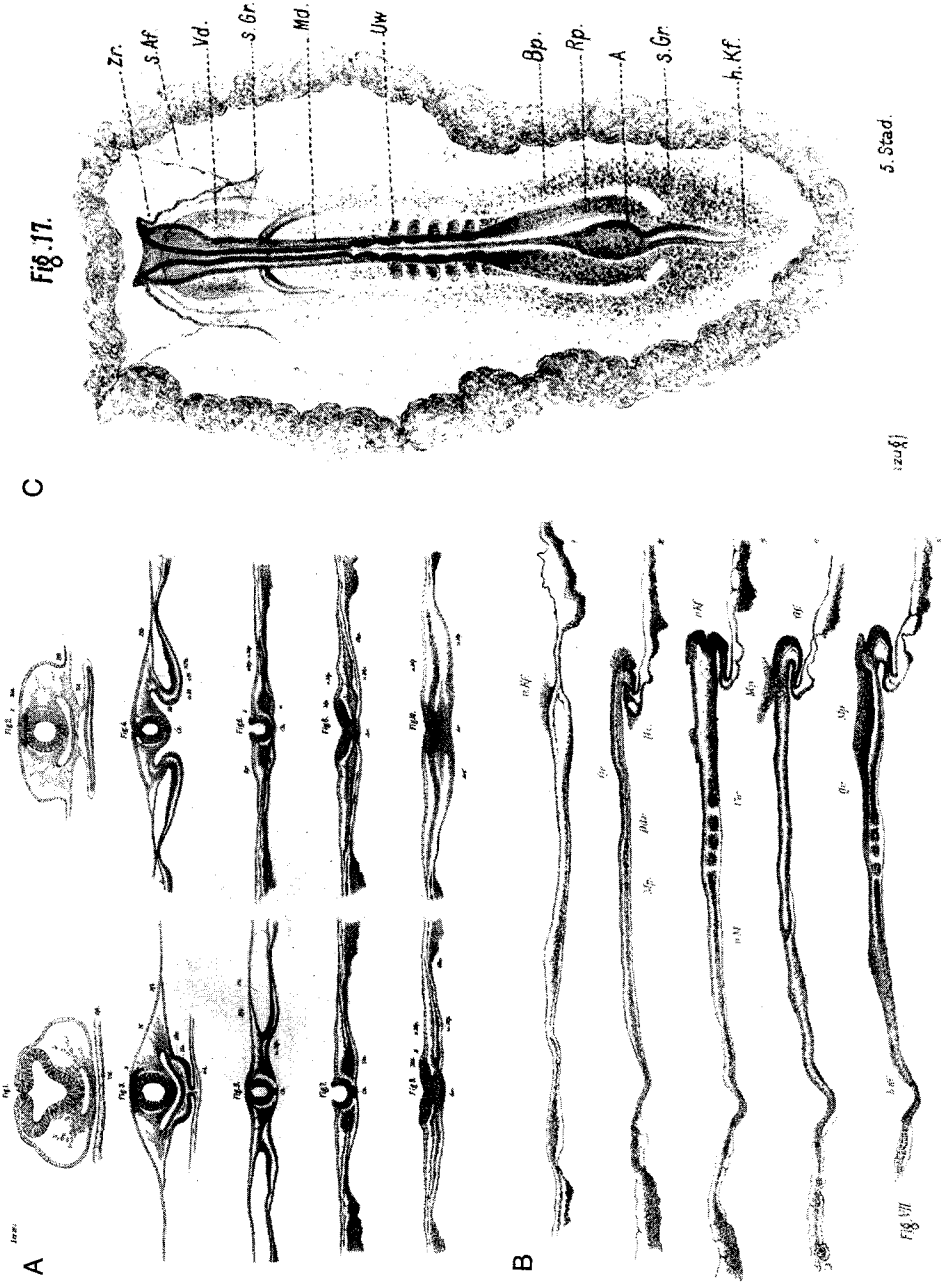
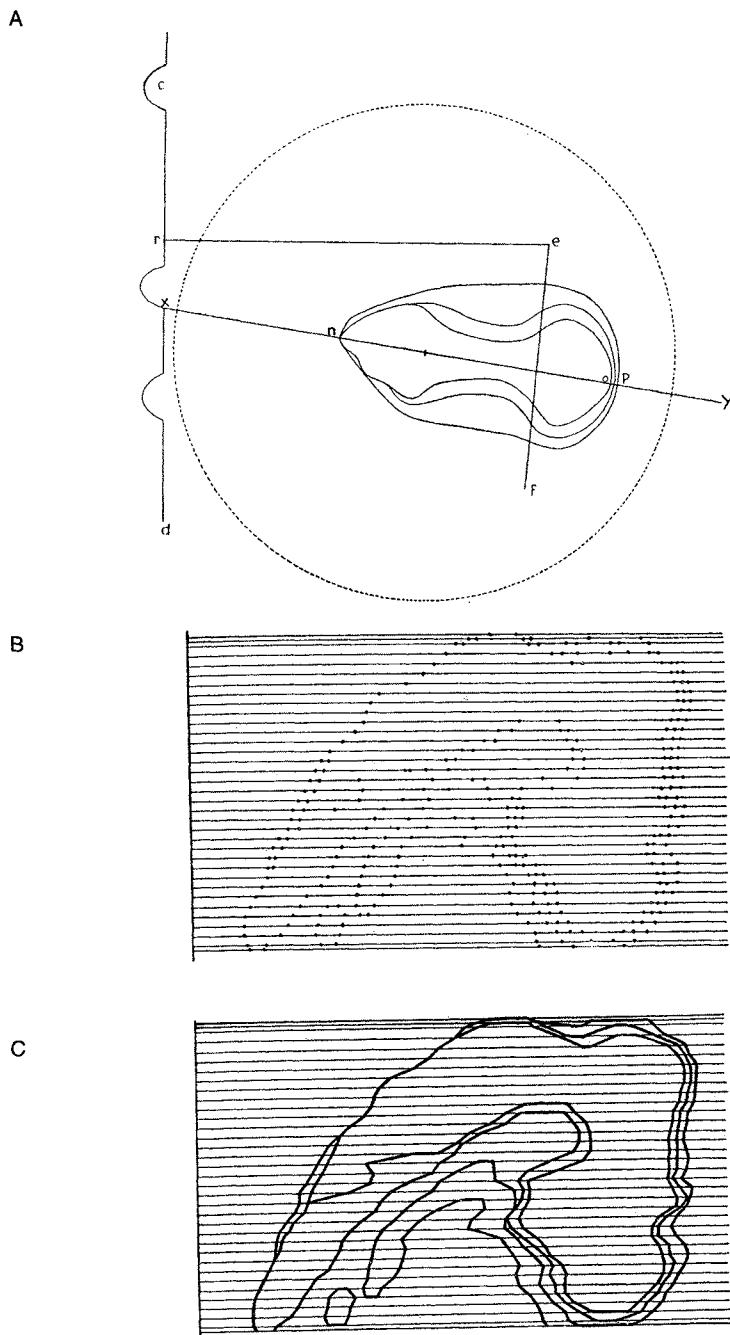


