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TEMPORALITY AND ATTENTION IN ICONOGRAPHIES OF THE LIVING

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1. Introduction: developmental narratives

As Nick Hopwood has so aptly observed, development is not merely the subject matter of embryologists—it is their achievement. A fundamental aspect of this achievement is the construction of embryological time. Visual images, three dimensional models and text narratives of the story of development are both working objects and finished products of embryological research, whether practiced as observational, experimental, or theoretical science. In producing visual narrative objects, Hopwood identified two problems of judgment that must be solved: selection and sequence. The problem of selection is to choose which static images to include in a visual montage. The sequence problem is to arrange the images into a narrative-supporting spatial order.

In this preliminary report, I sketch a model of narrative organization for visual embryological representations and argue that such organization was twice constructed in 19th century embryology. These constructions were stimulated by shifts of theoretical attention that changed research programs and made embryology a locus of biological unification for heredity, development, evolution, and cytology.

I describe these constructions of embryological time in terms of double movements connected with a broader shift of attention toward the cellular level of biological organization in the second half of the 19th century. In the first movement, research attention shifted backward in embryological time, toward the cellular origins of germ-layers—endoderm, ectoderm, and mesoderm. Once the backward shift of attention to the earliest developmental stages had been made, cell-lineage work from the 1870s to the 1920s facilitated a second movement, tracing forward in embryological time, from the egg and early cleavage cells to future structures in larvae and adult organisms. These studies identified the fates of cells and the timing of determination of fate in development. Their technical innovations produced two visual abstractions which were important to the emergence, in the 20th century, of distinct narrative forms in transmission genetics and developmental biology: the genealogical time of the geneticist and the deterministic temporal order of the developmental biologist.

Discursive visual representations of development are central to my story. Visual representations are very often the primary goal of embryological research and certainly are key resources in developmental interpretation. Their arrangement into normal tables, cell lineage diagrams and other kinds of visual sequences contribute a narrative.

4 Hopwood (2000).
5 Griesemer and Winsatt (1989); Maierrechel (1991a).
framework to working objects and products of research to “tell the story of development” in pictures and models as well as in words, “Narratives,” according to my colleague George Wilson, writing on narrative and film, “assign meaning or significance to the events they incorporate by situating them within an explanatory pattern that typically delineates both their causal roles and their teleological contributions to the needs and goals of the characters.”

Visual objects, such as image montages and films, pose particular problems for theories of narrative discourse and the representation of time, just as do fictional literary texts. In the visual montages of cell-lineage embryology, the delineation of causal roles and teleological contributions become visually explicit: delineation is made explicit by means of lines marking diagrams and teleology is explicit in symbols marking fate. “Most narratives,” writes Wilson, “are devised from the outset to reach an ending that will realize the audience’s desire for the dramatic development to culminate in an apt and satisfying conclusion.”

Wilson’s comments on narrative in film describe precisely the project of 19th century descriptive embryological research. The ending is the adult form, the audience is (often, but not always) embryological specialists in morphology and physiology, and the apt and satisfying conclusion is seeing the emergence of a normal larval or adult type from the embryo. The embryological ending, to be satisfying, must be visualized as the sensible result of the coalescence of origin and fate in the egg and early cleavage cells, discovered by tracing cell lineage branches back from their bushy, unique ends to their shared stems. The emphasis in turn of the century narratives on the normal embryo were important because they supported a resistance of observational embryology to the call for experimental purism by practitioners of Entwicklungsmechanik, whom cell-lineage workers regarded as studying abnormal developments that could not yield completely satisfying endings for the story of development, however important for pathology they may be.

Because visual representations in 19th century embryology are static, the constructions of time I shall be exploring take on particular spatial dimensions as well. Temporal and causal order in embryogenesis is represented in spatial relations among image components and in symbolic marks within images. In general, temporal order is represented by means of visual abstractions. A visual abstraction reveals structure by removing features from one visualisation to produce another, more simplified image, such as a view of a specimen through a microscope, a “realistic” portrait of a subject, or a photograph. Visual abstractions were historically significant in late 19th century biology because it is by their means that the genealogical time of the geneticist was first distinguished from the temporal and causal order of the embryologist. Working objects of the embryologist – the bench images used to construct developmental narratives – became founded, theoretical knowledge for the geneticist. From the discursive practices

6 Wilson (in press).
7 Ibid.
8 Lütke (1898).
9 See Landecker and Kelty (2002), on the emergence of motion studies of development in the early 20th century.
10 Grieseimer and Wimsatt (1989).
of embryologists working at the microscope thus came theoretical abstractions fundamental to the emerging sciences of genetics and developmental biology.

