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VISUAL STANDARDS AND DISCIPLINARY CHANGE: NORMAL PLATES, TABLES AND STAGES IN EMBRYOLOGY

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When I worked in developmental biology between 1986 and 1991 only two books had permanent places on my bench. The first, 'Maniatis', was a manual of the molecular cloning methods that our Cambridge laboratory was using to identify genes that specify muscle development in the South African clawed frog, *Xenopus laevis*. The second was 'Nieuwkoop and Faber', a 'normal table' that describes *Xenopus* embryos, one of the half-dozen model systems on which most developmental biology has been done. I knew the ring-bound recipes of Tom Maniatis *et al*. inside out, but with its dense morphological descriptions Pieter Nieuwkoop and Job Faber's *Systematical and chronological survey of the development from the fertilized egg till the end of metamorphosis* seemed an alien work from a bygone age — it was first published in 1956 — and I read only those few of the 250 pages that give 'external and internal stage criteria' through early development. My attention focused instead on the fold-out plates, a series of stippled line drawings that I photocopied and stuck above the bench. By internalizing these images, first encountered in an undergraduate practical class, I learned to tell gastrulae from blastulae and neurulae, and then stage $10\frac{1}{2}$ early gastrulae from stage 11 mid-gastrulae, and so to see my frogspawn develop in the same way as other people saw theirs. "Embryos", the Methods sections of our papers reported, "were staged according to Nieuwkoop and Faber". Reproduced in journal articles, and even on stationery and T-shirts, the stage pictures that ordered the work became badges of membership in a community of researchers who gathered at regular '*Xenopus* meetings'.[1] Embryological research is now unimaginable without such standard series, yet they do not figure in our histories at all. This article reconstructs the rise over the last two centuries of normal tables and the related normal plates and stages, and reflects on the relations between visual standards and disciplinary change.

Once beneath historical notice, standardization is gaining a place in the history and sociology of the sciences, technology and medicine commensurate with the greater resources that have gone into agreeing and maintaining standards than on 'pure' research. Most attention has been devoted to metrology, and the ways in which standard measurements have enabled centralizing states, global commerce and long-distance military action. We also have growing literatures on, for example, psychological norms and anthropometric standards, drug standardization and model organisms.[2] In the nineteenth century embryology was a central approach to animal life and a pillar of Darwinism. But this weakly disciplinized, largely academic (and overwhelmingly German) science did not have a high profile in bureaucracies,

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industry or even hospitals, though it was used in legal medicine.[3] So, as in many other academic fields, its standards were relatively informal and local. Only in the course of the twentieth century have embryological norms become effectively binding.

Normal plates are visual standards. Standard images have played ever more crucial roles in constituting the 'working objects' of each domain of inquiry. Atlases of anatomy and geology, star charts and ornithological field guides have mapped the known and the normal, and so made it possible to distinguish the novel, the pathological and the experimental. Lorraine Daston and Peter Galison sketched a history of atlases in terms of the mid-nineteenth-century rise, and mid-twentieth-century decline, of 'mechanical objectivity', an ideal of non-intervention through self-restraint.[4] Yet though its rhetoric and practices can be found even in embryology,[5] mechanical objectivity has played only limited roles in the sciences of organic form; full mental participation in drawing as a means to understanding remained too central well into the twentieth century. In any case, deep changes in the self are both too general and too individual to explain how standards have been involved, as "products of agreement" and "agents of unity", in building communities within and between sciences.[6] To grasp these processes we need to explore how representational practices have been bound up with the interactions between disciplinary identity and ways of working, mainly analysis and experiment, that have produced the various kinds of embryology.[7]

More than any other science, embryology has organized its objects in developmental series. During the nineteenth century visual representations of development became more prominent than textual descriptions, and in embryology perhaps especially central.[8] Yet, extraordinarily, we are only beginning to ground its history in the routine practices of representing series that set the framework for research and teaching. It is clear, though, that dramatic changes in the decades around 1800 staked out a space of representation within which developing embryos were constituted as objects of a substantially new science.[9] The history of development did not end there, however; methods of collecting and analysing, and of depicting and distributing the results, have changed enormously since. Here I seek to recover significant differences among the later series. Drawing on Daston and Galison's history of representative images from types to individuals, which though less used is more generally relevant than their discussion of mechanically objective imaging techniques, I concentrate on the division of development, especially in the selection and arrangement of printed pictures.

The first extended history of standard embryological series,[10] this article shows how disciplinary conflict and cooperation, and changes in ways of working, shaped and were shaped by the representation of development on the printed page. It is organized as a deep study of a major monument of comparative evolutionary embryology, the *Normal plates on the development of the vertebrates* that were edited from 1897 by the German anatomist, Franz Keibel. This series of 16 volumes is now attracting biological interest again but has never been studied historically. Amidst dramatic innovations in embryology between 1880 and 1920 — once seen as a 'revolt from morphology' that led to modern, experimental biology — it appeared to represent a degenerating research programme, and perhaps did not seem sufficiently rich in embryological ideas.[11] For a history of developmental standards, by contrast, Keibel's original works offer a strategic vantage point from which to map much previously unexplored terrain. By reviewing the nineteenth-century resources on which he drew to make a new genre of developmental series, and then following how this was transformed into the visual standards that sustain developmental biology today, we can explore the continuity and change in the representation of development that should be at the heart of embryology's history. Among other things, this will significantly expand our picture of its transformation around 1900.

The first two sections outline the theoretical, institutional and representational problems that Keibel's normal plates were designed to solve. I review the emergence around 1900 of a well-known crisis in the comparative evolutionary embryology of the vertebrates, and then sketch how this was bound up with the little-known nineteenth-century history of picturing embryonic stages within and between species. In the third section, I show how and why Keibel combined recently-invented plates and tables to create a new genre from less formal stage descriptions. Negotiating critiques by comparative anatomists and anthropologists, including intense local concern with individual variation, the project enlisted wide international collaboration. Next I present the normal plates as an attempt to map an embryological empire in a publication series, showing how differences between species and authors played out. The fifth and sixth sections explore the fate of the plates. These did not lead to any theoretical synthesis, but did become standard laboratory tools and created networks within which the first specifically embryological society and research institutes were founded. After the First World War, experimental embryologists and researchers on human embryos transformed the comparative genre to suit their own contrasting demands. In developmental biology after the Second World War, normal stages — reduced from complex, bulky tomes to a few easily-photocopied journal pages — played key roles in organizing work on model organisms.

1. DEVELOPMENT IN THE DISCIPLINES

To grasp the problems that Keibel's normal plates were launched to resolve, we need to trace the relations between 'ontogeny', or individual embryonic development, and 'phylogeny', or the evolutionary development of the species, that had been established and challenged in the preceding decades. To appreciate the social pressures that made these problems urgent, we need to place the theoretical disputes in the inter- and intradisciplinary struggles that drove them.[12] These were intense, because although embryology was the paradigm science of development, and gained enormously from Darwinism, it was at the end of the nineteenth century still weakly, or at least diversely, institutionalized and riven by competing approaches.

Embryology had been created in the decades around 1800 from investigations into generation, natural histories of monsters, and man-midwives' anatomies of the gravid uterus. It joined comparative anatomy as one of the two pillars of morphology, the new science of organic form. Embryologists claimed that, while comparative anatomy was often at a loss to interpret adult structures, complex and obscured by function as they were, the history of development showed clearly how diversity arose from simple, shared beginnings. Embryology's most important nineteenth-century institutions were the German universities, but the science never achieved the status of an independent discipline with its own professor at every one. After the wars of liberation from French occupation it went on mainly in institutes of anatomy and physiology, where microscopical work resolved embryos into germ-layers and cells. But from the late 1840s physiologists oriented towards physics rejected morphology as failing to seek properly causal explanations, and claimed separate chairs. Embryology remained in the anatomical institutes and gained the newly-independent institutes of zoology as its other main homes. So embryology's institutional ecology was almost as complex as that of morphology itself. It was represented most importantly in the special courses in human embryology that by mid-century were becoming small but standard parts of the medical curriculum.[13]

We might assume that this embryology was fundamentally comparative. The morphological work that aspired to be 'higher' than descriptive anatomical studies prided itself on taking a comparative approach, and embryology's role in resolving taxonomic problems was a matter of lively debate. Did human embryos recapitulate the forms of all the major groups of adult animals, or was the animal kingdom divided into four separate types, within which development did not run in parallel but rather diverged? Yet embryology, especially anatomist-dominated vertebrate embryology, was only comparative up to a point. Key discoveries stressed unity rather than diversity, and detailed comparison focused on individual organs.[14] The major conclusion, that all vertebrates develop within a common type, served primarily to justify the use of chick and domestic mammalian embryos as surrogates for human development, the main medical and anthropological concern.[15]

From the 1860s Darwinists pushed to make comparison central. Though embryos had played major roles in earlier nineteenth-century transformism, Darwin's theory definitively turned ideal archetypes into real ancestors and made embryonic similarity evidence of common descent. The leading propagandist of Darwinism in Germany, the Jena zoologist Ernst Haeckel, led life scientists in recasting the relations between series of embryos and of adult animals. He generalized an evolutionized doctrine of parallelism as the 'biogenetic law' that individuals repeat in the course of embryonic development the most important changes through which their adult ancestors passed during the evolutionary development of the species, or, in the terms he coined, "ontogeny recapitulates phylogeny".[16] In the absence of abundant fossils, Haeckel assigned embryos, especially the early stages of the most primitive groups, a central role in recovering the history of life on earth. To bring the embryos of phylogenetically strategic species back to European collections, marine stations were founded, most importantly by Haeckel's student Anton Dohrn at Naples, and expeditions undertaken, notably by Richard Semon, another student, in Indonesia and Australia.[17]

The problem, Haeckel admitted, was that ontogenetic stages never corresponded exactly to ancestral ones. Just as repeated transmission and translation corrupted a text, so the phylogenetic record became more or less 'falsified' in ontogeny. Haeckel distinguished the faithful 'palingenesis' from the corrupting 'cenogenesis'.[18] Apart from the development of nutritive yolk, the major mechanisms of cenogenesis were 'heterochrony' and 'heterotopy', terms that he may have borrowed from his teacher, the pathologist Rudolf Virchow, who had used them to describe disease. Haeckel's ontogenetic heterochronies were changes in the timing of development; for example, in vertebrate ontogeny the heart appeared much earlier in relation to the other organs than it had in phylogeny. Heterotopies were changes in the place of development, especially shifts of cells from one germ-layer to another: the sex glands arose in the mesoderm, but must originally have developed from one of the two primary germ-layers.[19] So using embryos as evidence of descent was a matter of separating the cenogenetic chaff from the palingenetic grain. In this way the biogenetic law accommodated exceptions so readily that it could never be simply disproved,[20] but embryologists' conflicting choices made its application appear arbitrary, and this left them vulnerable to attack from disciplines that favoured other evidence of evolution, especially comparative (adult) anatomy, and, as fossils accumulated, palaeontology too.

Embryology and comparative anatomy had been supposed to cooperate in establishing phylogenies. In the 1860s Haeckel worked with his senior colleague and close friend, the leading comparative evolutionary anatomist Carl Gegenbaur, to make Jena the citadel of *Darwinismus*. But faced with Haeckel's increasingly overweaning claims for ontogeny, Gegenbaur, who moved to the chair of anatomy at the University of Heidelberg in Baden in 1873, began asserting anatomy's rights. By the late 1880s he was arguing that only the comparative anatomist, with knowledge of the completed, active states of animals, could identify cenogeneses.[21] In the 1890s bitter and inconclusive turf wars between Gegenbaur's comparative anatomical school and Haeckel's embryologist students were driving younger scientists away from evolutionary morphology altogether.[22]

Haeckel's approach also suffered radical critiques from outside morphology. The most uncompromising early opposition came from the Basel, later Leipzig, anatomist, Wilhelm His, who from the mid-1860s attempted to apply the mechanical methods of physicalist physiology to chick development. Though not opposed to evolution, he shared the new physiologists' withering view of morphological explanations and rejected Haeckel's subordination of embryology to the construction of evolutionary trees. His countered with a mechanics of development, driven by the bending and folding consequent on unequal growth.[23] During the 1870s he remained isolated among the overwhelmingly morphologically-inclined embryologists, especially the young zoologists who found rich pickings by following Haeckel. But by the late 1880s evolutionary morphology was in turmoil and many were casting around for new approaches.

The resulting transformation of embryology has long been a paradigm of the crisis of Darwinism around 1900. The most successful of various programmes to investigate more focused problems in more accessible systems was the ‘developmental mechanics’ of German anatomist Wilhelm Roux. Like His, Roux concentrated on the physiological causes of development; unlike His, he insisted on experiment as the only conclusive method.[24] By 1900 developmental mechanics was a lively field with a journal of its own, but in a stagnating university system in which the full professors kept a lid on the number of senior posts, very few independent chairs of embryology were established (mostly in Austria), and none of developmental mechanics. So those pushing the new biology looked beyond the universities. Developmental mechanics was actively cultivated at Naples and other marine stations, and included in the Kaiser Wilhelm Institute for Biology that opened in Berlin in 1915.[25]

This, it has long been clear, is not the whole story.[26] Here I wish to stress that though the rise of experimental embryology and the end of ‘classical descriptive embryology’ are usually both dated to the 1880s, experimentalists did not achieve dominance until a half-century later, and ‘descriptive embryology’ not only persisted, it also changed. ‘Descriptive’ had once been the worthy but dull other of physiological, i.e., comparative studies, and then also of phylogenetic work; now experimentalists extended the term to include these approaches as well.[27] Yet though this ‘descriptive embryology’ was thrown onto the defensive, the institutes of anatomy and of zoology, in which Roux’s followers only slowly gained a hold, continued to recruit non-experimenting embryologists and increasingly gave them separate sub-departments to direct. Because of the potential medical, anthropological and evolutionary importance, pressure was strong on the anatomists, especially, to study not just vertebrates, but preferably the then experimentally inaccessible mammalian embryos. Nor was their work merely institutionally entrenched, it was also being transformed by demanding techniques. His had pioneered sectioning and modelling methods for analysing complicated microscopic structures in much more depth, and in the early 1880s used them to refound human embryology as a productive field of anatomical research.[28]

Haeckel’s Darwinism, and these critical responses to it, raised the profile of embryology inside and outside the universities, but neither he nor his opponents were content with the situation of the science. The problem, as His presented it, was only in part the competing disciplinary alliances and rival programmes. It was also that the new descriptive methods made mastering embryos’ complex and changing forms so time-consuming that individual investigators could tackle special problems only, and these often from just one particular point of view. The result was such a bewildering wealth of detail that in an 1886 address to a general session of the Congress of German Naturalists and Physicians His could lament that embryology, “which has the task of bringing together and mastering large fields according to unified principles, appears to be falling victim to an increasing fragmentation and confusion”.[29]

His’s solution was also an organizational form that would transcend the limitations of university institutes. He proposed the establishment, in embryology as in brain research, of central institutions that would take on tasks individuals could not master and make the results generally available. The model was in part the Naples Station, which had provided embryological researchers from around the world with benchspace and organisms. The more general plan was to do for embryology what the geographical and geological surveys, meteorological institutes and statistical bureaux had already achieved, and the Imperial Physical-Technical Institute then promised, an ideal to which within the universities the botanical gardens and observatories came closest. His did not in that speech grind an axe for the mechanical approach and his was not a forerunner of the campaign for a special institute for developmental mechanics. The aim was rather to reduce the disadvantages of specialization by expanding the common empirical ground on which embryologists of all persuasions could meet.[30]

Several initiatives of the 1890s and early 1900s, including Keibel's normal plates, go back to His's proposal and use resources that he produced. Though moves were also made to unify the embryological nomenclature, these inventorizing projects were primarily visual. They centred on the collection and preparation of specimens, and the production of drawings, photographs and models through which to order and understand them. So, to provide a frame of reference for Keibel's series, this sketch of the theoretical and institutional history of vertebrate embryology needs to be complemented with an equally selective review of its less familiar representational practices and the visual world they produced.

2. SERIES AND STAGES, PLATES AND TABLES

Stephen Jay Gould highlighted the ideological power of easily-taken-for-granted representations, such as evolutionary trees and measurements of skulls.[31] In embryology, the basic representations are developmental series. They have been made by a set of linked procedures: collecting specimens and framing them as embryos; transforming initially unprepossessing objects into vivid images; arranging these in developmental order and selecting representatives deemed normal and appropriately spaced; and preparing the series for publication or display. These practices may seem less contentious than drawing trees and measuring skulls, but they have had their politics too, in part (only in part) because they have been bound up with theoretical debates, including over ontogeny and phylogeny. Here, with a view to charting the shifts that produced Keibel's resources, I survey the organization of development in print. I concentrate on how, within species, representatives were selected and arranged, and on how the development of different vertebrates was compared.

We can start with a work from 1828 that both represents the embryological culmination of the decades of change around 1800 and was still read around 1900 as the foundation of the science, the first part of Karl Ernst von Baer's *Über Entwickelungsgeschichte der Thiere* (*On the developmental history of animals*). The scholia, which reflect on his description of chick development and consider it in relation to the development of other animals, contain this extraordinary passage:

> If we wanted to draw a number of fully-grown chicks quite exactly ... on a plate, we would recognize some differences, but only insignificant ones, which can exert little influence on the relations of life, such as longer and shorter necks,

> stronger and weaker feet .... If embryos of the stage of development when the back is closing were drawn on a plate next to each other in the same way but magnified to the size of the adults, then quite apart from the quicker or slower progress of development as a whole, one would recognize the greatest differences, and believe these embryos could not develop to the same form .... [O]ne can hardly comprehend how these variations lead to the same result and how, next to perfect chickens, countless cripples do not arise. Since, however, the number of cripples among the older embryos and adult chicks is only very small, one must conclude that the differences are evened out and every deviation, as much as possible, is led back to the norm.[32]

For von Baer, this was evidence against materialism and that development was governed by the essence, what the Romantics called the 'idea', of the animal to be generated. Here I am primarily concerned, not with arguments about how the process of development is normed, but with the norms that embryologists imposed on their series. So though these issues continued to be linked, for my purposes von Baer's imaginary plate is remarkable as a mental picture of variation and as a contrast to the illustrations in his own work.

First, von Baer offers an unusually vivid image of individual embryonic variation, which he treated as a problem to be overcome by setting up consistent criteria, according to which to determine "the individual periods of development". This was necessary, because, "[i]f one does not hold to such principles, then one can deliver a quite monstrous embryology, the individual determinations of which do not fit together at all". Von Baer divided "inequalities in the periodicity of development" into two kinds: "in the association of the phenomena" and "in the progress of development as a whole". The former were not very significant, but visible between less closely related parts; gut development was more tightly associated with the mesentery than the brain. Yet, "[m]uch more variable than the relationship of association is the progress of development according to the duration of incubation, and a real nuisance for the observer who, when he wants to observe a particular moment, almost does not achieve his goal unless he pays attention to, and masters, all conditions". That meant especially temperature; von Baer had spent many a sleepless night minding the incubator. "Now, in order nevertheless to be able to determine times for the individual stages of development [*Entwickelungsstufen*]," he wrote, "I sought to determine a normal development [*Normal-Entwickelung*]", that is, "the most usual" under the "favourable conditions" he specified. Von Baer used this to divide development into 21 comparable days, grouped into three periods.[33] He thus broadly followed his friend Christian Pander, who split his pioneering embryology of the chick into what were effectively ideal hours and days.[34]

Second, von Baer's mental image could not be further from the idealized figures with which he and Pander in fact illustrated their work. Most of Eduard d'Alton's ten plates for Pander appear to have been based on particular specimens, though no details are given. Plate V aimed, exceptionally, to show "the variety of forms under which the embryo is accustomed to appear at the same stage of development

[*Entwickelungsstufe*]". But in general the figures represent the degree of development in an interval without any hint as to what made the embryos representative. Von Baer's first two plates show cross- and longitudinal sections that are as schematic as Pander's. There is no question of their representing individual embryos; each summarizes observations on dozens of eggs. The third plate contains more obviously "ideal" or schematic figures.[35]

The anatomists and physiologists who followed Pander and von Baer divided development in broadly similar ways. Since there was no great pressure to conform, investigators were free to set up whatever series seemed best to suit the particular material and special problems at hand. During the middle decades of the nineteenth century there appears to have been a shift, slow and patchy in specialist works and hardly apparent at all in classroom visual aids, towards drawing, not types, but characteristic individuals. The lithographs representing stages of chick development in the 1868 monograph that introduced His's mechanical approach depict embryos for which he gave hours and temperature of incubation and a date. But he stressed how well his numbered stages (*Stadien*) corresponded to Pander's divisions.[36]

Embryologists divided development differently according to species and disciplinary goals. The chick was studied because, von Baer's trials notwithstanding, many eggs could be incubated relatively easily, and sheer numbers allowed abstraction from individual specimens. Early mammalian, especially human, embryos were much more difficult to obtain and investigations proceeded case by case. A 1799 atlas by the anatomist Samuel Thomas Soemmerring is generally regarded as the first developmental series of human embryos. The engravings depict the "most beautiful" types, but show individual specimens in his collection.[37] Corresponding to the diverse purposes for which human embryos were described, the surveys that followed took several forms. Descriptive anatomists, man-midwives and physicians in legal medicine often presented 'characteristics' for each month as prose descriptions and tables summarizing development, especially of the foetal bones; textbooks of obstetrics included plates of developmental series. Researchers with comparative interests tended to offer plates or wood-engravings depicting seriations, not formal stage divisions, based on size, age estimates and morphology, of the earliest specimens they regarded as normal. Because human embryos mostly came from abortions, variations were generally seen as pathological, but normality was difficult to assess. For more advanced embryos, anatomist-physiologists concentrated on following separately the development of the different organs.[38]

Handbooks, textbooks and atlases synthesized work on the development of the chick, humans and other vertebrates, but even as illustrations became more abundant around mid-century, comparative images remained few and far between. Von Baer's schematics represent the common vertebrate type,[39] and there are comparisons of single organs or systems, but very few plates assemble pictures of the whole embryos of more than one vertebrate.[40] This is because in most surveys a coherent account that could stand for human development was the main aim; the most famous comparative studies used the 'embryological criterion' to deal with particular organs, such as the urogenital and respiratory systems and the skull; morphologists regarded arrangements of parts as more significant than external forms; and specialist readers who wanted comparative drawings of whole embryos could have made their own.