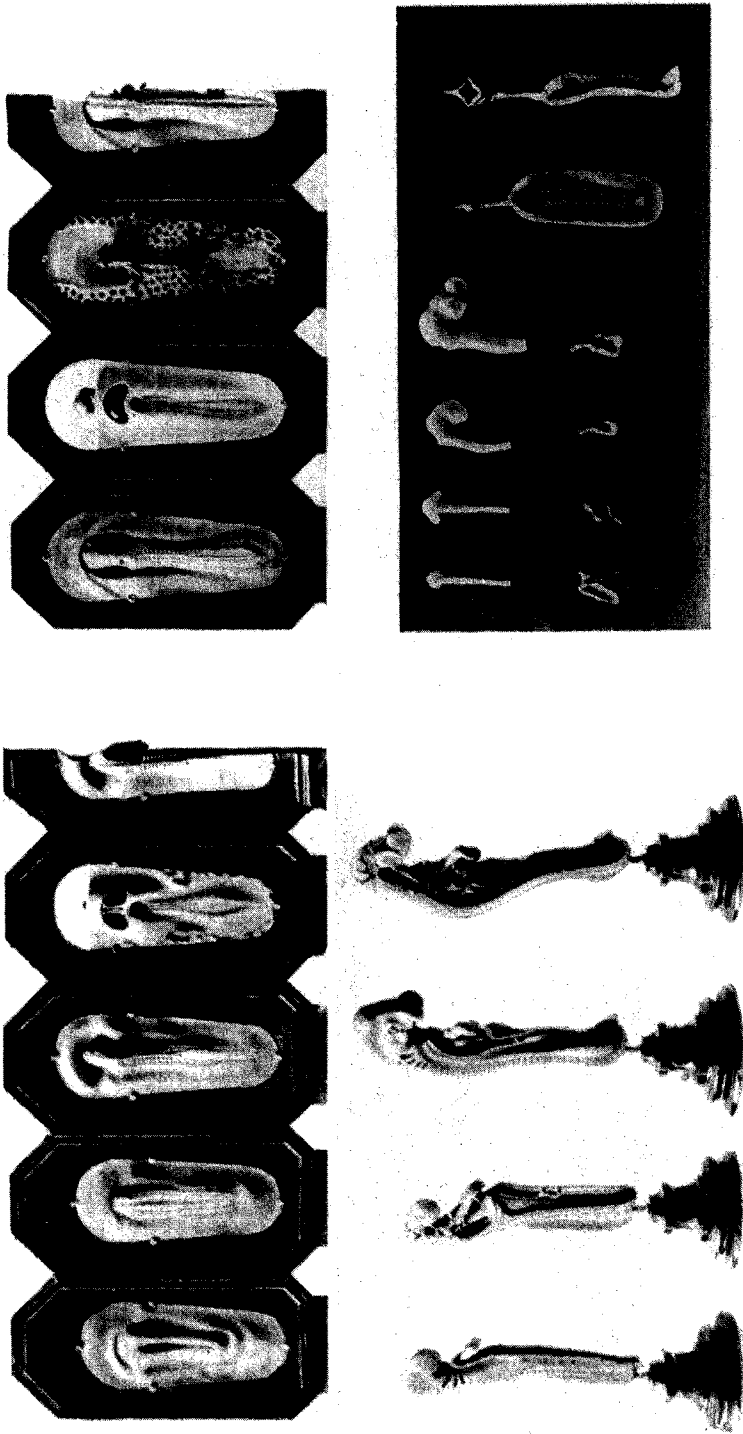
Figure 4. Stage 5 (two-day) chick embryo. (A) Cross-sections; (B) longitudinal sections; (C) surface view. From Wilhelm His, *Untersuchungen über die erste Anlage des Wirbelthierleibes: Die erste Entwicklung des Hühnchens im Ei* (Leipzig, 1868), Plates 7, 5, and 12. (By permission of the Syndics of Cambridge University Library.)

and elevations. The ideal would have been to view an embryo whole and then to investigate both cross- and longitudinal sections. But since no specimen could actually be sectioned twice, this had to be achieved indirectly. Before sectioning he drew the embryo in surface view, and after cutting, for example, cross-sections drew each section to the same magnification with the help of a camera lucida. His designed a special drawing apparatus that offered a convenient range of magnifications. But his major innovation was a method of “projective construction” for producing images of longitudinal or frontal sections from these cross-sectional drawings. He divided a piece of paper into parallel zones, each representing the thickness of a single section, and drew in a baseline, in the case of a sagittal construction the profile of the back with the appropriate curvature. Now he used a pair of compasses or callipers to measure on the cross-sectional drawings the various distances from the baseline of organs such as the medullary tube or the aorta and marked these in the correct places on the paper. The simplest way to do this was to plot for each section the points at which a particular line crossed the contours of the organs and to join the dots to produce a sagittal sectional image (Figure 5). The process could be repeated to make a series of longitudinal sections. It was also possible to project the whole of each cross-section at once and, after joining the dots, to add shading to produce a three-dimensional drawing. In this way, His regularly produced both frontal and profile constructions of cross-sectioned embryos, often focusing on particular organ systems or parts of the body. But the all-important next step was to use the drawings to make a model.

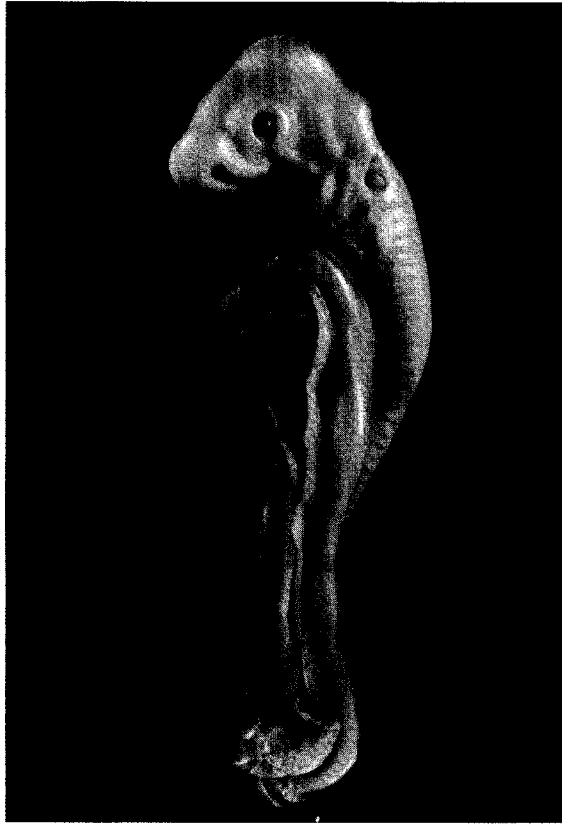
In the late eighteenth century wax models of the development of the chick were produced at La Specola in Florence and in Paris by André Pinson, modeler to the duc d’Orléans. His’s models differed not just in their purpose and audience but especially in exploiting sectional images. They were possible, however, only because he could draw on the skills of earlier modelers. His learned to model in wax from the leading embryological modeler Adolf Ziegler (1820–1889), who had qualified as an apothecary and then in medicine and settled as a physician in Freiburg in Baden. There he was employed as a zootomical *Assistent* under Ecker from 1854 to 1868, when he left his university job to devote himself to modeling full time. He subsequently dated the founding of his Studio for Scientific Modeling (*Atelier für wissenschaftliche Plastik*) to 1852, when he sold a series of twenty-five models on the development of the frog. By the mid 1860s, several series later, any embryologist looking for help with modeling would have turned to Ziegler. For His, only a few miles down the road in Basel, it would have been especially easy to avail himself of the modeler’s time. Unsatisfied with his own early efforts in lead and leather, His confessed that had it not been for “the tried and tested Freiburg artist” he might have given up: “I was made familiar by him with the manipulation of modeling clay and of wax, and in joint work we manufactured a series of models from specimens and sections, in the preparation of which we strove for the greatest possible accuracy and fidelity.” Ziegler reproduced and marketed a series of models on the early development of the chick to complement the plates of serial sections with which His illustrated the 1868 monograph. Thirteen mounted whole embryos at 40-fold linear magnification (about 30 cm high, including stands) correspond to stages 3–5 and 7–9 of the ten stages of embryogenesis that His had distinguished (Figures 6 and 7). Models of the earlier stages (the top row in Figure 6) were translucent, and when viewed against the light they were supposed to recreate the effect given by the embryo as light shone through it. Colored waxes differentiated germ layers and organs. The extra models were cut away to show internal systems, and ten additional organ models focused on the development of the brain, heart, and gut in the



**Figure 5.** Projective construction of a median section from a series of cross-sections. (A) Section through neck of a lizard embryo (c–d, guideline; x–y, line along which section is to be reconstructed). (B) Reconstruction of median section, with guideline left and points giving positions at which lines x–y cut the contours of the organs (the section shown in [A] corresponds to the eighth line from the top). (C) The points have been joined by straight lines. This method is based on Wilhelm His, *Untersuchungen über die erste Anlage des Wirbelthierleibes: Die erste Entwicklung des Hühnchens im Ei* (Leipzig, 1868), but the guidelines, at least, represent a more recent modification; he used the dorsal boundary of the embryo as a reference line. From Karl Peter, *Die Methoden der Rekonstruktion* (Jena: Fischer, 1906), Figures 21, 24, and 25. (Courtesy of the Anatomy Department Library, University of Cambridge.)



**Figure 6.** His-Ziegler wax models of the development of the chick. From Friedrich Ziegler, *Embryologische Wachsmodelle (Freiburg in Baden, probably 1920s)*. (Courtesy of the Medizinhistorisches Institut der Universität Bern.)



