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"Embodiments of theory:
Wax models of the Zoological Collection (ZCUV), with special regard to Berthold Hatschek's 3D publications of Trochophora and *Amphioxus*."

verfasst von / submitted by

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Embodiments of theory: Wax models of the Zoological Collection (ZCUV), with special regard to Berthold Hatschek's 3D publications of Trochophora and *Amphioxus*

Figure 1 Disciplining the eye, learning to see: Students at a zoological laboratory at Manchester's Owens College around 1900. Ziegler models of *Amphioxus* development are on display at the table in the center. The models carry descriptive labels, in order to train the students to recognise the relevant structures. A colour code makes it easier to understand the formation of germ layers, tissues and organs of these 3D ontogenetic snapshots. (Hopwood 2004). The *Amphioxus* models were produced first in 1882 after illustrations of the zoologist Berthold Hatschek (1854–1941) who later became professor in Vienna. Most *Amphioxus* models are still held at the Zoological Collection of the University of Vienna. Photo used with the permission of the John Rylands Library. Copyright University of Manchester.

To my late father,

to my mother.

Thank you.

1 Introduction

1.1 Motivation for this project

The first steps for this MSc project were taken while attending the course "Collection Sciences and Research". Ao. Univ.-Prof. Dr. Hans Leo Nemeschkal, Head of the Zoological Collection at the University of Vienna (ZCUV) and supervisor of this thesis, guided through this storage space at the "Biozentrum". He presented many fascinating specimens, including embryological wax models from the 19th century that had been used for teaching over many decades. Questions arose about these models that have been held at the Zoological Collection for approximately 130 years: Who made these models, and what purpose did they serve? Were any zoologists from the University of Vienna involved in the making of these wax models? And: Do these wax models still matter today?

It became apparent fast that the zoologist Berthold Hatschek[1] (1854–1941) was one of the scientific wax models authors. His visions were materialised in the form of mass-produced, tangible wax embryos: Twenty-five models of *Amphioxus* and five models of marine Trochophora larvae are among the many traces[2] that Berthold Hatschek has left.

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[1] Berthold Hatschek, born 1854 in the Moravian Skrbeň/Kirwein, studied Zoology in Vienna under the invertebrate morphologist Carl Claus and in Leipzig under Rudolf Leuckart. He also attended lectures of Ernst Haeckel at the University of Jena and formed a life-long bond with the latter. Hatschek's dissertation project was already dedicated to embryology, i.e. the development of Lepidoptera. He has deeply impacted the understanding of evolutionary embryology and the teaching practice at the University of Vienna. Being considered Jewish, the Nazis looted his possessions and analysed his works, probably because Hatschek was a supporter and friend of Ernst Haeckel. Whether or where Hatschek's scientific legacy (e.g. books, photographs, manuscripts) still exists, remains to be explored, see page 76. For biographical references, please see footnote 2.

[2] Hatschek's biography has gained some attention over the past years, e.g. in relation to the 650th anniversary of the University of Vienna. Among those sources are Coen 2007; Taschwer 2015; Müller & Nemeschkal 2015; Anonymous 2015; Huber 2015. A PhD thesis investigated the intellectual exchange between the Viennese musicologist Guido Adler, his friend Berthold Hatschek and the subsequent incorporation of Ernst Haeckel's works into Adler's newly developed methodology (Breuer 2011). Older sources for Hatschek's biography used in this thesis were Storch 1950; Haas 1958, Hatschek's personnel file at the Austrian State Archives (Österreichisches Staatsarchiv; AVA Unterricht allgemein (1848–1940); Universität Wien, Philosophie L-N; 902, Faszikel Nummer 865, Sign. 4G) and Hatschek's letters to Ernst Haeckel that are held at the Ernst-

Nevertheless, Hatschek's work as 3D author who publicised his most important model organisms in cooperation with a world-renowned wax model manufacturer is not familiar to most biologists. His wax models represented the becoming of an organism, displayed the formation of germ layers, were mass-produced and served many generations of students. *Amphioxus* and Trochophora in wax were on the one hand 3D snapshots of ontogeny, capturing specific moments in development, but at the same time tangible evidence for evolutionary theory.

Until today, research is almost nonexistent around these activities in Hatschek's early[3] career, years before he became professor in Vienna in 1896 and Head of the Second Zoological Institute for Comparative Anatomy[4] until his retirement in 1925 (sources for Hatschek's biography: please see footnote 2). Müller & Nemeschkal (2015) have pointed out the manifold ways in which Hatschek was forward thinking: for instance about the becoming of an organism which is influenced by "inner" phylogenetic programmes in inter-relationship with "outer" conditions. The same authors highlighted Hatschek's pionieering yet largely undiscovered insights into genetics that were published early in the 20th century (Hatschek 1905; Hatschek 1910).

Therefore, this thesis is dedicated to Berthold Hatschek's wax model authorship and its wider context; it also includes a documentation of the wax models that are still held at the ZCUV. These models are not only beautifully crafted objects of historical interest, but also precious evidence of evolutionary embryology teaching during the 19th century and beyond.

1.2 Aims of this project

In the course of this master thesis, the scientific and historic context of Berthold Hatschek as author of three-dimensionally expressed scientific theory and practice was explored. As leitmotif for this thesis, it was presumed that Hatschek's wax embryos were made not only to illustrate developmental pathways of elusive animals step by step, but also to be be read as representations of empirical evidence for evolution, an area of intense debate around 1880 (Nyhart 1995a). Being purchased by universities and museums, Hatschek's wax morphologies might well have served as mediators and tools for the popularisation of evolutionary thought among different audiences. Last but not least the models

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Haeckel-Haus in Jena (Best. A. Abt. 1. Nr. 1808/1-28). The latter is a plentiful resource for reconstructing the intellectual and personal exchange of Hatschek and Haeckel, it has been examined by authors from Jena (Krauße 1998; Uschmann 1959).

[3] Due to the nature of this project, only some of the early works of Berthold Hatschek were taken into account for this thesis. However, Hatschek's theoretical works on *Amphioxus*, Trochophora and several other topics (e.g. segmentation of the vertebrate skull) went far beyond the 1880s as was Hatschek's strong support of Ernst Haeckel's achievements (Storch 1950).

[4] Head of the First Zoological Institute [Erstes Zoologisches Institut] of the University of Vienna was Karl Grobben (1854–1945) (Haas 1958).

might have impacted on how embryos are seen at the Viennese Zoological Institute.

Among the most important questions of this thesis report were:

1. What organisms did Berthold Hatschek publish in 3D?
2. How was the cooperative process between scientific author and wax model manufacturer organised?
3. What did the models of Trochophora and *Amphioxus* convey about Hatschek's interpretation of embryology, morphology and evolution? To what extent were Hatschek's ideas about evolutionary theory reflected in these models? After all, the models were made and used at a time when Ernst Haeckel's[5] concepts about development and evolutionary theory had already deeply impacted on Hatschek and many of his contemporaries.

Another objective of this project was the creation of a comprehensive illustrated inventory of the wax models held at the ZCUV, including descriptions and photographs of more than 300 specimens. This current inventory might be of help for the future conservation and may even inspire further investigations around these exquisite wax models.

Due to the breadth of the topic and the pilot character of the current study, many questions could not be explored in detail. Many related issues have already been examined by various authors elsewhere, for instance:

- the roles of three-dimensional models, e.g. in embryology (Amundson 2005; Hopwood 2004; Ludwig et al. 2014; Grotz et al. 2015; Hopwood & Buklijas 2014; Hopwood 2009; Laubichler & Müller 2007; Chadarevian & Hopwood 2004; Kunst et al. 2010)

[5] In 1866, Ernst Haeckel wrote: "Die Deszendenztheorie ist die kausale Begründung der Entwickelungsgeschichte, und dadurch der gesamten Morphologie der Organismen. ... Es gibt keine andere Theorie, welche uns die gesamten Formverhältnisse der Organismen erklärt." (Haeckel 1906, page 186). His pionieering "Generelle Morphologie der Organismen" (1866) is considered his main theoretical work. Here, Haeckel introduced groundbreaking terminology, i. e. "ontogeny" and "phylogeny", explained the variety of species on the basis of the theory of descendence, depicted phylogenetic trees and wrote about inherited traits and acquired characteristics ("Characteres hereditarii" and "Characteres adaptivi"; Haeckel 1906, page 285). An advocate of materialism and recapitulationism, Haeckel sometimes is called "the German Darwin" (notwithstanding substantial disparities). Haeckel believed in a mechanistic nature, i.e. the causal relationship between atoms, molecules, chemical substances and the becoming of morphologies (Kraußе & Nöthlich 1990; Jahn 2000; Depew & Weber 1995). Ernst Haeckels influence on Berthold Hatschek is unmistakeable. In celebration of Haeckel's 80th birthday, Hatschek writes: "Einer jener Großen, deren geistiger Bannkreis uns – bewußt oder unbewußt – stetig umfangen hält!" (Hatschek 1914, page 233); "Er ist vor allem vergleichender Morphologe. Das Verständnis der Gestaltung als Ausruck der natürlichen Verwandtschaft der Organismen zu gewinnen, das ist sein Hauptziel. Die Fülle seiner bahnbrechenden Ideen – zum erstenmal in seiner vielbewunderten "Generellen Morphologie" niedergelegt – ist eine erstaunliche. Es gibt auf diesem Gebeite in jenen Jahrzehnten kaum eine neue Erkenntnis, die nicht von ihm begründet, vorbereitet oder beeinflusst ist" (Hatschek 1914, page 234f.).

- the (changing) roles of anatomy, morphology and embryology in connection to Darwinism, theory of descendence and EvoDevo (Hopwood 2009; Jahn 2000; Bowler 1996; Nyhart 1995a; Bredekamp & Bruhn 2013; Laubichler & Maienschein 2007; Hofer 1974; Depew & Weber 1995; Haeckel 1906)
- the visual culture of biology and the popularisation of science during the 19th century, including zoology and Darwinism in Vienna (Samida 2011; Ludwig 2013; Anderson & Dietrich 2012; Benesch 2014; Hochadel 2003; Taschwer 1997)
- the history of the ZCUV, other Viennese university collections and the related plans for a popular anatomy museum by Carl Brühl [anatomisches Volksmuseum] (Buklijas 2015; Feigl 2012; Buklijas 2010)
- the history of zoology as a discipline at the University of Vienna (Müller & Nemeschkal 2015; Haas 1958; Salvini-Plawen 1999; Salvini-Plawen 2010; Buklijas 2006)
- the developmental biology and evolutionary morphology of annelids and cephalochordates (Bleidorn et al. 2015; Nielsen 1995; Nielsen 2005; Gilbert 2014; Gilbert & Raunio 1997; Anderson 1973; Wanninger 2015b)

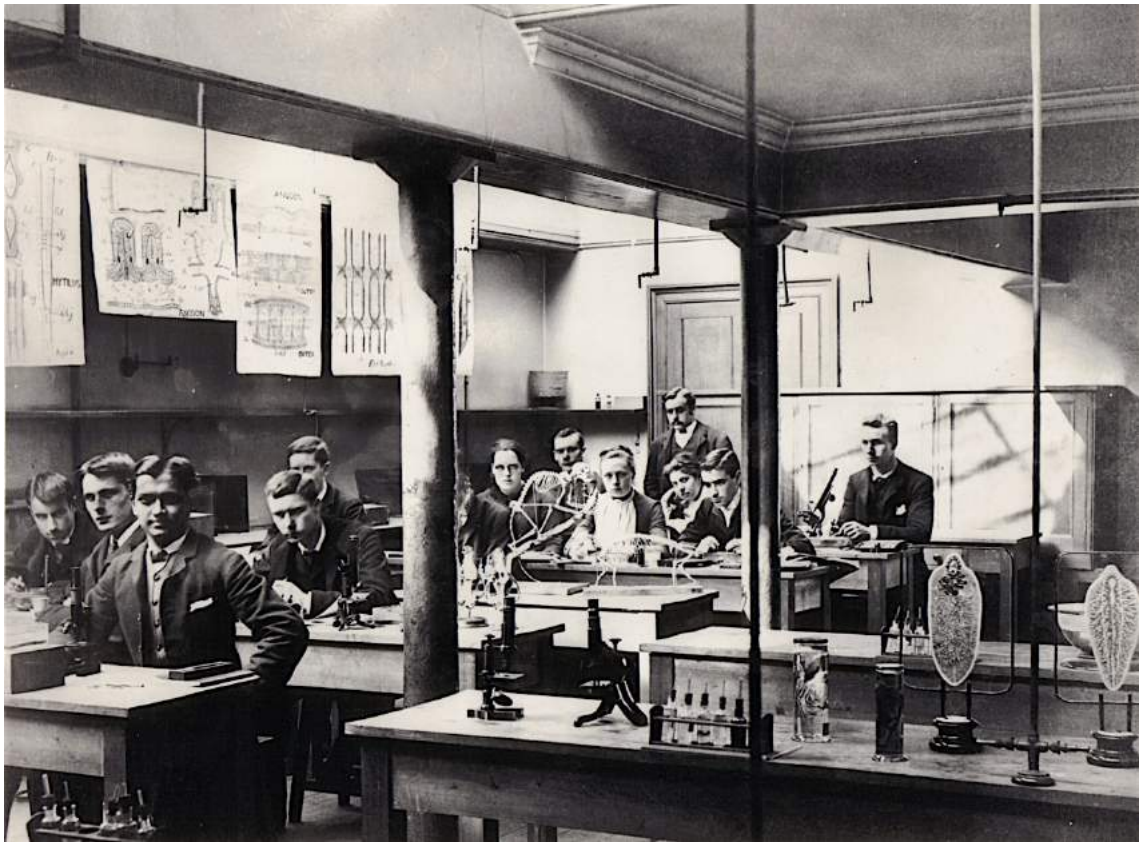

Figure 2 Students attending the "Longer Course in Practical Zoology" at the University College London in 1887. Typical for the rich visual culture in zoology of this time is the use of wallcharts, skeletons, wet preparations; the students were probably producing their own drawings as they were dissecting and gazing through the microscopes. Two Weisker models are on display (front table at the right): The glassplate wax models reveal the anatomy of parasitic worms (Davidson 2016). Photograph used with permission of University College London. Copyright UCL Grant Museum of Zoology.

2 Material and methods

The most important sources for this project were the wax models themselves. The examined models were held in five glass cabinets of the ZCUV within the "Trockensammlung" (collection of dry specimens, including skeletons, shells, feathers, taxidermied animals), a temperature-controlled underground storage that is part of the Department of Theoretical Biology, University of Vienna. In spring 2016, all available wax models were inspected thoroughly and photographed for this project.

Subsequently, the determination of the wax models was the core method of this project. The specimens were identified with the help of company catalogues (e.g. Weisker 1880; Ziegler 1893), inventory books, secondary sources and through email exchange with other collections. Several of the models had labels or handwritten inscriptions on their pedestals which were taken into account. Additionally, the online database www.universitaetssammlungen.de proved useful as well as the YouTube Channel of the Universiteitsmuseum Utrecht[6] with short films of their Weisker and Ziegler models.

Furthermore, several archives, collections, exhibitions and a conference were visited in person for this project in order to identify specimens and gain a deeper understanding of the science and culture of 3D publishing in the 19th century:

- Department for Historical Research at the Museum für Naturkunde in Berlin (Sabine Hackethal)
- Workgroup for Comparative Zoology, Institute for Biology at the Humboldt University in Berlin (Gerhard Scholtz)
- Phyletic Museum in Jena; Workgroup for Didactics of Biology at the University of Jena (Michael Markert, Uwe Hoßfeld)
- Archive at the Ernst-Haeckel-Haus, Institute of History of Medicine, Natural Sciences and Technology at the University of Jena (Thomas Bach)
- exhibition "modellSCHAU" at the Botanical Gardens in Berlin Dahlem (Grotz et al. 2015)
- conference "Naturgetreue Objekte? Moulagen und Modelle im Spannungsfeld von Wissenschaft und Ästhetik" at Medizinhistorisches Museum Hamburg
- Austrian State Archives in Vienna
- Vienna University Archive

[6] Youtube Channel; Universiteitsmuseum Utrecht
https://www.youtube.com/channel/UCEHmSgTfP5EaG2EU2vJVGnA

Nota bene: *Unless stated otherwise, all photographs used in this MSc thesis were taken by Patricia Julia Harlfinger. These photographs depict wax models and other sources, e.g. pages of an inventory book, and they are held at the Zoological Collection (ZCUV) of the Department of Theoretical Biology, University of Vienna. These working pictures were produced for documentations purposes with basic equipment and involved only minimal handling of the specimens. Images that were made by others and that are used with the permission of the respective institutions or persons carry details in their captions, e.g. regarding the copyright and location at which the respective object is held. Should there be any unintentional copyright violation, the author of this thesis kindly requests feedback of the respective person or institution.*

Figure 3 Embryos for a world market. Friedrich Ziegler, son and successor of company founder Adolf Ziegler, displayed his rich portolio of wax models at the World Fair in Chicago (1893), including Berthold Hatschek's Trochophora and *Amphioxus*. Twenty years earlier, Adolf Ziegler had exhibited his products at the World Fair in Vienna including wax models of chicken, frog and echinoderm development. Competitior Rudolf Weisker had presented parasite and dragonfly development in wax (Pokorny 1874). Image from a Ziegler catalogue (Ziegler 1893, page 39).

3 Results

At the time of the assessment, in spring 2016, there were 315 wax models held in five glass cabinets at the ZCUV. These models were produced in the decades around 1880. Most of them could be assigned to either Weisker's "Institut für Wachsbilderei" (65 models) or Ziegler's "Atelier für wissenschaftliche Plastik" (232 models). For 18 models, no manufacturing firm could be determined.

3.1 Weisker's "Institut für Wachsbildnerei"

This is one of the first attempts to assemble scattered information on the Weisker company and to document many of its products. Not much is reported apart from the fact that the company was located in Leipzig. It was founded by Rudolf Weisker in the 1870s and run by his successor Paul Loth until the turn of the century (Hackethal 2008). To date, one company catalogue (Weisker 1880) from around 1880 seems to be the only primary 2D source that is available.

Naturwissenschaftliche

ARBEITEN

aus dem

Institut für Wachsbildnerei

von

Rudolf Weisker

Dr. phil.

LEIPZIG.

Ehren-Preis:

der Kaiserl. Oesterreich. landwirthschaftlichen Academie zu Mödling-Wien;
der Ausstellung zu Dresden 1875;
des landwirthschaftl. Vereines zu Schaala-Rudolstadt;
der internationalen Fischerei-Ausstellung zu Berlin 1880.

1130

Figure 4 Catalogue of Rudolf Weisker's enigmatic "Institut für Wachsbildnerei", published around 1880 (Weisker 1880).

Nachstehende Universitäts- und Lehr-Institute sind bereits im Besitz theils ganzer Serien, theils von Auswahl Präparaten:

Die Anatomie und das zoologische Institut zu **Aberdeen.**
Die Anatomie zu **Amsterdam.**
Das pathologische Institut in **Bruxelles.**
Das landwirthschaftliche Museum in **Berlin.**
Das zoologische Institut zu **Charkow.**
Die anatomische Anstalt in **Cristiania.**
Die permanente grossherzogl. landwirthschaftl. Lehrmittelausstellung in **Carlsruhe.**
Die Thierarzneischule zu **Cureghem lez Bruxelles.**
Das zoologische Institut zu **Dorpat.**
Das zoologische Museum in **Dresden.**
Das zoologische Institut in **Erlangen.**
Das zoologische Institut in **Göttingen.**
Das zoologische Institut in **Graz.**
Die landwirthschaftliche Academie in **Halle a. S.**
Die landwirthschaftl. Hochschule zu **Kaschau** (Ungarn).
Das zoologische Institut zu **Kasan.**
Die Anatomie, das zoologische Institut, das Veterinair-Institut, die chirurgische Poliklinik zu **Leipzig.**
Das zoologische Institut zu **Louvain.**
Das zoologische Institut zu **Liège.**
Das zoologische Institut in **Lund.**
Das University-College in **London.**
Das zoologische Institut in **München.**
Das zoologische Institut in **Moskau.**
Das Anatomical-Departement in **Oxford.**
Das vergl. anatomische Museum in **Paris.**
Das zoologische Institut in **Strassburg.**
Das Science and art Departement in **South-Kensington.**
Das Science and art Departement in **Tokio** (Japan).
Die landwirthschaftl. Academie in **Ungar. Altenburg.**
Die Königl. Forstacademie in **Tharandt.**
Das zoologische Institut in **Wien.**
Die Thierarzneischule in **Wien.**
Das zoologische Institut in **Warschau.**
Die Landbauschule in **Wageningen** (Holland).