As embryology expanded, new techniques, especially for sectioning, printing and modelling, combined with new approaches, especially from Darwinism and experimental physiology, to produce significant visual diversification. Compared to the wood-engravings by a single artist in the long-standard 1861 textbook, the visual styles of the borrowed illustrations that were photomechanically reproduced in the first (1888) edition of its successor are very disparate indeed.[41] Among a bewildering number of specialized studies, the innovations of Haeckel and His stand out, visually as well as theoretically, as promoting syntheses of opposing kinds. Haeckel took what he found to hand and made it yield the comparative overview for which one otherwise searches in vain. His combined exhaustive analyses of individual specimens in selected species to visualize the development of embryos as wholes.

Even with much embryology now avowedly comparative, and the doctrine of the specificity of the germ-layers guiding internal comparisons, most pictures still did not actually compare whole embryos; they lined up organs or separately presented stages in the development of various groups. But from 1868 and 1874, respectively, Haeckel's semi-popular books, the *Natürliche Schöpfungsgeschichte* (translated as *The history of creation*) and the *Anthropogenie* (*The evolution of man*), used vivid icons to bring his Darwinist system to the reading public, and some of these compare whole vertebrate embryos. From the second (1870) edition of the *Schöpfungsgeschichte* a comparative plate is arranged in two rows for developmental stages and four columns for species; it shows divergence from a very similar moderately early stage. To make the comparison, and hence the evidence for common descent, as striking as possible, Haeckel figured each ideal-typical embryo at the same size and in the same view. By 1891 he had expanded the grid in the *Anthropogenie*, which concentrated on embryology, to three rows and 14 columns (Figure 1).[42] This space of representation invited indefinite extension, but Haeckel's plates were not easily integrated into academic embryology. His and others accused him of dishonestly making the first rows look more similar than they really were, and of inventing other illustrations.[43] His deployed a moderate mechanical objectivity and Haeckel countered by stressing the value of his own (and von Baer's) idealizing schematics.[44] Haeckel kept his place as the 'German Darwin', but with a tarnished reputation. The plates continued to be reprinted, but though distributed widely, were not for the moment copied into the leading embryology textbooks, only into more general works.[45] The post-Darwinian expansion and specialization of the field militated against the acceptance of simple, synoptic pictures.

If Haeckel's glib schemata illustrated the difficulty of aligning phylogenetic and ontogenetic series, His's sectioning, drawing and modelling deepened the microscopical description of development within species. Arguing that, in anatomy as in astronomy and geography, "standard book-keeping [*Standardbuchung*] ... in the form of pictorial representation" could approach the ideal of "absolutely objective

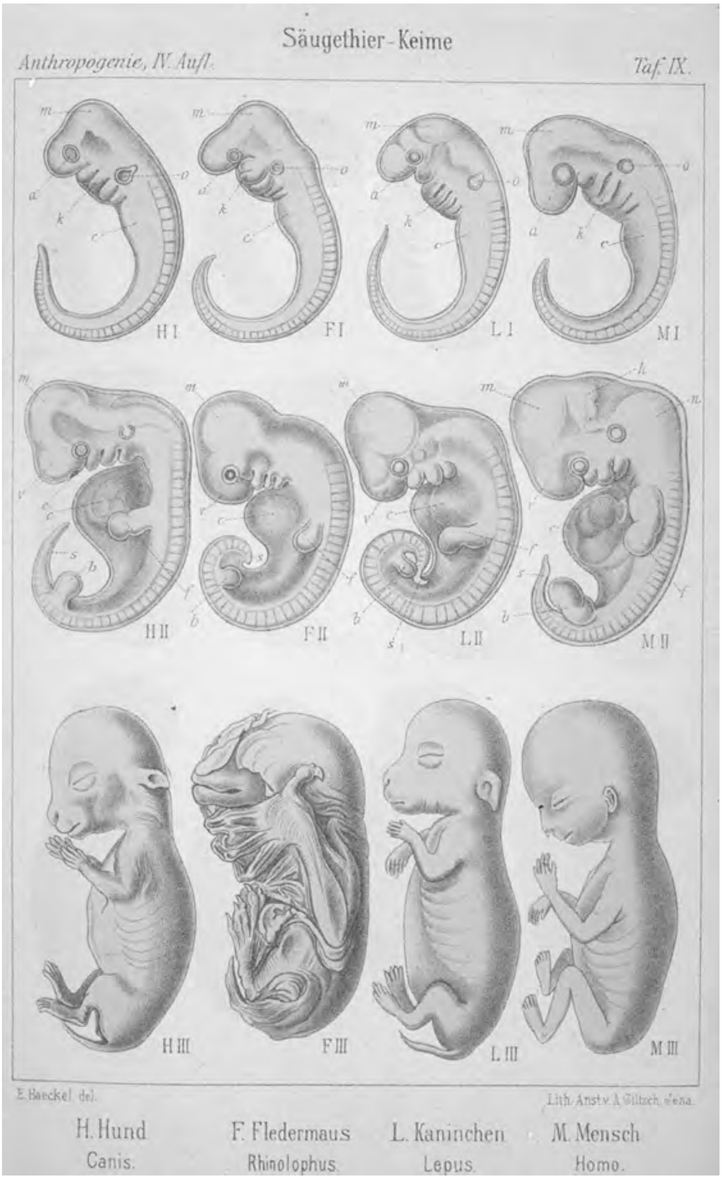


FIG. 1. Comparative plate of mammalian embryos in Ernst Haeckel's semi-popular *Anthropogenie*, showing dog (H), bat (F), rabbit (K) and human (M) at three developmental stages, "very early" (I), "somewhat later" (II) and "even later" (III). This is the last in a series of four lithographs by Adolf Giltsch after Haeckel's drawings that provided the most vivid survey of comparative vertebrate embryology when Franz Keibel was engaging with the biogenetic law. The fourth edition was less provocative than the earlier ones, but these pictures still included much that was controversial. From Haeckel, *Anthropogenie oder Entwickelungsgeschichte des Menschen: Keimes- und Stammes-Geschichte*, 4th edn (Leipzig, 1891), i, pl. IX.

norms", His intended his pictures and models to set more demanding and universal standards.[46] Though presented as providing a non-partisan foundation, such norms would also limit the room for manoeuvre and restrict the field to specialists. In the early 1880s, His applied the new methods to human embryology. The many rejected specimens included a human embryo Haeckel had deployed against him that he now reclassified as a bird.[47]

Exhaustively describing particular embryos also made it harder to set up stages. In the three instalments plus two atlases of the *Anatomie menschlicher Embryonen* (*Anatomy of human embryos*) we see His working from an unusually optimistic view of the possibility of staging human embryos — "it will not be difficult to set up stages [*Stufen*] according to the overall habitus of development that correspond with each other in the different classes of animals" — to a design that avoided such abstractions. In the first instalment (1880), he divided human development into stages (*Stadien*) like those he had set up for the chick, and distributed his own and other known specimens among them. Yet as he continued to analyse individual, named embryos and arrange those he selected in series, he abandoned his preliminary divisions, and worked instead to determine "norms", that is, "the relations of form and size that define each stage" (1882). Several redrawings later, the final instalment (1885) offered a lithograph of the external anatomy of embryos from the end of the second week to the end of the second month of pregnancy (Figure 2). Returning to a common practice in human embryology, but on the basis of far more specimens than a single researcher had ever analysed before, His no longer referred to stages, but simply arranged representative individuals in order. Finally replacing Soemmerring's out-of-date work, the figures no longer aspired to be ideal types but represented individuals judged to be characteristic. For this seriation His used the term *Normentafel*, or "plate of norms", to my knowledge for the first time; it would be translated as "normal plate" or kept in the German.[48]

His's authoritative work left human embryos better understood than those of any other mammal. The normal plate made it easy to assess new specimens and the models displayed the unprecedentedly detailed and accurate three-dimensional views of internal anatomy that serial sectioning and plastic reconstruction could achieve.[49] Though unusually systematic, His represents a more general trend to analyse individual specimens more thoroughly and to monitor more carefully the relations between figures, models and specimens. This made the wealth of new embryological detail look even more poorly organized and harder to grasp. Haeckel could synthesize it in new editions of the *Anthropogenie*, but it was a different matter for those actively involved in vertebrate embryology, especially the younger anatomists who both accepted the new techniques and saw the troubled relations between ontogeny and phylogeny as the major problem in the field. For them, the crisis of comparative evolutionary embryology was a crisis of staging, not just between species, but also within them.

In 1891 a systematic test of the biogenetic law showed how much, by the new standards, remained to be done. Albert Oppel, a newly-appointed prosector at Baden's

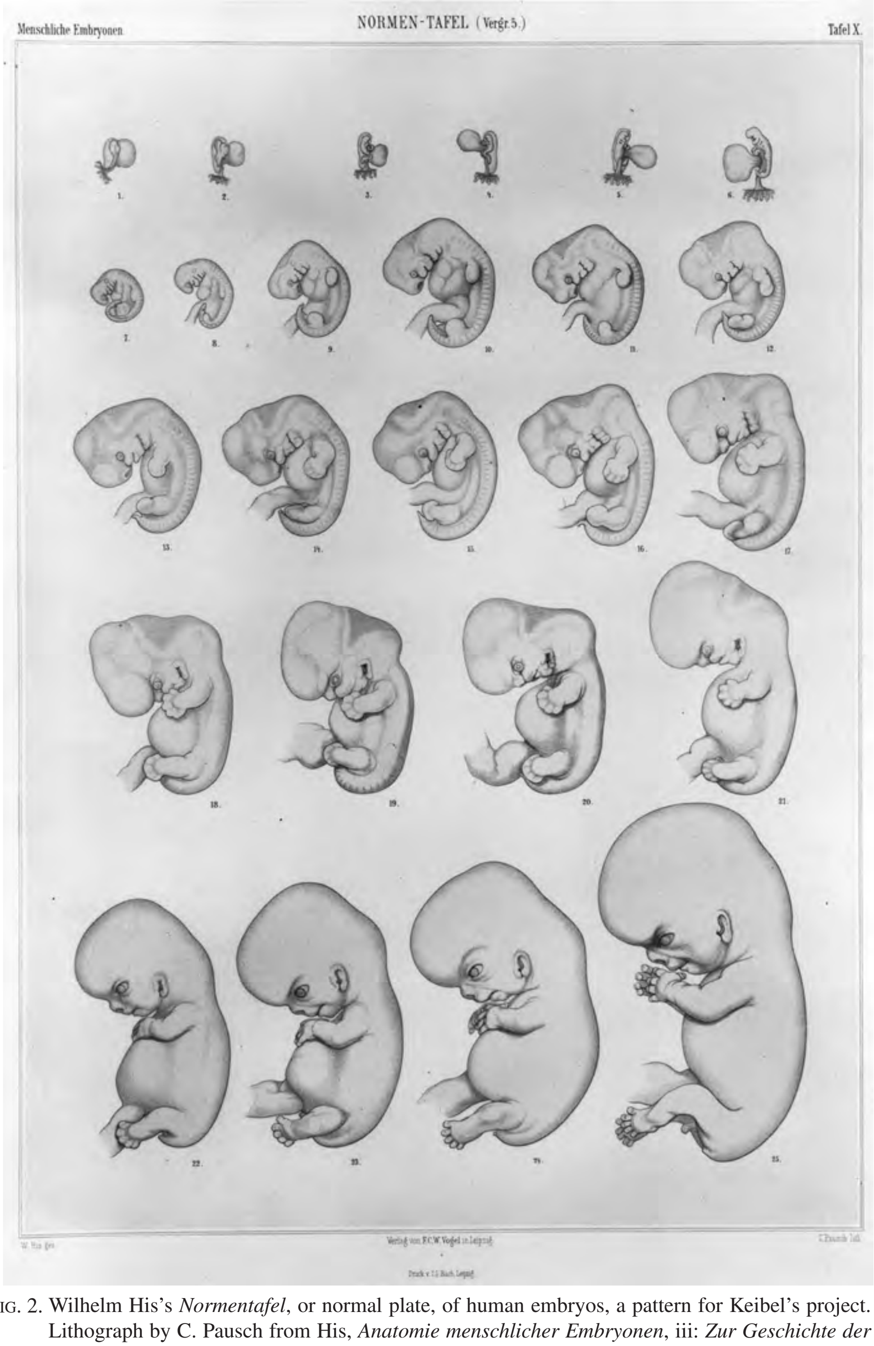


FIG. 2. Wilhelm His's *Normentafel*, or normal plate, of human embryos, a pattern for Keibel's project. Lithograph by C. Pausch from His, *Anatomie menschlicher Embryonen*, iii: *Zur Geschichte der Organe* (Leipzig, 1885), pl. X. Wellcome Library, London.

Nr.	Material	Länge	Alter	Körperform	Keimscheibe	Urwirbel	Chorda	Nervensystem	Auge	Ohr	Nase	Epiphyse Hypophyse	Mund	Verdauungstractus	Kiemenspalten	Urogenitalsystem	Herz und Gefäfse	Integument und Skelett	Extremitäten	Amnion	Allantois	Bemerkungen
18	Gasser 38					7—8 Urw.								Kopfdarmhöhle gewachsen			Verschmelzung der beiden Herzhälften					
19	Gasser 37					circa 8 Urw.										Wolffscher Gang im Entstehen						
20	Kupffer 50 Fig. 49	5,1 mm				8 Urw., Bildung des 9. angedeutet		Schlufs des Vorderhirns ist erfolgt. Schlufsstelle 2 Knöpfchen														Blut und Gefäfse im Gefäfshof. Anlage des Sinus terminalis
21	Gasser 47					8 Urw.	Läuft nach vorn in eine dicke Zellmasse aus	Gehirnnerven														
22	Gasser 47					9 Urw.																Pleuropericardialhöhle vorhanden
23	Gasser 38					10—11 Urw.											Blutkörperchen im Herz und in den Aorten					
24	Janosik 115					11 Urw.										Erster Anfang des Wolffschen Ganges						
25	Gasser 47				Primitivrinne noch vorhanden	12 Urw.		Medullarrohr klafft nur hinten noch ein wenig														
26	Braun 46	5 mm				13 Urw.																
27	Gasser 37					circa 14 Urw.										Wolffscher Gang, solider Strang						
28	Kupffer 50 Fig. 60		30 St.	Drehung des Kopfteils. Linke Seite gegen den Dotter		14 Urw.		Ganglion acusticofaciale	Beginnende Abschnürung der Augenblasen	Grube	nicht deutlich											
29	Gasser 47					14—15 Urw.		Medullarrohr vollständig geschlossen														
30	Gasser 37					16 Urw.										Wolffscher Gang zeigt deutliches Lumen						
31	M.			Embryo liegt auf der linken Seite		20 Urw.	Ch. im Vorderkopf. Verbindung mit den Mesodermflügeln	Hinterhirn segmentiert auch das Medullarrohr	Beginnende Bildung der sek. Augenblase. Linse: seichte Grube	Tiefe noch offene Grube			Rachenhaut nicht durchbrochen	Enddarm noch nicht geschlossen	1. u. 2. Kiemenspalte mit Verschlussplatte.					Niederes Kopfa. reicht nicht bis zum Mittelhirn	Nicht vorhanden	
32	Janosik 115					22 Urw.										W. G. reicht weiter caudalwärts als Urwirbel gebildet sind						
33	Hoffmann 68					24 Urw.								Schwanzdarm geschlossen							In der Anlage begriffen	
34	Janosik 115					30 Urw.										Primäre Urnierenkanälchen						
35	Janosik 115								Sek. Augenblase, Linsenanlage noch nicht abgeschnürt							W. G. hat im hinteren Abschnitt noch kein Lumen						Ist nach Janosik älter als No. 34

FIG. 3. Part of one of Albert Oppel's tables of development, which Keibel adapted for his normal plates. The rows represent specimens, the columns length, age, body form, germinal disc, somites, etc. This is one of several tables for the chick, because the authors described their material in incompatible ways, as either individual specimens (shown here) or stages. From Oppel, *Die Vergleichung des Entwicklungsgrades der Organe der Wirbelthiere* (Jena, 1891), 132–3. Original width 14.2 cm on each of the two pages.

other university, Freiburg, used the histological-embryological collection in Munich, to which he had had access as an assistant of Carl von Kupffer, as well as published descriptions, to compare the degrees of development of organs at different times in different vertebrates. Oppel highlighted the dependence of comparisons between species on staging, or rather not staging, within them, and criticized the easy-going practices that prevented him from using most of the literature. Some authors gave age or length as though these had any general significance. Many set up stages on the basis of whatever single organ they happened to be studying — organs that did not necessarily track the main developmental events — and aggregated features observed in different embryos into stages. But variations in the development of organs within species made arbitrary staging unreliable and the addition of new material difficult. Only from systematic descriptions of the development of many organs within a series of individual embryos — something that was lacking even for the chick — could effective comparisons be made. Oppel adapted a format for presenting internal analyses that could be easily compared and extended. Whereas the early nineteenth-century tables of human development had described bone development in measurements and short descriptions month by month, Oppel provided a series of tables, at least one for each species, in which the columns represented dimensions and organs, and the rows the progress of development (Figure 3). If possible, each row now corresponded to an individual specimen; if not, he listed stages.[50]

Surveying internal and external development as best he could, Oppel revealed temporal displacements (heterochronies) that confirmed the strict invalidity of the biogenetic law. Though he nevertheless set up "similar ontogenetic stages" across the vertebrates, from "pre-fish", "fish" and "land animal" to "proto-amniote", shortly after his book came out he announced a loss of faith.[51] Oppel's Freiburg colleague, Franz Keibel, would reject the law, but conclude that embryologists could still extract phylogenetic information from ontogeny. Rather than being put off by the temporal displacements, they should study them instead; and rather than relying on the literature, they would have to carry out much more thorough studies with the new techniques. This was the primary aim of his *Normal plates on the development of the vertebrates*, which drew on three of the innovations in presenting developmental series that I have just reviewed. On the one hand, Haeckel's comparative plates served as an inspiration and a warning, flawed Darwinist icons that Keibel aimed to supersede. On the other, His's *Normentafel* and Oppel's tables provided resources for comparative works that would respect the differences between species and even individual embryos.