**Figure 7.** His-Ziegler wax model of a four-day chick embryo, number 12 in the series shown in Figure 6. (Courtesy of the Anatomisches Museum Basel.)

later stages. These internal views show most clearly how much His and Ziegler had gained over Pinson by taking the detour via the sections.<sup>31</sup>

The campaign for modeling in anatomy that His waged for the next three decades offers a passionate argument for doubly embodied knowledge: insight a scientist gained through his body by "giving body" to his views. Rejecting passive contemplation, he argued that those who wished to grasp anatomical structure must actively engage in working through a reconstruction, reproducing the relationships they wished to understand. They must work not only with their brain and eyes but also with their hands. And they must not only draw but produce solid objects too. Taking what was by then a standard argument for drawing into the third dimension, His insisted that "one is within one's rights to demand that embryological researchers know, just as with the pencil, so also with the modeling spatula,

<sup>31</sup> His, *Erste Anlage des Wirbelthierliebes*, p. 182. The models are described in *Prospectus über die von Dr. A. Ziegler in Freiburg i. B. angefertigten Wachspräparate: Die erste Entwicklung des Hühnchens erläuternd* (copy in Biology Library, Univ. California, Berkeley). On anatomical modeling see the works cited in note 1, above. For the chick models of La Specola see Benedetto Lanza, Maria Luisa Azzaroli Puccetti, Marta Poggesi, and Antonio Martelli, *Le cere anatomiche della Specola*, 2nd ed. (Florence: Arnaud, 1997), p. 230; for Pinson's models see Michel Lemire, *Artistes et mortels* (Paris: Chabaud, 1990), p. 286. On Ziegler see Robert Wieder-sheim, "Adolf Ziegler †: Zum Gedächtnis," *Anat. Anz.*, 1889, 4:545–546.

how to give their conceptions of the spatial relationship of the represented parts plastic form and to adjust their descriptions accordingly." He modeled freehand but checked and corrected dimensions with a pair of callipers, using iron spatulas and spoons to add wax or take it away. Working on the same object from different aspects over a period of weeks built up a three-dimensional mental image. There was no substitute for this experience. If drawings were good, then drawing was held to be better; similarly, the modeler His agreed with the artist Ecker that "the pictures in the memory that have once made their way through the hand stick much more firmly in the head."<sup>32</sup>

Nevertheless, as with drawings so with models: not only was the process believed to transform the producer; the products were held to be indispensable in communicating with others who had not subjected themselves to this discipline. His relied on the models to give readers of the monograph the physical images that he argued the plates of serial sections alone could not supply. "As easy as it is to demonstrate the relationship of the anlage of the lung to the anlage of the liver on good models," he complained, "as difficult is it to give a clear presentation with words." The anatomist Wilhelm Waldeyer from Breslau drew attention to the "excellent" models, "which should contribute to understanding of the in many cases completely new views" that His presented. His also used the models in making the three-dimensional drawings with which he illustrated *Unsere Körperform* (compare Figures 1A and 1B with Figure 6), specifically to shade the surface of the body.<sup>33</sup> As a result, the visual language of the book contrasts strikingly with that of another chick-based introduction to embryology that had appeared a few months before. Michael Foster and Francis Balfour based their textbook on Foster's course in Cambridge. Intended for a narrower, student, audience with access to chick embryos and microscopes, it is less heavily illustrated than His's volume and uses mainly drawings of sections, several of them diagrammatic. Conventionally, the authors preferred "a simple razor . . . held in the hand" over a "section instrument," and they highlighted particular planes in which individual sections would be "most instructive." They nevertheless achieved images of three-dimensional structure by viewing the embryo under the microscope or a simple lens as an opaque and especially as a transparent object (whole mount). Yet the pictures His based on the models are much bolder and more detailed, giving the uninitiated reader without access to embryos or models an unprecedentedly vivid view of the developing chick. And he and Ziegler promoted the models so successfully that in the coming decades nearly every student of embryology—and certainly those in Cambridge—learned the development of the chick from them. His had trouble propagating his views, but not because the waxes failed to travel.<sup>34</sup>

<sup>32</sup> His, *Anatomie menschlicher Embryonen* (cit. n. 16), Vol. 1: *Embryonen des ersten Monats* (Leipzig, 1880), p. 12; and Ecker, *Hundert Jahre einer Freiburger Professorenfamilie* (cit. n. 28), pp. 140–141. His stressed the importance of solidity in a criticism of models in wire and thread, which "because of their incorporeality [*Unkörperlichkeit*] leave behind no lasting pictures in the memory": His, "Methoden der plastischen Rekonstruktion" (cit. n. 29), p. 391. On drawing see Soraya de Chadarevian, "Instruments, Illustrations, Skills, and Laboratories in Nineteenth-Century German Botany," in *Non-Verbal Communication in Science Prior to 1900*, ed. Renato G. Mazzolini (Florence: Olschki, 1993), pp. 529–562.

<sup>33</sup> His, *Erste Anlage des Wirbelthierleibes*, p. 145; [Wilhelm] Waldeyer, *Centralblatt für die medicinischen Wissenschaften*, 1869, 7:6–11, 21–24, 35–40, 54–57, 66–71, 82–85, 106–108, on pp. 36–37; and His, *Unsere Körperform*, p. 216.

<sup>34</sup> Michael Foster and Francis M. Balfour, *The Elements of Embryology* (London, 1874), pp. 250–251. For discussion of the illustrations in this work in relation to the problem of visualization in three dimensions see the anonymous review in *J. Anat. Physiol.*, 1875, 9:186–189, on pp. 188–189. When Adam Sedgwick and Walter Heape produced a revised edition in 1883 they asserted that "it is not possible to obtain satisfactory sections of embryos without . . . using a microtome"; see Foster and Balfour, *Elements of Embryology*, ed. Adam Sedgwick

## PLASTIC RECONSTRUCTION AND MECHANICAL REASONING

In addition to abstract mathematical "modeling," we have now seen His making two kinds of material model: reconstructions from sections and "simple experiments." But what could be—and were later often treated as—two distinct kinds of model were for him just two modes in which he modeled, the ends of a spectrum of uses. Not only did plastic reconstruction give His insight into and communicate developing form; it was central to his mechanical approach to development. He devised reconstructive modeling continuously with making the simple experiments, and he rated the activity of reconstruction among the strongest evidence for mechanical principles in embryogenesis.

We can distinguish His's mechanical models, the folded paper and the rubber tubes, from the plastic reconstructions in wax. The former were designed to mimic morphogenetic processes as vividly as possible, the latter to visualize three-dimensional structure as accurately as he could. For example, in the case of the gaping medullary folds, he used a slit and bent rubber tube to model the process and in the same passage where he described the slitting and bending appealed to a reconstructive model as showing more clearly than looking through sections that the surface of the embryo was indeed convex. In modeling static form, the wax model need not be, and generally was not, built by a process claimed to be nature's own way. But though analytically separable, His's production of the two kinds of model was continuous. Before Ziegler taught him to model in wax, he had used leather and lead plate. The lead models in Figure 8 show stages in the progressive folding of the body; they simultaneously demonstrate mechanical principles and represent form. But these materials, though flexible, apparently did not allow His to show structure sufficiently accurately; he found even these results "too crude to satisfy" and turned to the more malleable wax.<sup>35</sup> Lacking the mechanical properties of leather and lead, it was used principally for making very accurate reconstructions.

The point is not simply that, for His in the late 1860s, modeling could be one activity with two linked uses, representing form and demonstrating mechanical processes. It is, further, that he assigned to modeling in general a crucial role in grasping mechanical principles. Claiming that he had arrived at his physiological embryology through modeling, from which he had "gained quite unexpected insight into the relations of form and of growth," he reported on what, specifically, he had learned from plastic reconstruction about the mechanics of development: "The consequences of the principle of folding impose themselves in the course of such work with a much more irresistible force than through the mere contemplation of sections." We could object that, while this may have been true

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and Walter Heape, 2nd ed. (London, 1883), p. 432. By this time Cambridge scientists had designed an automatic microtome that produced ribbons of sections; see M. J. G. Cattermole and A. F. Wolfe, *Horace Darwin's Shop: A History of the Cambridge Scientific Instrument Company, 1878 to 1968* (Bristol/Boston: Hilger, 1987), pp. 166–178. Sydney Smith, "A Remarkable Case of Survival during Two Periods of Severe Environmental Stress" (unpublished, undated MS, Museum of Zoology, Univ. Cambridge), reports that the Ziegler chick models were bought for Balfour and Sedgwick's teaching, on which see Gerald L. Geison, *Michael Foster and the Cambridge School of Physiology: The Scientific Enterprise in Late Victorian Society* (Princeton, N.J.: Princeton Univ. Press, 1978), pp. 124–130. The very wide distribution of the models is attested by the list of 162 towns around the world that Adolf's son, Friedrich Ziegler, claimed to have supplied by 1893; see *Prospectus über die zu Unterrichtszwecken hergestellten Embryologischen Wachsmodelle von Friedrich Ziegler (vormals Dr. Adolph [sic] Ziegler)* (Freiburg in Baden, 1893), p. 5 (copy in Cornell Univ. Library, Ithaca, N.Y.). For a case in which the poor mobility of films was an issue see James Strick, "Swimming against the Tide: Adrianus Pijper and the Debate over Bacterial Flagella, 1946–1956," *Isis*, 1996, 87:274–305.

<sup>35</sup> His, *Erste Anlage des Wirbelthierleibes*, p. 87 (rubber tube); and His, "Methoden der plastischen Rekonstruktion" (cit. n. 29), p. 384 (quotation).