2 VII 1130

Figure 5 List of 34 institutions that held Weisker's series and specimens around 1880, among them "Das zoologische Institut in Graz", "Das zoologische Institut in Wien", "Die Thierarzneischule in Wien", but also distant institutions such as the Japanese "Science and art Department in Tokio" (Weisker 1880).

Unfortunately, it remains unknown how Rudolf Weisker and his successor Paul Loth worked, e.g. on which grounds they chose their model organisms or which modelling techniques they used. However it became clear from the catalogue (Weisker 1880) that Rudolf Leuckart, professor at the University of Leipzig, pioneer in parasitology and teacher of Berthold Hatschek, was intensely involved.

According to Weisker's catalogue, a variety of approximately 190 different wax models could be purchased.

- Numerous models of **parasites** were available, particularly "Vermes" (cestodes, nematodes, trematodes, acanthocephales) and mites, relevant for the health of humans and lifestock.
- Models displaying **human anatomy** were offered, e.g. a sagittal cut of the head demonstrating the hearing organ or a lifesize model of the Nervus sympathicus. The latter came in a polished black cabinet, cost 1000 Mark and therefore was by far the most expensive product listed the catalogue, with the other products ranging from 10 Mark (e.g. Tornaria larva or head of the tapeworm *Taenia solium*) to 275 Mark (salmon development).
- About two thirds of the Weisker models offerend around 1880 represented the **development of invertebrates and vertebrates**, most of these embryos being part of a multipiece series, e.g. *Echinorhynchus* development, see Figure 6.

Figure 6 Development of *Echinorhynchus angustatus* ["Kratzer"], a complete and beautifully preserved series. This series is not held at the ZCUV. Source: Museum für Naturkunde Berlin[7]; Historische Bild- u. Schriftgutsammlungen (Sigel: MfN, HBSB); Bestand: Zoologisches Museum Signatur: B XII/80–84 and 293.

[7] Thankfully provided by Dr. Sabine Hackethal. She also guided through the collection and granted access to the related files held at the Museum für Naturkunde.

3.2 Weisker models at the ZCUV

All in all, a total of 65 Weisker specimens were identified at the ZCUV, many of them still in good condition. Damaged models were harder to identify, e.g. a tapeworm embryo, see page 23.

Apart from the company's catalogue (Weisker 1880), the ZCUV's inventory book (Anonymous, 19th century), visits to other collections (Humboldt University[8] in Berlin; Museum für Naturkunde in Berlin) and email exchange with the Grant Museum for Zoology, University College London[9] provided several clues and allowed for cross-checking.

The majority of Weisker's animal models (zootomical specimens, developmental specimens) that were available around 1880 are now or at least once were part of the ZCUV. In contrast, models from the sections "anatomical specimens" (human anatomy) and "Diversa" (pathologies and oddities, e.g. club foot) are almost absent from the ZCUV apart from two rather bizarre molds taken from an embryonic whale, see page 29.

According to the inventory book of the ZCUV, the following Weisker models were once purchased, but cannot be found anymore at the ZCUV: *Echinorhynchus* (1 specimen); heart with all its chambers opened (1); sagittal cut of human skull with nerves (1); *Clepsine* (38); *Amphioxus lanceolatus*[10] (1).

Most interestingly, Weisker also offered a 9-piece-series depicting the development of an Ascidian, including an Appendicularia larva. In the course of this thesis, this series could not be retrieved in Vienna or elsewhere. Still, a wide array of Weisker specimens has remained at the ZCUV for about 130 years. All in all, the Weisker stock provides a very good overview of this company's work, including models depicting development.

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[8] Access to inventory lists was thankfully provided by Univ.-Prof. Dr. Gerhard Scholtz who also guided through the collection held at the Humboldt University.

[9] Thank you to Tannis Davidson, MSc for this fruitful exchange, for sharing Weisker model images and for information from inventories of the Grant Museum of Zoology.

[10] Weisker might have, apart from this model of an adult *Amphioxus*, at some stage also offered wax models of *Branchiostoma* development, see page 62.

3.3 Developmental models by Weisker at the ZCUV

A total of 33 developmental Weisker specimens were identified at the ZCUV. They belong to 8 series or sale units: *Actinotrocha branchiata* (1 specimen), Annelid larva (1), *Ramphogordius* (2), Tornaria (1), *Comatula* (1), Salmon (5), Dragonfly (12), Crayfish (10).

3.3.1 Marine larvae [*Actinotrocha branchiata* vor der Metamorphose; Anneliden-Larve; *Ramphogordius*, Larve und beginnende Ausstülpung; Tornaria; *Comatula*]

Six marine larvae (5 sales units) that were offered in Weisker's catalgoue (Weisker 1880) are held at the ZCUV. (For a comparison of Weisker models and Ziegler's marine larvae, please see 75ff.)

Figure 7 *Ramphogordius* 1, eary larva [Larve]

Figure 8 *Ramphogordius* 2, with starting elongation [beginnende Ausstülpung]. Nota bene: Although this specimen presumably was sold as a Nemertean of the genus *Ramphogordius*, beginning segementation is clearly visible and also mentioned in the model's description. However segmentation is not part of Nemertean development, but is a key feature in annelids.

Figure 9 Larva of an unspecified Annelid; segmentation and bristles are visible, both charateristic for Polychaete development.

Figure 10 Pedestal of a *Ramphogordius* model. It is most likely that this model was customised by its Viennese users. The handwritten inscription on the wooden pedestal and the ZCUV's label are now reading "*Polygordius*" instead of "*Ramphogordius*". The same was done with the second *Ramphogordius* and the unnamed Annelid specimen.

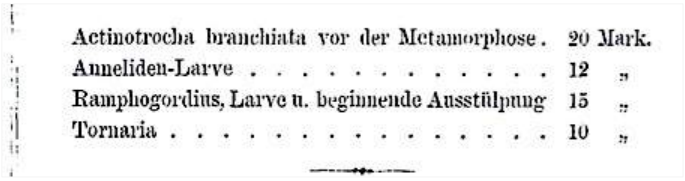
Figure 11 *Actinotrocha branchiata* before metamorphosis

Figure 12 Tornaria[11]

Figure 13 *Comatula*[12].

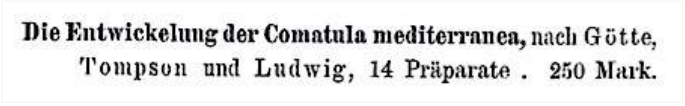
[11] The inventory book for the collection held at Workgroup for Comparative Zoology at Humboldt University lists this Weisker specimen as "*Balanoglossus*".

[12] It is not clear whether this crinoid larva is one of 14 stages of Weisker's *Comatula* after "Götte, Tompson and Ludwig" that was available around 1880. The inventory book at the Workgroup for Comparative Zoology at Humboldt University lists the purchase of an individual "*Antedon*" by Weisker. This might be the same single item that was bought for the collection in Vienna. The inventory book in Vienna, too, does not mention several stages.



Actinotrocha branchiata vor der Metamorphose .	20 Mark.
Anneliden-Larve	12 „
Ramphogordius, Larve u. beginnende Ausstülpung	15 „
Tornaria	10 „

Figure 14 Marine larvae entries in Weisker's catalogue (Weisker 1880) in the section "zootomical specimens"



Die Entwickelung der Comatula mediterranea, nach Götte, Tompson und Ludwig, 14 Präparate . 250 Mark.

Figure 15 *Comatula* entry in the section "developmental history"

Figure 16 "1. Tornaria 3 Präparate (Weisker in Leipzig)"; entry in the the ZCUV's inventory book (Anonymous 19th century). The Tornaria specimen probably were identical.

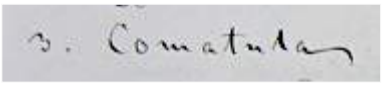


Figure 17 "3. *Comatula*"; entry in the ZCUV's inventory book

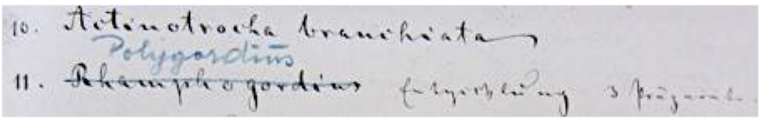


Figure 18 "10. *Actinotrocha branchiata*; 11. ~~*Rhamphordius*~~ *Polygordius* Entwicklung 3 Präparate"; entry in the ZCUV's inventory book. Weisker's models of two Nemertean *Ramphogordius* and of one unnamed Annelid were re-named and then possibly used at the University of Vienna to demonstrate Annelid development and Trochophora formation according to Berthold Hatschek's theories.

3.3.2 Fish development [Die Entwickelung des Lachs (trutta salar)]

This seems to be an incomplete series since 9 pieces are mentioned in the Weisker catalogue. However the inventory book of the ZCUV lists only the purchase of specimens 1 – 5. In their appearance and dimensions the fish stages appear similar to Weisker's *Astacus* series, see page 20. They were produced after "original models" provided by Professor His.

Figure 19 Five stages of salmon development, probably in their original box by Weisker

Entwickelungsgeschichte.

Die Entwickelung des Lachs, (trutta salar) nach den Originalmodellen des Herrn Prof. His, 40fach vergrössert, 9 Piecen . . . . . 275 Mark.

Figure 20 Entry in Weisker's catalgoue

Figure 21 Entry in the ZCUV's inventory book "Die Entwicklung des Lachses (nach His) 1 – 5"; this is an indication that only 5 pieces were bought, and not the complete series as offered in the catalgoue.

3.3.3 Dragonfly development [Libellula-Entwickelung. *Calopteryx* virgo]

The series of the dragonfly *Calopteryx virgo* demonstrates the development of a hemimetabolous insect with incomplete metamorphosis. The series is complete and contains twelve stages. In 1873, the *Calopteryx* series was shown at the World Exhibition held at Vienna (Pokorny 1874) where, by the way, also Joseph Hyrtl's corrosion specimens gained much attention (Buklijas 2015).

Apart from this insect development series, the ZCUV contains insect series of Coleoptera and Diptera development, i.e. Ziegler's *Hydrophilus* development after Heider (see page 44) and Ziegler's *Chironomus* development after Weismann (see page 43).

Figure 22 *Calopteryx virgo* stages 1 – 6. The numbers are inscribed on the models themselves which are mounted on two separate wooden boards, they are held in place by velvet-covered wire.

Figure 23 *Calopteryx virgo* stages 7 – 12. Both boards carry the original Weisker brand sticker and a handwritten label of the ZCUV.

Figure 24 Original Weisker brand sticker [Verfertiger naturwissenschaftlicher Wachspräparate. Rud. Weisker, Leipzig]

Figure 25 Handwritten *Calopteryx virgo* label, [Zoologische Verlgeichend-Anatomische Sammlung, Universität Wien]

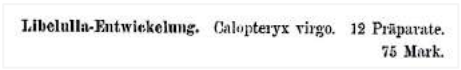


Figure 26 Entry in Weisker catalogue

Figure 27 Entry number 13 in the inventory book of the ZCUV: "Entwicklung des Eies von *Calopteryx virgo* 1 – 12 (Weisker in Leipzig)"

3.3.4 Development of *Astacus fluviatilis* [Die Entwickelung von *Astacus fluviatilis*]

This series is a complete set of 10 developmental stages of the European crayfish *Astacus fluviatilis*. Stages 1 – 8 are held in a box, probably the original container provided by the Weisker firm. Another *Astacus* series is kept at the Humboldt University's zoological collection in Berlin. Gerhard Scholtz reported about these models in great detail (Scholtz 2014).

Figure 28 *Astacus fluviatilus*, stages 1 – 8, probably in their original cardbord box

Figure 29 *Astacus fluviatilis*, stages 9 and 10

Figure 30 *Astacus fluviatilis*, stages 9 and 10

Die Entwickelung von Astacus fluviatilis. 10 Präparate.
75fach vergrössert . . . . . 200 Mark.

Figure 31 *Astacus fluviatilis* entry in Weisker catalogue

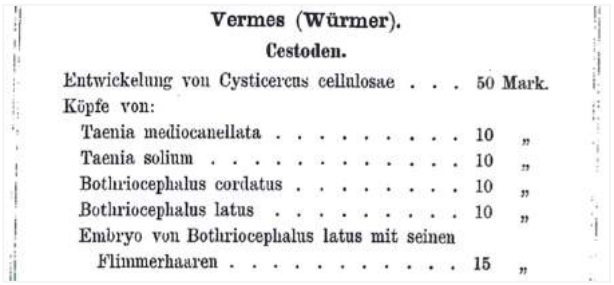
Figure 32 Entry number 34 in the ZCUV's inventory book: "Entwicklung v. *Astacus fluviatilis* 1 – 10"

3.4 Non-developmental Weisker models at the ZCUV

Apart from the developmental series, there are more Weisker models, mainly parasites, that are still held at the ZCUV. Of the 32 specimens (including 3 duplicates), almost of all of them represent "Vermes" and could be purchased individually.

All of these specimens were already offered in the catalogue from around 1880. They were listed in the section "zootomical specimens" and produced under the "special guidance" [specielle Leitung] of Rudolf Leuckart (Weisker 1880). Only the rather peculiar whale specimens (see page 29) were advertised in the "Diversa" section at the end of Weisker's catalogue.

3.4.1 Tapeworms [Vermes; Cestoden]



Vermes (Würmer).

Cestoden.

Entwickelung von Cysticercus cellulosae . . .	50	Mark.
Köpfe von:		
Taenia mediocanellata	10	„
Taenia solium	10	„
Bothriocephalus cordatus	10	„
Bothriocephalus latus	10	„
Embryo von Bothriocephalus latus mit seinen Flimmerhaaren	15	„

Figure 33 Weisker's catalogue, listing a total of 10 tapeworm models; 5 of them are still held at the ZCUV.

3.4.1.1 Tapeworm cysticercosis [Entwickelung von *Cysticercus cellulosae*]

Figure 34 This is the only (incomplete) stage, held at the ZCUV, of Weisker's *Cysticercus* development with 5 models

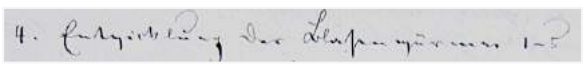


Figure 35 Entry in the inventory book of the ZCUV: "Entwicklung der Blasenwürmer 1 – 5"

3.4.1.2 Tape worm heads [Köpfe]

Figure 36 *Bothriocephalus latus*; *Taenia mediocancellata*; *Taenia solium*

Figure 37 Handwritten label reading "*Bothriocephalus latus*"

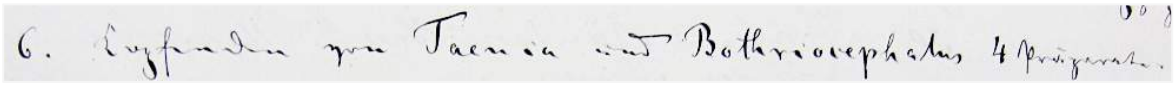


Figure 38 Corresponding entry in the ZCUV's inventory book

3.4.1.3 Tapeworm embryo [Embryo von *Bothriocephalus latus* mit seinen Flimmerhaaren]

Figure 39 *Bothriocephalus* embryo (damaged). The larva's characteristic hooks are visible, but the ciliated oncosphere is lost[13].

[13] Video clip of the complete specimen, held at the Universiteitsmuseum Utrecht: https://www.youtube.com/watch?v=HsiZcnfjsSk

3.4.2 Tapeworms on glassplates [Vermes; Proglottiden-Entwicklung]

Proglottiden-Entwickelung
(auf Glasplatten mit Messingträgern.)

Junges Glied	von Taenia solium	20	Mark.
do.	von Taenia mediocanellata . . .	20	„
Form des Uterus	von Taenia solium	15	„
do.	von Taenia mediocanellata .	15	„
Anatomie von Bothriocephalus latus (Doppelplatte)		30	„

Figure 40 Entry in Weisker's catalogue, listing the available glass plate models of tapeworms

3.4.2.1 Uterus of *Taenia* [Form des Uterus]

Figure 41 Wax model on a glassplate, displaying the uterus shape of *Taenia solium*. The original brass frame was replaced by a wooden frame.

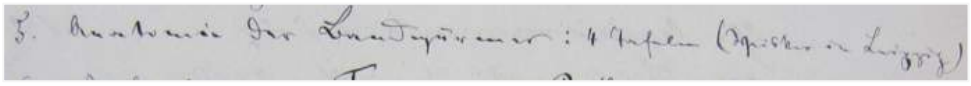


Figure 42 Entry in ZCUV's inventory book: "5. Anatomie der Bandwürmer: 4 Tafeln (Weisker in Leipzig)"

3.4.3 Roundworms [Vermes; Nematoden]

Nematoden.

Kopf von Ascaris lumbricoides	15	Mark.
Endspitze mit Spicula und Darm von demselben	20	„
Kopf von Dochmius duodenalis mit Querschnitt	20	„
Bursa von Dochmius duodenalis	20	„
Sclerostomum equinum	25	„
Trichina spiralis, Männchen und Weibchen . .	30	„
5 Präp. über die Wanderung i. d. Muskelfaser .	50	„
Oxyuris vermicularis ♀ u. ♂	30	„

Figure 43 Entry in Weisker's catalogue listing the available Nematode models. All of them are still held at the ZCUV.

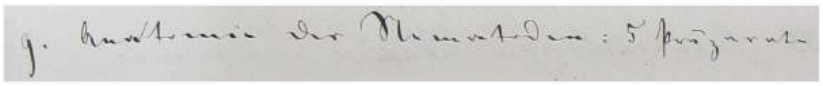


Figure 44 Corresponding entry in the ZCUV's inventory book: "Anatomie der Nematoden: 5 Präparate"

3.4.3.1 Roundworm *Ascaris* [Kopf von *Ascaris lumbricoides*; Endspitze mit Spicula und Darm von demselben]

Figure 45 Weisker's *Ascaris lumbricoides*, head section and end with spicula.

Figure 46 The same specimens: Head and posterior end of *Ascaris lumbricoides*.

3.4.3.2 Hookworm *Dochmius* [Kopf von *Dochmius duodenalis* mit Querschnitt; Bursa von *Dochmius duodemalis*]

Figure 47 Head and bursa of *Dochmius dudodenalis* (now: *Ancylostoma dudodenale*)

Figure 48 The same specimens: Anterior end, bursa of *Dochmius dudodenalis*

3.4.3.3 *Sclerostomum equinum*

Figure 49 Weisker's *Sclerostomum equinum*, anterior end can be taken apart to display a longitudinal section

3.4.3.4 Male and female *Trichinella* [*Trichina spiralis*, Männchen und Weibchen]

Figure 50 Male (top) and female (below) *Trichinella*, in their original box, with colouration. It is likely that these models were used in conjunction with the models demonstrating the parasite's invasion of muscles, see Figure 52.

Figure 51 Duplicate pale *Trichinella* models, without colouration

3.4.3.5 Migrating *Trichinella* [5 Präp. über die Wanderung i.d. Muskelfaser]

Figure 52 Five *Trichinella* models in their original box, demonstrating the migration of the larvae into the host's muscle, including the formation of cysts.

Figure 53 Entry of 7 *Trichinella* models in the ZCUV's inventory book: "26. *Trichina spiralis* ♀ und ♂ 1 – 2; 27. Wanderung derselben in die Muskelfaser 1 – 5"

3.4.3.6 Male and female pinworm [*Oxyuris vermicularis*, weiblich und männlich]

Figure 54 Male (top) and female pinworm (*Enterobius vermicularis* syn. *Oxyuris vermicularis*), complete set of 2 models, held in their original box

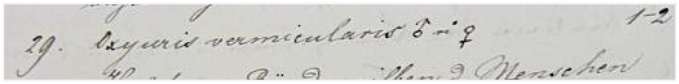
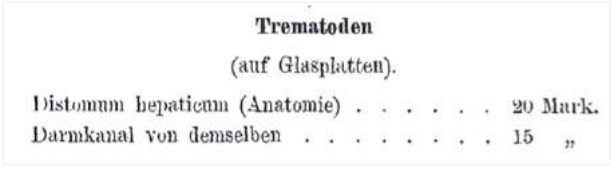


Figure 55 Entry in the inventory book "29. *Oxyuris vermicularis* ♂ und ♀ 1 – 2"

3.4.4 Flukes on glassplates [Vermes; Trematoden]



Trematoden

(auf Glasplatten).