3. NORMAL PLATES BETWEEN LOCAL CRITIQUES AND INTERNATIONAL COLLABORATION

His had proposed that "standard book-keeping" should go on in central embryological institutions. The most important early initiative in this direction was not an institute but loose collaboration on Keibel's normal plates. He had a specific agenda, to provide more complete descriptions in order to reinvestigate the relations of ontogeny and phylogeny, and had to respond to a set of locally intense comparative anatomical and

FIG. 4. Portrait photograph of the German anatomist Franz Keibel, editor of the *Normal plates on the development of the vertebrates*. Frontispiece to H. Stieve, "Franz Keibel zum Gedächtnis", *Zeitschrift für mikroskopisch-anatomische Forschung*, xviii (1929), 1–4. By permission of the Syndics of Cambridge University Library.

anthropological critiques. But the desire for what His had shown were useful laboratory tools was shared widely enough for the project to gain international support.

The son of a West Prussian landowner, Keibel (Figure 4) studied medicine in Berlin and then at the Imperial University of Strasbourg in occupied Alsace, where in 1887 the anatomist-anthropologist Gustav Schwalbe supervised a craniological dissertation and employed him as an assistant for three years. In 1889 Keibel was appointed a prosector to Robert Wiedersheim at the nearby University of Freiburg, where he remained until 1914. After the dissertation Keibel's research was all in embryology. Though he belonged to no school, he credited Wilhelm Waldeyer's Berlin lectures with sparking his embryological interest and also claimed inspiration from the other Berlin anatomy professor, Haeckel's renegade student Oscar Hertwig, and His.[52]

At least as important were the distinctive demands on embryology in a triangle of anatomical institutes at universities in the German south-west: Freiburg, Heidelberg and Strasbourg. While medical faculties were generally reluctant to appoint comparative anatomists, whose claims to expertise in preparing physicians and surgeons were relatively weak, Gegenbaur and his student and successor Max Fürbringer at Heidelberg and Wiedersheim at Freiburg ran two of the anatomical institutes most dedicated to comparative research.[53] While most anatomists did some anthropology on the side, Schwalbe led the way in bringing investigations of variation into the dissecting room.[54] So in this anatomical community, which was held together by regular group excursions,[55] comparative studies of humans and other vertebrates were looked on especially kindly, but the concerns of comparative adult anatomy and anthropology were dominant. Keibel had to take seriously the devastating criticisms of embryology that circulated in the Gegenbaur school and among Schwalbe's anthropologically engaged colleagues.

This is evident in Keibel's first major investigation, in which he sectioned and modelled pig embryos. In two long articles in Schwalbe's *Morphologische Arbeiten* Keibel asserted that embryologists could not trace the development of complex adult structures from the only apparently simple relations of the germ, or draw phylogenetic conclusions, as easily as they had assumed. The initial flourishing of evolutionary embryology had generated synoptic but superficial works — he surely had Haeckel's in mind — and the new methods had been applied only to particular periods and/or individual organs, which were relatively easy to arrange in phylogenetic series. This had left embryologists without a single really complete embryology of any vertebrate. The time had come, Keibel argued, to go back to "monographic" studies of individual species, which should proceed from the "characteristic, well marked particularities of the completed being", or at least from more advanced embryos, back to the less clear earlier conditions. This had always been done in human embryology, and he had fewer pig specimens than His had had human embryos, but it was the opposite of the usual argument for embryology as allowing a morphologist to work from the simple to the complex. That had also been the justification for studying evolutionarily primitive species. Doubting that amphioxus and selachians were really as primitive as had been assumed, Keibel defended mammals as relevant to humans and of intrinsic evolutionary interest.[56]

Keibel presented his study as a test of the biogenetic law. Unable to fit tables that he constructed for the pig into Oppel's stages, he concluded more generally that the temporal "jumblings up" (*Durcheinanderschiebungen*) — "displacements" was too mild a term — were such that, for mammals at least, the law was false. One could not distinguish a fish, let alone a generalized land-animal stage. "Temporal separation is inherent in the concept of *stage*", Keibel argued, "and to me at least it appears impossible to speak of stages temporally displaced through or over one another". Yet he did not doubt that mammalian ancestors must be counted among fish and amphibians, or that the embryos of present-day mammals preserve their traces, and he recognized that the development of other animals might well repeat characteristic major stages.[57] Defending the phylogenetic value of embryology against Gegenbaur's claim that adult anatomy should always be the final court of appeal, Keibel insisted that this more complex embryological evidence of evolution could be unlocked by making those troublesome temporal displacements the topic of research.[58]

Normal plates on the development of the vertebrates would provide embryology with the foundation from which to contribute to evolutionary studies from a position of strength. In October 1895 Keibel called in the *Anatomischer Anzeiger* and personal letters for collaborators. He needed help — no lone embryologist could have studied enough vertebrates in the kind of detail now demanded — and since many libraries would buy all of a series, this was a better economic proposition than individual volumes. By February 1896 the anatomists' house publisher, Gustav Fischer of Jena, had agreed to bring out the plates.[59]

Keibel proposed that studies of the relations between the development of different organs in particular species, and of particular organs across species, would also reveal physiologically important interactions. In this way, comparative and experimental approaches converged on the problem of 'correlation', the interdependence of parts in ontogeny and in phylogeny.[60] Keibel valued Roux's experiments on dependent versus independent differentiation,[61] but insisted that "the laws of the process of organic development can in their essence be deciphered only by *comparative* reflections". Comparing related processes of development would allow the same results to be traced back to the same factors, and hence their mechanical explanation.[62]

We might see Keibel as turning each column of Haeckel's famous–notorious comparative plates into a complex monograph in which the heterochronies that prevented specialists from simply lining up embryos at particular stages could be explored. Keibel established a new genre of embryological atlas by combining plates (*Tafeln*) modelled on His's and tables (*Tabellen*) that modified Oppel's design. The first issue — which re-published Keibel's work on the pig — set the pattern for quarto volumes of plates, tables and text. The text was little more than legends to the plates plus a substantial bibliography. Two plates illustrated the external morphology of individual embryos selected to form a continuous series up to the completion of the external organization (Figure 5). The third gave more highly magnified images of the earliest stages, though cleavage and gastrulation were to be shown, if at all, only in enough detail to indicate the type of development. The tables complemented the plates by describing internal structures. Based on serial sections, they indicated the degree of development of the overall body form, the primitive streak, somites, notochord, nervous system and so on (Figure 6).[63]

In contrast to the selective plates, Keibel intended the tables to include as many individual embryos as possible. For His in 1872, "the variability of the structure of our body" still stood only "as an obstacle in the way" of "the pictorial determination of absolute norms".[64] Now, even embryology, which tends to be held up as a bastion of essentialism, participated modestly and temporarily in a movement to investigate variation. Naturalists' engagements with Darwinism were an important inspiration, though a by no means overwhelmingly Darwinist anthropology is the more immediate source.[65] By the early 1890s, Schwalbe was turning the dissecting-room routine into an opportunity to explore variations throughout the adult body. He and his prosector Wilhelm Pfitzner participated in a general discovery of variation as more than merely troublesome or curious. This put Keibel under pressure. In an article on variation in hands and feet, Pfitzner criticized the "much too apodictic-dogmatic" definition of "the normal". Ernst Mehnert, who joined Schwalbe as an assistant in

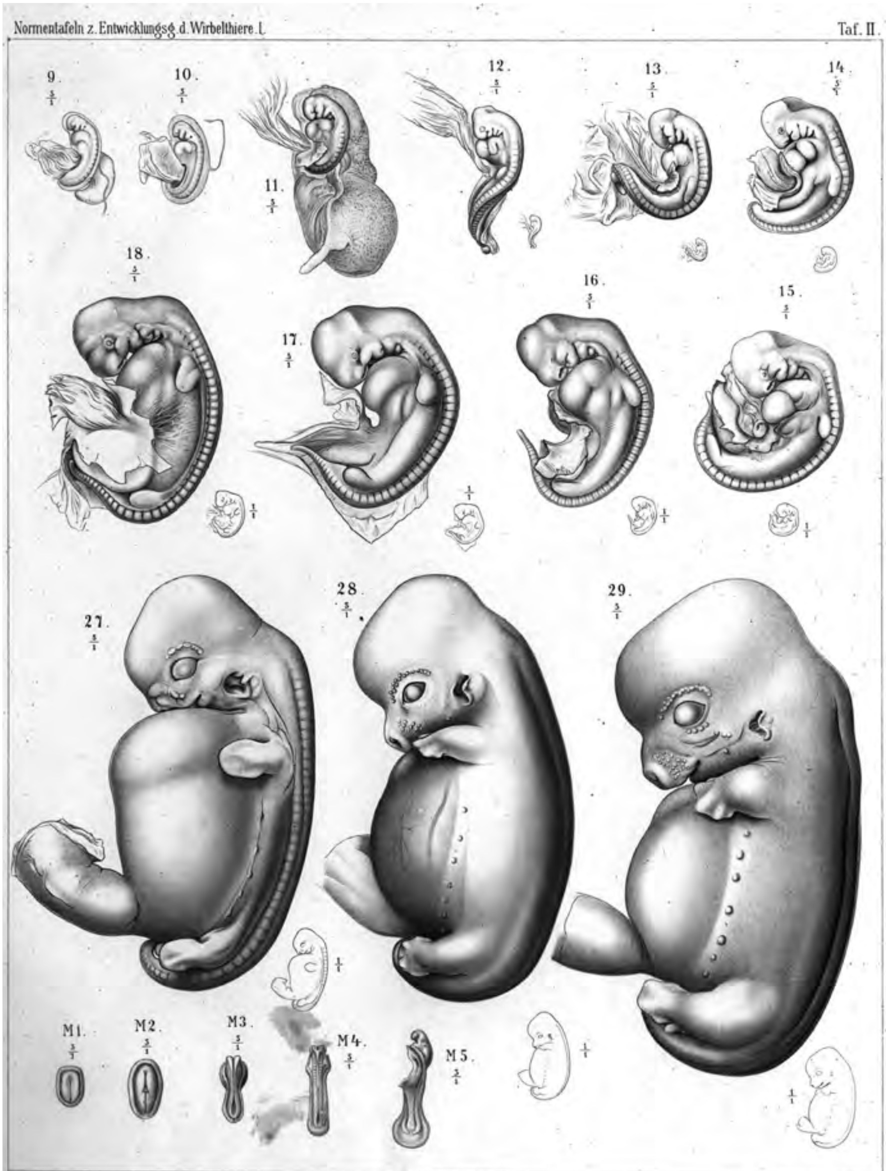


FIG. 5. Normal plate on the development of the pig from Franz Keibel's own first volume in his series. The 'M' figures show wax models. Lithograph by Adolf Giltsch from Keibel, *Normentafel zur Entwicklungsgeschichte des Schweines* (Sus scrofa) (Jena, 1897), pl. II. Original dimensions of border 26.3 × 20.4 cm.

Bez.	Maasse	Alter	Körperform	Primitivstr.	Urwirbel	Chorda	Nervensystem	Auge	Ohr	Nase
21 a S. 17. VIII 93. a. S. N. 243.	Gestreckt gedacht etwa 3,4 mm	16 Tage	Der Embryo ist leicht über die ventrale Seite gebogen.		0 (7) Urwirbel.	Chorda bis auf das vorderste Ende vom Entoderm unterwachsen.	Medullarrohr ganz offen.			
22 160. N. 4. L. 2. 28. März 92.	321 Schn. von 0,01 mm. L. nach Photographie 3,7 mm.	16 Tage 13 Stdn.	Kopfende beginnt sich eben abzuheben.	Länge d. Primitivstreifens ca. 0,4 mm, etwas mehr als ¼ der Körperlänge des Embryo, davor noch eine Strecke weit deutlicher Medullarspalt.	7 Urwirbel, 6 beiderseits abgegrenzte Urwirbel, der erste Urwirbel davor hat vorn keine Grenze. Auch die hint. Grenze des siebenten Urwirbels ist erst eben kenntlich. Ein achter Urwirbel ist in Bildung begriffen.	Chorda bis auf das vorderste Ende vom Entoderm unterwachsen.	Medullaranlage im vordersten Bereich des Kopfendes und ganz hinten im Bereich des Primitivstreifens noch nicht abgegrenzt, Ganglien kenntlich.			
23 258. 17./VIII. 93. c.	Nach der Zeichnung c. 3,7 mm.	16 Tage.			7 Urwirbel, 6 beiderseits abgegrenzte Urwirbel, davor der erste ohne Abgrenzung nach vorn; ein achter Urwirbel beginnt sich auch abzugrenzen.	Die Chorda bis auf das vorderste Ende vom Entoderm unterwachsen.	Die Medullarplatte nach vorn gegen das Ektoderm noch nicht abgegrenzt.			
24 263 u. 264 17./VIII. 93. K.	L. nach Zeichnung gestreckt c. 4 mm.	16 Tage.	Kopfende auf 18 Schnitten v. 0,01 abgehoben.		Zahl der Urwirbel, da einige Schnitte zerstört, nicht genau festzustellen.		Die Medullarplatte vorn gegen das Ektoderm noch nicht abgegrenzt.			
25 199. S. s. 10. 8. 31. März 92.	L., nach Zeichnung c. 3,7, dabei eine kleine Biegung ausser Acht gelassen.	14 Tage. 16 Stdn.	Kopfende auf 22 Schnitten v. 0,01 abgehoben.		7 Urwirbel, 6 Urwirbel beiderseits abgegrenzt, der erste Urwirbel ohne Grenze nach vorn. Ein 8. Urwirbel in Bildung.	Die Chorda bis auf wenige Schnitte am cranialen Ende vom Entoderm unterwachsen.	Medullarplatte vorn noch nicht gegen den Ektoblast abgegrenzt. Ganglienanlagen kenntlich.			
26 259 u. 260. S. 17. VIII. 93. g.	L. nach Photographie gemessen, c. 4 mm (gestreckt gedacht). Schnitte von 0,01 374.	16 Tage.	Das Kopfende auf 33 Schn. von 0,01 abgehoben.	Primitivstreifen incl. Medullarspalt 56 Schnitte von 0,01 mm; also c. ⅓ des Embryo.	7 Urwirbel, 6 Urwirbel beiderseits abgegrenzt, der 1. Urwirbel ohne Grenze nach vorn, ein 8. Urwirbel in Bildung begriffen.	Die Chorda bis auf wenige Schnitte am cranialen Ende vom Entoderm unterwachsen.	Das Medullarrohr ist an einer Stelle des Kopfgebietes dem Schluss nahe. Auch am vorderen Ende beginnt sich die Medullarplatte gegen das Ektoderm abzugrenzen.			
27 257. S. 17./VIII. f.	Länge nach Photogr. c. 3,8 mm.	16 Tage.	Kopfende 0,25 mm abgehoben.		7 Urwirbel, 8 Urwirbelanlagen kenntlich. Der 1. Urwirbel nach vorn nicht abgegrenzt. 6 beiderseits deutlich begrenzt.	Chorda am Vorderende in das Entoderm eingeschaltet.	Das Medullarrohr schickt sich zum Schluss an. Die Medullarplatte beginnt sich am vordersten Ende eben abzugrenzen.			

Bez.	Hypophyse	Mund	Verdauungstractus, Leber und Pankreas	Kiementaschen, Thyreoidea, Thymus, Trachea und Lungen	Urogenitalsystem	Herz und Gefässe	Integument	Skelet	Extremitäten	Amnion	Allantois	Bemerkungen
21 a		Mundbucht eben angelegt.	Kopfdarmbucht etwa 0,5 mm, Enddarmbucht 1,2 mm lang.			Erste Anlage des Herzens und der Herzbeutelhöhle. Gefässe auf dem Dottersack.				Amnionnabel noch 0,35 mm offen.	Die Allantois ist noch klein, zeigt jedoch schon Andeutungen der entodermalen Hörner.	N. T. Fig. 32. Studien II, Fig. 45 auf Taf. IV.
22		Mundbucht angelegt.			Erste Anlage des Excretionsapparates deutlich.	Pleuropericardialhöhle gebildet, Herz- u. Aortenanlagen; Gefässe auf d. Dottersack.				Bis auf den Amnionnabelstrang nahezu geschlossen.	Die entodermale Allantoisanlage noch ganz kurz; allererste Andeutung d. seitlichen Hörner.	N. T. M[4]. Pikrin-Schwefel-Chromsäure. Modell 3. Studien II, Fig. 46 u. 47.
23		Mundbucht angelegt.			Vornieren- resp. Urnierengang angelegt.	Pericardialhöhle, Herz und Gefässe angelegt.				Amnion bis auf den Amnionnabelstrang geschlossen.	Entodermale Allantois noch ganz klein, aber schon beginnende Hornanlagen.	Sagittalserie.
24		Mundbucht angelegt.			Vor- resp. Urnierengang angelegt.					Amnion bis auf den Amnionnabelstrang geschlossen.	Entodermale Allantois noch sehr kurz, erste Anlage der entodermalen Allantoishörner.	Kopfende quer, Caudalende längs.
25		Erste Anlage der Mundbucht.	Der Kopfdarm hat eine Länge von 52 Schn. von 0,01. Der Enddarm auf 84 Schnitten von 0,01 getroffen.		Erste Anlage des Vor- resp. Urnierenganges.	Pericardialhöhle, Herz- und Gefässanlagen.				Das Amnion noch auf 43 Schnitten von 0,01 offen.	Erste entodermale Allantoisanlage.	
26		Mundbucht deutlich angelegt.	Kopfdarm auf 49 Schn. von 0,01 mm getroffen. Enddarm auf 97 Schnitten von 0,01 mm getroffen.		Erste Anlage des Excretionssystems.	In der Herzanlage noch mehrfache von Endothel umgrenzte Lumina. In den Gefässen noch kein Blut.				Das Amnion bis auf den Amnionnabelstrang geschlossen.	Entodermale Allantoisanlage noch gering.	In zwei Stücken geschnitten, 259 Kopfende, 260 caudales Ende. Beide quer.
27		Erste Anlage der Mundbucht.	Kopfdarmbucht 0,4 mm. Enddarmbucht 0,9 mm.		(?)	Herzanlage u. Gefässe noch ohne Blut.				Amnion bis auf den Amnionnabelstrang geschlossen.	Allantois 0,1 mm lang, die Allantoishörner beginnen sich zu bilden.	Sagittal geschnitten.

Normentafeln zur Entwicklungsgeschichte der Wirbelthiere I. 6

FIG. 6. Table of pig development. From Franz Keibel, *Normentafel zur Entwicklungsgeschichte des Schweines* (Sus scrofa) (Jena, 1897), 40–41. Original width 20.5 cm on each of the two pages.