**Figure 8.** “Models by Prof. W. His,” presumably circa 1866–1867, showing successive stages of chick development in lead plate mounted on wood. (Courtesy of the Anatomisches Museum Basel.)

for His, many before him had presented development mechanically without taking the detour via the sections. One reviewer noted that the very terminology of invagination, evagination, and folding showed how mechanical early notions of development were. Von Baer and Theodor Bischoff had argued against a too-mechanical interpretation of processes that were pure phenomena of growth, but His had shown that growth itself was governed by mechanical laws.<sup>36</sup> Plastic reconstruction as His practiced it was not a precondition for discussing development mechanically—unless, perhaps, one had become estranged from the form of the whole embryo by contemplating isolated sections.

An eyewitness account of life in His’s laboratory shows how modeling and mechanism went together in his work. It also makes clear how much the practice of producing wax models would have to be reformed before it could even suggest mechanical views. The report is instructive as much for what it says as for the fact that it was Ziegler who wrote it to—of all people—Haeckel. In the mid 1870s, in the course of negotiations over making a set of models of the four forms of cleavage and gastrulation that he had described for the animal kingdom, Haeckel sent Ziegler a copy of *Ziele und Wege der heutigen Entwicklungsgeschichte*. Ziegler told the author of the “two exquisite hours” he had spent with the spicy and, for many scientists, scandalously offensive tract. It had interested him because he had “known personally two of the gentlemen named” (read: insulted): the late Louis Agassiz, idealist professor of zoology at Harvard, and His. Here is Ziegler’s lively description of His using the simple experiments to get across to one of his key collaborators, Hagenbach, what it was that he wanted to explain mathematically:

His appeared very vividly to my soul this afternoon as I read your *Aims and Approaches*. I sat beside him for a long time on that occasion in Basel when he had the university mathematicus come to determine with him the formula of growth; the stocky fat gentleman comprehended only with difficulty, and they made drawings, folded letters and finally experimented with the calf’s skin nailed on a board, until the two gentlemen at last agreed about things which—I no longer understood!

<sup>36</sup> His, *Erste Anlage des Wirbelthierleibes*, pp. vi, 182; and Anon. [Alexander Ecker?], *Archiv für Anthropologie*, 1870, 4:139.

Many a physician would have found the mathematics off-putting, but Ziegler's admission that he had not followed all the discussion was certainly diplomatic. We can glean two crucial points from the report. First, Ziegler's very presence in the laboratory shows that plastic reconstruction, simple experiments, and deriving equations were all going on simultaneously in one place. His was coordinating these three "modeling" practices in a single approach to development. The second point is that Haeckel, or anyone else, could not only use but even commission wax models without its signifying any commitment to mechanical physiology. His did not claim that looking at or handling a model would compel assent to his mechanical views but, rather, that the experience of modeling should. This Haeckel had not had and did not seek. He had not laboriously constructed the models of gastrulation; he just sent Ziegler an offprint and checked the waxes the modeler made from the plates.<sup>37</sup> This kind of relationship, sometimes involving specimens as well, was standard before anatomists adopted plastic reconstruction and so became modelers themselves. Until this happened, even potentially sympathetic scientists could hardly come to mechanical views through modeling.

To summarize, His sought to make two kinds of claim: about the changing form of the embryo and about the relevance of mechanical principles to its generation. He made these arguments using a range of models, which showed forms and mechanisms in varying degrees. At one extreme, he purported with the rubber tubes to mimic morphogenetic processes but admitted that they resembled the embryo only very crudely. At the other, he argued that the Ziegler waxes represented developing form with exceptional accuracy—and that in the course of making them he had gained new insight into mechanical moments in embryogenesis. (He also showed that mathematical modeling was possible in principle but did not exploit it in any detail.) The rest of the essay follows the fate of His's modeling practices among the next generation of embryologists. I begin by showing how anatomists came to accept his claim that in the microtome age they must reconstruct complex forms in three dimensions.

#### ANATOMISTS TAKE UP MODELING

The chick models rapidly joined Ziegler's earlier nonreconstructive series as regular teaching aids. Anatomists and zoologists readily agreed that models were an effective means of communicating with the less embryologically enculturated, who could not be expected to follow long verbal descriptions or build up a three-dimensional image from sections. But it was not until the mid 1880s that many scientists themselves began to model.<sup>38</sup> How, from such inauspicious beginnings, did plastic reconstruction become the most important research technique in embryological anatomy?

<sup>37</sup> Adolf Ziegler to Haeckel, 30 Nov. 1875, Ernst-Haeckel-Haus: "Ihre 'Ziele u. Wege' hat mich natürlich vielfach interessirt und mir zwei köstliche Stunden bereitet, da ich zwei der genannten Herren persönlich gekannt. . . . Hiss [sic] trat heute Mittag recht lebhaft an meine Seele, als ich Ihre 'Ziele u. Wege' las. Ich saß lange daneben, als er seiner Zeit in Basel den Universitätsmathematicus kommen lies, um mit ihm die Wachstumsformel festzusetzen; der untersetzte dicke Herr begriff nur schwer, u. es wurde gezeichnet, Briefe gefaltet u. schließlich mit dem auf ein Brett genagelten Kalbfell experimentirt, bis die zwei Herren sich endlich einigten über Dinge, die—ich nicht mehr verstand!" That Haeckel had sent his paper and would check the models is evident from other passages in the same letter. The plates accompanied Ernst Haeckel, "Die Gastrula und die Eifurchung der Thiere," *Jena. Z. Naturwissen.*, 1875, 9:402–508.

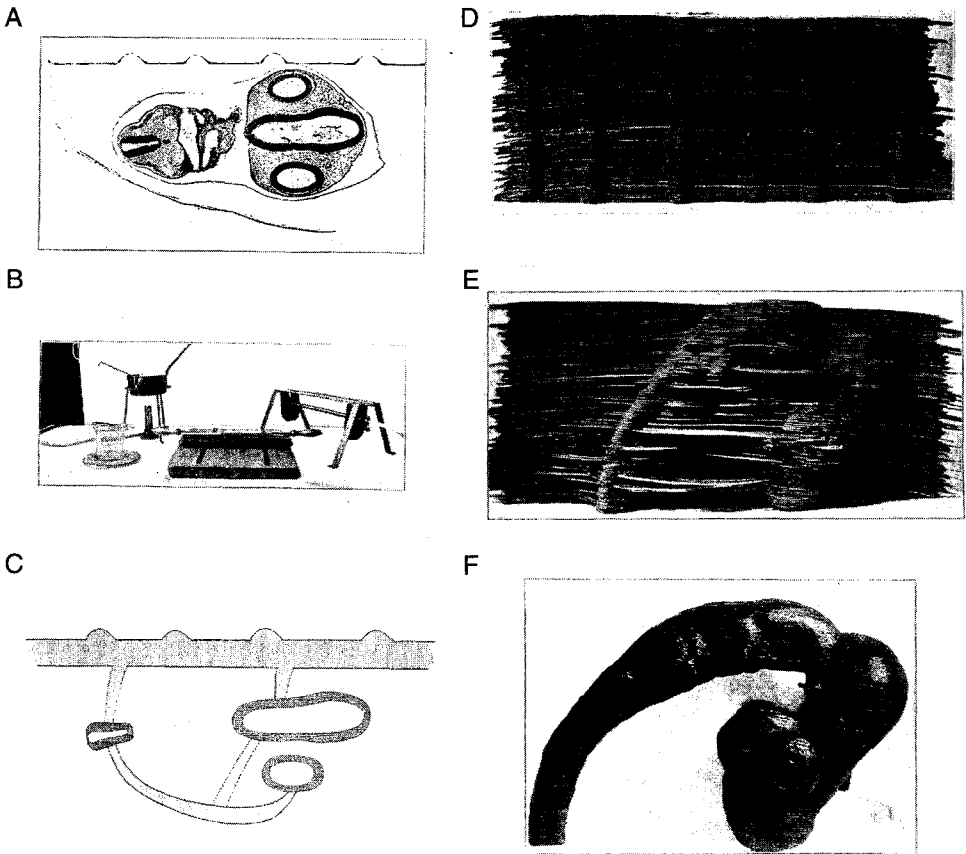
<sup>38</sup> In Joseph Priestley's terms, the models were much more easily accepted as "demonstration devices" than as "philosophical instruments"; see Simon Schaffer, "Machine Philosophy: Demonstration Devices in Georgian Mechanics," *Osiris*, N.S., 1994, 9:157–182, on p. 158.