Distomum hepaticum (Anatomie) . . . . . 20 Mark.
Darmkanal von demselben . . . . . 15 „

Figure 56 Entry in Weisker's catalogue; the glassplate specimens were probably used in conjunction with each other, but could be purchased separately.

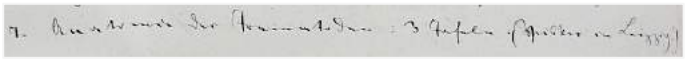


Figure 57 "Anatomie der Trematoden: 3 Tafeln (Weisker in Leipzig)", entry in the ZCUV's inventory book. The amount of glassplates (3) may imply that a duplicate of one specimen was purchased since only two different Trematode models are listed in the catalgoue from around 1880.

3.4.4.1 Liver fluke anatomy [*Distomum hepaticum* (Anatomie)]

Figure 58 Liver fluke *Fasciola hepatica* on a glassplate, customised for teaching in Vienna, with paper labels for organ identification

3.4.4.2 Digestive system of the liver fluke [Darmkanal von *Distomum hepaticum*]

Figure 59 Weisker's model of *Distomum hepaticum* (now: *Fasciola hepatica*). The flat glassplate model is without its original frame and pedestal. Please go to page 8 to see its use at a 19th century zoology lab.

3.4.5 Itch mites [Krätz-Räudemilben der Menschen und der Thiere]

Figure 60 Five mite models by Weisker

Die Krätz-Räudemilben der Menschen und der Thiere (400fach vergrössert).

Sarcoptes scabiei	♂	45	Mark.
	♀	45	„
Die Kauwerkzeuge derselben, ca. 1500fach vergr.		30	„
Dermatophagus ovis	♂	120	„
do.	do. ♀		
do.	do. Jugendform vor der Copula		
Dermatocoptes equi	♂	45	„
Demodex folliculorum		20	„

Figure 61 Entry in Weisker catalogue

Figure 62 Entry in the ZCUV's inventory book "30. Krätz- u. Räudemilben d. Menschen und der Thiere 1 – 8", indicating that the complete series was purchased

3.4.6 Blow holes and female genitalia of an embryonic whale [Naturabdruck der Spritzlöcher des Walfisches und weibl. äusseren Genitalien]

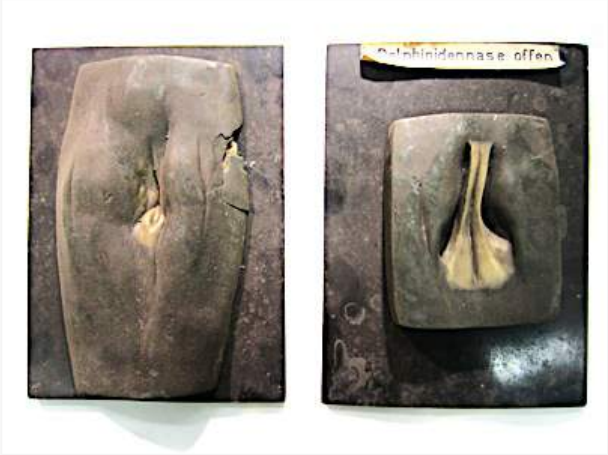


Figure 63 Weisker's wax molds of female whale genitalia and a whales's blowhole

Naturabdruck der Spritzlöcher des Walfisches und der weibl. äusseren Genitalien, vom 5 Meter langen Embrio des zoolog. Instituts . . . . . 20 Mark.

Figure 64 Entry in Weisker's catalogue

Figure 65 Entry in the ZCUV's inventory book: "Die Spritzlöcher d. Walfisches u die weibl äußeren Genitalien 1 – 2"

3.5 Ziegler models held at the ZCUV

At the time oft he assessment in spring 2016 a total of 232 Ziegler wax models (including 14 duplicates) were held at the ZCUV in glass cabinets. These models could be attributed to 21 series, depicting embryos of humans, invertebrates and vertebrates, representing normal development of individuals or organs in an idealised, abstracted way. Of the six botanical series that Ziegler made during the early years of the company, no models were located at the ZCUV.

In the following section, in most cases the models are listed according to their series numbers and series names as published in Ziegler's catalogue from 1912 (Ziegler 1912). Further main sources of this section and for the identification work were: Hopwood (2002), Ziegler (1893) and the ZCUV's inventory book with a 2-page-list.

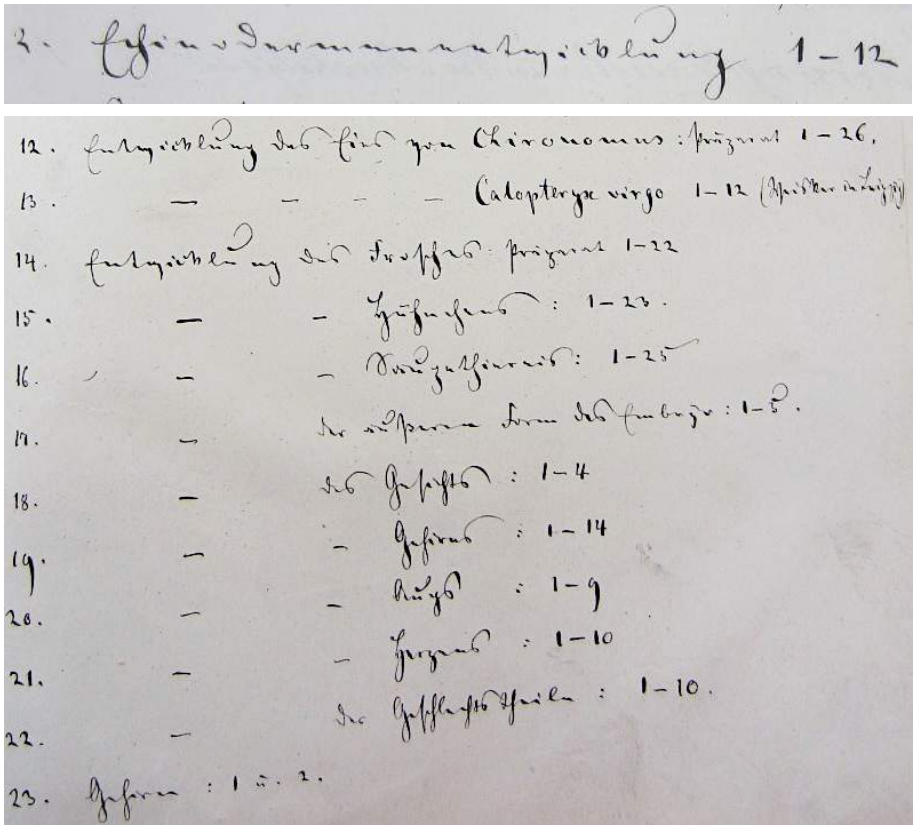


Figure 66 The ZCUV's inventory book from the 19th century contains 12 Ziegler models entries: "2. Echinodermenentwicklung 1 – 12; 12. Entwicklung des Eies von *Chironomus*: Präparat 1 – 16; (13. Entwickelung des Eies von *Calopteryx virgo* 1 – 12 (Weisker in Leipzig)); 14. Entwicklung des Frosches: Präparat 1 – 22; 15. Entwicklung des Hühnchens: 1 – 23; 16. Entwicklung des Säugethiereis: 1 – 25; 17. Entwicklung der äußeren Form des Embryo: 1 – 5; 18. Entwicklung des Gesichts: 1 – 4; 19. Entwicklung des Gehirns: 1 – 14; 20. Entwicklung des Augs 1 – 9; 21. Entwicklung des Herzens: 1 – 10; 22. Entwicklung der Geschlechtstheile: 1 – 10; 23. Gehirn: 1 u. 2"

The “Atelier für wissenschaftliche Plastik” was founded in 1852 by Adolf Ziegler (1820–1889), a medical doctor and general practicioner (Ziegler 1893). Ziegler started professional modelling as zootomical assistant of Alexander Ecker and would later call himself “plastic publisher” [plastischer Verleger] (Hopwood 2002). His son Friedrich (1860–1936), a trained artist, took over the business in 1886. The first commercially available series produced by Ziegler depicted the development of the frog (this series later got amended (Ziegler 1891)) and of the echinoderms. (Ziegler 1891; Hopwood 2002)

Ziegler’s model series were always developed in cooperation with a scientific author. Among those were leading scientists such as Wilhelm His, Alexander Ecker, August Weismann, Ernst Haeckel, Karl Heider and Philipp Stöhr. Their approval, together with Adolf Ziegler’s medical degree, gave authority to the wax models on a market with several competitors.

Ziegler’s wax objects were widely bought for teaching purposes and museums at a time when the underlying forces of development were explored and embryology had gained much attention as evolutionary theory was intensely discussed. The models were used along with wall charts, blackboard drawings, photographs and illustrated textbooks. The latter sometimes included images of embryos drawn after Ziegler’s wax models or were referring to wax models as demonstration objects, e.g. Kükenthal’s “Leitfaden für das Zoologische Praktikum”. A comprehensive commentary (Marshall 1891) and Ziegler’s supplementary leaflets materials that were available for some series (Ziegler ca. 1882; Ziegler 1891) provided more information on the developmental stages.

The first Ziegler series were modelled freehand after drawings and with the help observations of preserved specimens through the microscope. Later, microscopic photography and plate modelling[14] were applied in the production of some series in order to manufacture the models as precise as possible. Ziegler’s catalogue from 1893 dedicated a whole page to explain the methods for making “Plattenmodelle” and “Reconstructionsmodelle” (Ziegler 1893, page 4). The original prototypes could then be reproduced by casting and finished by handpainting. They were put on handles, pedestals or in customised boxes. Ziegler himself took responsibility for sales and worldwide distribution of his models as can be deducted from price lists and shipping information of the catalogues (Ziegler 1893; Hopwood 2002).

For more details, for example regarding scientific authorships, manufacturing techniques, corresponding print publications or publication dates of Ziegler wax models, please see Ziegler’s catalogues (Ziegler 1893) as well as Nick Hopwood’s publications, especially “Embryos in wax” (Hopwood 2002) which is an excellent reference for Ziegler’s wax models.

[14] The latter is in principle very similar to today’s imaging through computer tomography and 3D printing, indispensable tools of contemporary EvoDevo.

3.5.1 Human Embryos during the first month of development [Serie 1[15]; Modelle menschlicher Embryonen aus dem ersten Monat]

- 5 pieces
- incomplete series, models 2, 4, 5 are missing
- after Wilhelm His
- first published in 1885

Figure 67 Human embryos, Ziegler's series no. 1, models 1, 3, 6, 7, 8

3.5.2 Human embryos [Serie 1a; Modelle menschlicher Embryonen 1,3mm und 2,11 mm]

- 1 piece
- incomplete series, model 1 is missing
- after Auguste Eternod
- first published 1902 – 1908

Figure 68 Human embryo, Ziegler's series no. 1a, model 2

[15] The series numbers and series titles in this section correspond with those used in Ziegler's catalogue from 1912 (unless stated otherwise).

3.5.3 Development of the external shape [Serie 2[16]; Entwicklung der äußeren Form der menschlichen Embryonen]

- 5 pieces, complete series
- after Alexander Ecker
- first published in 1858 – 1861
- series listed in the ZCUV's inventory book

Figure 69 Development of the external shape, Zieglers series no. X (later no. 2), models 1 – 5

3.5.4 Anatomy of human embryos [Serie 3; Modelle der Anatomie menschlicher Embryonen]

- 6 pieces
- incomplete series, models 5 and 6 are missing
- after Wilhelm His
- first published in 1888

Figure 70 Human embryos, Ziegler's series no. 3, models 1, 2, 3, 4

Figure 71 Human embryos, Ziegler's series no. 3, models 7 and 8

Figure 72 Models 7 and 8, embryos at the end of the fourth week

[16] The ZCUV holds the older version of this series; the amended later version comprised only two specimens and was then called series no. 2.

3.5.5 Development of the human face [Serie 3b[17]; Entwicklung der äusseren Form des Gesichts beim Menschen]

- 4 pieces, complete series
- after Alexander Ecker
- first published in 1858 – 1861
- series mentioned in the ZCUV's inventory book

Figure 73 Development of the human face, Ziegler's series no. XII, models 1 – 4

3.5.6 Development of the brain convolusions [Serie 5; Entwicklung der Furchen und Windungen der Großhirnhemisphären im Fötus des Menschen]

- 14 pieces, complete series
- after Alexander Ecker
- published first 1868 – 1869
- models on wooden boards, can be removed for handling
- series mentioned in the ZCUV's inventory book

Figure 74 Development of the human brain, Ziegler's series no. 14, models 1 – 14

[17] The ZCUV holds the older version of this series; it was amended in the 20th century and then called 3b.

3.5.7 Adult brain with convolusions [Serie 6; Die Furchen und Windungen der Großhirnhemisphären des erwachsenen Menschen]

- 1 piece
- incomplete series, model 1 is missing
- after Alexander Ecker
- published first 1868 – 1869
- specimen on wooden board, may be removed for handling
- series mentioned in the ZCUV's inventory book

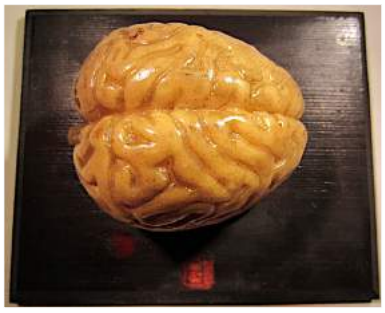


Figure 75 Brain of an adult human, Ziegler's series no. 6, model 2

3.5.8 Development of the vertebrate eye (Serie 8[18]; Entwickelung des Wirbelthierauges]

- 7 pieces
- incomplete series, models 1 and 5 are missing
- after Wilhelm Manz
- first published in 1876
- series mentioned in the ZCUV's inventory book

Figure 76 Development of the vertebrate eye, Ziegler's series no. 8, models 2 – 4, 6 – 9

[18] A later series after the Viennese researcher Ferdinand Hochsetter represented human eye development and was also called series no. 8.

3.5.9 Human heart development (Serie XVI[19]; Entwicklung des Herzens beim Menschen]

- 10 pieces, complete series
- after Alexander Ecker
- first published in 1858
- series mentioned in the ZCUV's inventory book

Figure 77 Development of the human heart, Ziegler's series no. XVI, models 1 – 10

3.5.10 Genital development in humans [Serie 14; Die Entwicklung der äußeren Geschlechtsteile des Menschen]

- 5 pieces
- incomplete series, models 3, 5, 6, 7, 9 are missing
- after Alexander Ecker
- first published in 1858
- specimens are mounted on wooden boards with metal eyelets so that they can be hung on a wall easily
- series mentioned in the ZCUVs inventory book

Figure 78 Development of external genitalia in humans, Ziegler's series no. 14, models 1, 2, 4, 8 and 10

[19] Another heart development series (after Wilhelm His, 12 specimen, series no. 11) was published first in 1885.

3.5.11 Development of the vertebrate primordial skull [Serie 15; Die Bildung des Primordialschädels]

- complete series with 5 specimens, held in their original boxes
- after Philipp Stöhr
- first published in 1882

Figure 79 Development of the primordial cartilage cranium, Ziegler's series no. 15, models 1 and 2: Axolotl at 7.5mm, Axolotl at 9mm

Figure 80 Primordial skull development, models 3, 4, 5: *Rana temporaria*, *Salmo salar* at 11mm, *Salmo salar* at 13mm

3.5.12 Lancelet development [Serie 22; Entwicklung des *Amphioxus*]

- 28 pieces (including doubles)
- incomplete series, missing stages : 2, 4, 6, 11, 12
- two specimens each of the following stages: 10, 13, 17, 19, 20, 21, 23, 24
- published first in 1882
- *Amphioxus* development series were analysed more extensively in this thesis since their scientific author was Berthold Hatschek, see page 74ff. and page 62ff.

Figure 81 *Amphioxus* development, Ziegler's series no. 22, overview of all models held at the ZCUV, models 1, 3, 5, 7 – 10, 13 – 25

3.5.13 Ray development [Serie 23; Entwickelung des Zitterrochens (*Torpedo*)]

- 2 pieces
- incomplete series, models 3, 4, 5 are missing
- after Friedrich Ziegler and his brother Heinrich Ernst Ziegler
- published first in 1892
- mounted on wooden boards

Figure 82 Stingray development, Ziegler's series no. 23, models 1 and 2

3.5.14 Development of the frog: original series and supplments [Serie 25; Entwickelung des Frosches]

- original series was made after Alexander Ecker
- first published in 1852
- original series mentioned in the ZCUV's inventory book (22 pieces)
- During the 1890s, several frog models (14 – 17; 23 – 25) were amended or replaced (Ziegler 1893; Ziegler 1891; Brazier & Duggins 2015) by Friedrich Ziegler and his brother Heinrich Ernst Ziegler.

Figure 83 Frog development, Ziegler's series no. 25, models 1 – 6

Figure 84 Frog development, models 7 – 12

Figure 85 Frog development, models 13 – 18

Figure 86 Frog development, models 19 and 20

Figure 87 Frog development, models 21 – 23

Figure 88 Overview, series no. 25, model labels 1 – 23

Figure 89 Ambiguous entry in the ZCUV's inventory book: "Die Entwickelung des Frosches (nach Goette) 1 – 8". This entry might either correspond to the supplemental Ziegler models. Or it might indicate that an (incomplete) frog series by Weisker (23 pieces, after Ecker and Götte) once was held at the ZCUV.

Figure 90 Supplements for frog development series, most likely by Ziegler. The supplemental models were made during the 1890s to amend the original frog series after Ecker from the 1850s. One of the models is affixed to a Ziegler pedestal including the typical Ziegler number label in red and gold (middle), reading "12". However six models are on wooden pedestals and metal holders that look similar to those used by Weisker and they do not carry numbered labels.

3.5.15 Early chick development (Serie 26; Entwickelung des Hühnchens]

- 23 models (plus 5 doubles)
- complete series; models 4, 7, 8, 10, 22 are duplicates
- after Wilhelm His
- published first 1868
- series mentioned in the ZCUV's inventory book

Figure 91 Chicken development, Ziegler's series no. 26, models 1 – 9 in their original frames

Figure 92 Chicken development, models 10 – 13

Figure 93 Chicken brain development, models 14 – 17

Figure 94 Chicken heart development, models 18 – 21

Figure 95 Digestive tract development, models 22 and 23

3.5.16 Mammalian development [Serie 28[20]; Die ersten Entwickelungsvorgänge bei Säugethieren bis zur Anlage des Embryo]

- 15 pieces
- incomplete series, missing numbers: 5, 12, 15, 17, 18, 19
- after Theodor Bischoff
- first published in 1852 – 1861
- series mentioned in the ZCUV's inventory book

Figure 96 Mammalian development, Ziegler's series no. 28, models 1 – 4, 6 – 11, 13 – 14, 16, 18, 20

3.5.17 Invertebrate pelagic larvae [Serie 30; Marine Larven]

- 6 models, plus 1 double *Eupomatus*
- incomplete series; models 1 (Pilidium), 6 (*Teredo*), 8 (Auricularia) are missing
- after Berthold Hatschek, Johannes Müller, Emil Selenka, Arnold Lang, Ilja Metschnikoff
- published first in 1882
- The marine larvae series and its context was extensively analysed since Berthold Hatschek served as ist scientific co-author, see page 49ff.

Figure 97 Marine larvae, Ziegler's colourful series no. 30, models 4, 3, 2, 5, 5, 7

[20] Series no. 28 was later replaced by the "Development of the pig".