1890 and helped measure the cadavers, would spearhead a moral campaign against casual pronouncements of embryological norms.[66]

Mehnert sharpened Oppel's critique of staging into a point of principle. Impressed by variations in the pelvic girdles of bird embryos, and of the turtle embryos he had collected on expeditions in his native Russia, in 1895 Mehnert compiled reports of variations from the literature. He railed against the assumption "that embryos of the same species belonging to the same stage are completely the same as each other and that as a result more or less any embryo may count as norm for the relevant stage of the species investigated". "Mostly *one embryo*, *one series is singled out* — which the author in question happens to find typical — *and described exactly*. The correlation of the organs found in this object is designated the 'norm' and the embryo in question registered as a 'stage'. These authors then also indicate exactly that this or that process begins at a certain number of somites." By contrast, embryologists who took the trouble to investigate many embryos found considerable variation. They avoided giving specific times for the appearance of a structure and speaking of 'stages'. They described development within a certain period, and took account of the individual deviations.[67]

Mehnert and Keibel shared enough common ground that Keibel presented a subsidiary purpose of the project as documenting individual variation, and Mehnert signed up to write normal plates on the turtle and the ostrich. But then they became embroiled in polemic. Gould discussed their disagreement over the biogenetic law,[68] but variation was at least as important a bone of contention and the two issues were linked. Reviewing Keibel's pig data, Mehnert found much more than the "not very significant" variation that Keibel was willing to acknowledge. Keibel repudiated Mehnert's tendentious reinterpretions of his work as based on the misunderstanding that for mammalian embryos one could rely on estimates of age. More generally, Keibel both insisted that embryonic variation was a truism and refused to accept that its range was as wide as his colleague claimed. The two men also fought over von Baer: Mehnert enlisted the imaginary plate in his defence, whereas Keibel relied on the preface.[69]

As Mehnert's health began to fail, he spent the nights and the holidays furiously writing long, speculative essays that drew far-reaching evolutionary conclusions from the very large variations he took to signal the independent development of parts. But though finding the most extreme cenogenesis, he insisted, absurdly in Keibel's view but to Haeckel's applause, that the biogenetic law was still valid — at the level of individual organs. Holding many variations to be palingenetic, Mehnert proposed that determining the range of variation for individual taxa would have phylogenetic value. Keibel upheld the importance of correlation. The row may have been enough for Mehnert to pull out of the plates before his early death in 1902.[70]

Schwalbe welcomed the normal plates because of the practical advantage, demonstrated by His for human embryology, that they allowed new embryos to be arranged easily. But, committed to statistical studies of variation and impressed by Mehnert's results, he declared in a chairman's opening address to the Anatomical Society that small numbers and the difficulty of standardizing estimates of age meant that "[t]he ideal of a *Normentafel* will, however, hardly ever be achievable. This would consist in setting down in measurements and figures, from a statistically sufficiently large number of embryos of the *same* age, the most frequent form and size, as well as the most frequent relationship of organization".[71]

We see here again how Keibel's main concern with comparing embryos of different species had to take account of the demand, which was perhaps pressed harder in the Strasbourg anatomical institute in the 1890s than anywhere else and at any other time, that descriptions of embryological material take account of individual variation. Keibel's defence highlighted the practical value of *Normentafeln* as tools, and acknowledged that they would never produce statistical norms. But that was wholly impracticable, he insisted; even determining age was not as easy as Schwalbe implied. Such extraordinary quantities of embryos would be required to gain significant results that investigations could be carried out only for very short periods of development; and usable measurements would in some cases be possible only on models reconstructed from serial sections, the labour of making which ruled out statistically significant numbers. Quantitative studies were best reserved for special investigations, such as the Austrian embryologist Alfred Fischel's measurements of parts of duck embryos along the anteroposterior axis. Embryologists' tables should provide materials for the study of individual variation, but not lose themselves in details straightaway.[72] Keibel prevailed because few embryologists were obliged even to consider the anthropological ideal of statistical norms.

More generally, Keibel recruited to the project because a consensus began to form on the usefulness of the plates beyond the reinvestigation of the relations between ontogeny and phylogeny that had attracted him. He always added that they would also serve as indispensable laboratory aids. But he accepted that a normal plate demanded a deceptively large amount of costly work for relatively little reward. The series sought to help authors over the great obstacles even to describing thoroughly the development of a single species and to make this a little less unrewarding.[73] In practice, Keibel signed up close colleagues and other embryologists who already had plans, and in several cases special grants,[74] to study particular species, and sought to persuade them that publishing (or republishing) with him would give their research wider significance and authority. To reinforce the moral obligation he had the names of authors and prospective authors printed on the title page of every volume — and removed as they pulled out.

Table 1 lists the normal plates that appeared, and more than as many again that were planned but did not. Keibel's team of over 40 anatomists and zoologists delivered 12 volumes covering 14 species before the First World War temporarily halted the project. Recruitment is patterned by discipline, seniority and nationality. Within the German-speaking universities Keibel, an anatomist advertising in the *Anatomischer Anzeiger*, attracted only anatomists; zoologists were in any case more likely to study invertebrate development. Some notable embryologists' conspicuous absence may simply indicate Keibel's limited power to persuade colleagues to take on a relatively unattractive task: an associate professor, he recruited no German scientist more senior than himself. Keibel, his medical students Karl Abraham and Curt Elze and a Japanese visitor, plus the Freiburg-trained Karl Peter and the Austrians Otto Grosser and Julius Tandler, did most of the work. Authors from outside the German universities cross these boundaries of discipline and to some extent seniority. The United States made the most significant contribution through the German-trained embryologist Charles S. Minot, who was building up a large collection at Harvard Medical School, and the University of Chicago zoologist Charles O. Whitman, but both enlisted junior colleagues, such as Richard E. Scammon.[75] The rest of the prewar plates were made by the zoological explorers, Semon, John Graham Kerr from Francis Balfour's Cambridge school, and A. A. W. Hubrecht of Utrecht; all had an interest in getting the most out of their hard-won material.

4. AN EMBRYOLOGICAL EMPIRE IN A PUBLICATION SERIES

Keibel edited normal plates that describe the embryos of various vertebrates in a single "standard series".[76] His authors collected biologically, geographically and socially diverse objects, and analysed them in a common framework, a precondition for comparative work. We might say that they mapped an embryological empire.[77] The plates vary because embryologists could study some species much more freely than others, and the difficulty of recruiting authors restricted Keibel's power to enforce a uniform approach. But these relatively subtle differences help to make clear just how much the plates shared. Though they appeared at irregular intervals, and so editor and contributors missed out on some of the discipline of serial publication, all were at some level committed to a common project that sought to be more than the sum of the parts.

Keibel's authors joined forces to analyse vertebrate species selected for their diverse systematic positions and because medicine, agriculture, hunting, fishing and tourism gave access to them. Embryologists had traditionally worked on humans when they could, and the rise of operative gynaecology made earlier normal specimens available from the clinics.[78] No longer acceptable as surrogates, except for the earliest stages, but invaluable for comparison, were domestic amniotes that embryologists could breed or have bred themselves: chicks and (before the rise of the laboratory mouse) rabbits. More unusually, Peter raised lizards in terraria over several summers.[79] Embryologists also cadged animals from farmers, hunters and fishermen or caught them in the wild. Keibel's father gave him six pregnant pigs and Keibel himself went with local hunters to cut the uteri from the warm bodies of the does they killed.[80] As a contrast to the chick Grosser and Tandler selected the lapwing because they expected its development to be unaffected by the "degenerative processes" that followed domestication, and because it was available. Being developed for holidaymakers, the village of Fonyód on the south-eastern shore of Lake Balaton served as a base for collection from the meadows adjoining the swamps.[81] It took Whitman, as director of the Allis Lake Laboratory at Milwaukee in the late 1880s, "years of persistent and patient effort" to discover nests and eggs of the mudpuppy,

TABLE 1. Series of normal plates on the development of the vertebrates. Franz Keibel's are listed first, followed by the successor series published under the auspices of the Institut International d'Embryologie, then plates that should have appeared in these series but were published separately, the many that are known to have been agreed but never published, and finally two proposals that were rejected. Dates of agreement with Keibel (or in the case of Ross Harrison, with Daniel de Lange), withdrawal and rejection are the earliest known; some will be many years after the event. Names in parentheses are of scientists who do not appear as authors but were involved in the work by passing on the commission, collecting material and/or starting the plate. Authors' locations are their places of work at the time of publication, or if the plate was not published, agreement or rejection. Species names are given, unmodernized, only when in the sources, except that I have provided a common name for every Latin name listed. Many of the authors who did not deliver had already published embryological work before they were signed up, from which one could speculate, for example, that Edward Bles would have contributed a plate on *Xenopus laevis*. Some will have authored articles that presented developmental series, but I have found no evidence of separately-published plates. Information is from title pages, prefaces (NT 1, 8, NT 2, 1, NT 3, pp. iii–iv, NT 5, 1–2, NT 12, 1, and de Lange and Nierstrasz, *Tabellarische Uebersicht* (ref. 125)) and letters from Keibel to Julius Tandler, 19 March 1906 (ref. 96), and to Gustav Fischer (refs 121–2).

No.	**Date**		**Author**				**Species**	
	Published/ withdrawn	Agreed/ rejected	Name	Dates	Location	Discipline	Latin name	Common name
Franz Keibel's *Normal plates on the development of the vertebrates* (Jena: Gustav Fischer)								
1	1897		Franz Keibel	1861–1929	Freiburg	Anatomy	*Sus scrofa domesticus*	Pig
2	1900		Franz Keibel Karl Abraham	1861–1929 1877–1925	Freiburg Freiburg	Anatomy Med. student	*Gallus domesticus*	Fowl
3	1901	1897	Richard Semon	1859–1918	near Munich	Phylogeny	*Ceratodus forsteri*	Australian lungfish
4	1904	1900	Karl Peter	1870–1955	Breslau	Anatomy	*Lacerta agilis*	Sand lizard
5	1905	1896 1903	Charles S. Minot Ewing Taylor	1852–1914 1874–1971	Harvard Harvard	Anatomy Histol., emb.	*Lepus caniculus*	Rabbit
6	1906	1905	Tsunejiro Sakurai (Franz Keibel)	1872–1928 1861–1929	Freiburg Freiburg	Anatomy Anatomy	*Cervus capreolus*	Roe deer
7	1907	1905	A. A. W. Hubrecht Franz Keibel	1853–1915 1861–1929	Utrecht Freiburg	Zoology Anatomy	*Nycticebus tardigradus* *Tarsius spectrum*	Slender loris Spectral tarsier
8	1908		Franz Keibel Curt Elze (Ivar Broman) (J. August Hammar) (Julius Tandler)	1861–1929 1885–1972 1868–1946 1861–1946 1869–1936	Freiburg Freiburg Lund Uppsala Vienna	Anatomy Med. student Anatomy Anatomy Anatomy	*Homo sapiens*	Human
9	1909	1906 1905	Otto Grosser Julius Tandler	1873–1951 1869–1936	Vienna Vienna	Anatomy Anatomy	*Vanellus cristatus*	Lapwing
10	1909	1905	John Graham Kerr (John S. Budgett)	1869–1957 1872–1904	Glasgow Cambridge	Zoology Zoology	*Lepidosiren paradoxa* *Protopterus annectens*	S. Amer. lungfish African lungfish
11	1910	1910 1910 1897	Albert C. Eycleshymer James M. Wilson (Charles O. Whitman)	1867–1925 1842–1910	St Louis St Louis Chicago	Anatomy Anatomy Zoology	*Necturus maculosus*	Mudpuppy

12	1911	1907	Richard E. Scammon	1883–1952	Harvard	Anatomy	*Squalus acanthias*	Spiny dogfish
		1896	(Charles S. Minot)	1852–1914	Harvard	Anatomy		
	1900	1896	(Alfred Schaper)	1863–1905	Harvard	Anatomy		
13	1922	1905	Otomar Völker	1871–1955	Brno	Anatomy	*Spermophilus citillus*	Ground squirrel
14	1925	1909	Leopold Glaesner	1885–	Hildesheim	Zoology	*Molge (Triturus) vulgaris*	Smooth newt
15	1937	1901	Bruno Henneberg	1867–1941	Giessen	Anatomy	*Rattus norvegicus*	Brown rat
16	1938		Tokuyasu Kudô	1888–1955	Niigata	Zoology	*Megalobatrachus japonicus*	Giant salamander
Institut International d'Embryologie *Monographs on the normal development of vertebrates* (Utrecht: Oosthoek)								
1	1932	1905	Hugo F. Nierstrasz	1872–1937	Utrecht	Zoology	*Tupaia javanica*	Javan tree shrew
		1917	Daniel de Lange	1878–1947	Utrecht	Zoology		
	1915	1905	(A. A. W. Hubrecht)	1853–1915	Utrecht	Zoology		
2	1937		Fokko J. Huisman	1898–	Utrecht	Zoology	*Manis javanica*	Malayan scaly anteater
			Daniel de Lange	1878–1947	Utrecht	Zoology		
Agreed, but published after the series had ceased to appear								
	1952	1897	Friedrich Kopsch	1868–1955	Berlin	Anatomy	*Rana fusca*	Brown grass frog
	1969	1936	Ross G. Harrison	1870–1959	New Haven	Zoology	*Amblystoma punctatum*	Spotted salamander
Agreed, but not published as separate works								
	1900	1897	Sándor Kaestner	1865–1924	Leipzig	Anatomy		Chick, duck
		1897	Friedrich Kopsch	1868–1955	Berlin	Anatomy		Trout
							Triton	
	1900	1897	Ernst Mehnert	1864–1902	Strasbourg	Anatomy	*Emys lutaria taurica*	Turtle
							Struthio africanus	Ostrich
	1922	1897	Adolphe Nicolas	1861–1939	Nancy	Anatomy	*Anguis fragilis*	Slow worm
	1922	1897	Jacob Reighard	1887–1942	Ann Arbor	Zoology	*Amia*	Bowfin
	1918	1897	Richard Semon	1859–1918	Jena	Phylogeny		Monotremes
	1901	1897	Johannes Sobotta	1869–1945	Würzburg	Anatomy	*Belone acus*	Garfish
	1929	1900	Franz Keibel	1861–1929	Freiburg	Anatomy		Duck
	1922	1900	Wilhelm Lubosch	1875–1938	Breslau	Anatomy	*Petromyzon planeri*	Lamprey
	1909	1900	Kakichi Mitsukuri	1857–1909	Tokyo	Zoology	*Trionyx japonicus*	Asian softshell turtle
	1906	1900	Georg Wetzel	1871–1951	Breslau	Anatomy		An ophidian

No.	Date		Author				Species	
	Published/ withdrawn	Agreed/ rejected	Name	Dates	Location	Discipline	Latin name	Common name
	1904	1901	Eugen Fischer	1874–1967	Freiburg	Anatomy		Mole
	1922	1901	Paul Martin	1861–1937	Zürich	Vet. anat.		Cat
	1922	1901	Johannes Sobotta	1869–1945	Würzburg	Anatomy	*Syngnathus*	Pipefish
	1928	1904	Bashford Dean	1867–1928	New York	Zoology		
	1921	1904	Albert H. Soulié	1867–1921	Toulouse	Anatomy		
	1922	1904	Frédéric Tourneux	1852–1922	Toulouse	Histology		
	1926	1905	Edward J. Bles	1864–1926	Glasgow	Zoology		
		1905	Jan Boeke	1874–1956	Helder	Anatomy		
	1922	1906	Albert Brachet	1869–1930	Brussels	Anatomy		
	1922	1906	Thilo Krumbach	1874–1949	Breslau	Zoology		
	1909	1907	Alfred Greil	1876–1964	Innsbruck	Anatomy		
	1922	1909	Hugo Fuchs	1875–1954	Strasbourg	Anatomy		
		1911	Miguel Fernández	1882/3–1950	La Plata	Zoology, comp. anat.		
		1911	James P. Hill	1873–1954	London	Zoology		
Offers rejected								
		1922	Aleksandr M. Zavadsky	1879–	Petrograd	Zoology		Sterlet
		1929	Oskar Schumacher	1894–1942	Vienna	Anatomy	*Chalcides ocellatus*	Lizard

a totally aquatic salamander common around the Great Lakes, but then the entire material for the normal plate was collected in a single May day.[82]

More-intrepid embryologists used imperial networks to bring home 'living fossils' and 'missing links', ancient species with ranges outside Europe and the U.S.[83] Looking back, an anatomist captured the aggressively comparative ambition of these explorers: "The jungles and hillsides of the world must be ransacked for out-of-the-way species which may fill the many gaps; embryos of squirrel and rabbit, sheep and dog must be set beside those of macaque and armadillo and of unheard-of creatures from distant lands like the tarsier [an arboreal and nocturnal primate of south-east Asia], tenrec [hedgehog-like Madagascan insectivores], and tupaia [south-east Asian tree-shrews]."[84] Semon, Kerr and his companion John Budgett went after lungfish on three continents because of their status as (relatives of the) links between fish and land animals. Semon went to Australia, while Kerr and Budgett fished the South American lungfish in the swamps of the Paraguayan Gran Chaco.[85] Budgett then independently found the African lungfish on an island in the River Gambia, but handed the embryos over to Kerr before dying of malaria and black-water fever caught on an expedition to observe the development of another ancient fish.[86] In Indonesia Hubrecht hunted prosimians as human ancestors.[87] The British Empire made Semon's trip possible, and the South American Mission provided Kerr with transport, accommodation and contacts.[88]

Bringing specimens through these networks into their laboratories, Keibel's authors extended embryology's intellectual dominion by framing as embryos objects that their suppliers had seen in very varied terms. Closest to home, anatomists, whose medical colleagues complained of women's ignorance of their own bodies, reinterpreted bleeds that had been experienced variously as unremarkable late periods, distressing miscarriages or desired restorations of menstrual flow, and discovered embryos in the bodies of patients who had not even known they were pregnant.[89] Fishermen's 'candles' became egg-cases.[90] Kerr and Budgett first encountered the South American lungfish *Lepidosiren* when they came across "a party of Indians cooking their supper". Known as "the Paisiapto or black-food people", "their main food was a dark-coloured eel-like fish that abounded in the swamps by which they lived". Kerr ate "a plate of the cooked lungfish ... 'con mucho gusto', for the flesh, rich with its deep orange red fat, was most tasty". Unlike the missionaries, he credited the Paisiapto "witch doctor", as "the common ancestor of our scientist, priest and physician", with "scientific knowledge of his environment".[91] Budgett, by contrast, described the West African "natives" as "entirely ignorant of any but the most obvious facts of natural history", though the "head fisherman, Sory" had found him the first "children of the 'Cambona'" and so taught him where to look for the *Protopterus* nests.[92] Hubrecht was brought fewer slender lorises than spectral tarsiers, although the former were more numerous, because the local people caught fewer alive; probably, he speculated, because of "certain superstitious ideas".[93] Prior interpretations were devalued as objects were endowed with enormous scientific value, but Kerr could still see the embryologists' cult of missing links from the outside. He reported that his old Cambridge professor, Alfred Newton, had been scandalized by the lungfish dinner, a "sacrilegious use of the sacred *Lepidosiren*".[94]

These diverse specimens were all to be analysed and presented in the same way, but limitations on what could be collected combined with local methodological preferences to make the plates a series of variations on Keibel's theme. Practices of the kind that have dominated discussions of mechanical objectivity — the microscopical and graphic procedures that converted specimens into highly magnified external drawings and internal descriptions — differed relatively little. Though Keibel soon abandoned a plan to have a single artist re-draw everything, the embryos were generally shown from the left or (for younger stages) the dorsal side at fivefold magnification (or multiples thereof).[95] Printing was generally by the highest-quality method, lithography, at Fischer's local firm.[96] The original design was for the first two plates to display post-gastrulation development (Figure 5), and the third to show supplementary pictures, especially of younger stages at higher magnification, but most authors preferred a single series across three or four plates. Embryos were sectioned for the internal analyses and the results summarized in the tables (Figure 6).