Embryologists modeled little in the 1870s, in part simply because microtomes were still not in regular use. They were arguably not worth using until methods of fixation and embedding had improved, and without the plane-parallel sections they produced it was generally acknowledged that no serious reconstruction could be undertaken. His was still giving sermons in the early 1880s about how early human embryos must go under the knife but be analyzed in such a way that a single set of sections could tell a whole story. It was, however, only around this time, with the perfection of the modern method of paraffin sectioning by scientists at the Naples Zoological Station, that "microtomy" became truly routine. Reconstruction from serial sections was one of a raft of methods that allowed anatomists and zoologists to use microtomes efficiently and to the best advantage. Whitman's text listed it along with the ribbon method of cutting serial sections, definitive ways of fixing sections on slides, section smoothers, and, not least, new fixatives and stains.<sup>39</sup> As microtomes gained ground, His's appeals had more chance of hitting home. At the same time many younger scientists, especially zoologists, under heavy competitive pressure in the 1870s, were probably sectioning so fast that they had no time to reflect on the alienation from solid forms that so worried their more leisured professors. Embryologists' resistance to following His into plastic reconstruction was ultimately overcome by his and some younger anatomists' exploitation of a new method. In the mid 1870s Gustav Born was working under Carl Hasse at Breslau on the evolutionary morphology of the nasal cavities of Amphibia. To grasp their complex form he devised a straightforward method of reconstruction. He produced a magnified copy of the relevant details of each section by transferring outlines of the structures in which he was interested from a drawing to a wax plate about 1 mm thick. The magnification of the drawing matched the increase in thickness that this represented. He then cut away the excess wax and stacked up the plates (Figure 9).<sup>40</sup>

Though it was later agreed to be a technical breakthrough of the first order, several years passed before anyone took up Born's method. A brief description may have reached only a limited audience because it appeared in a long paper on the nasolaryngeal duct; when the article came out in 1876 anatomists still felt it necessary to justify using a microtome. By the time Born published an extended account in 1883, not only had sectioning become completely routine, but his Würzburg friend Philipp Stöhr had used it to produce and had had Ziegler market models of amphibian brains. Soon other anatomists, especially N. Kastschenko in Leipzig and Born's one-time Breslau colleague Hans Strasser, then Robert Wiedersheim's prosector in Freiburg, introduced key technical improvements. Some, such as incorporating the sheets of paper bearing the sectional drawings into wax plates that were rolled rather than poured, made the wax-plate method easier; others, such as guideplanes to facilitate correct mutual orientation of the stacked sections, served

<sup>39</sup> For tissue preparation as a precondition for worthwhile microtomy and on the Naples school see Apáthy, *Mikrotechnik der thierischen Morphologie* (cit. n. 6); Irmgard Müller, "Die Geschichte der Zoologischen Station in Neapel von der Gründung durch Anton Dohm (1872) bis zum ersten Weltkrieg und ihre Bedeutung für die Entwicklung der modernen biologischen Wissenschaften" (unpublished Habilitationsschrift, Univ. Düsseldorf, 1976), pp. 255–271; and Christiane Groeben and Müller, *The Naples Zoological Station at the Time of Anton Dohrn*, trans. Richard Ivell and Christl Ivell (Paris: Goethe Institute, 1975). For His's calls to section human embryos see His, *Anatomie menschlicher Embryonen*, Vol. 1 (cit. n. 32), pp. 6–12, Vol. 3 (cit. n. 16), pp. 3–5; and for Whitman's list see *Methods of Research* (cit. n. 27), p. 2.

<sup>40</sup> See Nyhart, *Biology Takes Form*, pp. 193–204 (for competition in zoology), 284–285 (for Born). On Born see further Walter Gebhardt, "Gustav Born," *Anat. Anz.*, 1900, 18:139–143; and Max Born, Walter Brandt, and Gustav Born, "In Memoriam Gustav Born, Experimental Embryologist," *Acta Anatomica*, 1950, 10:466–475. Born first described the method in Gustav Born, "Ueber die Nasenhöhlen und den Thränennasengang der Amphibien," *Morphol. Jahrb.*, 1876, 2:577–646, on pp. 578–580; and more fully in Gustav Born, "Die Plattenmodellirmethode," *Arch. Mikr. Anat.*, 1883, 22:584–599.



**Figure 9.** Making a wax-plate model of an embryonic lizard brain. (A) Section with guideline at top. The relevant parts of the sections were drawn. (B) Instrumentarium for rolling the plates, including in the middle a lithographer's stone and a rolling pin. Each sectional drawing was incorporated into a plate and excess wax then removed. (C) Diagram of cut-out plate, with "bridges" keeping noncontiguous structures together. (D) Stacked cut-out plates seen from the guideplane side. (E) Stacked plates from the object side. (F) Model produced by removing guides and bridges and smoothing the edges; oil painting was the next and final step. This is the version of the method given by Karl Peter, a protégé of Born, incorporating Hans Strasser's and N. Kastschenko's improvements. From Karl Peter, *Die Methoden der Rekonstruktion* (Jena: Fischer, 1906), Figures 12, 30, 33, 34, 35, and 36. (Courtesy of the Anatomy Department Library, University of Cambridge.)

all methods (see Figure 9). Strasser began to engage in public discussion of the relative merits of His's 'free' modeling and Born's plate method. His's own publicity efforts continued, and as a deputy chairman of the new Anatomical Society and host of its first meeting in Leipzig in April 1887 he seized the opportunity to orchestrate a demonstration of his and others' models.<sup>41</sup> While His and his younger colleagues cooperated in advertising

<sup>41</sup> This is how His described the aims of the session to Strasser: "All in all it seems to me that none of the methods makes the others dispensable. . . . The main purpose of our papers seems to me to be to awaken interest in plastic methods and strongly to stimulate work in this direction." Wilhelm His to Hans Strasser, 20 Mar. 1887,

the benefits of modeling to the anatomical community, they engaged in spirited debate as to the pros and cons of their respective methods. By gaining anatomists' attention and then shifting the terms of the discussion from whether to how to model, the Anatomical Society meeting was decisive in making modeling a major research practice of the 1890s and beyond. It also forced the participants to make their methodological assumptions explicit, allowing historians not only to reconstruct why anatomists took up the plate method rather than free modeling but also to gain unusual insight into their attitudes toward these practices. In the end, Born's approach was accepted as quicker, easier, and more objective but still reconcilable with some anatomists' strong commitment to what the keen athlete Strasser called "stereometric gymnastics." His's free modeling was relegated to the prehistory of plastic reconstruction, though projective construction continued as a graphical method.<sup>42</sup>

First, and probably most important, Born claimed his method was easier than His's, which Born thought required "high artistic talent and skill." Each side accused the other of underestimating their own artistry and hence the hidden difficulties of their method, but His was on the defensive from the start. He admitted that "a certain stereoscopic grasp and a certain practice" were needed for freehand modeling but asked rhetorically whether a beginner could expect to match the achievements of the experienced in any area of research.<sup>43</sup> On precisely this key issue the Leipzig demonstration brought Born and Strasser a decisive victory. Born had a student use his method for the very first time and brought the resulting model to the meeting. Mr. Damm had made a chick's heart. With its thin walls, this was a challenging subject—Born doubted that any was more difficult; it was also one that His had famously modeled. Before the meeting Born had been nervous that Damm would produce nothing worthwhile at all; but he and Strasser now made the most of Damm's and another assistant's success. When one of their efforts was placed side-by-side with one of His's model in Leipzig, Born reported, "There was a striking agreement in all forms and relationships, but the plate model had the advantage . . . that it was the

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Briefsammlung der Bibliothek des Medizinhistorischen Instituts und Museums der Universität Zürich. For Strasser's initial views on the relative merits of the methods see Hans Strasser, "Ueber das Studium der Schnittserien und über die Hilfsmittel, welche die Reconstruction der zerlegten Form erleichtern," *Zeitschrift für Wissenschaftliche Mikroskopie*, 1886, 3:179–195. Strasser argued that compared to truly free modeling, His's method using exact measurements was "free" only in certain respects; see Strasser, "Ueber die Methoden der plastischen Reconstruction," *ibid.*, 1887, 4:168–208, 330–339, on p. 192. On Strasser see [Carl] Wegelin, "Prof. Dr. Hans Strasser †," *Anat. Anz.*, 1927, 64:193–199.

<sup>42</sup> Strasser, "Methoden der plastischen Reconstruction," p. 195. I have drawn on this paper extensively because it includes an unusually reflective discussion of plastic reconstruction, but it cut no ice with the Royal Microscopical Society's utilitarian reviewer (*Journal of the Royal Microscopical Society*, 1888, p. 853): "Prof. H. Strasser writes at great length and in copious detail on methods of reconstructing the object. All he has to say is practically a recapitulation of Born's procedure for making wax plates upon which the image of the object is drawn." See Karl Peter, *Die Methoden der Rekonstruktion* (Jena: Fischer, 1906), for the most thorough account of turn-of-the-century modeling methods and a full bibliography; for a later review in English see J. R. Norman, "Methods and Technique of Reconstruction," *J. Roy. Micr. Soc.*, 1923, pp. 37–56. Points relevant to the competition between plate and "free" modeling are raised in the discussion of methods of sectioning for rapid diagnosis during surgery by James R. Wright, Jr., "The Development of the Frozen Section Technique, the Evolution of Surgical Biopsy, and the Origins of Surgical Pathology," *Bull. Hist. Med.*, 1985, 59:295–326; and in an analysis of the introduction of ultrathin sectioning into electron microscopy by Nicolas Rasmussen, *Picture Control: The Electron Microscope and the Transformation of Biology in America, 1940–1960* (Stanford, Calif.: Stanford Univ. Press, 1997).