Figure 98 "*Eupomatus*" in handwriting on the wooden pedestal of model 5

Figure 99 Damaged Tornaria of *Balanoglossus* after Johannes Müller, showing ciliary bands (blue) and the the entodermal intestine (red)

3.5.18 Larvae of echinoderms [Serie 31; Larven der Echinodermen]

- 11 pieces
- incomplete series, model number 12 (Auricularia of a Holothuriuan) is missing
- after Georg Meissner
- first published in 1855 – 1859
- mentioned in the ZCUV's inventory book

Figure 100 Diversity of echinoderm larvae, Ziegler's series no. 31, models 1 – 11

3.5.19 Starfish development [Serie 32; Die Entwickelung von *Asterina gibberosa*]

- complete series with 11 pieces, showing larval development on day 4, 5, 6, 8 and 11
- held in original box, supplementary leaflet is missing
- after Hubert Ludwig
- first published in 1882

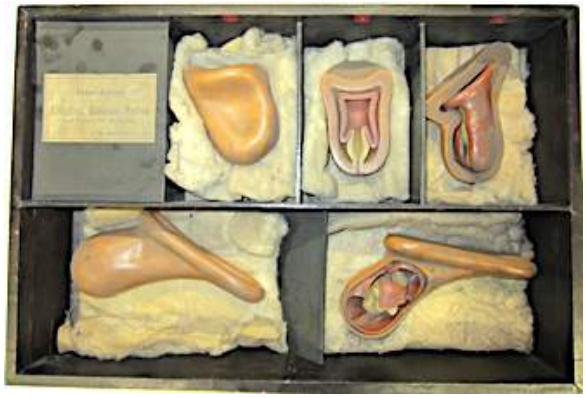


Figure 101 *Asterina gibberosa*, Ziegler's complete series no. 32, numbers 1 – 5

Figure 102 Ziegler's series no. 32, numbers 6 – 11, held in their original box

3.5.20 Development of a fly [Serie 33; Embryonalentwickelung von *Chironomus*]

- 25 pieces
- incomplete series, number 6 is missing
- after August Weismann
- first published in 1864
- series mentioned in the ZCUV's inventory book

Figure 103 *Chironomus* development, Ziegler's series no. 33 in original box, models 1 – 5, 7 – 25

3.5.21 Water beetle development [Serie 34; Die Entwickelung von *Hydrophilus* piceus L.]

- complete series, 11 specimens
- after Karl Heider
- first published in 1889

Figure 104 Development of the water beetle *Hydrophilus*, Ziegler's series no. 34, models 1 – 6

Figure 105 Ziegler's complete series no. 34, models 7 – 11

3.6 Undetermined models of the ZCUV

A total of 18 models could not be assigned to a manufacturer.

3.6.1 Human embryos displaying facial development

This series of 11 human embryos could not be allocated to a producer. At first glance, they resemble the wax models of human embryos made by Ziegler, but they were not part of the company's portfolio. This was confirmed by wax model expert Nick Hopwood (personal communication).

It might be that this series was described in the exhibition guide of a Viennese museum ("Präuscher's Nachfolger") with its "anatomical, pathological and ethnological displays" as mentioned in (Buklijas 2010). In this guide (Präuscher ca. 1875) a series of 12 wax models (numbers 413 – 424) is described. They represent the normal development of the face [Bildung des Gesichts] in the course of the first nine weeks, including jaws, oral cavity, tongue, eyes, nose, ears and heart. Although not shown on the wax embryos, the written description mentions developmental disorders that result in cleft palate [Wolfsrachen] and cleft lip [Hasenscharte]. However no manufacturer or other origin get mentioned in the guide book.

Figure 106 Human embryos of uncertain origin, stages 1 – 6

Figure 107 Human embryos of uncertain origin, stages 7 – 11

3.6.2 Mammalian brains

There were five brain models whose origins could not be determined further. Probably, the large brain models of an elephant, a dolphin and an orang utan were made by the same manufacturer; these three models carry inscriptions of the same style on their surface and have a similar appearance in general.

Figure 108 "Elephant"

Figure 109 undetermined wax models of a mammalian brain

Figure 110 "Delphin"

Figure 111 "Orang" (on a Ziegler wooden board)

Figure 112 Undetermined wax models of a mammalian brain

3.6.3 Tapeworm heads

These models could not be attributed to a certain company. They display, quite similary to Weisker, the heads of tapeworms, but are larger and bulkier. They might be dated to the 20th century and were possibly produced and sold by one of

the large German companies for teaching aids, such as “Lehrmittelwerkstätten Max Hummel[21]”.

Figure 113 Tapeworm heads of unknown origin

[21] Thankfully Dr. Michael Markert, researcher in the Workgroup for Didactics of Biology at the University of Jena, shared his extensive knowledge on several manufacturers of teaching aids.

SERIE 30.
Marine Larven.

Diese Reihe von Modellen stellt einige wichtige Typen freischwimmender mariner Larven dar. Die Auswahl der zu modellirenden Larven wurde von Prof. Dr. Heinrich Ernst Ziegler getroffen.

Alle Larven sind in der Medianebene halbirt dargestellt, so dass die inneren Organe sichtbar werden, und zwar ist bei allen die rechte Hälfte modellirt. Es sind durchgängig schematische Farben in der Weise verwandt, dass das Ectoderm und die ectodermalen Organe in blauer, das Entoderm in rother und die mesodermalen Gebilde in gelbbrauner Farbe gegeben sind. Die Cilien des Ectoderms sind theils körperlich dargestellt, theils soweit dies nicht möglich war, durch blaue Punkte oder blauen Farbton markirt. Die Grösse der Modelle variirt zwischen 10 und 12 cm.

Die Modelle und die Originalarbeiten, an welche sich dieselben anschliessen, sind folgende:

No. 1. Pilidium; **Metschnikoff**, Entwickelung der Echinodermen und Nemertinen, Mémoires de l'Académie Imp. des sciences Pétersbourg, VII. Série, Tom. XIV, Taf. IX, Fig. 8.

No. 2. Müller'sche Larve; **Lang**, Polycladen (Fauna und Flora des Golfes von Neapel, XI. Monographie) Taf. **XXXIX, Fig. 4, 5, 6.**

No. 3. Trochophora von Polygordius; **Hatschek**, Studien über Entwickelungsgeschichte der Anneliden, Arbeiten aus dem zoolog. Institut in Wien, Band I, Heft III, Taf. XXVII, Fig. 34.

No. 4. Trochophora von Polygordius, späteres Stadium; ebenda Taf. XXIV, Fig. 23.

No. 5. Trochophora eines Serpuliden; **Hatschek**, Entwickelung von Eupomatus, Arbeiten aus dem zoolog. Institut in Wien, Band VI, Heft I, Taf. XIII, Fig. 52.

No. 6. Trochophora von Teredo; **Hatschek**, Entwickelung von Teredo, Arbeiten aus dem zoolog. Institut in Wien, Band III, Heft I, Taf. II, Fig. 21—24.

No. 7. Trochophora von Pedicellina echinata; **Hatschek**, Embryonalentwickelung und Knospung der Pedicellina, Zeitschrift für wissenschaftl. Zoologie, Band XXIX, Taf. XXIX, Fig. 26.

No. 8. Auricularia von Holothuria; **Selenka**, Zur Entwickelung der Holothurien, Zeitschrift für wissenschaftliche Zoologie, Band XXVII, Taf. X.

No. 9. Tornaria von Balanoglossus; **Johannes Müller**, Ueber die Larven und die Metamorphose der Echinodermen, 4. Abhandlung. Abhandlungen der Berliner Akademie 1852.

Die Herren Professoren **Hatschek** in Prag, **Selenka** in Erlangen und **Lang** in Zürich hatten die Freundlichkeit, die Modelle, welche sich an ihre Arbeiten anschliessen, einer genauen Prüfung zu unterziehen. — Herr Prof. Elias **Metschnikoff** in Odessa hatte die Güte, die Modelle von Pilidium und Tornaria zu controliren.

Figure 114 Friedrich Ziegler published catalogues ["Prospectus"] in order to advertise his portofolio of wax models. On a market with several competitors, Ziegler's models gained authoritiy since they were always produced in cooperation with a respected scientist. The pelagic larvae of series no. 30 (F Ziegler 1893, page 35) were produced together with Berthold Hatschek and four other scientists.

4 Discussion

4.1 Hatschek, the (almost) secret 3D author

It is very notable that (almost) no evidence of Berthold Hatschek's activities as 3D author was retrieved during this project. Exceptions are the manufacturer's catalogues and rare short reviews (see Figure 147). There are no clues about Hatschek's involvement in wax modelling in his personnel file held at the Austrian State Archives[22], in his letters[23,24] to Ernst Haeckel (1876 – 1918) held at the Ernst-Haeckel-Haus in Jena or in the obituary written by Hatschek's former student Otto Storch (Storch 1950). This absence of information may be seen as an indication that authoring widely distributed models for teaching purposes was not perceived as relevant for a zoologist's career – or at least not as important as publishing in print and 2D (see Figure 144).

Contrary to this, Hatschek's contemporary Wilhelm His viewed sectioning, reconstructing and modelleling as essential processes and activities in embryology (Hopwood 2002). It is not known whether Berthold Hatschek was modelling himself as part of the theory building process, for instance in clay, in order to understand his study objects better. It remains obscure whether modelling was an activity that he suggested to his students or if he used (his own or other) wax models during lectures and practical courses.

4.2 Ziegler's series no. 30: pelagic larvae

Ziegler's series no. 30 "Marine Larven" [marine larvae] consists of nine wax models. They depict pelagic organisms early in their ontogeny that "differ very markedly in form, in structure, and in habitats from the adult" (Marshall 1891, page 71). These developmental stages of invertebrates were first published around 1886 and can be still found in Ziegler's catalogue from 1912. Amongst other Ziegler wax models, the marine larvae were presented at the World Exhibit in Chicago in 1893 (Ziegler 1912; Ziegler 1893; Hopwood 2002; Marshall 1891). In 1887, August Weismann praised this series in a short note[25] in the "Zoologischer Anzeiger" (Weismann 1887).

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[22]Personnel file of Berthold Hatschek, held at Österreichisches Staatsarchiv; AVA Unterricht allgemein (1848-1940); Universität Wien, Philosophie L-N; 902, Faszikel Nummer 865, Sign. 4G.

[23] About three dozen letters are held at the archive of the Ernst-Haeckel-Haus in Jena (Bestand A, Abt. 1, Nr. 1808). Most of them are written by Berthold Hatschek and addressed to Ernst Haeckel; furthermore there are letters concerning Berthold Hatschek's estate. These letters are written by Hatschek's former student Wilhelm Marinelli und Hatschek's daugther Augusta Dessauer who survived the Holocaust and kept vivid memories of her father's friendship with Ernst Haeckel.

[24] A letter that is kept at the Wienbibliothek at Vienna's Rathaus (former Wiener Stadt- and Landesbibliothek; call number 90.682) documents Hatschek's admiration for Haeckel's ideas. It was sent in November 1896, when Hatschek was, after about ten years of working in Prague, about to become professor at the University of Vienna: "Ich hoffe in Wien etwas von Ihrem Geiste in der Zoologie zur Geltung zu bringen, und ich hoffe auch dass Sie durch meine weitere Thätigkeit mich würdig befinden, zu Ihren Schülern zu zählen." More Haeckel letters and post cards (to Marie Eugenie delle Grazie): see call numbers 90.690 – 90.689

[25] "Vielleicht ist manchen Fachgenossen ein Dienst damit erwiesen, wenn ich auf die neuen Wachsmodelle der verschiedenen pelagischen Larvenformen aufmerksam mache, welche Herr Dr. Ziegler hier in recht

Figure 115 Ziegler's series no. 30, as shown in Ziegler's catalogue from 1912, represents the research results of five scientists, including Berthold Hatschek's Trochophora studies (Friedrich Ziegler 1912, page 30). The old series number was XX. (Hopwood 2002) At the ZCUV, five of these "invertebrate pelagic larvae" are still held, i.e. numbers 2, 3, 4, 5, 7 and 9.

The larvae models are approximately 10 to 12 centimetres high and medially cut in order to display the right hand side of the animals' inner organisation. Magnification is about 100 to 500 times (Marshall 1891). As in the *Amphioxus* wax models a colour code denotes ectodermal (bluish), entodermal (reddish) and mesodermal structures (yellowish, brownish). The wax models were "mass products" that looked similar, yet not the same since the finishing was handcrafted. This is clearly visible, for instance, when comparing the individual paintings of the ciliary structures (Stremmel 2006; Hopwood 2002).

Five of the nine marine larvae of Ziegler's series no. 30 were authored by Berthold Hatschek. Hatschek's direct involvment and quality control is documented for instance in Ziegler's catalogue (Ziegler 1893) and the "Zoologischer Anzeiger" (Wiedersheim 1883).

The remaining scientific authors of this series were the well-known professors Arnold Lang, Ilja Metschnikoff, Johannes Müller and Emil Selenka; they contributed one larva each. Their respective print publications had been published between 1852 and 1885. No other Ziegler series had such a large consortium of scientific authors and displayed such a wide systematic spread.

Figure 116 Ziegler's complete series no. 30. On the right: a previously damaged Trochophora of *Teredo* after professional restoration. This image, taken at Hessisches Landesmuseum Darmstadt by Jennifer Winkler (née Stremmel), is used with permission of the author (Stremmel 2006).

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passender Auswahl und in vortrefflicher Ausführung angefertigt hat. Die Serie von acht Typen ist wohl geeignet, eine lebendige Anschauung dieser Entwicklungsformen zu geben, und eignet sich gut sowohl zur Demonstration in der Vorlesung, als besonders auch zur Aufstellung in einer Instituts-Sammlung. Freiburg in Br., 4. April 1887. Weismann"

Model number 1:	**Pilidium**[31] **Larva of the Nemertean**[32] ***Cerebratulus*** (ribbonworm) after Ilja Metschnikoff[33] (1845-1916) (Metschnikoff 1869)
Model number 2:	**Mullerian Larva [Müller'sche Larve] of the Turbellarian**[34] ***Yungia aurantiaca*** (parasitic flatworm) after Arnold Lang (1855-1914) (Lang 1884)
Model number 3:	early **Trochophora of the Polychaete *Polygordius*** after Berthold Hatschek (1854-1941) (Hatschek 1878)
Model number 4:	later **Trochophora of the Polychaete *Polygordius*** after Hatschek (Hatschek 1878)
Model number 5:	**Trochophora of the serpulid Polychaete *Eupomatus unicatus*** after Hatschek (Hatschek 1885)
Model number 6:	**Trochophora of the Bivalve *Teredo*** ("ship worm") after Hatschek (Hatschek 1880)
Model number 7:	**Trochophora of the Endoproct *Pedicellina echinata***[35] after Hatschek (Hatschek 1877)
Model number 8:	**Auricularia of the Echinoderm *Holothuria tubulosa*** after Emil Selenka (1842-1902) (Selenka 1876)
Model number 9:	**Tornaria of the Enteropneust *Balanoglossus*** after Johannes Müller (1801-1858) (Müller 1852)

Table 1 The larval types of Ziegler's series no. 30.

[31] Hatschek considered the Nemertini (alternative term for Nemertea) to be Autoscolecida within the Zygoneura (Hatschek 1888-1891, page 395ff.). Furthermore, to him, the ciliated Pilidium larva represented an ancient developmental mode which therefore was not conserved anymore in all developing Nemertini.

[32] Nota bene: Weisker sold two wax models of a developing *Ramphogordius*, formally belonging to the Nemertea, but strangely showing beginning segementation. In Vienna, these ribbonworm models were re-labelled as "*Polygordius*", probably to demonstrate Trochophora morphology in annelids.

[33] Metschnikoff's work on phagocytosis and host resistance was based on the study of mesodermal lineages and metazoan ancestry. In his case, comparative embryology ultimately lead to the award of the nobel prize in 1908 (Hopwood 2009).

[34] Hatschek stated about the plathyhelminthic Turbellaria that the flatworm larvae ("Platodes") would only reach the Protrochula stage which he considered a predecessor of Trochophora (Hatschek 1888-1891, page 306ff).

[35] Hatschek tentatively put the Endoprocta within the zygoneural Scolecida – based on their larval morphology (Hatschek 1888-1891, page 370ff).

4.2.1 Hatschek's five Trochophora models

The Ziegler wax model company worked closely with scientists in order to produce high-quality models (Hopwood 2002; Hopwood 2004). Berthold Hatschek was one of those collaborators from academia and therefore managed to publish his concepts of evolutionary embryology in 3D. From 1882, his *Amphioxus* developmental series was produced by the "plastic publisher" Ziegler. Shortly thereafter, the epitome of Hatschek's Trochophora research was captured in wax and became part of the nine piece series "Marine Larven". Six of them are still held at the ZCUV, see page 41.

Hatschek's corresponding print publications about Trochophora larvae of various species were published between 1877 and 1885 (Hatschek 1880; Hatschek 1877; Hatschek 1878; Hatschek 1885) In the wax model catalogue, Ziegler lists these publications (see Figure 114) and even refers to the corresponding illustrations that served as 2D templates and reference for the 3D models.

Unfortunately, it could not be determined how the interaction between Ziegler and Hatschek evolved and how intense it became. However there is a note in the catalogue that it was Heinrich Ernst Ziegler, zoologist and brother of the owner Friedrich Ziegler who selected the larval organisms of series no. 30 that made it into the production (Ziegler 1893, page 35). The catalogue also states that Hatschek, at the time professor in Prague, had inspected the wax models. Therefore, it can be assumed that Hatschek had given his approval to the prototypes before serial production and marketing. The same is true for the other scientific authors of series no. 30.

Since Hatschek and Ziegler cooperated twice during the 1880s, amouting to an output of 25 *Amphioxus* models and five Trochophora models, it is likely that Hatschek was content with the overall outcomes. Different sources indicate that Berthold Hatschek had interest in the popularisation and public discussion of science and various educational issues (Hatschek 1898; Hatschek 1906; Hatschek 1896).

It is not clear how many pieces were sold or whether Hatschek yielded any financial profits. However Hatschek's marine larvae supposedly were widely distributed as teaching aids and therefore might have reached fairly large audiences since the Trochophora models can still be found many university collections and were advertised over several decades in Ziegler's catalogues. This indicates that Ziegler's series no. 30 was successful for a long time on the market of teaching aids.

Model number 3: Earlier Trochophora of *Polygordius*

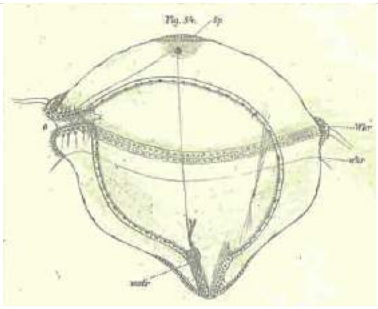

Figure 117 Earlier Trochophora, illustration by Berthold Hatschek, figure 34 (Hatschek 1878)

Figure 118 Earlier Trochophora wax model of *Polygordius*, held at the ZCUV, shortly after hatching. With apical plate (ectodermal, blue) and intestine (entodermal, red). Important mesodermal structures (yellow) are missing in this model, but can be seen in better conserved specimens (Stremmel 2006) (Marshall 1891): protonephridial excretion channels, i.e. head kidney [Kopfniere] and paired mesodermal bands [Mesodermstreifen] for later formation of "Ursegmente". Hatschek refused to use the term "Keimstreifen", considering it not to be precise enough (Hatschek 1878, page 5).

Figure 119 Earlier Trochophora of *Polygordius*, external view with the characteristic ciliary bands, i.e. preoral double prototroch and postoral single mesotroch (ectodermal). Ocelli (eye spot) are not visible in this picture.

Model number 4: Later Trochophora of *Polygordius*

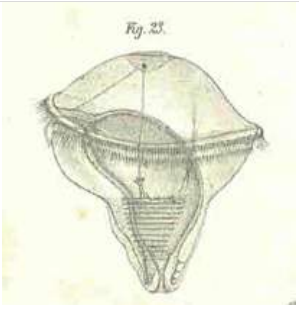

Figure 120 Later Trochophora, illustration by Berthold Hatschek, figure 23 (Hatschek 1878)

Figure 121 Later Trochophora wax model of *Polygordius*, held at the ZCUV, displaying nerves (ectodermal, black wire), digestive tract (red), head kidneys and extended mesodermal bands (yellow). Muscles are missing in this model.

Figure 122 Later Trochophora with ectodermal prototroch and metatroch [Wimpernkränze]. Elongation and segment formation are visible "by which the vermiform shape of the adult is gradually acquired" (Marshall 1891, page 76).

Model number 5: Trochophora of *Eupomatus*

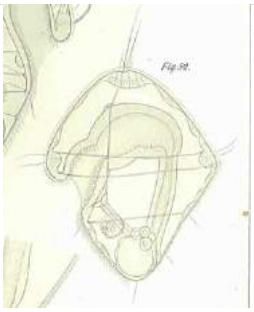

Figure 123 Hatschek's illustration of *Eupomatus unicatus*, figure 52 (Hatschek 1885)

Figure 124 Trochophora wax model of *Eupomatus unicatus*, held at the ZCUV, with apical plate, digestive tract, anal vesicle [Analblase], apical plate (ectodermal), otocysts or auditory vesicles [Gehörbläschen]. Not visible in this specimen are mesodermal cells and protonephridial structures also known as head kidneys [Kopfniere].