How were representatives selected and what did they represent? The project began with Keibel's inability to set up comparable stages, or divisions based on general characters, across the mammals; it was informed by Oppel's and Mehnert's criticisms of naïve staging within species. Yet though Keibel and his direct collaborators avoided the term 'stage' and offered selections of mere individuals, the other authors made individual embryos characterize stages. Semon conceded that his depicted and described 'stage 48' of *Ceratodus* referred in reality only to a particular unique individual, while as a stage it was an abstraction, even a fiction — but no more so, he argued, than every other division in the organic world. Peter acknowledged that his figures showed "individuals and not 'stages'", but for the "purely practical purpose" of ordering a lizard embryo according to figure and description, "one can surely with reference to the figures use that disreputable word 'stage'".[97]

Authors differed more in the extent to which, where enough material was available, they took advantage of the tables to document variation. Keibel, and especially Peter, included many more embryos in the tables than the plates, and commented on individual differences. We could view their presentation of larger numbers of less interpreted specimens than the previous generation as sharing in a more general alarm about eliminating subjectivity.[98] We might, more positively, see the tables as allowing them to analyse embryos thoroughly while avoiding decisions that had come to seem arbitrary, and as turning a nuisance into research materials. But we should recognize that several authors remained unconcerned. Kerr's tables describe only the lungfish specimens shown on the plates (Figures 7 and 8). Though in preliminary work he had been "greatly impressed by the variability observed amongst embryos of similar stages" and convinced "of the futility of trying to give a fair description of the embryology of any type unless one has a very large material to go upon", he found it unnecessary to indicate the range of variation or how he had selected 'stages'.[99]

The Harvard embryologists, working on relatively abundant embryos, approached

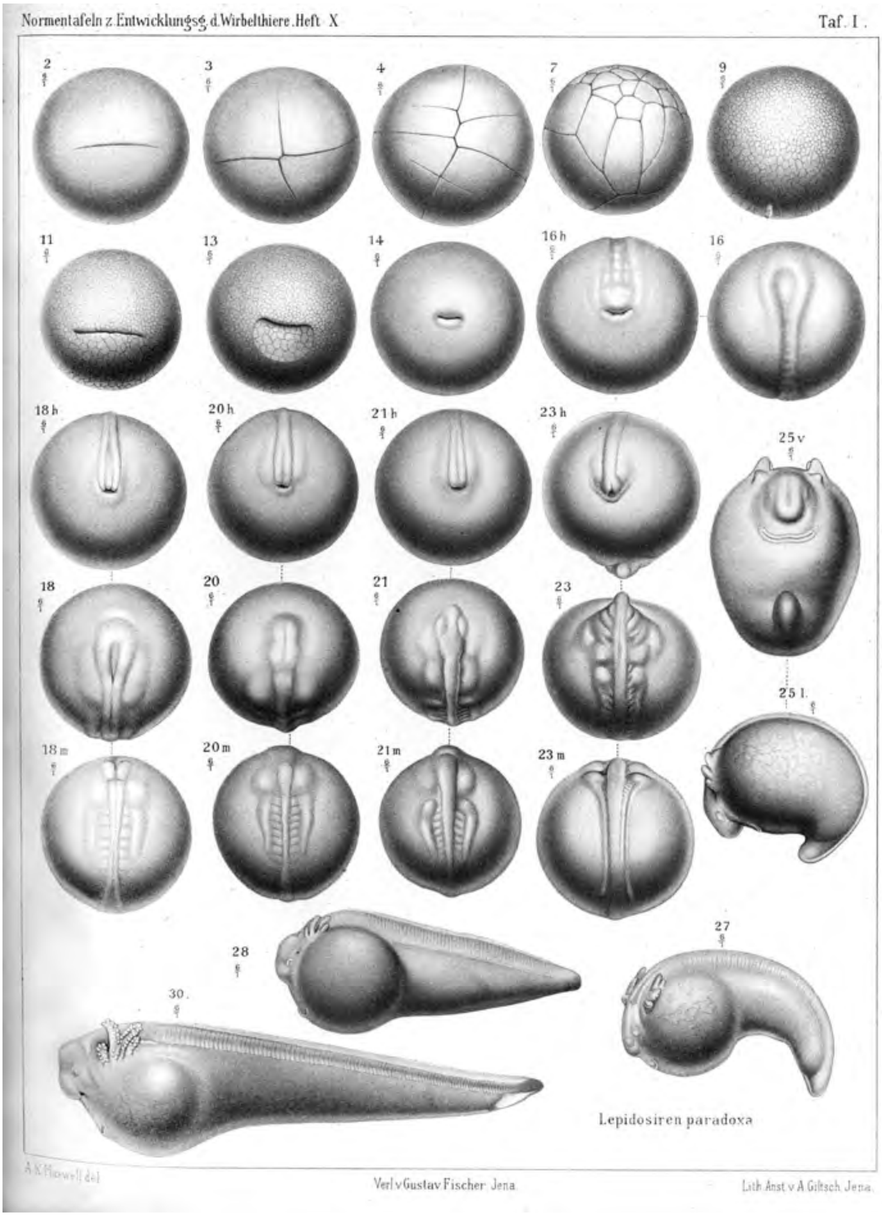


FIG. 7. John Graham Kerr's normal plate on the development of the South American lungfish, *Lepidosiren*. By contrast with Fig. 5, which represents scarce mammalian embryos, the regular arrangement heightens the sense of confident mastery of the whole of early development. Lithograph by Adolf Giltsch after drawings by A. Kirkpatrick Maxwell from Kerr, *Normal plates on the development of* Lepidosiren paradoxa *and* Protopterus annectens (Jena, 1909), pl. I. Original dimensions of border 26.3 × 20.0 cm.

Stage	External features	Segmentation cavity	Invagination	Archenteron	Dorsal wall of archenteron	External form	Metotic mesoderm segments	Nervous system	Eye	Otocyst	Visceral clefts	Urogenital system	Stage
2	First meridional furrow.												2
3	Second meridional furrow.												3
4	First four vertical furrows.												4
7	Egg completely segmented.	Hardly any chinks between blastomeres.											7
9	Late segmentation.	Appears as a larger chink amongst the blastomeres.											9
11		Fully developed. (Becomes traversed by spongework of macromeres about stage 12.)	Continuous latitudinal groove which may reach 120° in length.										11
13		Practically obliterated. Reduced to a few chinks.	Blastopore reduced in length: crescentic slit concave dorsally.	135° in length. (In other specimens of same external appearance 103°, 105°, 106°, 120°, 140°.) Inner end rounded with continuous cuticle.	Composed of large-yolked cells. Roof cells large yolked agreeing in character with rest of endoderm, not with ectoderm.			Deep layer of ectoderm of medullary plate decidedly thickened and beginning to be more than one cell thick.					13
14			Much shorter. Large yolk cells almost completely hidden.		(Mesoderm split off from endoderm except at outer edge: also separated by a split from the notochordal rudiment.)			(Very slight longitudinal depression along centre of medullary plate. The latter has grown down into a distinct keel by multiplication of its deep layer cells in the region of the mesial plane.)					14
16			Beginning to be enclosed by medullary folds.		(Mesoderm and notochord distinct.)		Mesoderm not yet segmented.	Medullary folds distinct. Medullary keel well developed.					16
18	Branchial eminence appears. (Pronephric swelling appears 17.)		Reduced to short slit-like opening.	225°.			Mesoderm segments (about 7) faintly discernible with central coelomic cavity beginning to appear.	Medullary folds have met along middle of trunk region.					18
20						Medullary folds have completely met.	About 12? Myocoeles present widely open.	Neural rudiment still solid.	Solid optic rudiment.	Begins as downgrowth of deep layer of ectoderm.	(3 solid rudiments [AGAR].)	Pronephric swelling opposite anterior segments.	20

FIG. 8. John Graham Kerr's table for *Lepidosiren*. Unlike Keibel's pig table (Fig. 6), which represents individual specimens, Kerr shows stages. From Kerr, *Normal plates on the development of* Lepidosiren paradoxa *and* Protopterus annectens (Jena, 1909), 12–13. Original width 18.7 cm on each of the two pages.

variation more systematically, but again, only in order to select the best series for thorough analysis. Minot claimed for rabbit embryos that he had largely determined "stages, which should be really nearly normal, i.e., representative of the median of the variations for each selected age", by taking the three individuals from the litter which for that age "appeared nearest central". "A typical embryo" was drawn and all three were sectioned, in orthogonal planes, as the basis for the tables. Of the "not very frequent" variations among the threes, "all the important ones" were noted. For the dogfish Minot stressed similarly that the "series have not been made at random, but by a carefully followed plan". As far as he could, Scammon based stage descriptions on three orthogonally sectioned specimens; he added carefully shaded graphical reconstructions to the text.[100]

Stages and norms were hard to compare. Grosser and Tandler related most of their lapwing embryos to Keibel and Abraham's chicks, but Kerr was unable to model his lungfish stages on Semon's or even to make those for *Lepidosiren* and *Protopterus* the same. Within species, since "[a]ny division into formal stages of a period of gradual change and differentiation is perhaps open to criticism as being arbitrary and artificial",[101] authors had to deal especially carefully with any predecessors in the field. Should one extend a previous system or attempt to supplant it? For human embryos His's celebrated *Normentafel* provided a universally used and flexible framework. Keibel and Elze managed to pay homage to His by dedicating the work to his memory and including a version of his plate as a first figure, and at the same time to stress its provisional character.[102] In a field already congested with competing series, Scammon took another approach. Balfour's elasmobranch stages were so well established that he had no choice but to relate his stages to them. So he reminded readers that Balfour's series mixed three species, fresh and fixed specimens, and various unspecified magnifications, and still contained major gaps. In a move that became standard for ambitious normal-plate-makers, he presented a "general correlation table" that subsumed Balfour's and nine other elasmobranch series within his own.[103]

In the different amounts of material Keibel's authors could collect, and through the various ways they treated it, biological, geographical and cultural distinctions were reproduced in the plates and tables. Yet the individual volumes did not need to be fully standardized for them to be seen as a series dedicated to a common project.

5. THEORETICAL FAILURE AND INSTITUTIONAL SUCCESS

Keibel's normal plates have a modest place in Gould's history of the "decline, fall, and generalization" of Haeckel's biogenetic law around 1900.[104] In grand theoretical terms, the series did fail, but as a practical and institutional success it still shapes embryology today.

Keibel promoted the plates as a resource for exploring correlation and variation. Several authors began to compare and identify heterochronies as they went along,[105] but no new synthesis emerged, and the project does not seem to have raised the status of embryos as evidence of evolution.[106] Nor did it lead to any general conclusion about variation — perhaps the numbers were just too small or the approach not quantitative enough — though Peter made variability a major (and controversial) strand of his research.[107] From the start, however, Keibel had promised that quite apart from the significance of the plates for the "highest and ultimate goals of embryology", they would provide "a good aid in embryological laboratories", i.e., in ordering and interpreting specimens in jars and on microscope slides, along with the corresponding drawings and models.[108] Reviewers agreed, and Kerr's textbook explained that "[w]here no normal plates exist the embryologist should make it his [*sic*] first business to construct one".[109]

Published in runs of only 300,[110] Keibel's plates were intended for university and institute libraries; they did not seek to change medicine or agriculture. Keibel and Elze's volume on human development could not have been used in eugenics, in spite of the involvement of Tandler, later active in this direction, because clinical access to embryos so early in pregnancy was still exceptional, as it was also for the few economically important mammals in the series. But authors who moved to related fields — Abraham to psychoanalysis and Scammon to foetal and infant anthropometry — may have drawn on their experience of staging embryos.[111] And the normal plates were called on as evidence in highly public disputes. Keibel and Elze's appeared in the middle of a second row over accusations that Haeckel had forged embryological illustrations. This one was started by the Kepler Federation, an anti-freethinking organization dedicated to reconciling scientific knowledge and Protestant belief. The campaign backfired when Keibel and other German anatomists and zoologists were cornered into a qualified defence of the ageing prophet against a greater threat.[112]

On the one hand, the normal plates represent a triumph of exact description, as different from Haeckel's popular works as could be. Keibel and Elze's plate, especially, consolidated just the kind of human embryology that His had used against him. His's student, Franklin P. Mall of Johns Hopkins, explained that "in the study of human embryology ... many of the specimens obtained are pathological, and on account of the wide interest in this subject are often extravagantly and poorly described". These criticisms targeted clinicians who analysed specimens that anatomists preferred them to hand over. Mall commended the new work "equally as much for what has been omitted from it as for what has been included". "The embryos ... have been carefully selected and the statements regarding them are sound and conservative."[113] On the other hand, Haeckel, who did not even aspire to be conservative, welcomed the "excellent" normal plates too. For him, no longer close to the cutting edge of research but with millions of readers around the world, the important point was still the fundamental agreement in the characteristic structure of all vertebrate embryos. While he regretted that, as an "exact embryologist" in the His mould, Keibel opposed the biogenetic law, he and his secretary used the comparative plates and His's *Normentafel* in their propaganda for a monist world-view.[114]

Keibel's normal plates established themselves as standard resources, but his own career might nevertheless seem to confirm a sense of failure. Though he made Wiedersheim's institute an international centre of research in comparative embryology, he was for a quarter-century unable to secure a chair of his own. But few anatomists will have objected to his doing descriptive rather than experimental work. The probable reasons are the usual ones: a general shortage of positions, a reputation as a dull teacher, a feeling that his research was so concentrated in a field with little clinical relevance, and then, once he had been passed over for years, that he was getting too old. So he remained in a subordinate position until the age of 53, when, in July 1914 — an inauspicious time, as things turned out — he was finally called to succeed Schwalbe in Strasbourg. Keibel presumably owed the appointment in part to connections at his alma mater and in part to the way that he had built an international reputation, especially with the normal plates, that compensated for lack of local power. He had honorary doctorates from two British universities and from Harvard.[115]

The project did not just benefit Keibel's career; it also helped institutionalize embryology. We saw that in the nineteenth century the science existed mainly as special courses, but lacked the trappings of a full discipline: there were very few chairs of embryology and embryologists met with anatomists and zoologists rather than among themselves. Only in the early twentieth century were separate embryological institutes and a specialist society created. Histories of biology lead us to expect that these would be the work of experimenting embryologists, but they made homes in biological institutes and marine stations. The new embryological institutions were founded by comparative and human embryologists who supported Keibel's project.

The normal plates are prominent among several initiatives that led to an international resurgence of human and comparative vertebrate embryology. Towards the end of his life, His had tried to use the International Association of Academies, a cartel of learned societies in which he represented Saxony, to create a central embryological institution that would house a collection and produce plates and models.[116] This did not happen, but the plan led more or less directly to the foundation in 1911 of the first specifically embryological society, the Institut International d'Embryologie (I. I. d'E.). Keibel, Hubrecht and another mammalian embryologist, Robert Bonnet, organized this exclusive club of European comparative vertebrate embryologists expressly to promote the collection and study of the embryos of endangered colonial mammals, and so to make material, not least from the Dutch colonies, available for central collections and further normal plates.[117] After Hubrecht's death in 1915 a laboratory was established in his memory at Utrecht, as the first of the international centres envisaged in the statutes of the I. I. d'E.[118] Though Hubrecht himself had highly controversial evolutionary views, collecting and describing embryos could now proceed relatively independently of such personal agendas. Perhaps embryology gained independence in part as this became more of an end in itself. The significance of Keibel's plates is as a practical project, not just proposals, on which cooperation had started two decades before.

Keibel also worked with Mall to establish human embryology. They co-edited a handbook and Mall got the Carnegie Institution of Washington to fund a new Department of Embryology in Baltimore. Devoted especially to the anatomy of human (and more generally primate) embryos, it would become the leading institution in that field. It also shows the difference that international (which increasingly meant

American) support could have made to Keibel personally. When combined with his new position as institute director in Strasbourg, the $100 per month that from 1914 he received as a research associate of the Department — as much, he told Mall, as his three sons cost — opened up the prospect of freedom from much of the drudgery of undergraduate teaching.[119]

The First World War ended the modest revival of comparative embryology and interrupted publication of the normal plates. Keibel, a scientific internationalist and pan-German campaigner for naval rearmament, endured his youngest son's death, the suicides of his wife and second son, and the confiscation of his scientific materials in the French reconquest of Strasbourg. Even after 1922, when he secured his own position by succeeding to Oscar Hertwig's chair in Berlin, he could not pick up where he had left off.[120] Many potential contributors had withdrawn from the project — some had died — and with access to material more restricted few offers came in. Keibel rejected a volume on the sterlet, a small sturgeon, probably because of the Russian author's "terrible" German,[121] and a proposal of another lizard as being too close to Peter's "very good and detailed" plate (Table 1).[122] During these years of economic crisis Fischer struggled even to bring out those plates to which Keibel was already committed.[123] The two that appeared in 1922 and 1925 were not the most attractive: a long-winded and hence expensive volume on the squirrel, and — on a newt, potentially of wide interest as a genus favoured for experiments — the far-from-confident performance of Leopold Glaesner, a former assistant in the zoological institute at Strasbourg who published little else.[124]

In 1930, a year after Keibel's death, Dutch embryologists led a revival of the Institut International (Figure 9), opening the club to experimentalists and attempting to continue the normal plates. In the depths of the world economic crisis, Fischer was not prepared to help. He had lost money on the last volumes and would publish more only if the authors bore 70% of the cost, but did not wish to give up his right to the name. So the Utrecht embryologists Daniel de Lange and Hugo Nierstrasz negotiated a new series with their local publisher Oosthoek. *Monographs on the normal development of vertebrates* were produced under the auspices of the Institut and promoted to the membership, but only two volumes, on Indonesian mammals, were ever produced (Table 1).[125] For the third, the Yale zoologist Ross G. Harrison promised the spotted salamander *Amblystoma punctatum*, but it never appeared. In the late 1930s Fischer published two last *Normentafeln* in the old series, one of them long-delayed plates on the Norwegian rat, for which increasing laboratory use had by the 1920s created significant demand (Table 1).[126]

Keibel's normal plates, which before the First World War had contributed to a revival of comparative embryology, shared in the field's mid-twentieth-century marginalization. With the organization in its last two decades of an 'evolutionary developmental biology' initially around precisely the problem of heterochrony, they are again attracting interest. The most thorough available descriptions of several rare vertebrate embryos, they have, for example, provided resources to debate the notion that all vertebrate embryos pass through a stage when they look the same.[127] It is

FIG. 9. Group portrait of the Institut International d'Embryologie in Utrecht, 4–5 September 1933. This was the fifth meeting, the second of four held between 1930 and 1938. Present were Thomas H. Bryce, James P. Hill, Otto Grosser, Giuseppe Levi, Walther Vogt, James T. Wilson, Martinus W. Woerdeman, Daniel de Lange, Jan Boeke, Johan F. van Bemmelen, Friedrich Kopsch, George L. Streeter (fifth from right), Jan W. van Wijhe, Ludwig Graeper and Edwin S. Goodrich. Photograph from Alan Mason Chesney Medical Archives, Johns Hopkins Medical Institutions, Baltimore: Carnegie Institution of Washington Department of Embryology Papers, record group 5, series 1, box 1, folder 18; names from list on portrait at Hubrecht Laboratory.

also likely that, as the traditions are traced that made 'evo-devo' possible, much mid-twentieth-century work using the plates will come to light. But just as making them wove networks through which the science gained a more general independence, so their uses were not bound to the mixed fortunes of comparative embryology. Suitably transformed, they also provided other approaches with laboratory tools.

6. FROM NORMAL PLATES TO STAGING SYSTEMS

From about 1914 two groups of embryologists began to adapt the *Normentafel* design to their own demands. Though neither was much interested in evolution or variation, they were at opposite poles of the science and so offer a useful contrast. Experimentalists sought convenient tools for rapid staging of living embryos, especially amphibians and the chick. Human embryologists invented a system for ordering detailed reconstructions of individual specimens in collections.

In the first three decades of the twentieth century experimental embryology gained greatly in sophistication and status. Roux's interventions had been rather crude, but the experiments of the central figures in the next generation, Harrison and the German zoologist Hans Spemann, relied on fiddly microsurgery to explant tissue and transplant it between embryos of different species and stages. By the mid-1920s, with such discoveries as Harrison's invention of tissue culture and the Spemann laboratory's 'organizer', this kind of work was dominant, though a great many non-experimental studies of embryos still went on.

Describing stages was obviously at the heart of human embryology, but normal plates have hardly counted as worthy topics for reflection among either experimental embryologists or their historians. In the preface to the major post-Second World War survey, the editors, Benjamin Willier, Paul Weiss and Viktor Hamburger, expressed "the hope ... that future accounts of embryological knowledge would emphasize the dynamic and causal aspects of embryogenesis rather than mere description and seriation of developmental stages".[128] In the same volume, Jane Oppenheimer's history celebrated "[t]he greatest progressive minds of embryology" as having "looked *at* embryos", rather than "searched *for* hypotheses" — she had the theoretical biologist Joseph H. Woodger in her sights — and promised to examine "[h]ow they have looked, and how they are looking now". But though critical of naïve experimentalism, her perfunctory chapter on "Methods and techniques" ignores normal plates and stages.[129]

Yet both Oppenheimer and Hamburger were deeply familiar with the genre. She had set up fish stages,[130] and he is most widely known as co-author of "a series of normal stages in the development of the chick embryo". Reprinting this most-cited paper in chick developmental biology, the editor worried, however, that praising "what is, after all, an organizational rather than an intellectual achievement" might "amount to damning with faint praise".[131] Making and using normal plates and stages is a prime example of the low-status analytical work that plays a crucial role in constituting experimental systems.[132] Drawn by experimentalist rhetoric to highlight the most distinctive features — the design, moment of operation and conclusions drawn — historical studies have obscured the more time-consuming work of identification and classification without which no experiment could be performed or interpreted. Paying "mere description and seriation of developmental stages" due attention brings out continuities with 'descriptive' embryology and shows how experimentalists transformed normal plates as 'normal' came to mean "without experimental intervention".