The backward movement of attention to embryological time can be described in terms of a "narrative relation," in which the selection and sequencing of entities, structures, positions, states, and times in the embryological past of a given present type – such as annelid, mollusk or ascidian; gastrula, larva or adult – serves the project of narrating a story of development of that kind or in which a comparative selection and sequencing serves the project of narrating an evolutionary story of common descent and homology.

The forward movement can be described in terms of a "fate relation," in which reference to determined entities, structures, positions, states, and times in the embryological future of a given type of present entity, structure, position, state or time (e.g. annelid, mollusk or ascidian / egg, cleavage cell, or blastula) serves the project of narrating a story of development of that kind.

It is also important to distinguish between narrational order – the represented time in the diagram sequences – and narrative order – the temporal framework in which events narrated by the scientists are embedded.\footnote{Wilson (in press).}

The images I discuss have non-visual analogues in the formal structures that analytical philosopher of history Arthur Danto calls "narrative sentences."\footnote{Danto (1985), Griesemer (1996a).} These are sentences which fundamentally relate two times but describe or are about the earlier ones. The second movement in each embryological construction I discuss can be forward-looking in virtue of a prior backward movement that established an end or outcome which will be realized by the developmental process. By attributing the relational property of a "fate" at an earlier time to cells or structures which are ordered into a sequence by cell genealogy, a fate relation – what embryological narrative sentences are about – is asserted in the second movement of the construction. In embryological narratives, fate connects two moments in time, completing the resources needed to construct a narrative account of development as a story of the unfolding of a causal process and realization of an end.

2. Two constructions of embryological time

19th century embryology concerned the process of development from egg to adult, whether this was to be interpreted as developmental history, evolutionary history, or causal developmental mechanics. In the mid-19th century, this process was divided into two phases by those who accepted the epigenetic viewpoint that development emerges during the life of the organism, not predelinated or preformed in the germ. Ernst Haeckel, for example, identified the phase transition with gastrulation, the process by which a homogeneous ball of cells becomes heterogeneous as a result of differential cell movements, as illustrated in this 1906 plate in stages 7 (upper) and 17 (lower) (see fig. 1).

The first phase (cleavage and blastulation) was a process of mere growth by cell division of homogeneous cells lacking morphological "value or significance," that is,
lacking any particular relation to the future morphology of the organism, other than serving as the material out of which the organism was to develop.

**Figure 1: Phases of Development according to Haeckel**

The second phase (gastrulation and organogenesis) was a process of differentiation of the heterogeneous germ-layers, tissues and organs that make up the larval (pre-metamorphic) or adult body. The similarities of early development and divergences of later development were sometimes used to argue in favor of a biogenetic law, in which descendant species “recapitulated,” in their ontogeny, the phylogeny of their ancestors. Haeckel had brought these various considerations together in his notorious “gastrea”

13 Reproduced from Haeckel (1900), plate V.
theory, which placed substantial weight on the gastrula as the critical point dividing the early homogenous phase from the late heterogeneous phase of development and thus made the evolution of gastrulation the key to the origin of higher organisms. The gastrula, for Haeckel, is the embryological form in which the differentiated germ-layers (endoderm, mesoderm, ectoderm) appear out of the undifferentiated mass of cells of the blastula.