<sup>43</sup> Born, "Plattenmodellirmethode" (cit. n. 40), p. 586; and His, "Methoden der plastischen Rekonstruktion" (cit. n. 29), pp. 385–386. As Born put it to Strasser, "Anyone can learn plate modeling, but to model freehand not one in ten"; see Gustav Born to Strasser, 24 Mar. 1887, Medizinhistorisches Institut Zürich. Neither side claimed that their method was invariably better, just that it was better for most purposes. Indeed, after Born had publicized his method, His revealed that in making the original chick models he had experimented with cutting out wax plates. "However I soon went over to free modeling controlled with callipers": His, *Anatomie menschlicher Embryonen*, Vol. 3 (cit. n. 16), p. 5. Ziegler claimed that they had cut sectional images out of sheet metal; see *Prospetus über die Embryologischen Wachstumsmodelle* (cit. n. 34), p. 4.

first attempt of a beginner in this technique, whilst there will be few people who are in a position to imitate the artworks of the Leipzig anatomist."<sup>44</sup> A second advantage claimed for Born's method was speed, and this His scarcely contested. He had admitted that his method was extremely labor intensive and time consuming, that a single reconstruction could take "weeks or even months of uninterrupted work," some of which he would gladly unload onto a technician. Born's method still required the sections to be drawn, and this remained a long job. But thereafter it was far quicker, because it lent itself to the division of labor: a significant proportion of the work could be assigned to relatively unskilled technicians. Born reported that a servant could make fifty plates in a few hours and that "every intelligent servant" could be trained to cut them to shape.<sup>45</sup>

In their discussions of plate versus free modeling, some anatomists were concerned not just with ease and speed but with how each method involved them physically and mentally in reconstructing spatial relationships. His had argued that the activity of reconstruction produced not just a model but also an anatomist with an incomparable appreciation of form. Strasser considered the possibility that free modeling could in this respect have the edge: "Might it be thought . . . that precisely the surplus labor of free modeling represents its most important advantage, insofar as a better mental processing of the relations of form is linked to it?" No, he concluded. Most of the additional work was in measuring distances that were not themselves important. But when the mind had to deduce the form of a surface from the individual sections there were also more purely geometrical or stereometrical images to manipulate. "I am," he noted, "far from wishing to present such hard gymnastics in stereometric thinking in general or for the microscopist as superfluous. The better the latter is able without special aids from mere consideration of the successive sections to reach conclusions about the cut surfaces of the body, the better." But the very best training in such a skill was in fact to follow the progress of plate modeling, so this did not lag behind free modeling even "with respect to gymnastics."<sup>46</sup>

There was another aspect to an anatomist's mental involvement in modeling—and a fourth way in which plate modeling won the day. His had judged it necessary even in 1868 to preempt the charge that his models were too subjective: "Anyone who does not attempt plastic work of this kind can hardly imagine the strict control that it guarantees. Every detail, every apparent irregularity of a section receives its peculiar significance, every lack of clarity revenges itself through an error in the plastic object, and the detailed working through of such models with compasses and ruler gives a certainty of visualization that is hardly achievable in any other way." He emphasized the self-disciplining intolerance of the procedure. Were any part not of the right form and size and in the right place, then it would throw neighboring parts out of kilter. Anything short of complete mastery of the object left only two alternatives: giving up or a deliberate fudge. But at a time when scientists generally were growing increasingly alarmed about subjectivity and striving for its mechanical elimination, Born was careful to recommend his method as "objective."<sup>47</sup>

<sup>44</sup> Gustav Born, "Noch einmal die Plattenmodellirmethode," *Z. Wissen. Mikr.*, 1888, 5:433–455, on p. 435; see also Strasser, "Methoden der plastischen Reconstruction" (cit. n. 41), p. 196. For Born's lack of confidence—"Colleague Damm is supposed now hurriedly to model a couple of chick hearts, but what he will produce I do not yet know"—see Born to Strasser, 24 Mar. 1887.

<sup>45</sup> His, *Anatomie menschlicher Embryonen*, Vol. 3 (cit. n. 16), p. 3; His, "Methoden der plastischen Rekonstruktion" (cit. n. 29), p. 391; and Born, "Plattenmodellirmethode" (cit. n. 40), pp. 596, 599.

<sup>46</sup> Strasser, "Methoden der plastischen Reconstruction" (cit. n. 41), p. 195.

<sup>47</sup> His, *Erste Anlage des Wirbelthierleibes*, p. 182; and Born, "Plattenmodellirmethode" (cit. n. 40), p. 584. On mechanical objectivity see Simon Schaffer, "Astronomers Mark Time: Discipline and the Personal Equation," *Science in Context*, 1988, 2:115–146; and Lorraine Daston and Peter Galison, "The Image of Objectivity," *Representations*, 1992, 40:81–128.

Strasser claimed that the plate method need not be merely mechanical, but the fact that it was so much less dependent on an anatomist's judgment surely counted heavily in its favor. "Artworks" could be admired, but they were perhaps not the most reliable science.

After the Anatomical Society meeting plate modeling became a standard microtechnique, especially in embryology and brain research. It was just within the reach of advanced students, but so time consuming that only a few actually tried it.<sup>48</sup> Free modeling, by contrast, was presented as too subjective and demanding to produce publishable results even in the hands of an expert. It continued to be used in research to produce "sketch" models and appears to have been introduced into anatomical, including embryological, teaching in the early twentieth century "to demonstrate the change in certain forms quickly or to awaken the sense for forms in the first place."<sup>49</sup> Generations of medical students have associated embryology with trying to make lumps of plasticine gastrulate. But it was plate modeling that in the decades around 1900 became the most important way to visualize complex structures in vertebrate embryos. In addition to those already mentioned, Franz Keibel, Karl Peter, Hermann Braus, Ernst Gaupp, Oscar Hertwig, Ferdinand Hochstetter, Auguste-François-Charles d'Éternod, and Florence Rena Sabin contributed to the three dozen or so series that Adolf Ziegler's son Friedrich sold between the world wars. The models were not universally appreciated. In 1895 His, as editor of the leading anatomical journal, had to insist that any works that relied for the determination of complex anatomical forms on looking through sections, without using them to undertake the exact reproduction of the form, should be regarded as "incomplete in their method and thus as lacking evidential value in science." Enough anatomists followed him that many journal articles effectively became descriptions of models—which His argued were actually the more important publications. Anatomists valued the waxes themselves, even above drawings or photographs of the models, because they could view them from all sides, feel their surfaces with their fingers, and cut them up. Having given three-dimensional "body" to their representations, they could more readily work on them as though they *were* bodies.<sup>50</sup>

Anatomists' acceptance of plastic reconstruction marks the end of a dramatic shift in the location of embryological modeling, the relationship between scientists and modelers,

<sup>48</sup> Paul Mayer, *Einführung in die Mikroskopie* (Berlin: Springer, 1914), p. 122, warned beginners off reconstruction; and Albert Oppel, *Leitfaden für das embryologische Praktikum und Grundriß der Entwicklungslehre des Menschen und der Wirbeltiere* (Jena: Fischer, 1914), p. 50, explained that time constraints allowed him only to demonstrate the procedure and have students practice individual operations. Students in the Zoology Department at Cambridge in the 1950s did cut their own sections of a frog embryo and reconstruct a part from them; see Sydney Smith, "The Use of Models in the Teaching of Embryology," in *Models and Analogues in Biology*, ed. J. W. L. Beament (Symposia of the Society for Experimental Biology, 14) (Cambridge: Cambridge Univ. Press, 1960), pp. 214–229, on pp. 216–217. For later innovations in reconstructive methods see esp. W. A. Gaunt and P. N. Gaunt, *Three Dimensional Reconstruction in Biology* (Tunbridge Wells: Pitman, 1978); and Randle W. Ware and Vincent LoPresti, "Three-Dimensional Reconstruction from Serial Sections," *International Review of Cytology*, 1975, 40:325–440.

<sup>49</sup> E. Pernkopf, "Technik der Herstellung anatomischer Präparate," in *Methodik der wissenschaftlichen Biologie*, ed. Tibor Péterfi, 2 vols., Vol. 1: *Allgemeine Morphologie* (Berlin: Springer, 1928), pp. 1154–1263, on p. 1189. On modeling in anatomy teaching see B. Henneberg, "Zum anatomischen Unterricht," *Anat. Anz.*, 1921, 54(Suppl.):106–111; and Johannes Brodersen, "Die Einfügung der Modellierungen in den anatomischen Unterricht," *ibid.*, 1927, 63:37–43. For a late defense of "free" modeling see David Waterston, "Reconstruction in Modelling Clay: A Rapid Method of Plastic Reconstruction from Serial Sections," *J. Anat.*, 1914, 48:19–23.