Figure 125 Trochophora model of *Eupomatus unicatus* with ciliary tufts, apical plate, ciliary bands and ocelli.

Model number 6: Trochophora of *Teredo*

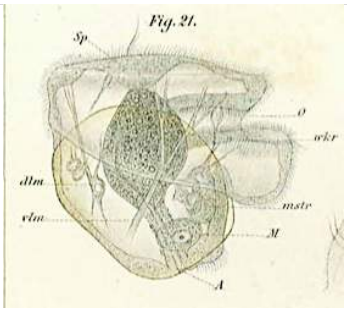

Figure 126 Hatschek's illustration Teredo, figure 21 (Hatschek 1880)

Figure 127 This model is not held at the ZCUV: Trochophora of *Teredo*, with apical plate and ganglion, digestive tract, preoral and postoral ciliary bands, mesodermal cell masses (yellow) and the shell at the dorsal end. This image was taken in the course of restoration works at Hessisches Landesmuseum Darmstadt by Jennifer Winkler (née Stremmel) and is used here with her permission (Stremmel 2006).

Figure 128 External view of "Muschellarve" *Teredo* (image used with permission of Stremmel 2006).

Model number 7: Trochophora of *Pedicellina echinata*		
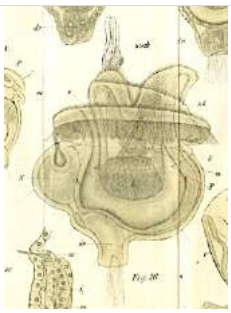		
Figure 129 Hatschek's illustration of *Pedicellina* (Hatschek 1877), figure number 26	Figure 130 Trochophora wax model of *Pedicellina echinata*, held at the ZCUV, displaying mesodermal cells, digestive tract with "liver" (red), and an (sensory) apical gland [Kittdrüse] (blue), bud [Knospe], mesodermal cells and excretory organs (yellow)	Figure 131 *Pedicellina* with apical plate, tuft, ciliary bands, ectodermal folds

Table 2 Wax models of Trochophora larvae, produced by Ziegler's "Atelier für wissenschaftliche Plastik" contrasted with their corresponding illustrations from print publications, authored by Berthold Hatschek. All models are held hat the ZCUV (unless stated otherwise).

4.2.2 More marine larvae by Ziegler

The marine organisms of series no. 30 were not the first larvae of the sea in Ziegler's portfolio. A variety of Echinoderm larvae types (12 models, e.g. Pluteus, Bipinnaria, Auricularia) and starfish larvae (11 stages of *Asterina*) had been published earlier (Hopwood 2002; Ziegler 1893; Ziegler 1912).

Figure 132 Ziegler's larvae of Echinoderms (Friedrich Ziegler 1912, page 30), first published around 1855. The old series number was II. (Hopwood 2002) This series is held at the ZCUV; see page 42 .

Figure 133 Ziegler's starfish development (Friedrich Ziegler 1912, page 31). The old series number was III, the models were published first in 1882 (Hopwood 2002). This series is held at the ZCUV; see page 43.

There are two more series representing marine larvae that were probably both published after series no. 30. The author of these series was Heinrich Ernst Ziegler (1858–1925), renowned zoologist and brother of the second company owner Friedrich Ziegler. These series represent the development of the sea urchin *Echinus* (15 stages, series no. 31a) and the crinoid *Ophiotrix fragilis* (7 stages, series no. 32a) (Hopwood 2002; Stremmel 2006).

4.2.3 Framework of Hatschek's Trochophora research

In the course of the analysis of the broader context of Berthold Hatschek's early work on Trochophora and its subsequent 2D and 3D publications, several typical features were detected. Selected sources for the following brief overview (i. e. all bullet points below) are: Hopwood 2009; Jahn 2000; Hoßfeld et al. 2016; Müller and Nemeschkal 2015.

- Hatschek had great interest in **marine organisms** and relatively easy access to sea animals, for instance through the Zoological Research Station in Trieste [k. k. Zoologische Station in Triest] that was supported by the University of Vienna and whose co-founder was Hatschek's teacher Carl Claus.
- Already during his student years, spending time in Leipzig and Jena, Hatschek had developed strong links to leading researchers in **Germany. This country was the epicentre** of morphological and embryological research during the 19th century and its corresponding rich visual culture.
- Hatschek's research was facilitated by better **microscopes** and new techniques for **fixating and staining** small research objects such as fragile marine organisms. Furthermore, the invention of the **microtome** enabled the cutting of specimens to become substantially faster. The serial sectioning of embryonic bodies made the exact reconstruction of morphologies feasible (e.g. Hopwood 1999).
- Searching for **evolutionary evidence in embryonic development** had become a very common approach during the last decades of the 19th century. Evolutionary theory had permeated zoology, and ontogenetic morphologies were meant to provide proof for the theory of descent. Proponents of this strategy were for instance Ernst Haeckel (who developed the controversial Gastraea[36] Theory about the monophyletic origin of all Metazoa) and Alexander Kowalevsky; they created "evolutionary taxonomies guided by the study of individual development and separated from the study of the organism's function and its relation to the external environment" (Nyhart 1995b, page 168).

[36] Ernst Haeckel's "Main types of cleavage and gastrulation" were published by Ziegler in 1876; the series comprised 22 models (Hopwood 2002).

- Hatschek's early Trochophora studies and the subsequent phylogenetic theories were strongly influenced by Haeckel's "law" of recapitulation. According to Haeckel's concept, embryos of more "highly" developed taxa progress, as they move through their own ontogeny, through their ancestors' adult phases in a rather linear manner. Therefore, his models may be seen as embodiments of theory rather than mere illustrative teaching aids (please also see page 60).

4.2.4 Fishing for evidence[37]

Trochophora larvae had an enormous importance throughout Berthold Hatschek's career. By publishing this larval type in wax and 3D, Hatschek's concept of Trochophora became a more and more common view to students, researchers and possibly even a wider (lay) audience.

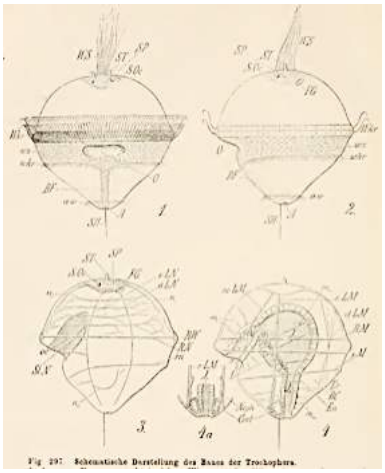

Figure 134 Protagonist of Hatschek's research: Trochophora, as depicted in his incomplete textbook. (Hatschek 1888-1891, page 308)

Being the tangible embodiments of Hatschek's extensive 2D publications, the wax models were to communicate in brief: Primordial and modified Trochophora larvae are key organisms for reconstructing phylogenies. They are essential for understanding the evolutionary relationships of annelids, molluscs and further invertebrate groups – by tracing homologies in the course of development.

In short, bringing forward arguments from ontogeny and morphology, Hatschek ultimately organised the bilaterian Metazoans into three major groups: Ambulacralia, Chordonii and Zygoneura. The latter comprised the majority of the invertebrates and, as Hatschek postulated, shared a Trochophora-like ancestor by

[37] According to Hatschek, evidence for the theory of descent could be found in morphology, i.e. comparative anatomy and embryology. "Für die Descendenztheorie liefern noch eine Reihe von Beweisen: 1)Die Paläontologie ... 2)Die Thier- und Pflanzen-Geographie ... 3)Die Morphologie (vergleichende Anatomie und Embryologie der Thiere und Pflanzen)." (Berthold Hatschek 1888-1891, page 18)

the name of "Trochozoon". Despite different current terminology the broad outline of Hatschek's systematic framework has in general stood the test of time.

But back to the start: Published in 1878, "Studien über Entwicklungsgeschichte der Anneliden. Ein Beitrag zur Morphologie der Bilaterien" (Hatschek 1878) was a milestone in Berthold Hatschek's work. Having received his doctorate for a thesis about Lepidoptera embryology just the year before, he now meticulously described the development of the aquatic earthworm *Criodrilus* (from the Danube wetlands around Linz) and the marine polychaete *Polygordius* (caught in the Adriatic Sea near Triest) and its Trochophora larva.

The pelagic larvae of *Polygordius* carry two ciliary bands. These so-called trochophores, situated anterior and posterior to the mouth opening, presumably serve locomotion, stabilisation and nutrition. Due to the prominent structure Hatschek re-named[38] this larval type "Trochophora" (derived from Greek: "wheel-carrier") in his richly illustrated essay.

On the grounds of its larval morphology Hatschek declared *Polygordius* to be primitive[39]. He suggested a close relationship between *Polygordius* and the hypothetical ancestor[40] by the name of "Trochozoon"; this term that was also coined by Hatschek. According to his "Trochozoon Theory" the ancient Trochozoon would have carried its trochophores throughout its complete ontogeny, quite unlike *Polygordius* that featured this plesiomorphic structure only at the beginning

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[38] It was the Swedish zoologist Sven Ludvig Lovén who had described this larval type first in 1840. The ancient larval type [uralte Stammform] had since been known as "Lovén's Larva" [Lovén'sche Larve] or Cephalotrocha. The British zoologist E. Ray Lankester later used the term "Trochosphaera". Both researchers got acknowledged by Berthold Hatschek (Hatschek 1878, page 23 and page 80).

[39] Hatschek denotes, for example, the segmentation of *Polygordius* as ancestral feature (Hatschek 1878, page 58ff): "Die Segmentirung des *Polygordius* ist ferner in der äusseren Körperform noch nicht zur Ausprägung gekommen, sie ist nur auf die inneren Organe beschränkt. Auch hierin erkennen wir ein ursprünglicheres Verhalten, denn die Segmentirung tritt bei allen Anneliden auch ontogenetisch zuerst nur als eine innere, anfangs nur das Mesoderm (Ursegmente) betreffende, auf, und erst später erstreckt sie sich auch auf die äussere Form des Körpers. Auch bei den einzelnen Organen von *Polygordius* finden wir vielfach Verhältnisse als bleibende vor, welche bei den meisten Chaetopoden als vorübergehende Entwicklungsstadien durchlaufen werden"; "Aus den hier angeführten Verhältnissen ergibt sich, dass *Polygordius* nicht etwa eine durch Rückbildung vereinfachte, sondern die ursprünglichste, der gemeinschaftlichen Stammform der Anneliden am nächsten stehende Gattung repräsentirt."

[40] Hatschek's "invention" of the Trochozoon might remind of the "Gastraea", Ernst Haeckel's hypothetical ancestor of all metazoans. At this time, Hatschek supported Haeckel's monophyletic theory and wrote in his report on *Teredo* development (Hatschek 1880): "As long as we view the construction of phylogenetic stages only as an embodiment of our abstractions and continually remind ourselves that its significance is predominantly heuristic, we can adopt without fear a series of the hypothetical forms set out by Haeckel" (cited after Nyhart 1995b, page 198).

of its life. Furthermore, Hatschek claimed that the Trochozoon would have been very similar to the recent Rotatoria[41] (now: Rotifera).

After the crucial publication on the Trochophora of *Polygordius*, Berthold Hatschek continued his work on marine larvae. In several publications to come, he claimed that homologous Trochophora larvae are present in Annelids, Molluscs and several "Vermes", e.g. (Hatschek 1885; Hatschek 1880), pointing to the common ancestor Trochozoon. As he consequence, he linked the phylogenies of these major groups closely together.

Ultimately, Hatschek's Trochozoon Theory gave rise to the generation of the Zygoneura[42], a major clade of bilateral metazoans in Hatschek's "Zoological System" [Zoologisches System] (Hatschek 1888-1891), amended in 1911 to the "New Zoological System" [Neues Zoologisches System] (Hatschek 1911). In short, the Zygoneura comprised the following groups: Scolecida ("Vermes" without Annelida), Articulata (Annelida, Onychophora, Arthropoda); Tentaculata (Phoronida, Bryozoa, Brachiopoda) and Mollusca.

Despite altered terminology[43], e.g. Grobben's "Protostomia" instead of Hatschek's "Zygoneura" and Grobben's "Deuterostomia" instead of Hatschek's "Ambulacralia" and "Chordonii" (Nielsen 2010; Grobben & Heider 1911), Hatschek's phylogenetic vision is still of relevance. For instance, the relatively new Lophotrochozoa concept[44] based on molecular data is in accordance with (several of) Hatschek's morphological and embryological observations, as Andreas Wanninger reported as recently as 2015. Wanninger also valued Hatschek's "comparative evolutionary and developmental approach as an important intellectual forerunner of today's EvoDevo" (Wanninger 2015a, page 2).

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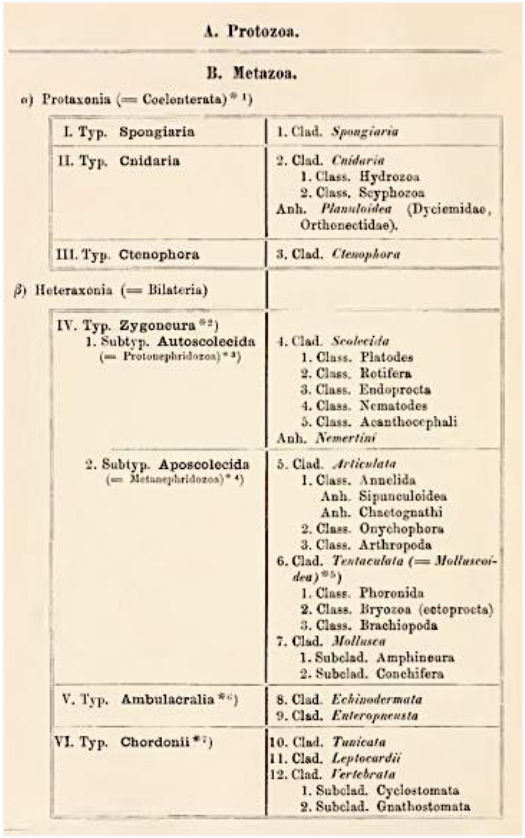
[41] "Wir werden weiterhin nachweisen, dass die Anneliden von einer Rotatorien-ähnlichen Stammform abzuleiten sind."; "Die Homologie der Wimperapparate der Rotatorien und der Trochophora der Anneliden ist durch die Lage, den Bau, die Function, und die Entwicklungsgeschichte dieser Organe unzweifelhaft erwiesen." (Hatschek 1878, page 74 and page 84)

[42] The clade's name refers to the nervous system with paired ("zygo") nerve chords: "Der Name Zygoneura, Paarnervige, ist nach den paarigen Längsnerven gewählt, die entweder in ganzer Länge oder wenigstens im Bereich der Schlundkommissur zeitlebens getrennt bleiben." (Hatschek 1888-1891, page 41)

[43] Much to Hatschek's dismay, Grobben introduced the term "Protostomia", basically replacing the "Zygoneura". "Nach altem Herkommen gilt der Name, der für eine richtig abgegrenzte und nach richtigen Prinzipien bekannte Gruppe zuerst eingeführt wurde und er darf nicht willkürlich geändert werden." (Berthold Hatschek 1911, page 30). Grobben, professor at the University of Vienna and head of the First Zoological Institute, replied to Hatschek's accusations. (Grobben & Heider 1911)

[44] Briefly, the Lophotrochozoa consist of two large protozoan divisions, the Lophophorata and the Trochozoa respectively. The Trochozoa include the following phyla: Mollusca, Annelida, Nemertea and Sipuncula. The Lophophorata (sometimes called Tentaculata) include the Phoronida, Bryozoa and Phoronida.



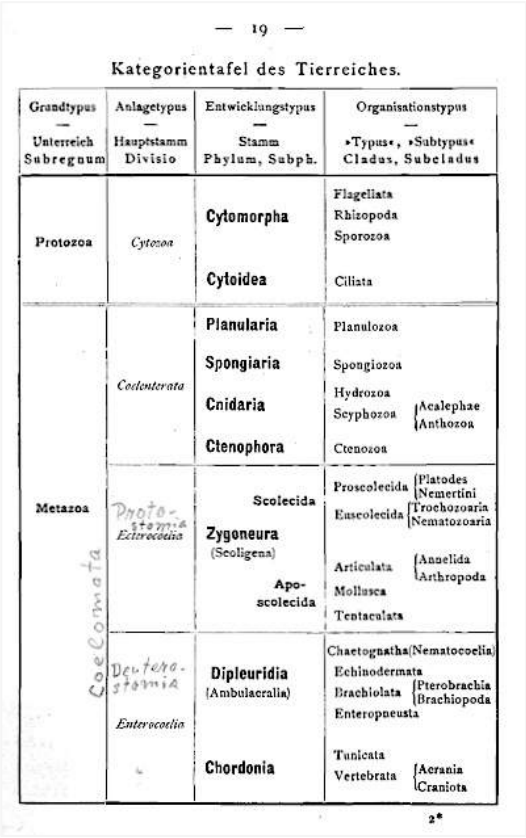
A. Protozoa.

B. Metazoa.

α) Protaxonia (= Coelenterata) *1)

I. Typ. Spongiaria	1. Clad. *Spongiaria*
II. Typ. Cnidaria	2. Clad. *Cnidaria* 1. Class. Hydrozoa 2. Class. Scyphozoa Anh. *Planuloidea* (Dyciemidae, Orthonectidae).
III. Typ. Ctenophora	3. Clad. *Ctenophora*
β) Heteraxonia (= Bilateria)	
IV. Typ. Zygoneura *2) 1. Subtyp. Autoscolecida (= Protonephridiozoa) *3)	4. Clad. *Scolecida* 1. Class. Platodes 2. Class. Rotifera 3. Class. Endoprocta 4. Class. Nematodes 5. Class. Acanthocephali Anh. *Nemertini*
2. Subtyp. Aposcolecida (= Metanephridiozoa) *4)	5. Clad. *Articulata* 1. Class. Annelida Anh. Sipunculoidea Anh. Chaetognathi 2. Class. Onychophora 3. Class. Arthropoda 6. Clad. *Tentaculata (= Molluscoidea)* *5) 1. Class. Phoronida 2. Class. Bryozoa (ectoprocta) 3. Class. Brachiopoda 7. Clad. *Mollusca* 1. Subclad. Amphineura 2. Subclad. Conchifera
V. Typ. Ambulacralia *6)	8. Clad. *Echinodermata* 9. Clad. *Enteropneusta*
VI. Typ. Chordonii *7)	10. Clad. *Tunicata* 11. Clad. *Leptocardii* 12. Clad. *Vertebrata* 1. Subclad. Cyclostomata 2. Subclad. Gnathostomata

Figure 135 Hatschek's zoological system (1888), prominently featuring the Zygoneura, Hatschek's new clade (Hatschek 1888-1891, page 40).



— 19 —

Kategorientafel des Tierreiches.

Grundtypus — Unterreich Subregnum	Anlagetypus — Hauptstamm Divisio	Entwicklungstypus — Stamm Phylum, Subph.	Organisationstypus — »Typus«, »Subtypus« Cladus, Subcladus
Protozoa	*Cytozoa*	Cytomorpha	Flagellata Rhizopoda Sporozoa
		Cytoidea	Ciliata
Metazoa	*Coelenterata*	Planularia	Planulozoa
		Spongiaria	Spongiozoa
		Cnidaria	Hydrozoa Scyphozoa {Acalephae, Anthozoa}
		Ctenophora	Ctenozoa
	Proto-stomia *Ecoelomata*	Scolecida	Proscolecida {Platodes, Nemertini} Euscolecida {Trochozoaria, Nematozoaria}
		Zygoneura (Scoligena)	Articulata {Annelida, Arthropoda}
		Apo-scolecida	Mollusca Tentaculata
	Deutero-stomia *Enterocoelia*	Dipleuridia (Ambulacralia)	Chaetognatha (Nematocoelia) Echinodermata Brachiolata {Pterobrachia, Brachiopoda} Enteropneusta
		Chordonia	Tunicata Vertebrata {Acrania, Craniota}

2*

Figure 136 Hatschek's new zoological system with amendments, published in 1911 (Hatschek 1911, page 19). Hatschek stressed the importance of fundamental "Entwicklungstypen" [fundamental types] for his phylogenies – versus Cuvier's "Organisationstypen" [organisational types] (Hatschek 1911, page 23).