By the 1870s and 80s, many embryologists, anatomists and zoologists were exploring various possible temporal locations and characteristics of the causes of visible germ-layer differentiation. My interest is in those embryologists who identified themselves as doing "cell-lineage work." These were scientists who aimed to trace the origin of germ-layer (as well as larval and adult organ) differentiation back to its cellular sources in the blastula, in cleavage cells, in the maternal organization of the egg, or to even earlier causes acting in the maternal body. Classical cell-lineage work spanned the period from the late 1870s to the early decades of the 20th century, perhaps to about 1925, when Walther Vogt achieved a merger of experimental embryology and cell fate mapping by experimentally marking individual cells with dyes and with mica chips to trace their movements in development and E. B. Wilson published the third and last edition of his text, The Cell in Development and Heredity, marking an end to the classical descriptive period of cyto-embryology.

The first construction of embryological time by means of the double movement of attention flowed from, and in reaction to, Haeckel’s use in the 1860s and 70s of evolutionary comparative methods to theorize a notion of embryological time in his version of the biogenetic law: the recapitulation of phylogeny in ontogeny. The systematic evolutionary relationships of adult forms was to be reconstructed by studying those taxa that are relatively undifferentiated in their adult states and to study their homologies in a common embryological groundform, the "gastrula," from which the phylogeny of the higher forms could be inferred. Haeckel’s reasoning, building on von Baer’s embryological work in the first half of the 19th century, supported the fundamental division of ontogeny into the two phases I mentioned: a homogenous phase from first origin in an ovum to the origin of the germ layers in gastrulation, and a second, heterogeneous phase from gastrulation to the development of the organs which constitute the characteristic adult form. By recognizing in the gastrula a mode of organization homologous across the animal kingdom, Haeckel’s recapitulation principle provided a theoretical tool for constructing a universal ontogenetic narrative to be explained by phylogeny.

Once this shift of attention backward from adult form to the gastrula as the selected locus of material causal origins of the heterogeneous adult form has been made, a return tracing could be made forward from the gastrula to the several adult organs. The organization of narrative structure depends on the round trip from adult form to gastrula

16 Wilson (1925). Cell-lineage work became popular again in the 1970s with the "worm project" to trace every cell line in the nematode C. elegans, making this classical object of study into a modern "model system" for molecular developmental biology.
and back again: once the outcome or ending is recognized in the adult form, then the causal pathway of development can be narrated "teleologically" from the universal gastrula – in terms of the anticipated end point. An important kind of forward tracing was carried out by Haeckel's student Oscar Hertwig, among others, who studied the origin of the mesoderm, or middle germ layer, in lower invertebrates such as the medusa, from a two layered gastrula composed of endoderm and ectoderm. Hertwig also studied the organogenesis of musculature, reproductive organs, gastro-vascular system, and nervous system. In keeping with Haeckel's fundamental "periodization" of ontology, Hertwig considered that cells developed new faculties as they separated from the germ-layers identified in the gastrula and not before.

These shifts of attention in the first narrative construction can be summarized in a diagram (see fig. 2).

![Diagram of the first construction of narrative time](image)

**Figure 2: First Construction of Narrative Time**

**Haeckel's Two Phase Ontogeny**

The narrative structure achieved by these movements is the temporal ordering of selected items into a causal sequence within the represented story of development. Times are represented visually by spatial structures – classically by portraits of embryos, subsequently by lineage diagrams. The classical style of developmental narrations are stage diagram montages. The *Normentafeln* of Wilhelm His described by Nick Hopwood in his talk at this conference is a good example. His took great care in standardizing the sequence of human development to represent time order in the spatial organization of his plates; the contrast with the rather less-organized representations in work both before and after His is striking. In well-ordered developmental diagram montages, time or temporal order is represented in two ways: (1) in the blank spaces between the spatial images of embryos in different states of development and (2) by means of numerical or alphabetical symbols marking each portrait in the montage and serving as a surrogate for

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20 Griesemer (1996b).
22 See also Ratcliff (1999).
temporal order in virtue of symbol-reading conventions. I will show that in the cell-
lineage work of the late 19th century, particular symbols marking diagram elements take
on added roles.