In embryology as in other biological sciences, experimental work was concentrated on an ever more limited range of species. Early twentieth-century experimenters, noticing the plates for lungfishes and the lapwing, soon felt their lack for the groups, sea urchins and amphibia, that they used most. Like other series, Keibel's project created gaps that cried out to be filled. Fresh from his *Normentafel* of the lizard, Peter regretted that researchers on the sea urchin had to use terms such as "young and old gastrula", or "pluteus with short or with long arms", which "can give the reader no exact picture of a specific phase of development".[133] The first widely adopted 'normal stages' by an experimenting embryologist were Harrison's for the salamander, begun long before those negotiations with the I. I. d'E. Trained in part by German anatomists, Harrison wrote in 1918 that, "[i]n the absence of a set of 'normal plates' of *Amblystoma*, a series of stages have been designated arbitrarily" — he later described this as like taking "a few frames ... from a motion picture film" — "and type specimens preserved".[134] By 1925 his visiting German artist Lisbeth Krause had "standardized" the "normal development of *A. punctatum* ... by a series of drawings", to which he referred, and some of which he reproduced as line drawings, in articles.[135] But he never quite got around to publishing the full series. A notoriously dilatory publisher, Harrison doubtless prioritized research, but he also struggled with variation and the "differences in degree of development which we find according as we adopt one criterion or another for staging the embryos".[136] In spite of his own repeatedly expressed intention, prods from colleagues, an offer of help from two graduate students,[137] and the I. I. d'E.'s soliciting the work, the stages were left for his assistant to include in his posthumous 1969 book.[138]

Remarkably, this "essential reference for embryologists" had nevertheless long been in general use.[139] The stages were well known because Harrison was a leading figure who trained large numbers of researchers and teachers at Yale. There was demand because the more elaborate experiments became, the more necessary it was to standardize stages of operation and of assay, within a single experiment, through an experimental series, and to establish a "'common language'" between laboratories,[140] including those working on different, but closely related, species. Harrison's students received various salamander projects that often involved late stages, for which fine distinctions matter more. So his correspondence is full of inquiries from researchers who feared that their results would remain unintelligible until he published. He responded by distributing Krause's drawings free of charge. Figure 10 shows the first sheet of the set owned by Harrison's student William W. Ballard, a zoologist at Dartmouth College, New Hampshire. It is a photograph of a series of elegant wash-drawings, which themselves mimic the effect of photography, but allowed the artist more freedom to heighten definition. Harrison had by the 1940s distributed them to nearly 90 laboratories, mainly in the U.S. and Germany.[141] But this restricted effective communication to his own network. Thanking him for an offer to send the pictures, one anatomist made the desperate plea: "What I really need worse than anything else, however, is to be able to refer to the various stages in publication with some assurance that folks will know what I'm talking about. The only way I know to get this, is for you to publish said figures.... Please sir, HELP."[142] In the early 1940s Harrison's stages were in fact published. Since no one could start an experiment without staging embryos, the new manuals of experimental embryology reproduced drawings of his and other series.[143] So while Harrison's failure to publish might at first seem to indicate that normal stages were a low priority, the effort put into communicating them by other means shows that they had become indispensable.

Experimenters in the other most important laboratory, Spemann's zoological institute in Freiburg, took similar initiatives. In 1924, during his doctoral research, Viktor Hamburger made a small normal plate for the frog *Rana fusca* because an (unsuccessful) attempt to resolve discrepant results by postulating a short critical

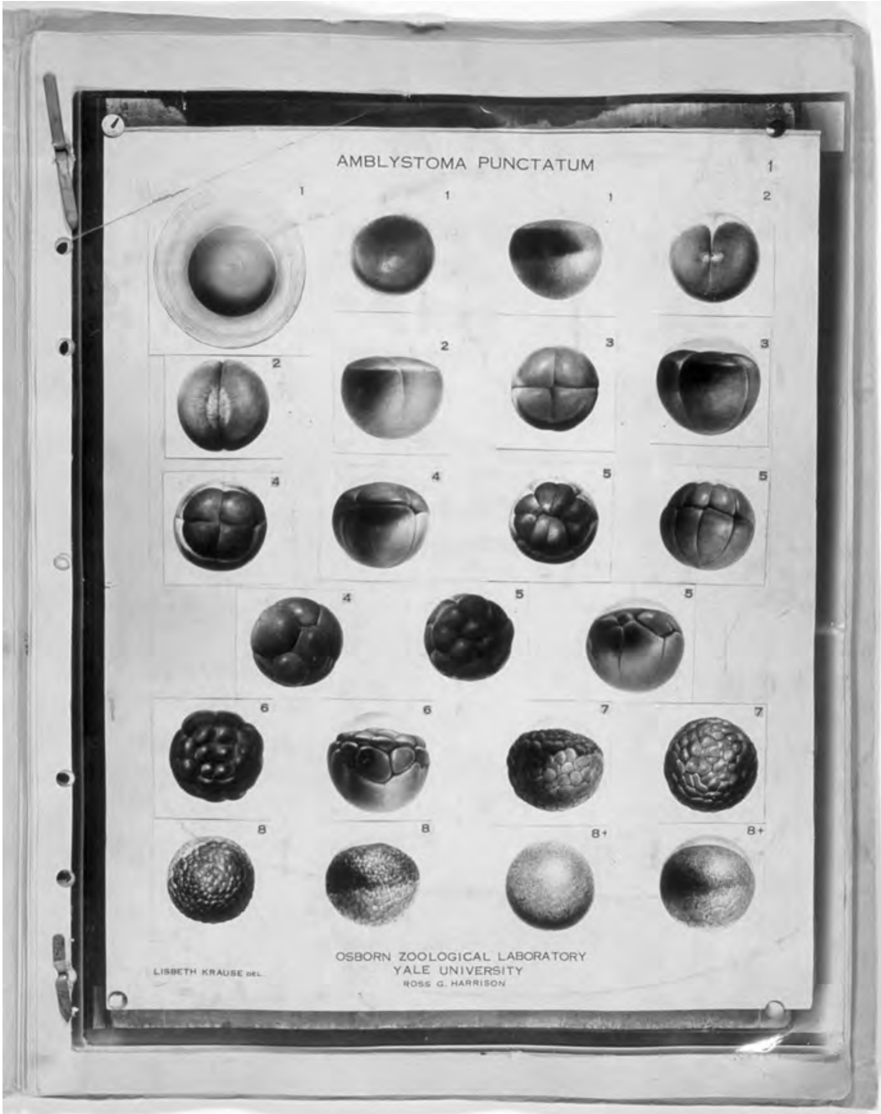


FIG. 10. The first of seven sheets of photographs of Lisbeth Krause's wash-drawings representing Ross G. Harrison's normal stages of *Amblystoma punctatum*. The first picture is of an unsegmented egg (stage 1), including the jelly, the last of an early blastula (stage 8). Harrison gave this set to his student William W. Ballard of Dartmouth College, New Hampshire, who himself authored several sets of normal stages. Original page 27.9 × 21.4 cm. Gift of Michael Dietrich.

period depended on operating on precisely defined stages.[144] Subsequently, he and a student, Eckart Rotmann, needed normal stages of limb development for grafting between two newt species, and another student, Salome Glücksohn (later Waelsch), was set to work them out. Hamburger had now obtained Harrison's stages and in the interests of consistent "norming of the urodeles" had her extend them. Unhappy with this gendered division of labour, she would much later contrast her "rather boring descriptive study" with Rotmann's "quite exciting experimental problem".[145] But Hamburger had spent a little of his own time in a similar way, and kept an appreciation of normal plates when the Nazis forced him to emigrate to the mid-western U.S. In the late 1940s the Iowa zoologist Howard L. Hamilton was revising Chicago biologist Frank R. Lillie's standard textbook on chick embryology — chick embryos were now more widely used than ever in biological research — and Hamburger persuaded him to replace the unillustrated table it contained with a series of normal stages that they also published separately (Figure 11).[146]

The makers of the new normal stages were inspired by Keibel's *Normentafeln*, but also dissatisfied with them. Even the volumes on relevant species, such as the chick and a newt, had not become popular with experimentalists. This was only partly because they were relatively inaccessible and unwieldy; the pictures were also reckoned inadequate for rapid identification and/or inconveniently spaced.[147] Their authors had been concerned primarily to represent whole embryos, rather than focus on diagnostically decisive parts; they generally used lithography, the softness of which could achieve a high degree of verisimilitude but at the expense of definition; and in some cases (e.g., Glaesner) they were simply not as expert. By contrast, the experimentalists' own stages not only proved uncontroversial themselves, by helping to hold coherent groups together they also reduced controversy over other issues.[148]

Experimentalists' complaints point to their two main desiderata, Hamburger's "ground rules".[149] First, rapid staging in the course of an experiment should be possible from sharply defined external features alone. This meant using characters that were changing prominently, for the chick at fairly early stages the number of somites, later the limb buds (Figure 11). Second, successive stages should cover the whole period of interest closely. This meant balancing good coverage of intervals when a lot was happening but external morphology changed little, most importantly gastrulation, with avoiding minor differences as stage criteria. Hamburger and Hamilton reassured readers that they had taken account of the "complications which derive from the independent variations of different characters" and "tried to establish average or 'standard' types by comparing a considerable number of embryos in each stage". They thus acted like those of Keibel's authors with abundant material and no wish to investigate variations. Each stage was defined by a short description, which replaced the tables of internal development with a list of criteria, plus, instead of lithographs, a photograph of a whole embryo that "appeared typical".[150] For some stages extra photos and/or an artist's outline or lightly shaded drawings of key diagnostic features were also given (Figure 11).

This work turned large-format monographs into 20-page articles containing just

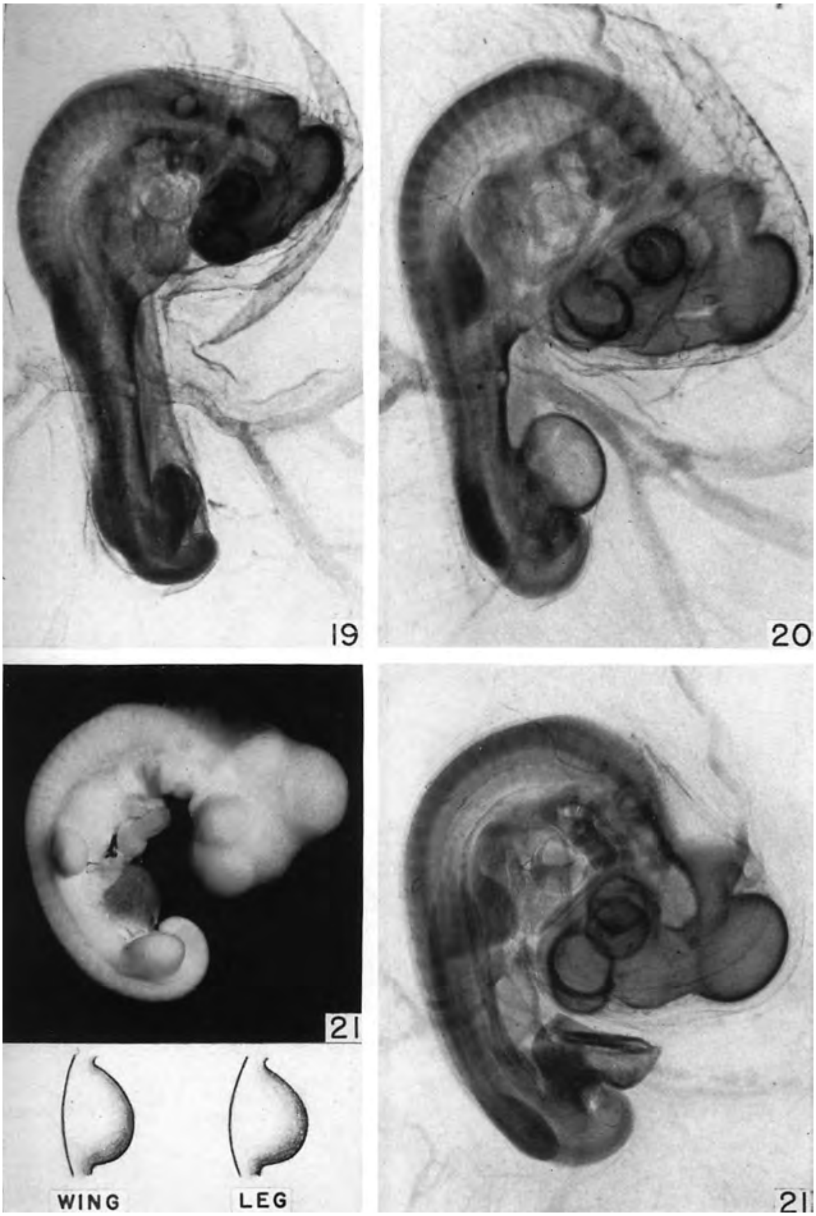


FIG. 11. Journal page with plate of Hamburger and Hamilton chick stages 19 to 21. The photographs (both cleared and opaque for stage 21) are supplemented by drawings of the diagnostically important limb buds. From Viktor Hamburger and Howard L. Hamilton, "A series of normal stages in the development of the chick embryo", *Journal of morphology*, lxxxviii (1951), 49–92, pl. 6 on p. 79. Reprinted with permission of Wiley-Liss, Inc., a subsidiary of John Wiley & Sons, Inc.

drawings of external morphology plus stage criteria. By the middle of the twentieth century *The anatomical record* and the *Journal of morphology* were filling with short papers reporting "stages in" or "tables for the normal development of" various lower vertebrates, most presented as tools for experimental work. (The 'tables' were not summaries of internal development in Oppel's sense but drawings plus information about age and/or length.) Exceptions prove the rule. Few can have held their breath while the Berlin anatomist Friedrich Kopsch took till 1952 to complete a *Normentafel* that was "nearly ready" in 1922 and he had promised Keibel in 1897.[151] Far more significant was the 1956 *Xenopus* normal table, which combined continuity with the older normal plates in its production with innovation in its form and use.

Harrison demonstrated the power of a leading researcher and teacher to promote normal stages; the *Xenopus* project illustrates the strength of scientific internationalism. The Hubrecht Laboratory in Utrecht, as seat of the I. I. d'E. (from 1968 the International Society of Developmental Biologists), home of the Central Embryological Collection, and from 1949 to 1980 publisher of the *General embryological information service* newsletter, had re-established itself after the Second World War as the closest thing to a global embryological institution. Producing a normal table would keep up the laboratory's prewar tradition and enhance the international mission. The director, Pieter Nieuwkoop, chose *Xenopus laevis*, a South African amphibian that pregnancy testing had introduced into the laboratories of the world. In contrast to the spring laying of amphibia native to Europe and North America, hormone injection would induce *Xenopus* to lay eggs all year round. Having shown that it was suitable for experiments, Nieuwkoop, who not unusually combined comparative and mechanistic interests, was intrigued by the "rather aberrant development of this systematically somewhat isolated species".[152]

Deciding to use embryos laid in South Africa, Nieuwkoop sent the master's student Job Faber to Jonkershoek Fish Hatchery near Stellenbosch, which was already producing adult *Xenopus* for export, and he stayed for eight months. They had determined stages up to the tailbud in Utrecht, and Faber established the rest in the field, following Harrison's model. Faber photographed anaesthetized living embryos, and back in Utrecht used the drawing experience gained during a course in taxonomic botany to make pencil drawings, which the Zoology Department's scientific illustrator, J. J. Prijs, took into ink for publication as ten fold-out plates (Figure 12). These plus the 27 pages of internal and external stage criteria correspond to the Harrison stages. The bulk of the book was devoted to "the systematic description of the internal development", equivalent to Keibel's *Tabellen* but with little attention to variation, on which Nieuwkoop had organized international collaboration by distributing sections among 24 contributors in nine countries for analysis.[153] Nieuwkoop and Faber included "a comparative table of anuran normal tables", but the Iowa embryologist Emil Witschi's 1956 proposal that, for "the comparative and generalizing evaluation of developmental processes" and for teaching, series of normal stages — he counted over 50 — should themselves be standardized across the vertebrates, was not widely taken up.[154]

During the 1960s experimental embryology began to be recast as 'developmen-

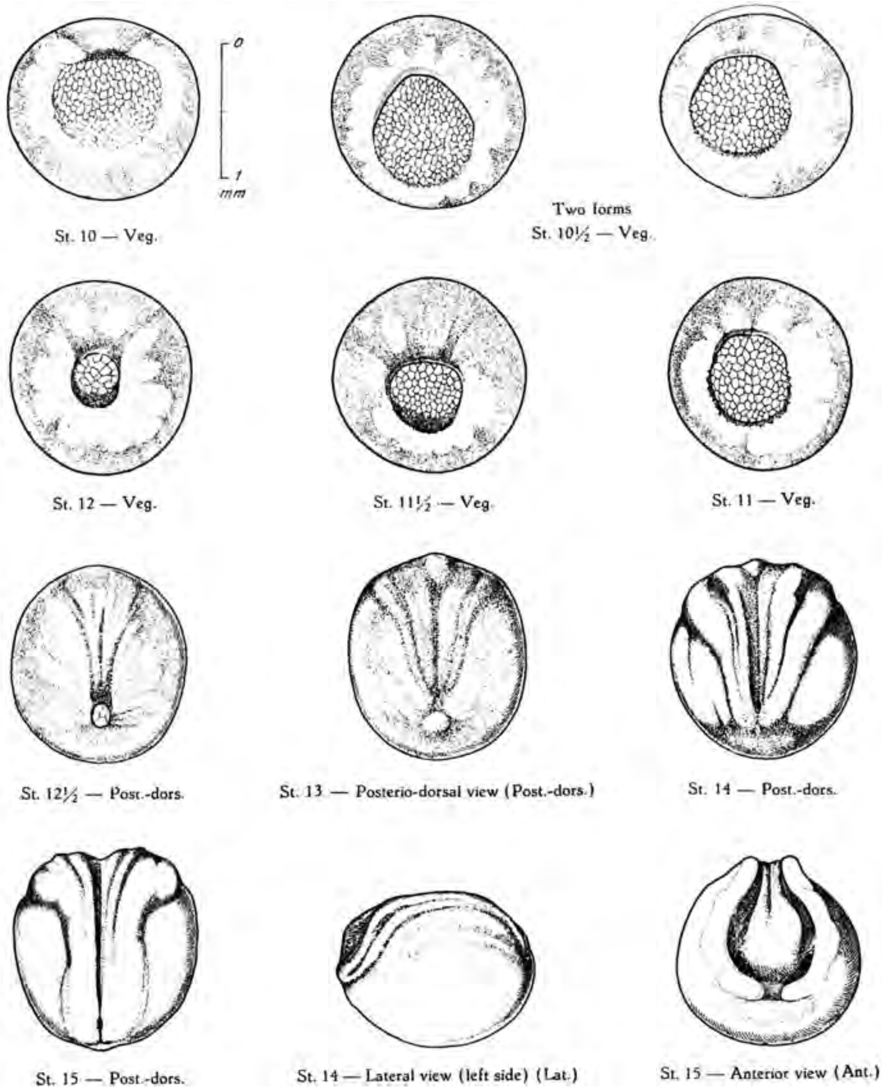


FIG. 12. Plate from the Nieuwkoop and Faber normal table of the South African clawed frog, *Xenopus laevis*. For these relatively early embryos, from initial gastrula to early neural-fold stage, staging followed Harrison's closely. From P. D. Nieuwkoop and Job Faber (eds), *Normal table of* Xenopus laevis *(Daudin)*, 2nd edn (Amsterdam, 1967), pl. III.

tal biology'. This joint initiative of self-consciously 'modern' embryologists, and geneticists, biochemists, cell biologists and molecular biologists who saw a field ripe for their skills, took over the problems and practices of experimental embryology but sought an expanded role in explaining development and differentiation throughout the living world. Focusing on principles it claimed would be universal, it could take whatever species was most convenient.[155] As a key 'literary technology' of laboratory domestication, the normal table helped *Xenopus* oust local amphibians, including Harrison's *Amblystoma*, Hamburger's *Rana* and Glücksohn's *Triton* (now *Triturus*), and become one of the select few model systems on which by the 1980s most developmental biology was done. Much of the demand came from biochemists who, entering the field in the early 1960s, had no interest in "aberrant" development, but wanted to establish general principles at the molecular level.[156] To start a developmental biology laboratory it was and is necessary to obtain animals, tanks and/or incubators — and a set of normal stages.[157] 'Hamburger & Hamilton' and 'Nieuwkoop & Faber' were reprinted respectively in 1992, and in 1967, 1975 and 1994.