4.2.5 Haeckel, Hatschek and Trochophora

In "Studien über Entwicklungsgeschichte der Anneliden. Ein Beitrag zur Morphologie der Bilaterien" (Hatschek 1878) Berthold Hatschek hardly ever mentioned his "adored friend and master[47]" Ernst Haeckel. However, Hatschek's approach in the aforementioned research report often was in accordance with Haeckel's biogenetic "law" and the strong intertwinement of ontogeny and

[47] Hatschek adressed Haeckel as "innigstverehrter Freund und Meister" (letter dated May 1st, 1911). Haeckel and Hatschek corresponded from 1876 on. Hatschek had been visiting Haeckel's lectures in Jena and met him for the first time in 1877 in Trieste. Haeckel supported Hatschek on numerous occasions. According to Hatschek's daughter Augusta Dessauer, they were friends and even spent holiday time together, see Uschmann 1959; Krauße 1998; letters at Ernst-Haeckel-Haus archives, Best. A. Abt. 1. Nr. 1808.

phylogeny[48]. The stepwise recapitulation[49] of a more or less linear phylogeny in the course of ontogeny has, over the years, aroused criticism by many (Barnes 2014; Gilbert 2014; Hoßfeld et al. 2016).

Hatschek, too, admitted that his pieces of evidence and the subsequent phylogenetic theories were associated with a certain amount of unlikelihood[50] since his concepts could not be proven straightforwardly[51]. In his textbook (Hatschek 1888-1891), he also critically commented on the pitfalls of comparative ontogeny. Nevertheless he drew his conclusions from a relatively small number of case studies, i.e. a few hand-picked marine larvae. Unlike some of his influential contemporaries, Hatschek, at least in his early works, was not so much interested in mechanical constraints as was for instance Wilhelm His (although there is a section in his *Amphioxus* paper on "Mechanics of developmental processes", Hatschek 1881, page 45ff.) or environmental conditions that might as well govern the unfolding of an embryo.

Müller & Nemeschkal (2015) reported that, around 1900, Vienna's zoological research kept moving further away from Haeckel's concept of recapitulation. Instead, mechanistic analyses of developmental processes[52] were favoured, and

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[48] In 1866, Ernst Haeckel writes in "Generelle Morphologie" (edition from 1906): "Die Ontogenie oder Entwickelungsgeschichte der physiologischen Individuen ist aber unzertrennlich und auf das innigste verbunden mit der Phylogenie der Entwicklungsgeschichte der genealogischen Stämme (Phylen). Jedoch haben in der ganzen Biologie kaum zwei Wissenschaftszweige so weit voneinander entfernt gestanden, als die Ontogenie und die Phylogenie." (Haeckel 1906, page 167)

[49] "Die ontogenetische Reihe ist auf die phylogenetische Reihe der Endstadien zurückführbar" (page 22); "Die phylogenetische Veränderung geht also in den meisten Fällen so vor sich, dass eine Hinzufügung an das Ende der ontogenetischen Formenreihe erfolgt" (pages 23 and 24); "Die Methode der vergleichenden Ontogenie ist eine Erweiterung der vergleichend anatomischen Methode (Feststellung von Homologie und Anatomie) durch Anwendung derselben auf Formenreihen" (page 26); "Der metamerische Bau kommt zuerst durch Wiederholung der inneren Organe zum Ausdruck. Bei *Polygordius* bliebt er auf dieser Stufe der Entwicklung stehen, bei den anderen Anneliden beginnt sich die Gliederung auch in der äusseren Körperform, durch segmentweise Einschnürungen und durch die äusseren Anhänge und Gliedmassen, auszuprägen" (page 72). (Hatschek 1878)

[50] "Die Ergebnisse der vergleichenden Ontogenie haben stets nur den Werth von Wahrscheinlichkeitsschlüssen … Die relative Sicherheit … hängt nur von der Menge der Prämissen und von der Schärfe des Schliessens ab."; "Die Uebereinstimmung einer entwickelten Thierform mit dem Larvenstadium einer anderen Classe – eine für die Entwicklungstheorie bedeutungsvolle Erscheinung – geht hier so weit, dass man die Trochophora der Anneliden, wenn sie auf dieser Entwicklungsstufe geschlechtsreif würde, der Classe der Rotatorien einordnen müsste" (Hatschek 1878, page 26 and page 80f.)

[51] "Wie alle solche weitreichenden, experimentell nicht beweisbaren Gedankenrekonstruktionen ist auch die Trochophoratheorie Hypothese geblieben und mancherlei Einwänden unterworfen." (Storch 1950, page 288)

[52] "Eine weitere Veränderung in den Zielsetzungen der zoologischen Forschung ergab sich aus der zunehmenden Abkehr vom Studium der Embryologie als Ablesevorgang für typologisch-taxonomische Einordnungen im (rekapitulationistischen) Sinne Haeckels und der Zuwendung zur mechanistischen Analyse von Entwicklungsprozessen." (Müller & Nemeschkal 2015, page 359)

experimental embryology gained (even more) momentum. An indication of Hatschek's sympathy for this pathway is his continuous support of his former students Hans Przibram (1874–1944), Paul Kammerer (1880–1926) and the establishment of the Vivarium (also known as "Biologische Versuchsanstalt") where the roots of Vienna's Theoretical Biology lay. However Hatschek's early works that formed the basis for the 3D wax publications of *Amphioxus* (1882) and Trochophora (1886) exhibit a strong advocacy of the recapitulation concept. Embryonic homologies are the leitmotif in Hatschek's research of the 1880s.

4.3 Modelling the ancestral *Amphioxus*

Berthold Hatschek cooperated twice with Ziegler's wax model company. The first series was published from 1882 onwards and comprised 25 specimens that represented the development of the lancelet *Amphioxus* (Ziegler 1893; Ziegler 1912).

Figure 137 *Amphioxus* models based on Berthold Hatschek's illustration. This image is taken from Ziegler's 1912 catalogue (Ziegler 1912). A colour code made it easier to understand the migration of cells and the formation of germ layers, tissues and organs: grey – stages during cleavage; light blue – ectoderm (epiblast[53]); white – neural plate, neural tube; red – entoderm (hypoblast[54]); yellowish, reddish – mesoblast; crimson red – notochord

In Ziegler's catalogue from 1893, the *Amphioxus* series (no. 22) cost 130 Mark; for comparison: the development of the chicken cost 210 Mark; development of the brain convulsions in humans cost 35 Mark; the marine larvae cost 90 Mark. In a separate leaflet that was not part of the regular catalogue (Ziegler ca. 1882) Hatschek's corresponding *Amphioxus* illustrations were listed. They all stem from Hatschek's richly illustrated research report that had been published in 1881 (Hatschek 1881).

In these "Studien über Entwicklung des *Amphioxus*" (Hatschek 1881) Hatschek, then at the beginning of his career, strongly referred to the works of the Russian embryologist Alexander Kowalewksy from the 1860s and 1870s. However Hatschek did not mention Ernst Haeckel's (Hopwood 2015) preoccupation with

[53] terminology used by (Marshall 1891)

[54] terminology used by (Marshall 1891)

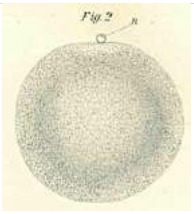
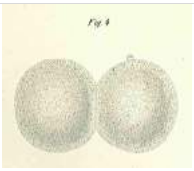
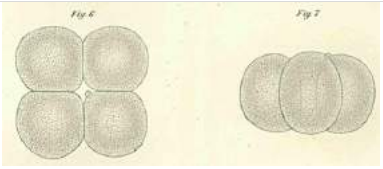
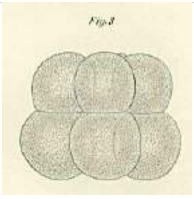
the primitive chordate *Amphioxus* – and the controversy that had arisen around Haeckel's theories[55]. To Haeckel, *Amphioxus* with its Ascidian-like development joined invertebrates and vertebrates. The lancelet ultimately provided, as a vertebrate ancestor, a key to understand the development of humans, it was "flesh of our flesh and blood of our blood'' (cited after Hopwood 2015, page 372). Haeckel's popularisation of *Amphioxus*, achieved for instance with the help of illustrations in "Natürliche Schöpfungsgeschichte", preceeded Hatschek's 2D and 3D publications by several years.

With his primarily descriptive approach Hatschek attempted to add to Kowalewsky's publications, to close some gaps, to correct several errors. Hatschek had acquired his living specimens during a 10-week-stay near Messina in 1879; he was catching, keeping, observing, illustrating and preserving *Amphioxus* developmental stages himself (Hatschek 1881). As can be seen in the wax models, the development of the germ layers and their respective tissues were of major importance to Hatschek. In the models, a special colour code was used which illustrated the becoming of ectodermal, mesodermal and entodermal structures more explicity than Hatschek's drawings alone.

The *Amphioxus* series was still advertised in Ziegler's catalogue from 1912 (Ziegler 1912). The University of Manchester devoted a long section in its "Descriptive Catalogue of Wax Models" (Marshall 1891) to these models (see Figure 1). The *Amphioxus* models still can be found in several university collections (see www.universitaetssammlungen.de). Reviewer Robert Wiedersheim classified them as highly useful and hands-on teaching aids (see Figure 147). During the 20th and 21st century other model makers produced similar *Amphioxus* series (see page 71ff.). All of this indicates that the sales of Ziegler's and Hatschek's joint *Amphioxus* series was successful in the long term. Last but not least it has to be mentioned that models of Branchiostoma – after Berthold Hatschek – are still produced today by the German company "SOMSO Modelle" (see Figure 146).

[55] For detailed information about the debate over vertebrate origins, the ascidian theory, the annelid theory, please see e.g. Bowler (1996) or Holland (2015).

4.3.1 Ziegler's *Amphioxus* series

***Amphioxus* models 1 - 7**			
Citations from: Prospectus über die Unterrichtsmodelle zur Erläuterung der Entwickelung des *Amphioxus* (Ziegler ca. 1882)	Images of specimens held at the ZCUV	Corresponding illustrations from Hatschek's *Amphioxus* publication (Hatschek 1881)	Citations extracted from: Descriptive Catalogue of the Embryological Models (Marshall 1891, page 1ff.)
"Ei mit Richtungskörper"; **model 1**			**"Ovum before fertilisation"** "The small bead on top is the polar globe."
"Zweizelliges Stadium" ; **model 2**	not held at the ZCUV		**"Two-celled stage"** "The ovum, after fertilisation, has divided, by a vertical cleft, into two halves of equal size."
"Vierzelliges Stadium"; **model 3**			**"Four-celled stage"** "By a second vertical cleft, at right angles to the first, each of the two cells of the preceding stage."
"Achtzelliges Stadium"; **model 4**	not held at the ZCUV		**"Eight-celled stage"** "By a horizontal or equatorial cleft each of the four cells of stage 3 is divided into two."

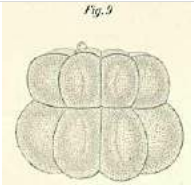
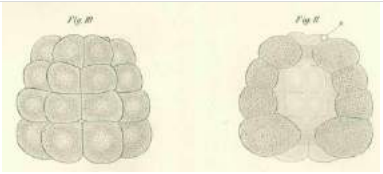
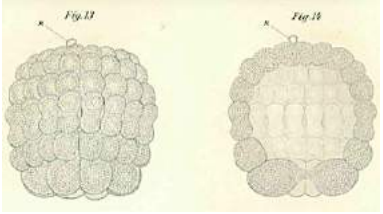
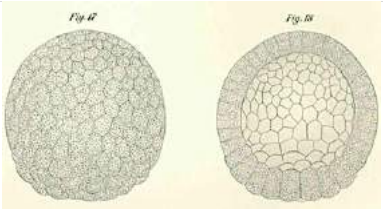
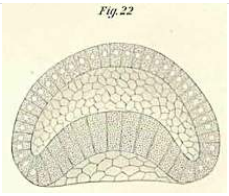
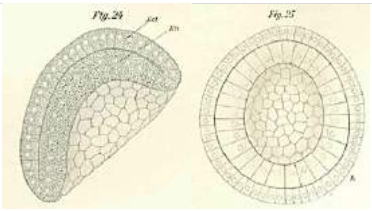
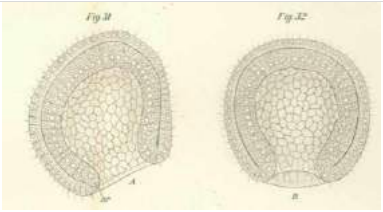
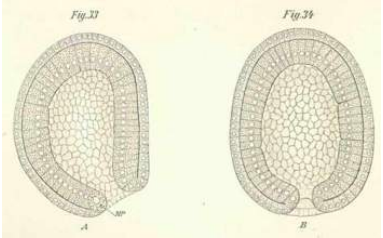
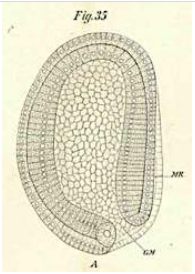
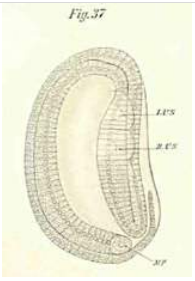
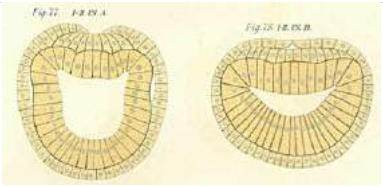
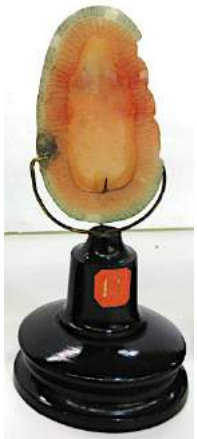
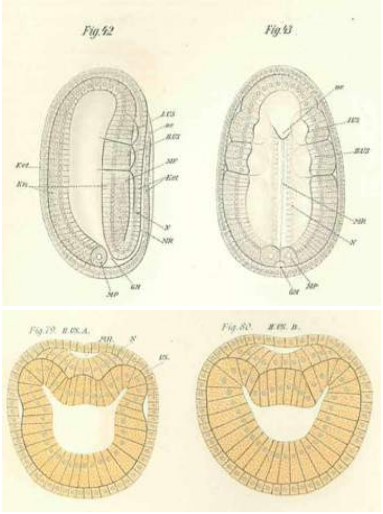
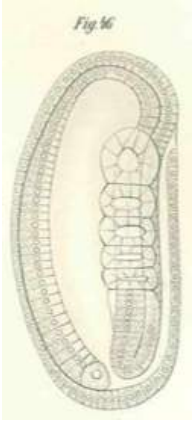
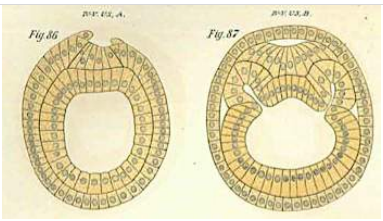
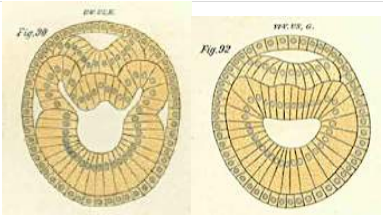
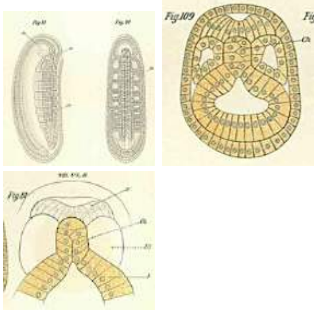
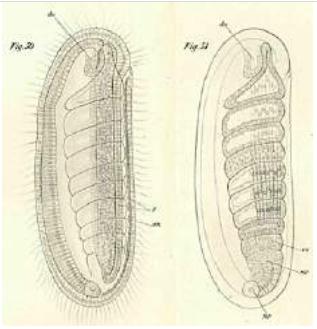
"Sechzehnstelliges Stadium"; **model 5**			**"Sixteen-celled stage"** "The embryo now consists of an upper tier of eight smaller cells, and a lower tier of eight larger cells."
"Zweiunddreissigzelliges Stadium"; **model 6**	not held at the ZCUV		**"Stage with thirty-two cells"** "The central space … is now almost closed by approximation of the cells of the upper and lower tiers respectively."
"Weiteres Furchungsstadium, halbirt"; **model 7**			**"Blastula stage"** "The segmentation cavity or blastocoel is now closed above, but is still open at its lower pole."

Table 3 *Amphioxus* development, stages 1 – 7: Cleavage. Model enlargement: 350 times

***Amphioxus* models 8 - 25**			
Citations from: Prospectus über die Unterrichtsmodelle zur Erläuterung der Entwickelung des *Amphioxus* (Ziegler ca. 1882)	Images of specimens held at the ZCUV	Illustrations from Hatschek's *Amphioxus* publication (Hatschek 1881)	Citations from: Descriptive Catalogue of the Embryological Models (Marshall 1891, page 1ff.)
"Blastula halbirt"; **model 8**			**"Completed blastula stage"** "The blastocoel is now completcly closed; the embryo being in the form of a hollow ball with a wall composed of a single layer of cells."
"Ein Stadium der Einstülpung halbirt"; **model 9**			**"Commencing gastrula stage"** "The hypoblast (red) is becoming doubled up within the epiblast (blue). The blastocoel or segmentation cavity is still of considerable size."
"Stadium der vollendeten Einstülpung halbirt"; **model 10** (2 specimens held at ZCUV)			**"Gastrula"** "The segmentation cavity is obliterated by the invaginated hypoblast coming in contact with the epiblast. The blastopore or gastrula mouth is of large size."
"Weiters Stadium der Gastrulation, rechte Hälfte"; **model 11**	not held at the ZCUV		**"Gastrula"** "The blastopore has become greatly reduced in size … it marks the posterior end of the embryo."
"Gastrula; Andeutung der Bildung der Medullarplatte und der Mesodermfalte, rechte Hälfte"; **model 12**	not held at the ZCUV		**"Completed gastrula"** "The embryo has elongated considerably, and is now egg-shaped. The blastopore has narrowed still further"

"Stadium mit Rückenfurche und erstem Ursegment, welches durch Abpräparieren des Ektoderms sichtbar gemacht ist, rechte Hälfte"; **model 13** (2 specimens held at ZCUV)			"The right half of a free-swimming embryo at the commencement of the period: part of the epiblast of the right side has been removed. The embryo is increased in length."
"Weiteres Stadium, das zweite Ursegment ist in Bildung, ebenso das Medullarrohr, rechte Hälfte"; **model 14**			"The neural plate (white) has become slightly depressed so as to form the floor of a longitudinal neural groove along the back of the embryo. The epiblast (blue) along the sides of the groove forms ridges"
"Weiteres Stadium, Embryo in der Region des ersten Ursegments und im hintern Viertel quer durchschnitten"; **model 15**			"The neural plate (white) lies on the dorsal surface: it is overlapped by the lateral epiblastic plates (blue), which have not quite met in the median plane."
"Stadium mit zwei Ursegmenten, dorsale Hälfte. Die Ursegmente sind durch Abpräpariren des Ektoderms sichtbar gemacht"; **model 16**			"In the anterior half of the embryo two pairs of myotomes are seen arising as lateral pouchings of the archenteron."

"Stadium mit fünf Ursegmenten; rechte Hälfte *Nota bene: the wax model and both the illustration and the description do not correspond. Obviouly, stage 17 and 19 were interchanged and relabelled.* (2 specimens held at ZCUV)			"The right half of an embryo with six pairs of myotomes."
"Stadium mit fünf Ursegmenten; Querschnittsegment aus der vordern Hälfte des Embryo"; **model 18**			"The plane of section passes through the neuropore, below which the neural plate (white) is seen. The archenteron (red) is cut in front of the first pair of myotomes."
"Stadium mit fünf Ursegmenten; Querschnittsegment aus der hintern Hälfte des Embryo; No. 18 und 19 können in der Längsrichtung aneinander gestellt werden *Nota bene: the wax model and both the illustration and the description do not correspond. Obviouly, stage 17 and 19 were interchanged and relabelled.* (2 specimens held at ZCUV)			"The neural plate is grooved dorsally, and its two sides folded longitudinally."