The second construction of embryological time was not so much driven by theory as
was Haeckel's, but rather by adoption of new study organisms and new methods to
extend the first construction and, ultimately, to reject it. In the late 1870s, as I
mentioned, many embryologists questioned whether the embryo was homogeneous
before gastrulation, or that the cells within and among the germ layers really constituted
undifferentiated masses of equivalent cells. Kowalevski in 1871 traced the metoblast of
the earthworm (Lumbricus) back from the gastrula to two individual posterior pole cells.
Wilhelm His and Oscar Hertwig challenged Haeckel's claim, to his "gastrula theory,"
that development before gastrulation was little more than growth. In effect, they turned
Haeckel's narrative structure on its head, since they did not accept phylogeny as the
appropriate causal narrative means to explaining embryological ends.

Following Jane Maienschein, I focus on American "cell-lineage" work from the late
1870s to about 1905, which extended the European challenges to Haeckel's phylogeny
as an explanation of ontogeny. But where Maienschein emphasized the transformation
of traditions through study of new organisms and adoption of the cell-lineage method, I
emphasize the consequences of shifts of attention in and to visual representations
developed in the course of cell-lineage work, particularly in the development of camera
lucida techniques to work with living as well as preserved and sectioned material.

Figure 3: Camera Lucida Microscope

The cell-lineage workers also completed a double construction, first shifting attention
backward from the gastrula to the cleavage cells and egg to seek the origins of

24 Ibid., p.93.
embryological form, and then tracing forward from those earlier stages in pursuit of cell fate in the germ-layers of the gastrula and beyond.

They faced special difficulties in their visual constructions because they followed embryos at such early stages and because tracing lineage required, wherever possible, following cell divisions in living materials since they aimed at a complete and accurate assessment of causal origins of each cell. Because they studied embryos at the cell-rather than the tissue- or germ-layer level of organization, microscopical techniques had to be refined, both to visualize structure on a finer scale and to view and represent it in living material. Moreover, to follow every cell in a living embryo is a daunting observational challenge. The challenge was met by specific technical means: the camera lucida microscope. It allowed subtle shifts of attention between embryo and drawing—between "embryological content" and "genealogical form," as it were—while the embryo developed.

Figure 4: Diagram of How the Camera Lucida Works

In figure 3, a simple microscope from 1892 with a camera lucida device fitted to its ocular is pictured. Figure 4 is a diagram showing how the device works. The prism attached to the microscope ocular transmits an image from the microscope to a mirror, which reflects the image to a drawing surface adjacent to the observed specimen. Because the observer can also look through the prism, one can view the specimen under the microscope and at the same time see a "virtual" image that appears superimposed on the specimen on the drawing surface. The observer can draw the specimen—tracing outlines, putting in shading to indicate three dimensions, and add symbols and notes—all without taking eyes off the specimen. Camera lucida thus affords the most subtle and minute management of shifts of visual attention possible.

26 Reproduced from Clarke (1940), p.276.
The *camera lucida* microscope facilitated not only the second movement in the cell lineage workers' construction of time, but also an important visual abstraction of time. As the working drawings were made, symbolic marks could be added that helped organize the causal representation of an observed embryological sequence. But also, after an episode of observing was finished, the drawing could be further articulated and developed in isolation from the specimen. This further development of the visual representation disconnected the observer's attention from the immediate events of development happening under the microscope and facilitated visual abstraction from the portraits drawn from life.

![Diagrams](image)

**Figure 5: Sequence of Cell Lineage Diagrams, Showing Visual Abstraction**

In following each cell's lineage, the observational project became genealogical — a matter of cellular descent or heredity — in addition to sequential staging — a matter of embryological growth and development. Moreover, the visual representations gradually abstracted the genealogical form or structure from the embryological, cellular content of observation. As embryos develop, they increase in complexity. This complexity was managed in the visual representations by means of a symbolic notation to track lineages. But as the embryo further developed, the structure of the visual representations became more abstract. A montage of embryo portraits at different times, following the classical techniques of stage diagrams, became inadequate. The lines that were in the first place inscribed as working representations of lineage within embryo portraits were visually extracted from that observational context to fill the temporal blank spaces between images. The result is the "table of cleavages" with genealogical time marked as lines connecting images. Eventually, these lines between the images became the subject of primary attention as cyto-embryologists provided one path to the origin of genetics.28

In the sequence of three figure panels above (see fig. 5), one sees the emergence of lineage lines from embryo portraits as a new subject of theoretical attention. The first figure shows an example of the visual portrayal of embryo development as a sequence of

increasingly complex images. The next two show the visual innovation of marking arrows on the portraits to indicate direction of cellular movement.