Normal tables help order laboratory work. They are used to recognize when a mutant stock begins to develop abnormally, to determine the timing of microsurgery and assays, and to decide when samples should be fixed or frozen for histological or biochemical analysis. These tools of time management make it possible to coordinate 'investigator time' and 'phenomenon time'.[158] For example, by distributing *Xenopus* eggs fertilized at different times to incubators held at different temperatures, development can be simultaneously stretched and contracted over a wide range. By monitoring control dishes of unoperated embryos, periods of operation and assay can usually be organized around mealtimes and bedtimes. When the results of such work are a stage series of descriptions and pictures of histological or biochemical analyses, normal stages order communication too.

It is instructive to compare the experimentalists' normal stages with a mid-twentieth-century series produced in a different branch of embryology: human embryology as practised by Mall's successor, George L. Streeter, at the Carnegie Department in Baltimore. This laboratory gained such a dominant position that the third director could dub it a "bureau of standards for human embryology"; another Carnegie embryologist has suggested that it is to the earliest human embryos what the Folger Library is to Shakespeare first folios.[159] The problem here, to order a collection that was expanding to some 8,000 specimens plus associated drawings and models, was much more like Keibel's authors' than the experimentalists', except that the numbers were much larger and interspecies comparison was a secondary concern.[160]

So standardized staging was a key aim,[161] but also immensely challenging. In 1942, shortly after his retirement, Streeter began to publish a survey of human embryos that superseded the preliminary stages Mall had set up in 1914. This effectively replaced the *Normentafel* seriations, which had the practical disadvantage that if a new embryo was more advanced in one respect but less so in another it might not fit with the norms. Yet Streeter at first fought shy of "the term stage, with its implication of precision". Instead, he segregated embryos more flexibly into "age groups" that "represent levels

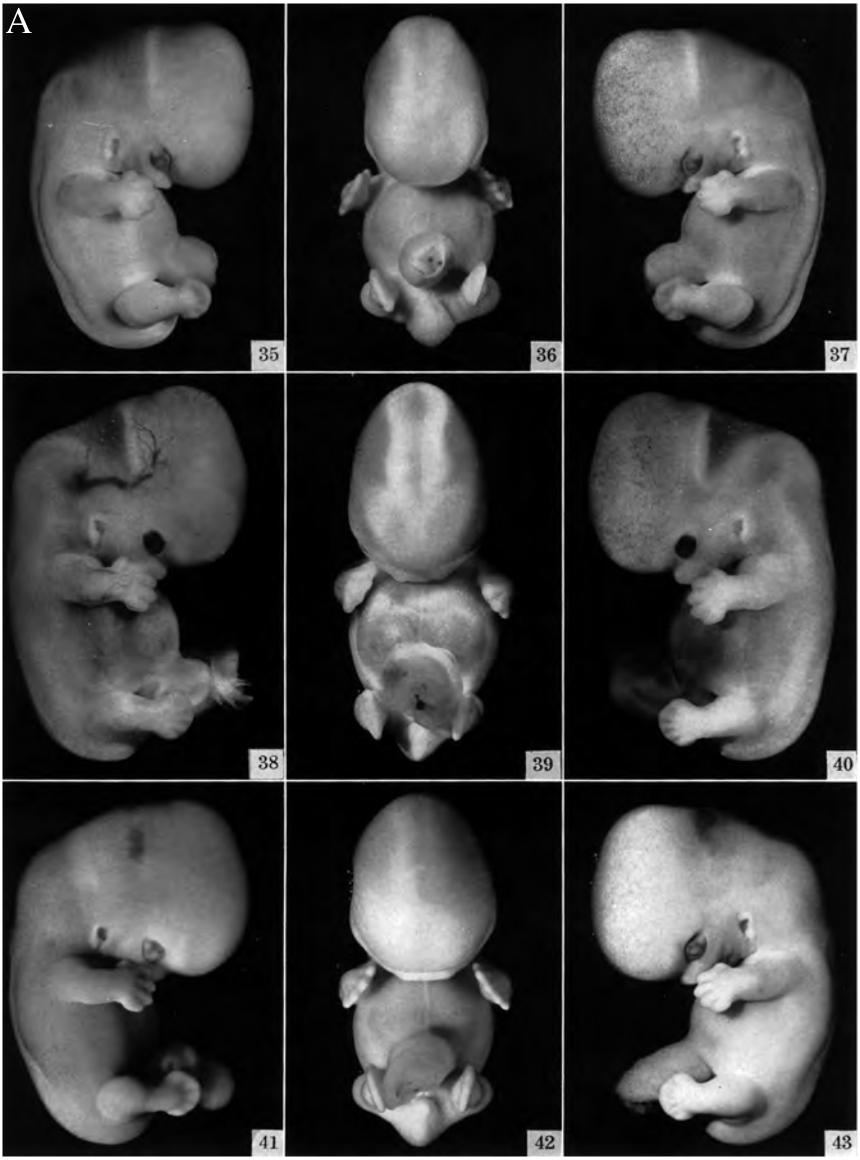
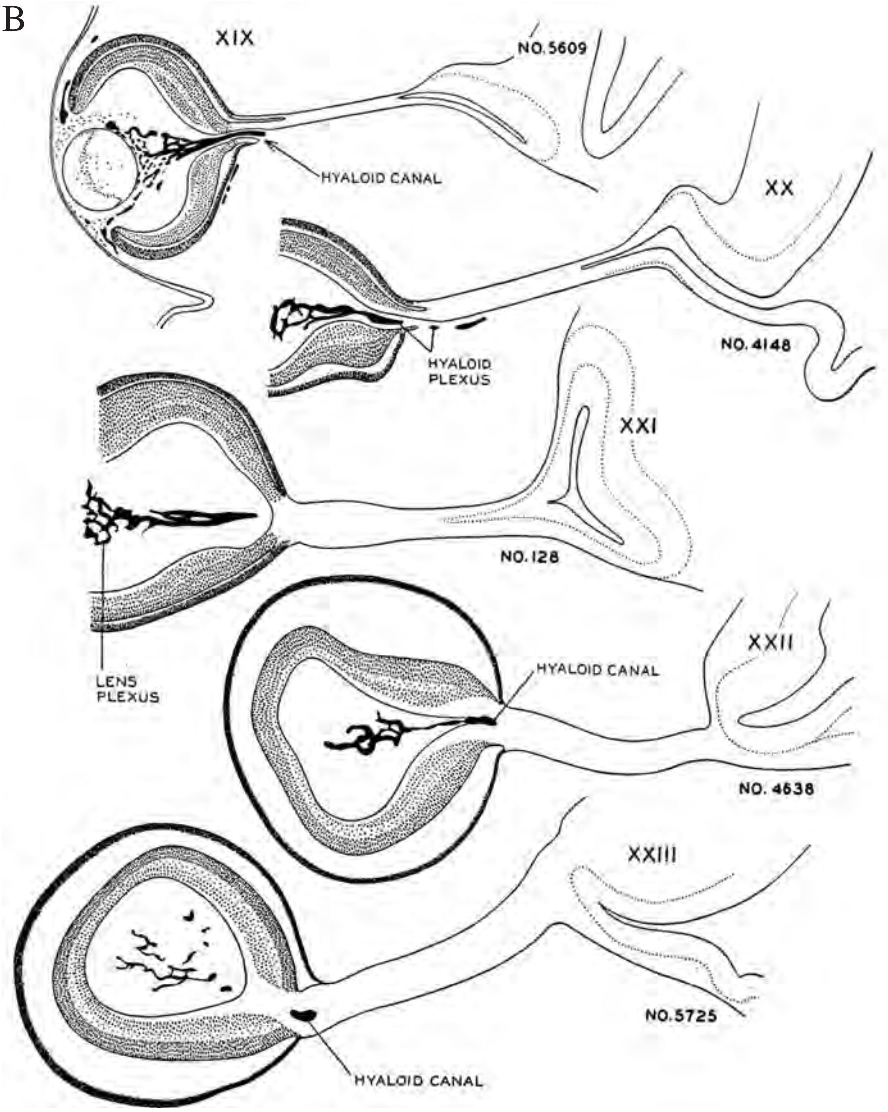


FIG. 13. Developmental horizons in human embryos. (A) "Photographs of three embryos belonging to horizon XIX"; the numbers (35–43) are figure numbers. (B) "Drawings of sections through the eye and optic nerve in age groups xix to xxiii." The optic nerve was one of eight arbitrarily chosen structures that Streeter assigned point scores. Roman numerals stand for horizons, Arabic are specimen numbers in the Carnegie collection. From George L. Streeter, "Developmental horizons in human embryos: Description of age groups XIX, XX, XXI, XXII, and XXIII, being the fifth issue of a survey of the Carnegie Collection", *Contributions to embryology*, xxxiv (1951), 165–96, pl. I, XIX and fig. 4 on p. 174. By permission of the Syndics of Cambridge University Library.

B


XIX
NO. 5609
HYALOID CANAL
XX
HYALOID PLEXUS
NO. 4148
XXI
NO. 128
LENS PLEXUS
HYALOID CANAL
XXII
NO. 4638
XXIII
NO. 5725
HYALOID CANAL

in their structural organization as a whole". Opposed to Haeckel, Streeter insisted that "embryos not only develop but they must also live", and presented these levels as corresponding to integrated functional states. To denote his age groups, he borrowed the term 'horizons' from geology and archaeology, and sought, like fossils for strata, several morphological criteria for each one.[162] So Streeter's revision of the *Normentafel* started from caution about having one supposedly 'typical' specimen represent a stage, and the human-embryo collector's respect for the individual case.

Streeter went on to investigate the "degree of correlation in the development of the different organs" and concluded that, for all the variation, "a definite and invariable schedule of organ correlation does occur", i.e., that for each developmental level he could distinguish "a syndrome of characters, ... the presence of any one of [which] in a given embryo betokens the existence of the others". The embryo was thus like "a form of intricate clockwork, in which each part is accurately geared".[163] But when the survey reached the later embryonic horizons, a scoring system was devised for these, with each horizon defined by a range of point scores for the presence of marked transformations in key organs.[164]

Since many specimens had been sectioned, internal criteria were more important than external. Streeter concentrated on "characters that can be clearly and easily recognized and that do not require special staining techniques, or elaborate reconstructions, for their identification", i.e., features that could be easily scored as present or absent in sections.[165] Yet though the aim was to order specimens efficiently, this could presumably take hours rather than seconds. Streeter's papers in the department's lavish *Contributions to embryology* offered photographs of whole embryos in several views, and of sections, and drawings of the more significant structural and diagnostic features (Figure 13). He objected to schemata,[166] and used photographs wherever possible; even the most vivid diagrams were based on actual sections or models of identified embryos.

After Streeter's death, Ronan O'Rahilly took over the collection and the project, which was no longer at the centre of the department's research, extending it to the earliest embryos and revising the other horizons. He went back to 'stages', because the "term is simpler, clearer, of widespread usage, and can be employed as a verb", but prized the flexibility of Streeter's system over the *Normentafel* design. For the earliest stages a single criterion was sufficient; later ones needed more criteria and ranges from less to more advanced members.[167] Carnegie stages eclipsed the few rival systems.[168]

So, in the second quarter of the twentieth century researchers in experimental and in human embryology revised the normal-plate design in contrasting ways according to their disciplinary agendas and the different kinds of work that amphibian and chick versus human embryos allowed. Experimentalists reduced the large volumes to a few pages of text plus drawings or photographs that they could use to stage living embryos rapidly for operations. Human embryologists adapted the *Normentafel* to the arrangement of a much larger collection in cohorts of not-quite-synchronously-developing specimens.

DISCUSSION

Rather than continuing to write histories of concepts of development, it now appears more productive to explore a history that was, in the first place, material and social. For unless we start, as embryologists did, with the "mere description and seriation of developmental stages", we shall always be coming into the story after most of the hard work has been done. It makes sense to begin with the most authoritative series, those that in the course of the twentieth century became standards of development. Studying how this happened not only enriches our understanding of the routine work that has been so sorely neglected, but also revises our picture of the theoretical and institutional transformations that have loomed so large. This is because normal plates, tables and stages shaped, as well as being shaped by, disciplinary change.

Once we acknowledge the everyday work that made the plates and tables, we can appreciate how comparative evolutionary embryology relied at the most basic level on medicine, agriculture, hunting, fishing and empire, and brought diverse objects into the form of embryos that could be compared. Then it also becomes clear how resolution of the highest theoretical questions could be blocked by mundane difficulties with developmental series, and that the troubles in the field around 1900, exacerbated by interdisciplinary competition, led to a crisis in methods of staging, within as well as between species. It is in this context that, for some, individual embryonic variation stopped being just a nuisance and became an attractive object of study. Keibel's normal plates did not bring the hoped-for resolution, but did promote an international revitalization of comparative vertebrate embryology, which though cut short by the First World War, nevertheless created institutes and a professional society that have endured. Since in so many accounts it is still 'experimental embryology' that by the early 1900s makes all the running, it is worth stressing that a major step towards embryological independence was taken in these very years, but elsewhere. The first embryological research organizations were founded by ignored representatives of 'descriptive embryology' and experimentalists were not at first welcome in these clubs. The other most important legacy of His's and Keibel's normal plates was as the starting point from which embryologists of very different kinds created visual standards of development. In the mid-twentieth century experimentalists' demands produced normal stages as analytical tools that have played crucial roles in holding together communities of researchers working on model systems.

How does this case study of embryology relate to Daston and Galison's synoptic history of atlases, the most ambitious attempt to chart changes in scientific images? Embryological series fit this ideal-typical scheme less, the more we take 'mechanically objective' image-making to be the key issue. Keibel's plates unsurprisingly incorporate only certain features of a 'regime of objectivity', and Harrison's, Hamburger and Hamilton's and Streeter's share only some characteristics of the post-1920 'regime of judgement' that Galison proposed for atlases in other fields.[169] And yet, it is in the decades around 1900, roughly the heyday of mechanical objectivity in other fields, that staging embryos, i.e., selecting and grouping them, became a serious problem in some of the most important centres of production. Arranging and dividing development had been fairly relaxed before, whether in stages or as seriations, and by the mid-twentieth century was dealt with rather confidently in systems of formal stages. But His abandoned staging human embryos, Keibel and Oppel found it incompatible with presenting their material in a form others could use, and Mehnert would have made 'stage' a dirty word; Harrison kept delaying publication. I have suggested that His's move came in part because his experience with human embryos brought him back to what had been common practice in that field, and in part through his interest in establishing norms against Haeckel. I have explained the calls to stop selecting single embryos as representing stages and to take individual variation seriously in terms of the interdisciplinary struggles to which embryology in this period, especially in south-west German anatomy, was unusually vulnerable.

For local problems we surely need specific explanations, but deeper and more general shifts may have provided a critical repertoire and an extra moral charge. Galison has offered a "characterological history of the author-scientist" — a succession of 'personae' from genius around 1800 through bureaucrat, manufacturer or *Bildungsbürger* around 1900 to expert in the mid-twentieth century — associated with regimes of truth, objectivity and judgement, respectively, and Daston interpreted the Haeckel–His controversy in terms of the clash of the first two.[170] I am not convinced that the terms of this analysis fit the sciences of organic form, but nor is it obvious how to develop the scheme so as to explain the pattern of communities reinforced through visual standards, while other scientists with similar training and jobs took opposing approaches. Changes in disciplinary identity and their interactions with innovations in ways of working are surely not the whole story, but they do offer resources at an appropriate level of generality.

How and to what extent was agreement achieved to recognize developmental series as standards? Complaints in the 1890s that the proliferation of arbitrary 'stages' was making communication ineffective and work unusable illustrate how little the division of development had been standardized before. Following His and Oppel, Keibel's project put staging on the agenda. In the mid-twentieth century consent to stage systems appears to have depended on their proposers having the authority that went with strategic institutional positions — which widely-used stages then reinforced. At the Hubrecht Laboratory, and especially the Carnegie Department, those responsible for repositories of rare material were uniquely well placed to promulgate stages; having directed the latter for over two decades Streeter could be described by his successor as "unquestionably the best-qualified expert". Successful stages were also proposed by individual researchers — the "master embryologist" Harrison is the prime example — at the centre of webs of training and research, within which the stages helped to promote cohesion and reduce potential controversy further.[171] By contrast, Keibel's plates failed experimentalists because their authors, who lacked authority in those communities, had produced them for a different purpose. It would be interesting to know more about controversies over stages, competition between staging systems and uses by non-embryologists, for example, obstetricians in the clinic or collectors in the field.[172]

The degrees of coordination of developmental series have constrained and been constrained by the organization of embryology. If stage systems were relatively unproblematic for single species studied by well-connected groups of researchers, comparison between species was much more fraught. This is in part because such second-order standardization — not to mention bringing adult animals and fossils into the frame — demanded synthesis across entrenched lines. Early in the nineteenth century, the most influential work defined itself against grand and controversial attempts to compare embryos throughout the animal kingdom. Much more embryology treated a few embryos as universal vertebrates than sought a comprehensive comparison. The debates over Haeckel's innovative plates — which were not, he protested, intended for exact research — show what could happen when almost all of the conditions for maximum controversy were met. Keibel's dull, collaborative project reacted against this, but the rigorous design made comparison much more difficult. Attempts to standardize stages across the vertebrates have failed.

This article has described the creation and transformation of a genre of technical publication that might be placed alongside anatomical nomenclatures, mathematical tables, organism-based newsletters and trade catalogues as guides to the contents of scientific fields, once unsung but increasingly recognized as determining. Further work could explore how, within embryology, normal stages were used with other special tools, notably fate maps, as well as more routine items, to order research and structure communication. It would also be worth investigating more generally how, beyond importing the notion of 'horizons' from geology, the production and uses of embryological plates and tables responded to or even promoted innovation elsewhere.

For all the basic similarity, it is in the contrasts between series that we shall discover how the pace, rhythm and texture of development have changed. Here I have said little about changes in drawing and printing, let alone modelling, but have highlighted shifts in the selection of representatives and their arrangement on a page, in a book and through a publication series. Even in these respects, my account of the differences between earlier nineteenth-century works, the various volumes in Keibel's series, and standards in human and experimental embryology has only scratched the surface. Much more could be said, for example, about defining the limits of developmental series in relation to life cycles. The general challenge is to invent more subtle, but not unreasonably detailed, ways of historicizing series. To meet it, we shall need to look beyond the most authoritative standards and for features that were shared across the sciences.

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5. See, e.g., Nick Hopwood, "'Giving body' to embryos: Modeling, mechanism, and the microtome in late nineteenth-century anatomy", *Isis*, xc (1999), 462–96, pp. 490–1. Embryological experts were exposed to few of the public challenges, which, it has been suggested, elicit 'mechanical objectivity' as a defence; see Theodore M. Porter, *Trust in numbers: The pursuit of objectivity in science and public life* (Princeton, 1995); and Ken Alder, "Making things the same: Representation, tolerance and the end of the *ancien régime* in France", *Social studies of science*, xxviii (1998), 499–545.
6. M. Norton Wise, "Precision: Agent of unity and product of agreement", in *idem* (ed.), *Values of*

precision (ref. 2), 92–100, 222–36 and 352–61; Simon Schaffer, "Accurate measurement is an English science", *ibid.*, 135–72, pp. 135–7.

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8. Nick Hopwood, "Producing development: The anatomy of human embryos and the norms of Wilhelm His", *Bulletin of the history of medicine*, lxxiv (2000), 29–79; *idem*, "Embryonen 'auf dem Altar der Wissenschaft zu opfern': Entwicklungsreihen im späten neunzehnten Jahrhundert", in Barbara Duden, Jürgen Schlumbohm and Patrice Veit (eds), *Geschichte des Ungeborenen: Zur Erfahrungs- und Wissenschaftsgeschichte der Schwangerschaft, 17.–20. Jahrhundert* (Göttingen, 2002), 237–72; *idem*, *Embryos in wax: Models from the Ziegler studio, with a reprint of "Embryological wax models" by Friedrich Ziegler* (Cambridge and Bern, 2002); *idem*, "Plastic publishing in embryology", in Soraya de Chadarevian and Nick Hopwood (eds), *Models: The third dimension of science* (Stanford, 2004), 170–206. On developmental series in other sciences, see, e.g., Martin J. S. Rudwick, "Charles Lyell's dream of a statistical palaeontology", *Palaeontology*, xxi (1978), 225–44; *idem*, *Scenes from deep time: Early pictorial representations of the prehistoric world* (Chicago, 1992); David K. van Keuren, "Museums and ideology: Augustus Pitt-Rivers, anthropological museums, and social change in later Victorian Britain", *Victorian studies*, xxviii (1984), 171–89; and David Armstrong, "The temporal body", in Roger Cooter and John Pickstone (eds), *Medicine in the twentieth century* (Amsterdam, 2000), 247–59.
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11. Stephen Jay Gould, *Ontogeny and phylogeny* (Cambridge, Mass., 1977), 174. For revisionist views of the 'revolt', see Jane Maienschein, *Transforming traditions in American biology, 1880–1915*

(Baltimore, 1991); *idem*, "The origins of *Entwicklungsmechanik*", in Scott F. Gilbert (ed.), *A conceptual history of modern embryology* (Baltimore, 1994), 43–61; Lynn K. Nyhart, *Biology takes form: Animal morphology and the German universities, 1800–1900* (Chicago, 1995), 243–361; and Hopwood, "Embryology" (ref. 3).