"Stadium mit fünf Ursegmenten; dorsales Stück"; **model 20** (2 specimens held at ZCUV)			"On the ventral surface the enlarged anterior end of the archenteron is seen in front: behind it are six pairs of myotomes; the hindmost or sixth pair not yet completely formed. At the posterior end of the model is the neurenteric canal: a wire has been inserted into it"
"Stadium mit sechs Ursegmenten. Um die Chordafalte sichtbar zu machen, ist die ventrale Hälfte des Embryo abgetragen und durch das erste Ursegment ein Querschnitt geführt"; **model 21** (2 specimens held at ZCUV)			"The dorsal portion of the body of an embryo with seven pairs of myotomes."
"Stadium mit acht Ursegmenten. Der Embryo ist durch das erste und das fünfte Ursegment quer durchgeschnitten; zeigt die Weiterentwicklung der Chorda"; model number 22			"A segment cut from an embryo with eight pairs of myotomes."
"Stadium mit neun Ursegmenten. Auf der linken Hälte des ganzen Embryo ist das Ektoderm mit Ausnahme der Medullarplatte abgetragen"; **model 23**			"An embryo with nine pairs of myotomes."

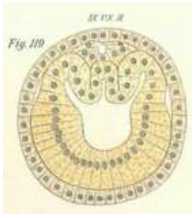
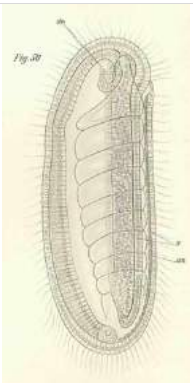
"Stadium mit neun Ursegmenten. Derselbe Embryo quer geschnitten durch das vierte Ursegment und durch die ungegliederte Mesodermfalte"; **model 24** (2 specimens held at ZCUV)		 	"The neural canal is now completed, the side walls having grown in and met each other so as to form a roof to the canal, independent of the external epiblast."
"Stadium mit neun Ursegmenten, rechte Hälfte des Embryo"; **model 25**			"The neuropore … leads into the neural canal (white), which runs the whole length of the embryo, and opens behind through the neurenteric canal into the hinder end of the archenteron or gut. The notochord (crimson) is a longitudinal rod lying between the neural tube and the gut…"

Table 4 Ziegler's *Amphioxus* development after Hatschek, stages 8 – 25: Gastrulation and formation of the somites, notochord etc. Models are enlarged 350 times until stage 11, then 420 times.

4.3.2 More *Amphioxus* representations

The German company SOMSO still produces Branchiostoma models after Berthod Hatschek (see Figure 146). They are not made from wax anymore but from the company's own material "SOMSO Plast". Apart from these teaching aids, several *Amphioxus* models and drawings were detected in the course of this project that not made by Ziegler. Here is a very brief pictorial summary:

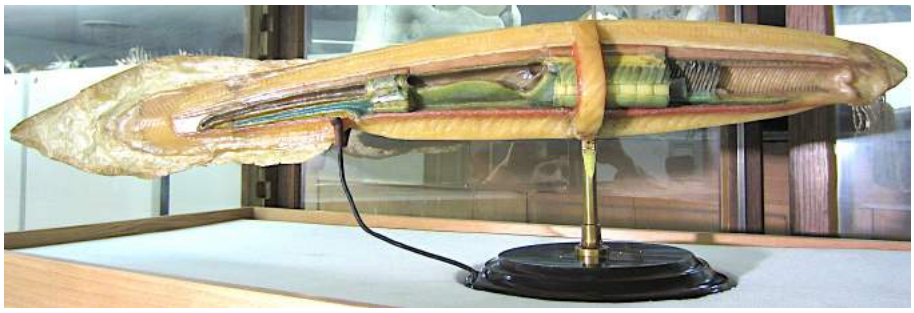


Figure 138 Berthold Hatschek's assistant Heinrich Joseph built this *Amphioxus* around 1900, utilising wax and pig's bladder as materials. It is likely that this unique specimen was used along Ziegler's *Amphioxus* models in order to demonstrate full development (Siderits 2009).

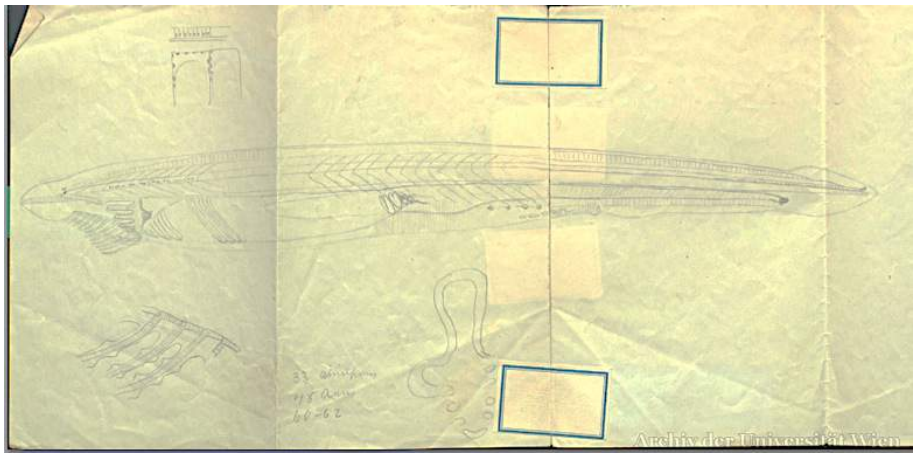


Figure 139 This *Amphioxus* sketch belongs to Heinrich Joseph's scientific estate. It is part of various notes and drawings that probably were prepared jointly by Joseph and Hatschek who were working closely together as teachers and researchers. The *Amphioxus* sketch is held in a "Vertebrata" file and testifies that teaching the anatomy *Amphioxus* was still considered relevant for Hatschek decades after his first 2D and 3D publications on this model species. The sketch is held at the Vienna University Archive: "Nachlass Heinrich Joseph, box 836, call number 131.98; Praktikumsskizzen ca. 1908 – 1921; Zootomisches und Histologisches Praktikum"

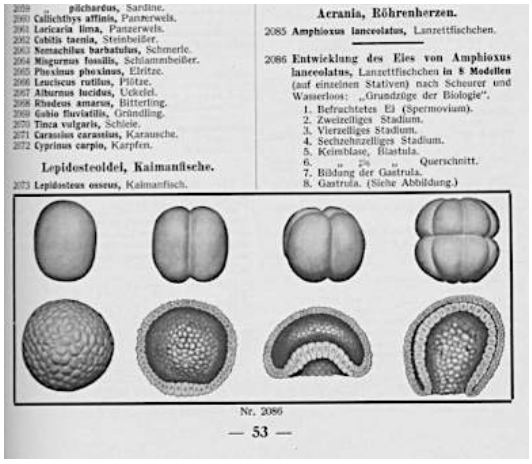


Figure 140 *Amphioxus* wax models (20865) and preseved specimens (2085) were offered in the catalgoue of Dr. Schlüter & Dr. Mass, Naturwissenschaftliche Lehrmittel-Anstalt, Jubiläumskatalog Nummer 290. Access to catalogue from 1928 thankfully provided by Michael Markert, University of Jena.

Figure 141 Take-apart *Amphioxus* model, held at the depot of the Phyletic Museum in Jena. Its label is reading "Louis Meusel", a company that also produced *Amphioxus* developmental stages early in the 20th century. Access to the model thankfully provided by Matthias Krüger, Phyletic Museum in Jena.

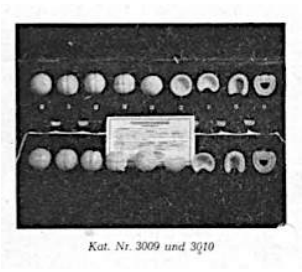


Figure 142 Early development of *Amphioxus*: Nine wax models with corresponding box and glued-in information leaflet, sold by "Lehrmittelwerkstätten Max Hummel" in Leipzig and listed in the catalogue "Lehrmittelerzeugnisse für Universitäten, Institute, Krankenhäuser und Schulen aller Art". Access to specimens and corresponding catalogue from 1950 thankfully provided by Michael Markert, University of Jena.

4.4 Reflections on Weisker models

Ziegler's "Atelier für wissenschaftliche Plastik" (Freiburg, Germany) was not the only wax publisher to make and sell wax models of developing marine organisms. Weisker's "Institut für Wachsbilderei" (Leipzig, Germany) also advertised a variety of marine larvae. According to the catalogue[56], Weisker had these marine larvae models available around 1880:

- 1 ***Actinotrocha branchiata*** before metamorphosis
- 1 **Annelid** larva. There is no indication of species in Weisker's catalogue. The specimen held at the ZCUV carries a handwritten label on its pedestal, reading "*Polygordius*". Seemingly, it was used together with both Ramphogordius larvae and they all were renamed "*Polygordius*".
- 2 ***Ramphogordius*** larvae (probably representing an earlier and later Trochophora). The Ramphogordius models at the ZCUV carry a label reading "*Polygordius*". Likewise, the corresponding entry in the inventory book was changed from "*Ramphogordius*" (a Nemertean) to "*Polygordius*" (an Annelid).
- 1 **Tornaria**. There is no indication of species in the catalogue.
- 14 stages of the crinoid ***Comatula*** after "Götte, Tompson and Ludwig"
- 11 stages of an **Ascidian**, including an Appendicularia larva

Weisker's *Actinotrocha*, Tornaria, an annelid larva and both *Ramphogordius* larvae were identified at the ZCUV of Vienna. Furthermore, one crinoid larva is left which might be a specimen remaining of the 14-piece *Comatula* series.

Neither Weisker's *Amphioxus* (see page 74) nor the extremely interesting Ascidian development series could be located at the ZCUV or elsewhere. The fact that Ascidian and *Amphioxus* development models were on offer reflects a significant question of the time: Evolutionary embryology was used to reconstruct the origin of vertebrates and their phylogenies.

Apart from six marine larvae, Weisker offered several developmental series:

Development of...	**Number of stages**	**Section in catalogue**	**held at the ZCUV?**
Taenia / *Cysticercus cellulosae* (Cestodes)	5	Zootomische Präparate [Zootomical Specimens]	1 specimen left at ZCUV
Bothriocephalus (Cestodes)	1 (embryo)	Zootomische Präparate	yes
Echinorhynchus angustatus (Acanthocephala)	6	Zootomische Präparate	no see Figure 6

[56] To date, information on the Weisker company is extremely sparse. Weisker's catalogue from around 1880 (Weisker 1880), held at the Landesbibliothek Mecklenburg-Vorpommern (D-19053 Schwerin, Germany) and located during this thesis project, was found to be an extremely useful source for identifying the ZCUV's Weisker models.

Salmon (*Trutta salar*) after Professor His	9	Entwickelungsgeschichte [Developmental History]	5 specimens held at ZCUV
Clepsine (Hirudinea), after C.O. Whitman, at the institute of Professor Leuckart	38 (e.g. cleavage, development of organs)	Entwickelungsgeschichte	entry in the ZCUV's inventory book, but no specimen retrieved
Frog after Ecker and Götte	23	Entwickelungsgeschichte	no
Dragonfly *Calopteryx*	12	Entwickelungsgeschichte	complete series held at the ZCUV
Astacus fluviatilis	10	Entwickelungsgeschichte	complete series held at ZCUV

Table 5 Weisker' wax models available around 1880, depicting invertebrate and vertebrate development (except for marine larvae, see page 73). Weisker also offered microscopic slides (not wax models) of chicken development, from day 1 to 10 (Rudolf Weisker 1880, page 8).

4.4.1 Weisker's enigmatic *Amphioxus*

Weisker's catalogue entry of *Amphioxus* [*Amphioxus lanceolatus* mit Anatomie] (Rudolf Weisker 1880, page 8) does not state a number of stages. The ZCUV's inventory book indicates that there was only one model. Furthermore, this specimen is not listed in the "development section" [Entwickelungsgeschichte] (Rudolf Weisker 1880, page 6). Therefore, it seems likely that at least this *Amphioxus* model by Weisker was a single item representing the adult animal's anatomy and did not demonstrate the larval development of *Amphioxus* over several stages[57] as Ziegler and other model manufacturers did.

However, there is a short note in the "Cornell Daily Sun" about the arrival of Weisker models, including 33 *Branchiostoma*[58] models "from the egg to the time when the adult form is recognisable" (Anonymous 1884). "An admirable wax colored model of Branchiostoma, 61 cm long", available from Weisker, is also mentioned in the "Proceedings of the American Association for the Advancement of Science", plus "a series of embryonic stages and transections" (Wilder 1886). Furthermore, Robert Wiedersheim (Wiedersheim 1883) cites Berthold Hatschek who obviously thought that his *Amphioxus* wax models (published by Ziegler) were superior to Weisker's; see page 86. Therefore, Weisker might have offered different *Branchiostoma /Amphioxus* specimens as time went on.

[57] Shortly thereafter, in 1882, Hatschek's representations of *Amphioxus* development were published by Ziegler, following Hatschek's publication "Studien über die Entwicklung des *Amphioxus*" from 1881.

[58] Interestingly, these models obviously were sold as "*Branchiostoma*", not as "*Amphioxus*".

4.4.2 Three unnamed Trochophora[59] larvae

Since their respective portfolios included developing marine organisms, both Weisker and Ziegler obviously responded to a market that was receptive to embryology, morphology and evolution of invertebrates from the sea, but the execution of Ziegler's and Weisker's specimens is quite dissimilar.

Compared to the marine larvae of Ziegler, Weisker's models are not only smaller. The marine larvae from Leipzig also convey less information due to their comparatively reduced form. The larve are not cut open to reveal the inner structure, and they lack Ziegler's colour code for the germ layers and the descending tissues and organs. Nevertheless, the position of ciliary bands is also emphasised in Weisker's larvae, for instance in the so-called "Ramphogordius" and the Annelid. The darker prototrochs and metatrochs contrast the pale body. Ciliary bands are also visible in the models of Tornaria and *Comatula*. The latter even sports a ciliary tuft, possibly made of horse hair.

Figure 143 Weisker's "*Ramphogordius*" (2 models) and "Annelid" (far right), held at the ZCUV; see page 16. Their dark ciliary bands (prototroch, metatroch) are a main feature. The further developed *Ramphogordius* model (middle) cleary shows segmentation and the becoming of the vermiform shape. Therefore, it cannot be classified as Nemertean (ribbon worm). It is unclear how this systematic confusion came along and whether Berthold Hatschek reacted towards it; he had reported that it was still unclear whether the Nemertini had a metameric structure. (Hatschek 1878, page 76ff.)

4.4.3 Did Hatschek co-operate with Weisker?

It is unknown whether Berthold Hatschek's publication on *Polygordius* development and his Trochozoon Theory (Hatschek 1878) spurred Rudolf Weisker to design the Trochophora-like larvae of *Ramphogordius* and an unspecified Annelid. If so, Rudolf Leuckart, Hatschek's former doctoral supervisor from the University of Leipzig, could have played a role in this.

This is conceivable since Leuckart both knew Berthold Hatschek well and collaborated[60] with Weisker: Models of the Weisker catalogue section "zootomical

[59] The term "Trochophora" is not used in Weisker's catalogue from around 1880. This "systematic-structural type of larval organisation" was critically reviewed, amongst others, by Salvini-Plawen (1980) with reference to Berthold Hatschek's works.

specimens" [Zootomische Präparate] that included various parasitic worms, were published under Leuckart's direction [specielle Leitung] which is explicitly stated in the the corresponding catalogue. It is also in this section that the three worm larvae are listed. Furthermore, it is most likely that Rudolf Leuckart was familiar with the activities of Berthold Hatschek in the years around 1880.

Leuckart was not always in agreement with his former student's approach[61]. However he must, in general, have thought highly of his mentee: Leuckart asked Hatschek whether he was interested in taking over his professorship as Leuckart's retirement approached[62].

What cleary speaks against Hatschek's direct involvement in Weisker's Trochophora production is the fact that two of them were sold as larval stages of the ribbonworm *Ramphogordius* (sometimes also spelled "R**h**amphogordius"). Additionally, Hatschek called the Nemerteans' Pilidium larva "Protrochula" and classified it as phylogenetically earlier[63]. Furthermore, the term "Trochophora" does not get mentioned in the catalogue. Ultimately, this makes it unlikely that Berthold Hatschek's role – if he played an active one – was highly valued in this process.

Whatever Hatschek's participation might have been: Weisker's worm larvae show that morphology and embryology of marine life forms were most relevant for academic teaching around 1880. Even though not sold or labelled as "Trochophora", Weisker's models might have helped to manifest Hatschek's views on invertebrate homologies and evolution in lecture halls, zoological laboratories and anatomical museums.

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[60] Apart from Rudolf Leuckart more scientists are mentioned in the catalogue: Professors His and Braune, directors of the anatomical institute of the University of Leipzig, and C. O. Whitman from Boston (Weisker 1880)

[61] In 1876, Rudolf Leuckart (University of Leipzig) wrote to Carl Claus (University of Vienna) about their respective student's passion for evolutionary theory as it was interpreted and popularised by Ernst Haeckel "Dr. Hatschek, too, although he has an undeniable technical and scholarly talent, is infected by the Jena epidemic, as is Herr Dr. V. Ihering."; cited after Nyhart (1995), page 196f.

[62] In November 1896, Rudolf Leuckart was about to retire. He wrote to Berthold Hatschek, then still a professor in Prague, that he needed to suggest a substitute. Leuckart asked Hatschek whether he would appreciate being offered professorship in Leipzig and signed himself as "your old teacher and friend" [Ihr alter Lehrer und Freund]. This letter is part of Berthold Hatschek's personnel file, held at the Austrian State Archives (Österreichisches Staatsarchiv; AVA Unterricht allgemein, 1848–1940; Universität Wien, Philosophie L-N; 902, Faszikel Nummer 865, Sign. 4G).

[63] Hatschek hypothesised in his textbook (Hatschek 1888-1891, page 317): "Die Protrochula ist eine Wiederholung des Protrochozoon, d. i. der gemeinsamen Stammform aller Zygoneura. – Die Trochophora ist die Wiederholung des Trochozoon, d. i. der gemeinsamen Stammform aller über den Platoden stehenden Zygoneura."

Wenn ich in dieser Sache das Wort ergreife, so ist es nicht wegen einer kleinlichen Rechthaberei, sondern weil ich die Verpflichtung fühle, einmal für die wissenschaftliche Wertschätzung der der Oeffentlichkeit übergebenen Modelle ausdrücklich einzutreten. Schon seit manchen Jahren habe ich Gelegenheit gehabt, wahrzunehmen, daß die im Handel befindlichen Modelle als wissenschaftlich nicht zu Recht bestehend behandelt werden. In Jahresberichten und in Monographien werden sie ignorirt, und auch solche Fachgenossen, für welche die bezüglichen plastischen Darstellungen erreichbar sind, pflegen ihnen kaum die gebührende Beachtung zuzuwenden.

Es steht also die Frage so: Hat ein Autor, welcher die Ergebnisse seiner Forschung in Form plastischer Modelle veröffentlicht hat, für diese Modelle, gleich wie für gedruckte Schriftstücke, die Rechte wissenschaftlicher Urkunden zu beanspruchen?

Ich selber bin über die Bejahung dieser Frage durchaus nicht in Zweifel. So wie ich complicirte räumliche Verhältnisse erst dann für wirklich verstanden ansehe, wenn dieselben in plastischer Darstellung vorliegen, so meine ich, ist auch das Modell, noch mehr denn das geschriebene Wort, die entscheidende Urkunde über die Formauffassung des betr. Forschers. Jeder erfahrene Anatom wird mir darin beistimmen, daß es Formverhältnisse giebt, die einem, auch wenn man sie einmal sorgfältig durchgearbeitet hat, doch nicht jeden Augenblick geläufig sind, die man sich aber durch Ansehen des körperlichen Objectes oder eines guten Modelles sofort wieder völlig ins Bewußtsein rufen kann. Auch darüber möchten wohl diejenigen, die selber modellirt haben, eins sein, daß eine plastische Form manche Einzelheiten wiedergeben kann, deren Schilderung durch das Wort nur sehr umständlich und schwierig zu geben ist. Ich bin mir wenigstens bewußt, daß in meinen Modellen aus älterer und neuerer Zeit Vieles liegt, worüber ich mich schriftlich nur nebenher oder gar nicht geäußert habe. Auch habe ich aus den Modellen anderer Forscher stets viel unmittelbarere Formeindrücke bekommen und mehr daraus gelernt, als aus schriftlichen Darstellungen, und ich bin überzeugt, daß es Anderen damit geht wie mir.