<sup>50</sup> His, *Anatomie menschlicher Embryonen*, Vol. 3 (cit. n. 16), p. 4; and Wilhelm His, "Ueber die wissenschaftliche Wertung veröffentlichter Modelle," *Anat. Anz.*, 1895, 10:358–360, on p. 359. For these points about the value of the waxes and further investigation of how the Zieglers and their clients produced and used the models see Nick Hopwood, "Publishing in Wax: Modelers and Anatomists in Embryology around 1900," paper presented at a symposium on "Models in the Sciences, Technology, and Medicine: Displaying the Third Dimension," Wellcome Institute for the History of Medicine, 13 Nov. 1998.

and the status of wax models in embryology. Traditionally, a scientist had produced specimens or drawings and was approached by or employed a modeler to have them rendered in wax. However much, as vivid and widely distributed representations of amphibian development, Ziegler's models of Ecker's tadpoles became canonical, they stood in a subordinate relationship to the plates of the atlas and to the fresh or fixed specimens. Then, in a key transfer of skills, Ziegler went to His's laboratory and helped him make the original models there, returning to his workshop only to produce the reproductions. Now distributed in slices over a series of slides, the specimens could—His argued—be reconstituted only as a model, of which a drawing or a photograph was a pale imitation. It took nearly two decades and the technical innovations and surrounding debates I have discussed here before the anatomical community agreed. Taking up the plate method definitively shifted the—now very different—work of modeling the originals into anatomists' laboratories, where they made it the primary means of visualizing embryos and brains. (Where no reconstruction was required, as generally for zoologists' invertebrate embryos, traditional practice continued.) The modelers now had less input, but, since they were still needed to finish, reproduce, and distribute models that had become central to communicating form, they nevertheless did more business.<sup>51</sup>

Plastic reconstruction has been especially significant in human embryology. In the early 1880s His established thorough investigation of individual sectioned specimens as the pattern of research in the science and modeling as the primary means of visualizing human embryonic form. In 1914 the Johns Hopkins anatomist Franklin Paine Mall obtained funds from the Carnegie Institution of Washington for a Department of Embryology devoted to extending and refining His's work. Plastic reconstruction was so crucial that the department employed an in-house modeler, Osborne O. Heard, to make models for a reference collection. Similarly, the Göttingen anatomist Erich Blechschmidt, who directed the other major project to describe human development, had by the 1960s filled a room in his institute with a collection of fifty plastic embryos, on average 1.8 m tall, and each reconstructed from thousands of serial sections.<sup>52</sup>

But what of His's claim that the experience of modeling would compel insight into the mechanics of development? He returned to it in 1894, nearly three decades after he had begun the work on the chick. Fighting the same battle, he began by attacking those morphologists who still looked to phylogeny rather than mechanics, lamenting that "the importance of mechanical processes in the development of organic beings even today finds stubborn doubters, and . . . the mystics have not died out who imagine heredity causes the material of developing organisms to move according to other laws than those which are valid in nature as a whole." He then pointed to the rise of modeling and optimistically invoked his view that the reconstructive visualization of form implied its mechanical explanation:

Such unclear points of view will, I hope, soon be overcome, and precisely the increasing appreciation that methods of plastic reconstruction are finding among younger researchers must in this respect have a purifying effect. When working plastically it is indeed nearly impossible to close one's eyes to the basic processes of the development of form. I too long ago was forced

<sup>51</sup> Hopwood, "Publishing in Wax."

<sup>52</sup> O'Rahilly, "One Hundred Years of Human Embryology" (cit. n. 7); Erich Blechschmidt, *Vom Ei zum Embryo: Die Gestaltungskraft des menschlichen Keims* (Stuttgart: Deutsche Verlags-Anstalt, 1968), p. 21; and Klaus V. Hinrichsen, "In memoriam des Anatomen und Embryologen Erich Blechschmidt (1904–1992)," *Annals of Anatomy*, 1992, 174:479–484.



to mechanical views not through abstract considerations but through the empirical results of my first attempts at modeling.

His maintained to the last the link between plastic reconstruction from serial sections and mechanical approaches to development. Mechanical discussion was largely absent from the methodological discussions I have reviewed, but it would be worth examining specific passages of research in embryological anatomy for such links. Blechschmidt much later held an uncannily His-like package of commitments: he developed plastic reconstruction of human embryos to a new pitch of perfection, argued for the importance of mechanical moments in development, and was even highly critical of evolutionary interpretations of embryogenesis.<sup>53</sup> But around 1900 many embryologists clearly modeled from sections without associating themselves with mechanical views. It was, moreover, not work based on plastic reconstruction that in the 1880s and 1890s most successfully took up His's call to investigate the proximate, physiological causes of development but, rather, the *Entwicklungsmechanik* program of the Breslau anatomist Wilhelm Roux.

#### EFFACING THE WAXES

Roux's "developmental mechanics" traced a lineage to His's "mechanics of development" but also demarcated itself from it. During the 1880s Roux moved away from the tradition of mechanical anatomy in which he had begun his career with an investigation of the effect of blood flow on vessel formation. By "mechanics" he increasingly meant not just the relatively crude pressures and pulls by which His had explained the form of the body; his use of the term signaled a more general, Kantian commitment to causal explanation.<sup>54</sup> His's "simple experiments" did inspire a line of work in *Entwicklungsmechanik*, but Roux insisted on going beyond analogy to test hypotheses experimentally on living embryos. He split the power of experiment to determine the causal factors of development from a worthy but inconclusive "descriptive" embryology in which plastic reconstruction became indispensable to elucidating the forms of higher vertebrate embryos. The first experimentalists favored early amphibian and sea urchin embryos, simpler systems in which they could intervene much more easily and that they did not need to model for months in order to visualize their results. Reconstruction hardly figured in this research, and His's wax models accordingly had little place in their image of him.

His's embryological contemporaries had regarded the simple experiments as at best suggestive and at worst laughable. The rubber tubes were never fully rehabilitated—for a long time even sympathetic authors first had to mention the scorn they had attracted—but the approach was formalized as what Ludwig Rhumbler called "methods of imitation": generating possible explanations by mimicking developmental processes in materials chemically unlike but physically resembling the cells and tissues themselves.<sup>55</sup> Roux did

<sup>53</sup> His, "Mechanische Grundvorgänge thierischer Formenbildung" (cit. n. 16), p. 2; and Blechschmidt, *Vom Ei zum Embryo*.

<sup>54</sup> On Roux see Frederick B. Churchill, "Chabry, Roux, and the Experimental Method in Nineteenth-Century Embryology," in *Foundations of Scientific Method: The Nineteenth Century*, ed. Ronald N. Giere and Richard S. Westfall (Bloomington: Indiana Univ. Press, 1973), pp. 161–205; Reinhard Mocek, *Wilhelm Roux—Hans Driesch: Zur Geschichte der Entwicklungsphysiologie der Tiere* ("Entwicklungsmechanik") (Jena: Fischer, 1974); and Nyhart, *Biology Takes Form*, pp. 278–305.

<sup>55</sup> See Strasser, "Methoden der plastischen Reconstruction" (cit. n. 41), p. 169 (on scorn for His's rubber tubes); and Ludwig Rhumbler, "Methodik der Nachahmung von Lebensvorgängen durch physikalische Konstellationen," in *Handbuch der biologischen Arbeitsmethoden*, ed. Emil Abderhalden, Sect. 5, Pt. 3A: *Methodik*

model in this way but showed the distinctiveness of his approach even in two studies inspired directly by His's work. In the first, he made a "developmental model" of the chick embryo out of five to ten balls of dough, to each of which he had added a certain amount of yeast or baking powder. Placing the dough in an incubator led to the formation of structures that depended on the arrangement of the balls and their different contents of yeast. Though admittedly not much like an embryo, these could demonstrate the power of differential growth; the lack of the necessary cohesion showed, Roux said, that other factors were also at work. While His had stressed the importance of mechanical forces in the blastoderm as a whole, Roux claimed that the activities of the cells, which His had considered only in passing and were not well mimicked by the model, were more important. This little-known model is surprisingly His-like; Roux used an earlier and much more familiar study to highlight how he was going beyond him. The older anatomist had argued from simple experiments in lead plate that the medullary folds arose passively as a result of pressure "backing up" from the lateral parts of the embryo. Roux turned His's argument into a question: Was neural folding driven passively from the "sides" or did the cells of the medullary plate participate actively in pushing it forward? He also refused to recognize His's attempts to mimic the process as "experiments," which he limited to hypothesis testing on the embryo itself. Roux cut out the central region and showed that since the folds appeared in the isolated explant the factors responsible must lie largely within the medullary plate, not laterally to it, and presumably in the activities of the cells.<sup>56</sup>