The next figure (fig. 6) shows the crucial visual abstraction, in which the cells or embryo regions of the previous representation are reduced to nodes or vertexes between the genealogical lines of cell lineages.

![Figure 6: E. B. Wilson's Cell Genealogy Diagrams, Showing Visual Abstraction](image)

I have argued elsewhere that this form of visual abstraction was used to represent, in addition to cell-lineages leading to the three germ-layers, also the embryology of germ-cells. Because the embryology of germ-cells was of concern to 19th century theories of heredity, the visual abstraction of genealogical time became connected with the problem of the relation between heredity and development, particularly in the work of Boveri and E. B. Wilson. Wilson’s representation of Weismann’s theory of the continuity of the germ-plasm inside germ-cells is a direct extension of his table of cleavages representation of cell-lineage (see fig. 7).

![Figure 7: Wilson’s Representation of Weismannism](image)

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29 Reproduced from Wilson (1892), p.382.
30 Reproduced from Wilson (1896), p.11.

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A second abstraction emerges from the cell-lineage visualization work as well: cell fate as a causal mapping between developmental stages. Rather than the temporal lineage notion that represented conceptions of genetic continuity and symbolized in diagrams by lines connecting cells across times, the fate map abstracted from lineage relations to identify the “morphological significance” of an embryonic region or cellular part at a given time in terms of its relation to future structure, position, or state. In fate mapping, embryological time is represented as a collection of abstract causal mappings rather than as an extended, linear or branching structure. Symbols for future states (and so forth) are superimposed on diagrams representing states at a given present rather than linking images representing different times in a montage. The lineage concept is preserved in the relational scheme that relates cells of a given cell generation as descendants from immediate ancestors, but lineage per se is not represented. For example, in figure 8, Conklin labels the figure of a single cell—the first cleavage cell—with the future fates of areas of the first cleavage cells in terms of their eventual place in the germ layers: ectoderm (ect.), endoderm (end.), mesoderm (m.s.), mesenchyme (m/ch), neural plate (n.p.), chorda (ch). The planes of division this first cell will go through are represented by the vertical and horizontal lines. The symbols cannot refer to the present state of the cell because the labels refer to states assumed by distinct cell populations while only one cell is pictured.

![Diagram](image)

*Figure 8: Cell Fate Map*

In the second construction of embryological time (see fig. 9), like the first, there is a double movement of research attention. This time, the backward shift is from the gastrula with its germ-layers to the egg, prior to any cellular organization of the embryo. The forward shift traces cell-lineage and cell fate back to particular cells and germ-layers as well as larval and adult structures.

In both constructions, there is first a shift of attention backward from later form to a search for embryological origins of that form in earlier stages of development. In each construction, the shifting of attention concerns primarily a different phase of development, as defined by Haeckel’s original concern with gastrulation. Second, there is a shift forward from those early origins to trace fates in the genesis of form. The double movement leads to a narrative construction of embryological time in which the

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31 Reproduced from Conklin (1905), p.108.
movement backward solves the selection problem at the same time it creates narrational possibilities of causal sequencing. That is, particular stages of development are identified (on theoretical grounds) as appropriate candidates from which to narrate the origins of known adult forms. The movement forward in time, tracing fates, creates new narrative possibilities in the technical abstractions created in representing forms changing over embryological time. But these technical abstractions transformed the sciences that gave rise to them, and thus, their narrative purposes.

<table>
<thead>
<tr>
<th>egg</th>
<th>homogeneous</th>
<th>gastrula</th>
<th>heterogeneous</th>
<th>adult</th>
</tr>
</thead>
</table>

**First shift of attention**
Trace backward from gastrula to the origin of gastrula structure in the phylogenetically common forms of cleavage.

**Second shift of attention**
Trace forward from egg to the origin of gastrula structure in the phylogenetically common forms of cleavage.

*Figure 9: Second Construction of Narrative Time
Cell-Lineage Workers' Two-Phase Ontogeny*
References