Figure 144 In, 1895, the Swiss anatomist Wilhelm His wrote about the low scientific appreciation of 3D models. He critised that the publication of 3D models did not receive the credit that they deserved. Congruently, Berthold Hatscheks's activities as model author are unbeknownst to many until today whereas his 2D publications still receive attention (His 1895, page 359f.).

5 Summary and conclusion

The Zoological Collection (ZCUV) is among the most fascinating research environments of the University of Vienna. In the course of this MSc project, **315 wax models from the ZCUV, dating back to the 19th century, were documented**. The majority of these specimens depict developmental series that comprised several stages of humans, vertebrates and invertebrates. They were used to instruct many generations of students.

Almost all wax specimens could be identified and ascribed to two German manufacturers, either Ziegler's "Atelier für wissenschaftliche Plastik"or Weisker's "Institut für wissenschaftliche Wachsbildernei". **These models once served as teaching aids in lecture halls, laboratories and museums.** With the help of these tangible specimens, students of biology and medicine were to understand developmental processes, ontogenetic morphologies and evolutionary embryology.

One of the scientific wax models authors was Berthold Hatschek (1854 – 1941), a zoologist who was trained at the University of Vienna and later became Head of the Second Zoological Institute. Hatschek was a supporter and friend of Ernst Haeckel. Unbeknownst to many, he published his most important model organisms in 3D in close cooperation with "plastic publisher" Ziegler.

It was one of the main goals of this project **to highlight for the first time Hatschek's activities as wax model author**. It seems that authoring wax models was not seen equivalent to publishing in 2D since no evidence of Hatschek's 3D publications was found in the sources analysed.

Nevertheless Hatschek's models were distributed world-wide through the manufacturer Ziegler: **the lancelet *Amphioxus* (25 models) and Trochophora, a marine larval type (5 models)**, published in 1882 and 1886 respectively. Both, *Amphioxus* and Trochophora, were protagonists in Hatschek's theorical work over decades. Being produced after Hatschek's drawings and authorisation, these models might well have contributed to the popularisation of evolutionary thought, providing evidence for the theory of descendence and reaching large audiences.

Berthold Hatschek's models were not just mere illustrations of the morphologies of obscure sea animals early in their ontogenies. ***Amphioxus* and Trochophora were embodiments of Hatschek's theories on evolutionary embryology.** The wax models served as powerful communication tools, they made theory tangible, aesthetically pleasing and accessible.

6 Zusammenfassung

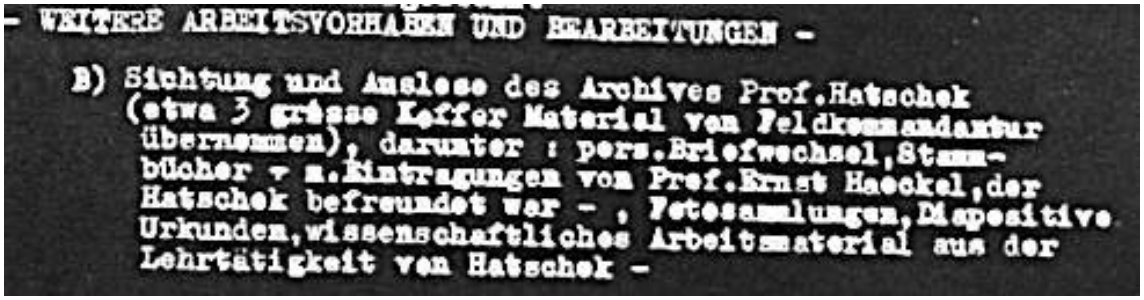
Im Rahmen der vorliegenden Masterarbeit wurden 315 Wachsmodelle aus der Zoologischen Sammlung der Universität Wien (ZCUV) zum ersten Mal dokumentiert: Die meisten Modelle gehören mehrteiligen Serien an und stellten Entwicklungsstadien von Menschen, Vertebraten und Invertebraten dar. Die Modelle, produziert im 19. Jahrundert, dienten Generationen von Studenten als Lehrmittel.

Fast alle Wachsmodelle konnten identifiziert und einem von zwei Herstellern zugeordnet werden: 232 Modelle stammten aus Zieglers „Atelier für wissenschaftliche Plastik“ (Freiburg), 65 Modelle wurden von Weiskers „Institut für wissenschaftliche Wachsbildernei“ (Leipzig) hergestellt. Mit Hilfe dieser bunten, massenhaft fabrizierten Modelle wurde die Entwicklungsgeschichte von Organismen begreiflich – sie veranschaulichten komplizierte Entstehungsprozesse, das Werden von Morphologien und letztlich auch das Zusammenspiel von Evolution und Entwicklung.

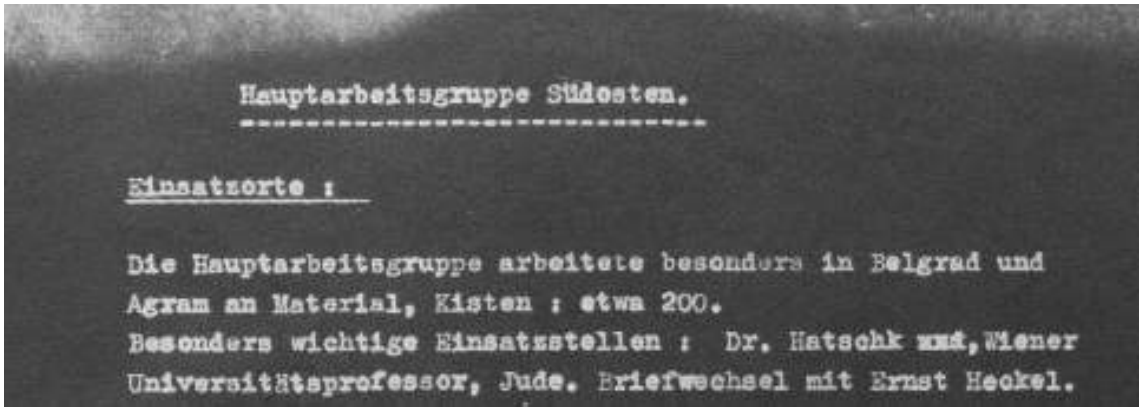
Einer der Wachsmodellautoren war Bertold Hatschek (1854 – 1941). Der Zoologe hatte u.a. in Wien studiert, wurde 1896 Vorstand des Zweiten Zoologischen Instituts der Universität Wien und prägte die Disziplin. Zu Beginn seiner wissenschaftlichen Laufbahn publizierte er seine wichtigsten Modellorganismen in Wachs und 3D gemeinsam mit dem „plastischen Verleger“ Adolf Ziegler. In enger Zusammenarbeit mit Ziegler entstanden 25 *Amphioxus*-Modelle (Verkauf ab 1882) und 5 Trochophora-Modelle (Verkauf ab 1886). Diese Organismen sollten über Jahrzehnte Protagonisten in Hatscheks theoretischen Arbeiten bleiben, die übrigens maßgeblich von Ernst Haeckel beeinflusst wurden.

Ein Ziel dieser Masterarbeit war es, Hatscheks so gut wie unbekannte Wachsmodell-Autorenschaft zu beleuchten. Denn dieser Teil von Hatscheks wissenschaftlicher Karriere ist bis jetzt kaum bekannt. Offenbar hatte diese Form der Publikation in der „Scientific Community“ nicht denselben Stellenwert wie Veröffentlichungen auf Papier und in 2D.

Die Wachsmodelle von *Amphioxus* und Trochophora, die weltweit vertrieben wurden und noch immer in etlichen Museen und Universitätssammlungen zu finden sind, waren nicht nur bloße Illustrationen der frühen Ontogenie von morpholgisch interessanten Meerestieren. Vielmehr waren die Wachsmodelle die Verkörperung von Hatscheks Theorien zum Zusammenspiel von Entwicklung und Evolution. Somit dienten die Modelle (auch) als gewissermaßen anrührende Kommunikationsinstrumente: Sie machten biologische Theorien nahbar, ästhetisch und begreifbar.


- WEITERE ARBEITSVORHABEN UND BEARBEITUNGEN -

B) Sichtung und Auslese des Archives Prof.Hatschek (etwa 3 grösse Koffer Material von Feldkommandantur übernommen), darunter : pers.Briefwechsel,Stammbücher - m.Eintragungen von Prof.Ernst Haeckel,der Hatschek befreundet war - , Fotosammlungen,Dispositive Urkunden,wissenschaftliches Arbeitsmaterial aus der Lehrtätigkeit von Hatschek -


Hauptarbeitsgruppe Südosten.

Einsatzorte :

Die Hauptarbeitsgruppe arbeitete besonders in Belgrad und Agram an Material, Kisten : etwa 200.
Besonders wichtige Einsatzstellen : Dr. Hatschk xxx,Wiener Universitätsprofessor, Jude. Briefwechsel mit Ernst Heckel.

Figure 145 Hatschek's archives were plundered. The looted scientific and teaching materials were brought to Belgrade to be documented and scrutinised by Einsatzstab Reichsleiter Rosenberg, Hauptarbeitsgruppe Südosten. Source for images of filing cards: Bundesarchiv, BArch NS 30/193 and BArch NS 30/32.

7 Epilogue: "Universitätsprofessor, Jude"[64]

Many questions around Berthold Hatschek's life and work could not be answered, for instance: Was Hatschek content with his models? Did his colleages value the wax models as scientifc publications in 3D? Did Hatschek make models himself in order to build, test and deconstruct his theories?

Hatschek's scientific estate might have been able to provide some answers. However his property (correspondence, photographs, diapositives, manuscripts, books etc.) was looted and inspected by the Nazis (Weinberger 2012; Grimsted 2005). It is likely that the close scientific and personal bonds between Berthold Hatschek and Ernst Haeckel accounted for the vivid interest in analysing Hatschek's works. At least three suitcases with scientific materials were brought to Belgrade, scrutinised by Einsatzstab Reichsleiter Rosenberg, Hauptarbeitsgruppe Südosten and later brought to Ratibor, at least partially. Traces of these belongings can be found at the Bundesarchiv in Germany where the activities of Einsatzstab Reichsleiter Rosenberg[65] are documented.

Hatschek and his wife who both were classified Jewish got expelled from their home in Vienna after the so-called „Anschluss". Their "Villa Hatschek" in Badgastein was "aryanised" (Lichtblau 2004). Hatschek passed away[66], on 14 January 1941. His funeral at the Viennese Zentralfriedhof was attended by two colleagues only: Heinrich Joseph, Hatschek's assistant over many years and creator of a unique *Amphioxus* model (see Figure 138) and his former student Otto Storch who wrote an obituary in 1950 (Storch 1950). Hatschek's wife, the painter Marie Hatschek-Rosenthal (*1869) whose possessions were looted as well, was deported[67] to a concentration camp in Yugloslavia[68]. The couple's daughters, Augusta Dessauer und Anna Marie Geschwind, survived the Holocaust in the USA and Great Britain.

There whereabouts of Hatschek's looted estate could not be examined further in the course of this thesis. However a thorough examination and reconstruction of these events is long overdue. Berthold Hatschek's material and immaterial legacy must not be forgotten.

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[64] Bundesarchiv; NS 30/32 (page 38) Schriftwechsel mit der HAG Südosten http://www.argus.bstu.bundesarchiv.de; see Figure 145

[65] http://www.bundesarchiv.de; see Einsatzstab Reichsleiter Rosenberg NS 30

[66] Death certificate of Berthold Hatschek http://rocek.gli.cas.cz/hatschek_soubory/Death_certificate.pdf

[67] Wilhelm Marinelli, a Viennese zoologist and former student of Berhold Hatschek, wrote to Georg Uschmann in 1968 that Marie Rosenthal-Hatschek had "travelled" to Yugoslavia, probably with her sister. Marinelli also mentioned that he had tried to trace or retrieve some of Hatschek's library, correspondence and files – to no avail. This letter is kept at the archive of the Ernst-Haeckel-Haus in Jena. (Bestand A, Abt. 1, Nr. 1808).

[68] Dokumentationsarchiv des Österreichischen Widerstandes DÖW http://www.doew.at/

Figure 146 Contemporary *Amphioxus* [Lanzettfischchen] models as currently sold by SOMSO Modelle GmbH, Ziegler's successor[69] since 1936. Until today, the German family-run business produces models of *Branchiostoma lanceolatus*, apart from many other teaching aids. Hence the 3D publications of Berthold Hatschek, first published in wax in 1882, have transcended to the 21st century.

[69] Source: http://www.somso.de/fr/zoologie/evolution-zoologique/*Amphioxus*/, image used with permission of Hans Sommer, director of SOMSO Modelle. The family business was founded in 1876 and bought Ziegler's business in 1936. Hans Sommer supported this MSc project for instance by sending catalogues and providing information on the extremely interesting history of his family's company.

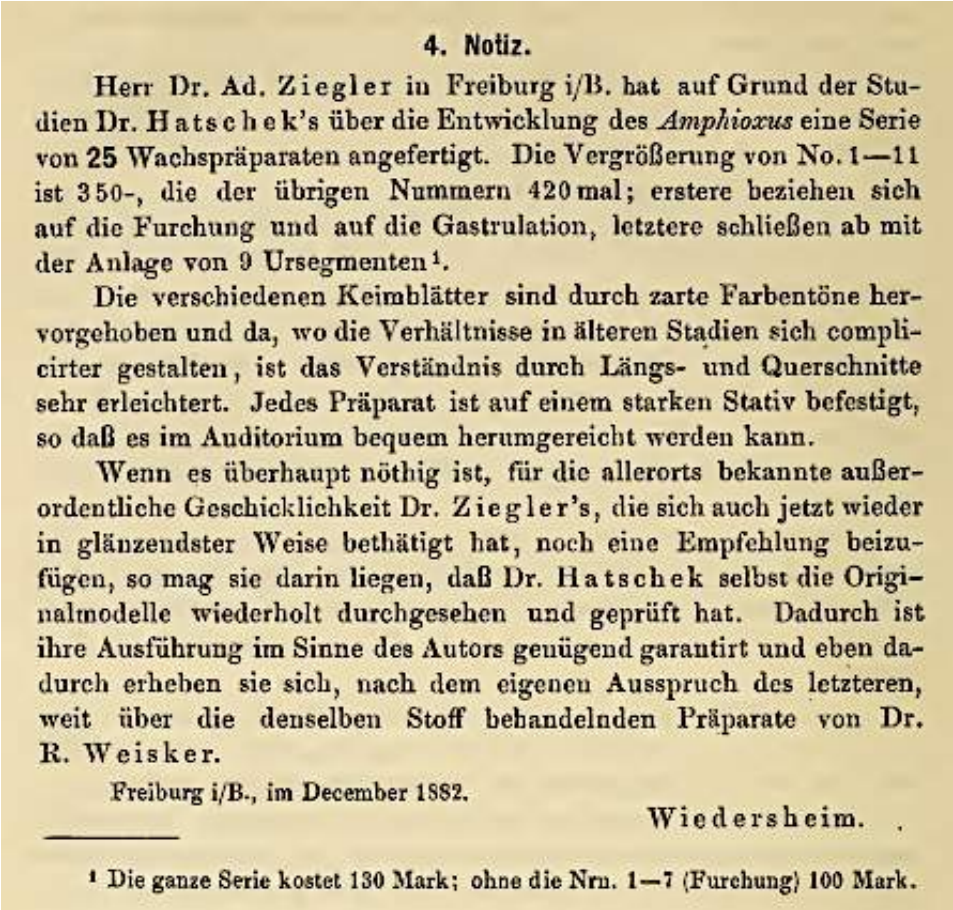
8 Acknowledgements

First of all, I would like to express my thanks to my thesis supervisor Univ.-Prof. Dr. Hans Leo Nemeschkal for suggesting this topic and embarking on this interdisciplinary project. Professor Nemeschkal, Head of the Zoological Collection (ZCUV), provided guidance throughout the project and granted access to one of the most inspiring research environments of the University of Vienna: the ZCUV. Both, Professor Nemeschkal and Maximilian Petrasko, Assistant Curator of the ZCUV, supported this project in various ways, for example by sharing their knowledge on the history of zoology and providing literature sources. Additionally, Univ.-Prof. Dr. Dr. Gerd Müller, Head of the Department of Theoretical Biology, facilitated this thesis.

Furthermore, I am indebted to the following people (in alphabetical order):

Jack Ashby MA, Manager of the Grant Museum of Zoology, University College London; Tannis Davidson MSc, Curatorial Assistant at the Grant Museum of Zoology, University College London; Dr. Sabine Hackethal, Head of the Department for Historical Research, Museum für Naturkunde in Berlin; Dr. Nick Hopwood, Reader in History of Science and Medicine at the Department of History and Philosophy of Science, University of Cambridge; Univ.-Prof. Dr. Uwe Hoßfeld, Head of the Workgroup for Didactics of Biology, University of Jena; Matthias Krüger, Taxidermist at the Phyletic Museum in Jena; Dr. Michael Markert, Researcher, Lecturer and Collection Specialist at the Workgroup for Didactics of Biology, University of Jena; Univ.-Prof. Dr. Stefan Richter, Head of the Institute für Zoology, University of Rostock; Univ.-Prof. Dr. Rüdiger Schultka, Institute for Anatomy and Cell Biology, Medical Faculty, University of Halle (Saale); Univ.-Prof. Dr. Gerhard Scholtz, Head of the Workgroup for Comparative Zoology, Institute for Biology at the Humbolt University in Berlin; Hans Sommer, Director of SOMSO Modelle GmbH in Coburg; Diplom- Restauratorin (FH) Jennifer Winkler (neé Stremmler) freelance restaurator in Berlin.

My sincere thanks go out to everyone who generously shared their passion for wax models, provided insights and various sources, let me access collections and discover otherwise hidden specimens.



4. Notiz.

Herr Dr. Ad. Ziegler in Freiburg i/B. hat auf Grund der Studien Dr. Hatschek's über die Entwicklung des *Amphioxus* eine Serie von 25 Wachspräparaten angefertigt. Die Vergrößerung von No. 1—11 ist 350-, die der übrigen Nummern 420 mal; erstere beziehen sich auf die Furchung und auf die Gastrulation, letztere schließen ab mit der Anlage von 9 Ursegmenten[1].

Die verschiedenen Keimblätter sind durch zarte Farbentöne hervorgehoben und da, wo die Verhältnisse in älteren Stadien sich complicirter gestalten, ist das Verständnis durch Längs- und Querschnitte sehr erleichtert. Jedes Präparat ist auf einem starken Stativ befestigt, so daß es im Auditorium bequem herumgereicht werden kann.

Wenn es überhaupt nöthig ist, für die allerorts bekannte außerordentliche Geschicklichkeit Dr. Ziegler's, die sich auch jetzt wieder in glänzendster Weise bethätigt hat, noch eine Empfehlung beizufügen, so mag sie darin liegen, daß Dr. Hatschek selbst die Originalmodelle wiederholt durchgesehen und geprüft hat. Dadurch ist ihre Ausführung im Sinne des Autors genügend garantirt und eben dadurch erheben sie sich, nach dem eigenen Ausspruch des letzteren, weit über die denselben Stoff behandelnden Präparate von Dr. R. Weisker.

Freiburg i/B., im December 1882.

Wiedersheim.

[1] Die ganze Serie kostet 130 Mark; ohne die Nrn. 1—7 (Furchung) 100 Mark.

Figure 147 In 1882, the German anatomist Robert Wiedersheim commented on Hatschek's *Amphioxus* series in the widespread "Zoologischer Anzeiger" (Wiedersheim 1883). Wiedersheim (who would publish 3D vertebrate brains with Ziegler in 1887, Hopwood 2002) highlighted that the *Amphioxus* models by Ziegler and Hatschek were tangible and could easily be passed around in lecture halls. Different colouration of the germ layers and sections would facilitate the understanding of complex developmental process. Furthermore, Wiedersheim stressed that Berthold Hatschek had inspected the prototypes and therefore taken responsibility for their validity. Wiederheim reports Hatschek viewed his *Amphioxus* models (by Ziegler) as far superior to Weisker's *Branchiostoma*, see page 74ff. However the latter could not be retrieved for the purpose of comparison during this thesis.

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***Nota bene**: For reasons of clarity, the sources of several references other than books or journal articles (e.g. archival files, websites, images, videos) are quoted directly in image captions or footnotes.*

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