If *Entwicklungsmechaniker* gave the "simple experiments" only qualified approval, they would have even less time for plastic reconstruction. Born and Strasser, who in the early 1880s worked alongside Roux in Breslau and helped to frame the new approach, had also made important contributions to reconstructive methods.<sup>57</sup> Some anatomists with experimental interests—for example Braus—also devoted much energy to plastic reconstruction. Yet Roux himself had not participated in the debates over modeling and stands out as one of the few embryologically active anatomists of the period to have left no Ziegler models bearing his name. As His acknowledged, visualization of developing form played a minimal role in Roux's work: "Roux and I obviously work in different ways; he begins with theoretical considerations and in his case experiment follows such considerations. When I work visualization [*Anschauung*] usually comes first, thinking this through follows,

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*der Entwicklungsmechanik* (Berlin/Vienna: Urban & Schwarzenberg, 1923), pp. 219–440. Rhumbler, professor of zoology at the Forestry College in Hannover-Münden, himself worked in the tradition, which went back at least to the Heidelberg zoologist Otto Bütschli some decades before, of modeling cellular protoplasm as a foam emulsion; see Arthur Hughes, *A History of Cytology* (London/New York: Abelard-Schuman, 1959), pp. 112–130. Methods of imitation in embryology and cytology are related to the "mimetic experimentation" that Peter Galison and Alexi Assmus identified in late nineteenth-century physical science; see Galison and Assmus, "Artificial Clouds, Real Particles," in *The Uses of Experiment: Studies in the Natural Sciences*, ed. David Gooding, Trevor Pinch, and Simon Schaffer (Cambridge: Cambridge Univ. Press, 1989), pp. 224–274.

<sup>56</sup> Wilhelm Roux, "Meine entwicklungsmechanische Methodik," in *Handbuch der biologischen Arbeitsmethoden*, ed. Abderhalden, Sect. 5, Pt. 3A, pp. 540–616. For the *Entwicklungsmodell* see, e.g., Roux, *Die Entwicklungsmechanik: Ein neuer Zweig der biologischen Wissenschaft* (Leipzig: Engelmann, 1905), pp. 99–100. Explanation of the medullary plate is discussed in these two works; for the original report and discussion of His's views see Roux, "Beiträge zur Entwicklungsmechanik des Embryo," *Zeitschrift für Biologie*, N.S., 1885, 3:411–526.

<sup>57</sup> In a report on the Anatomical Society meeting of 1887 Strasser tackled the relationship between the "phantoms" of leather, rubber, and lead that His had exhibited, plastic reconstruction, and Roux's work. He agreed with His that the most perfect possible familiarity with spatial relationships was a precondition not just for investigating the "mechanical correlation of masses" but for every other problem of *Entwicklungsmechanik*. See Strasser, "Methoden der plastischen Reconstruction" (cit. n. 41), p. 169.

and the gaps that come to light I seek to fill through new visualizations.”<sup>58</sup> The leading *Entwicklungsmechaniker*—Roux and, even more, Hans Driesch—began not with *Anschauung* but with hypotheses that they sought to test experimentally on the simplest and most readily visualized biological material they could find.<sup>59</sup>

Wax models were also too static for a program focused on the dynamics of development. In the early 1920s the Viennese experimentalist Hans Przibram, seeking to model the processes of life, disparaged models of the kind Friedrich Ziegler produced: “The commercially available so-called models of egg development in hard wax, glass, or wood are nothing but copies of the individual successive developmental stages, thus not models of egg development, but at most of individual points thereof. It is impossible to form from them an image of how from an egg fragment under certain conditions a whole embryo, under others a half is formed.”<sup>60</sup> Instead, he recommended a soft, painted rubber ball that could be ligated with a thread. In this view, the His-Ziegler models reproduced a succession of developmental stages but did not show development itself. Used most prominently in drilling medical students, they eventually came to epitomize everything—description, higher vertebrates, and undergraduate teaching—that the most militant experimentalists despised.

Different embryological traditions did not just take up His’s modeling practices in different ways; they created and still maintain correspondingly different images of His. Human embryologists celebrate “the Vesalius” of their science and the inventor of plastic reconstruction, but the dominance of experimental embryology and its post-World War II successor, developmental biology, has kept this a minority view.<sup>61</sup> Experimental embryologists commemorate the pioneer of the embryology of proximate causes who, however, never made the breakthrough to experiment on the living embryo. The studies on the chick have a secure place in the experimentalist canon but are mined for physiological

<sup>58</sup> His, “Mechanische Grundvorgänge thierischer Formenbildung” (cit. n. 16), p. 52. This contrast is reminiscent of that drawn in Herbert Mehrten’s history of mathematics; see Mehrten, *Moderne Sprache Mathematik* (cit. n. 1). To the mathematical modernism of David Hilbert, which rejected representational views of mathematical truth for the mathematician’s free creative play in mathematical language according to the rules of the axiomatic method, he counterposed the mathematical countermodernism of Hilbert’s Göttingen colleague Felix Klein. Also modern in rejecting representation and transcendence, countermodernists sought the “ground” in which mathematics was “rooted” and claimed to find it in *Anschauung* and *Intuition*. Mehrten argues that models were the crucial instance of Klein’s obsession with *Anschauung*, that pedagogical collections made concrete the countermodernist message that abstract maths could be seen and enjoyed.

<sup>59</sup> It is important not to overstate the contrast, at least among the anatomists. Roux accepted that experimentation presupposed knowledge of normal development, and plate modeling appealed to him as a mechanically objective morphological method, even if it was not important in his own work. In an obituary for Born, he singled out the “universal, mechanical method of reconstruction” that allowed the conversion of the microscopic into the macroscopic “without the involvement of an intuitively active intelligence” as his dead colleague’s “most far-reaching achievement.” Embryology (*Entwicklungsgeschichte*) owed the great progress of the preceding decades to plate modeling and the microtome; both, Roux predicted, would remain indispensable aids in descriptive and hence also in developmental mechanical research. See Wilhelm Roux, “Professor Dr. Gustav Born,” *Archiv für Entwicklungsmechanik der Organismen*, 1900, 10:256–259, on p. 259. The Würzburg zoologist Theodor Boveri gave Hans Spemann, who became the leading embryological experimenter in the generation after Roux, a habilitation topic that involved graphical reconstruction of larval head skeletons. But as soon as he set his own research agenda Spemann abandoned such work. See Peter E. Fäßler, *Hans Spemann 1869–1941: Experimentelle Forschung im Spannungsfeld von Empirie und Theorie: Ein Beitrag zur Geschichte der Entwicklungsphysiologie zu Beginn des 20. Jahrhunderts* (Berlin: Springer, 1997), pp. 145–149.

<sup>60</sup> Hans Przibram, “Methodik der Experimentalzoologie,” in *Handbuch der biologischen Arbeitsmethoden*, ed. Emil Abderhalden, Sect. 9, Pt. 1 (1st half): *Allgemeine Methoden* (Berlin/Vienna: Urban & Schwarzenberg, 1924), pp. 1–96, on pp. 53–54.

<sup>61</sup> O’Rahilly, “One Hundred Years of Human Embryology” (cit. n. 7), p. 89.

and mechanical insights; the simple experiments are remembered, while the "merely descriptive" wax models are filtered out.

Until recently, a theory-dominated historiography conspired with experimentalist condescension toward the work of visualizing form to hide plastic reconstruction from view. In the last few years the situation has begun to change, not just in history of science but perhaps also in embryology. Developmental biologists interested in the mechanisms of embryogenesis can hardly fail to notice how much of their time is now spent inventing new and often computerized means of visualizing intricate patterns in two dimensions and, increasingly, in three. This may have helped to make His's work of representing form visible once again and the wax models newly relevant. We can recover his drive to grasp form in three dimensions and appreciate his claim that an embryologist's view of the mechanisms of development is a product of the way she or he represents form. In his own practice, growth equations represented the germinal disc as an imperfectly elastic plate extending at an uneven rate; simple experiments in everyday materials sought to show concretely that mechanical principles were at work in development; but modeling from sections made the form of the embryonic body tangible in the first place and, he claimed, persuaded him of the importance of mechanical principles in its development.

The prospects are bright for exploring further the production, manipulation, and display of three-dimensional representation devices in embryology and in the sciences, technology, and medicine more generally. There is much to find out about such models, both as research tools and as means of communicating scientific visions to wide audiences. We may wish to keep two challenges in view. First, taking models in three dimensions into account can most effectively expand our appreciation of the variety of representational activity in the sciences if we avoid fetishizing an isolated class of objects. We ought, rather, to aim for a deeper understanding of the often fraught relations between practices of representation in two dimensions and three. Second, we could ask how innovations in modeling in embryology related to changes in making other medical or biological, geological, engineering, chemical, mathematical, or physical models. Exploring specific inventions might prompt a more general reevaluation of how, across the sciences, modeling practices have changed.