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13. For reviews, see Frederick B. Churchill, "The rise of classical descriptive embryology", in Gilbert (ed.), *Conceptual history* (ref. 11), 1–29; and Hopwood, "Embryology" (ref. 3). On morphology's institutional situation, see Nyhart, *Biology takes form* (ref. 11); and on the courses, Hopwood, *Embryos in wax* (ref. 8), 33–39.
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18. Ernst Haeckel, "Die Gastrula und die Eifurchung der Tiere", *Jenaische Zeitschrift für Naturwissenschaft*, ix (1875), 402–508, pp. 409–12. For the confused Greek etymology of *Cenogenese* or *Caenogenese*, see Franz Keibel, "Das biogenetische Grundgesetz und die Cenogenese", *Ergebnisse der Anatomie und Entwickelungsgeschichte*, vii (1898), 722–92, p. 731.
19. Rudolf Virchow, *Die Cellularpathologie in ihrer Begründung auf physiologische und pathologische Gewebelehre: Zwanzig Vorlesungen gehalten während der Monate Februar, März und April 1858 im pathologischen Institut zu Berlin* (Berlin, 1858; facsimile edn, Hildesheim, 1966), 57; Ernst Haeckel, *Anthropogenie oder Entwickelungsgeschichte des Menschen: Gemeinverständliche wissenschaftliche Vorträge über die Grundzüge der menschlichen Keimes- und Stammes-Geschichte* (Leipzig, 1874), 634, 717; *idem*, "Gastrula" (ref. 18), 412–16. Haeckel's possible

borrowing from pathology is suggested by quotations from a translation of a later handbook in the *Oxford English dictionary*, but I am not aware that attention has been drawn to it before.

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22. Nyhart, *Biology takes form* (ref. 11), 243–77.
23. Hopwood, "'Giving body'" (ref. 5).
24. Frederick B. Churchill, "Chabry, Roux, and the experimental method in nineteenth-century embryology", in Ronald N. Giere and Richard S. Westfall (eds), *Foundations of scientific method: The nineteenth century* (Bloomington, Ind., 1973), 161–205; Maienschein, "Origins of *Entwicklungsmechanik*" (ref. 11); Reinhard Mocek, *Die werdende Form: Eine Geschichte der Kausalen Morphologie* (Marburg, 1998).
25. Irmgard Müller, "Die Wandlung embryologischer Forschung von der deskriptiven zur experimentellen Phase unter dem Einfluss der Zoologischen Station in Neapel", *Medizinhistorisches Journal*, x (1975), 191–218; Jeffrey Werdinger, "Embryology at Woods Hole: The emergence of a new American biology", Ph.D. dissertation, Indiana University, 1980; Philip J. Pauly, "Summer resort and scientific discipline: Woods Hole and the structure of American biology, 1882–1925", in Ronald Rainger, Keith R. Benson and Jane Maienschein (eds), *The American development of biology* (New Brunswick, N.J., 1991), 121–50; Jonathan Harwood, *Styles of scientific thought: The German genetics community, 1900–1933* (Chicago, 1993), 30–31; Nyhart, *Biology takes form* (ref. 11), 243–361; Ulrich Sucker, *Das Kaiser-Wilhelm-Institut für Biologie: Seine Gründungsgeschichte, seine problemgeschichtlichen und wissenschaftstheoretischen Voraussetzungen (1911–1916)* (Stuttgart, 2002).
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27. E.g., [Gabriel Gustav] Valentin, "Foetus", in D. W. H. Busch *et al*. (eds), *Encyclopädisches Wörterbuch der medicinischen Wissenschaften*, xii (Berlin, 1835), 355–89, p. 355, with reference to "descriptive anatomy"; Ernst Haeckel, *Generelle Morphologie* (ref. 16), ii, 16; *idem*, *Anthropogenie oder Entwickelungsgeschichte des Menschen: Keimes- und Stammes-Geschichte*, 4th edn (2 vols, Leipzig, 1891), i, pp. xx–xxi; Wilhelm Roux, C. Correns, Alfred Fischel and E. Küster, *Terminologie der Entwicklungsmechanik der Tiere und Pflanzen: Eine Ergänzung zu den Wörterbüchern der Biologie, Zoologie und Medizin sowie zu den Lehr- und Handbüchern der Entwicklungsgeschichte, allgemeinen Biologie und Physiologie* (Leipzig, 1912), 91–92. The term was not only negative; a sympathetic obituarist praised Keibel's normal plates as having laid a foundation for "deskriptive Embryologie"; see [Curt] Elze, "Franz Keibel †. Geb. 6. Juli 1861, gest. 27. April 1929", *Klinische Wochenschrift*, viii (1929), 1335.
28. On His, see Hopwood, "'Giving body'" (ref. 5); and *idem*, "Producing development" (ref. 8); for the range of vertebrate embryology, Oskar Hertwig (ed.), *Handbuch der vergleichenden und experimentellen Entwickelungslehre der Wirbeltiere* (3 vols, Jena, 1906); and on the mass of new evolutionary research around 1900, Peter J. Bowler, *Life's splendid drama: Evolutionary biology and the reconstruction of life's ancestry, 1860–1940* (Chicago, 1996).
29. Wilhelm His, "Die Entwicklung der zoologischen Station in Neapel und das wachsende Bedürfnis nach wissenschaftlichen Zentralanstalten", *Biologisches Centralblatt*, vi (1886), 545–54, p. 554. All translations are mine.

30. *Ibid.*, 549–54.
31. Stephen Jay Gould, *The mismeasure of man* (Harmondsworth, 1984); *idem*, "Ladders and cones: Constraining evolution by canonical icons", in Robert B. Silvers (ed.), *Hidden histories of science* (London, 1997), 37–67. On evolutionary trees, see further especially G. Uschmann, "Zur Geschichte der Stammbaum-Darstellungen", in Manfred Gersch (ed.), *Gesammelte Vorträge über moderne Probleme der Abstammungslehre*, ii (Jena, 1967), 9–30; (with care) Mary Bouquet, "Family trees and their affinities: The visual imperative of the genealogical diagram", *Journal of the Royal Anthropological Institute*, n. s., ii (1996), 43–66; and Julia Voss, *Darwins Diagramme — Bilder von der Entdeckung der Unordnung* (Max-Planck-Institut für Wissenschaftsgeschichte Preprint 249; Berlin, 2003); and on craniometry, Zimmerman, *Anthropology and antihumanism* (ref. 2), 86–107; and Michael Hagner, *Geniale Gehirne: Zur Geschichte der Elitegehirnforschung* (Göttingen, 2004).
32. Karl Ernst von Baer, *Über Entwickelungsgeschichte der Thiere: Beobachtung und Reflexion*, part 1 (Königsberg, 1828; facsimile edn, Brussels, 1967), 147–8.
33. *Ibid.*, 4–7. On the sleepless nights, see *idem*, *Autobiography of Dr Karl Ernst von Baer*, 2nd edn, transl. by H. Schneider, ed. by Jane M. Oppenheimer (Canton, Mass., 1986), 212.
34. Christian Pander, *Beiträge zur Entwickelungsgeschichte des Hühnchens im Eye* (Würzburg, 1817), 30; *idem*, "Dissertation inaugurale établissant l'histoire de la métamorphose que subit l'œuf au cours des cinq premiers jours d'incubation" [Latin original, 1817], in *Les textes embryologiques de Christian Heinrich Pander (1794–1865)*, ed. and transl. by Stéphane Schmitt (Turnhout, 2003), 61–94.
35. Pander, *Beiträge* (ref. 34); von Baer, *Entwickelungsgeschichte* (ref. 32). So much remains to be done on the visual language of embryology that even the illustrations in these major works have yet to receive serious historical attention.
36. Daston and Galison, "Image of objectivity" (ref. 4), 84–98; Wilhelm His, *Untersuchungen über die erste Anlage des Wirbelthierleibes: Die erste Entwickelung des Hühnchens im Ei* (Leipzig, 1868), 56–60.
37. Samuel Thomas Soemmerring, "Icones embryonum humanorum", in *Schriften zur Embryologie und Teratologie*, transl. by Ferdinand Peter Moog, ed. by Ulrike Enke (Basel, 2000 [Latin original, 1799]), 165–89; Barbara Duden, "The fetus on the 'farther shore': Toward a history of the unborn", in Lynn M. Morgan and Meredith W. Michaels (eds), *Fetal subjects, feminist positions* (Philadelphia, 1999), 13–25; Enke, "Schönheit der Embryonen" (ref. 9).
38. For a review, see Valentin, "Foetus" (ref. 27). Tables are included in Carl Friedrich Senff, *Nonnulla de incremento ossium embryonum in primis graviditatis mensibus: Dissertatio inauguralis ...* (Halle, 1801); and Johann August Heinrich Nicolai, *Beschreibung der Knochen des menschlichen Foetus: Ein Beitrag zur Anatomie des Foetus und zur Bestimmung des Alters der Embryonen und des Foetus aus der Beschaffenheit der Knochen* (Münster, 1829); plates in J. J. V. Coste, *Histoire générale et particulière du développement des corps organisés* (Paris, 1849); and Alexander Ecker, *Icones physiologicae: Erläuterungstafeln zur Physiologie und Entwickelungsgeschichte* (Leipzig, 1851–9); and woodcuts in Kölliker, *Entwicklungsgeschichte* (ref. 15).
39. Von Baer, *Entwickelungsgeschichte* (ref. 32), pl. III.
40. The most striking comparisons I have found are *ibid.*, part 2 (Königsberg, 1837; facsimile edn, Brussels, 1967), pl. IV (legend in *ibid.*, *Schlussheft*, ed. by Ludwig Stieda (Königsberg, 1888), 396–7); and Rudolph Wagner, *Icones physiologicae: Tabulae physiologiam et geneseos historiam illustrantes. Erläuterungstafeln zur Physiologie und Entwickelungsgeschichte* (Leipzig, 1839), pl. V.
41. Kölliker, *Entwicklungsgeschichte* (ref. 15); Oscar Hertwig, *Lehrbuch der Entwicklungsgeschichte des Menschen und der Wirbelthiere* (Jena, 1888). Hopwood, *Embryos in wax* (ref. 8), 38, mislabels a figure of Hertwig's as a wood-engraving.

42. Haeckel, *Natürliche Schöpfungsgeschichte* (ref. 16), pls II–III; *idem*, *Anthropogenie*, 4th edn (ref. 27), i, pls VII–IX. Compare the wood-engravings in Francis M. Balfour, *A treatise on comparative embryology*, ii (London, 1881).
43. Reinhard Gursch, *Die Illustrationen Ernst Haeckels zur Abstammungs- und Entwicklungsgeschichte: Diskussion im wissenschaftlichen und nichtwissenschaftlichen Schrifttum* (Frankfurt am Main, 1981).
44. Daston, "Objectivity versus truth" (ref. 4), 28–29.
45. I am preparing a book on Haeckel's pictures of embryos.
46. Wilhelm His, *Über die Aufgaben und Zielpunkte der wissenschaftlichen Anatomie: Rede, gehalten beim Antritt der anatomischen Professur der Universität Leipzig den 4. November 1872* (Leipzig, 1872), 9–10. Is it significant that His referred to norms (for the first time in print?) on joining the Leipzig medical faculty, where Carl Wunderlich was promoting a view of disease as deviation from a thermometrically measured norm of temperature (Volker Hess, *Der wohltemperierte Mensch: Wissenschaft und Alltag des Fiebermessens (1850–1900)* (Frankfurt am Main, 2000), 146–65)?
47. Hopwood, "Producing development" (ref. 8).
48. Wilhelm His, *Anatomie menschlicher Embryonen* (3 vols, Leipzig), i: *Embryonen des ersten Monats* (1880), 147–68 (quote on p. 147); ii: *Gestalt- und Grössenentwicklung bis zum Schluss des 2. Monats* (1882), 2 (quote), 23–71; iii: *Zur Geschichte der Organe* (1885), 236–42; Hopwood, "Producing development" (ref. 8). Use of the term 'norm' was not new; Gustav Valentin had written that a certain embryo could be taken "[a]s norm of the fifth week" (Valentin, "Foetus" (ref. 27), 363), and incidentally, also of Soemmerring's "normal figures" (*ibid.*, 357–8).
49. Hopwood, "Producing development" (ref. 8), 70–76.
50. Albert Oppel, *Vergleichung des Entwicklungsgrades der Organe zu verschiedenen Entwicklungszeiten bei Wirbeltieren* (Jena, 1891). There are parallels to recent concerns about gene expression data. Oppel, who was later a colleague of Roux in Halle, is perhaps more widely known as co-author of a microscopy manual; see P. Eisler, "Albert Oppel †", *Anatomischer Anzeiger*, xlviii (1915), 414–15; and Wilhelm Roux, "† Albert Oppel", *Archiv für Entwicklungsmechanik der Organismen*, xlii (1917), 261–6.
51. Albert Oppel, "Dritter Theil: Entwicklungsgeschichte. Zweiter Abtheilung: Entwicklungsgeschichte der Wirbelthiere", *Jahresbericht über die Fortschritte der Anatomie und Physiologie*, xx (1892), section, 608–747, pp. 683–6.
52. Karl Peter, "Franz Keibel: Ein Nachruf", *Anatomischer Anzeiger*, lxviii (1929), 201–20; [Rudolf] Fick, "Gedächtnisrede auf Franz Keibel", *Sitzungsberichte der Preussischen Akademie der Wissenschaften, Physikalisch-mathematische Klasse*, 1929, pp. cvii–cxxii; Elze, "Keibel" (ref. 27); H. Stieve, "Franz Keibel zum Gedächtnis", *Zeitschrift für mikroskopisch-anatomische Forschung*, xviii (1929), 1–4; G[eorge] L. S[treeter], "Franz Keibel", *Science*, lxix (1929), 637; E. Th. Nauck, *Franz Keibel: Zugleich eine Untersuchung über das Problem des wissenschaftlichen Nachwuchses* (Jena, 1937). Nauck celebrated Keibel as a pioneer of a holistic embryology. For an autobiographical account from 1892, see Universitätsarchiv Freiburg: B37/535.
53. Nyhart, *Biology takes form* (ref. 11), 207–40. On the Freiburg institute, see further Hopwood, *Embryos in wax* (ref. 8) and literature cited therein.
54. On Schwalbe, more prominent in histories of embryology for supervising Roux's doctoral dissertation, see Franz Keibel, "Gustav Albert Schwalbe †", *Anatomischer Anzeiger*, xlix (1916), 210–21; and J. M. Le Minor and J. L. Kahn, "Histoire de l'anatomie à Strasbourg", *Archives d'anatomie, d'histologie et d'embryologie normales et expérimentales*, lxxii (1989), 125–55, pp. 142–7.
55. The excursions are mentioned as regular events in Robert Wiedersheim to Max Fürbringer, 7 June 1910, and Ernst Gaupp to Fürbringer, 18 June 1911, Universitätsbibliothek Johann Christian Senckenberg, Frankfurt am Main: Fürbringer Papers.

56. Franz Keibel, “Studien zur Entwicklungsgeschichte des Schweines (*Sus scrofa domesticus*)”, *Morphologische Arbeiten*, iii (1893), 1–139, pp. 1–10. The corresponding models are illustrated in Hopwood, *Embryos in wax* (ref. 8), 111 and 149, and their making discussed on pp. 57–59.
57. Franz Keibel, “Studien zur Entwicklungsgeschichte des Schweines. *(Sus scrofa domesticus.)* II”, *Morphologische Arbeiten*, v (1895), 17–168, pp. 75–78.
58. *Idem*, “Das biogenetische Grundgesetz” (ref. 18), 731–6.
59. Franz Keibel, “Normentafeln zur Entwickelungsgeschichte der Wirbeltiere”, *Anatomischer Anzeiger*, xi (1895), 225–34; *idem*, “Mitteilungen über die ‘Normentafeln zur Entwickelungsgeschichte der Wirbeltiere’”, *ibid*., xi (1896), 593–6. Personal approaches include Keibel to Max Fürbringer, 17 and 24 October 1895, Fürbringer Papers (ref. 55), the latter mentioning Semon; Keibel to Friedrich Merkel, 17 October 1895, Niedersächsische Staats- und Universitätsbibliothek Göttingen: Philos. 187, 14; and Keibel to Jacob Reighard, 17 October 1895 and 15 June 1897, Bentley Historical Library, University of Michigan: Reighard Papers, box 1; none of these led directly to a publication in the series, but see Jacob Reighard, “Exhibition of figures for a *Normentafel* of *Amia* with an account of methods of photographing the embryo”, *Science*, xi (1900), 251. Keibel also presented the project to the German Anatomical Society and received His’s support (*Verhandlungen der Anatomischen Gesellschaft*, 1896, 81); see also Wilhelm His, “Ueber wissenschaftliche Centralanstalten und speciell über Centralanstalten zur Förderung der Gehirnkenntniss”, *Berichte über die Verhandlungen der mathematisch-physischen Classe der Königlich Sächsischen Gesellschaft der Wissenschaften zu Leipzig*, liii (1901), 413–36, p. 427. Keibel surely used conferences to recruit internationally too. On serial publication, see, e.g., Leslie Howsam, “Sustained literary ventures: The series in Victorian book publishing”, *Publishing history*, xxxi (1992), 5–26.
60. Keibel, “Entwicklungsgeschichte des Schweines” (ref. 56), 5; *idem*, “Ueber den Entwickelungsgrad der Organe in den verschiedenen Stadien der embryonalen Entwickelung der Wirbeltiere”, in *Handbuch der vergleichenden und experimentellen Entwicklungslehre der Wirbeltiere*, ed. by Oskar Hertwig, iii/3 (Jena, 1906), 131–48. For a contemporary history, see Em[anuel] Rádl, “Ueber die Bedeutung des Prinzips von der Korrelation in der Biologie”, *Biologisches Centralblatt*, xxi (1901), 401–16, 490–6, 550–60, 585–91, 605–21; and for an experimentalist’s statement, Hans Spemann, “Zum Problem der Correlation in der tierischen Entwicklung”, *Verhandlungen der Deutschen Zoologischen Gesellschaft*, xvii (1907), 22–48. In work on the statistical norming of development, Alexander Gurwitsch took a distinctive approach to this complex of problems; see Alexander Gurwitsch, “Über Determination, Normierung und Zufall in der Ontogenese”, *Archiv für Entwicklungsmechanik der Organismen*, xxx (1910), 133–93; and Lev V. Beloussov, John M. Opitz and Scott F. Gilbert, “Life of Alexander G. Gurwitsch and his relevant contribution to the theory of morphogenetic fields”, *International journal of developmental biology*, xli (1997), 771–9.
61. Keibel occasionally encouraged students to pursue developmental mechanical investigations, but — as one might expect of a Hertwig student (Weindling, *Darwinism* (ref. 26), 119–30) — was critical of Roux’s inaccuracies and exaggerations; see Franz Keibel, “Bemerkungen zu Roux’s Aufsatz: ‘Das Nichtnötigsein der Schwerkraft für die Entwickelung des Froscheies’”, *Anatomischer Anzeiger*, xxi (1902), 581–91; *idem*, “Bemerkung zu Wilhelm Rouxs Aufsatz: ‘Über die Ursachen der Bestimmung der Hauptrichtungen des Embryo im Froschei’”, *ibid*., xxiii (1903), 224. Keibel’s most extensive reflections on the subject include this statement: “We have, then, every reason to welcome experimental embryology and can readily overlook the way that some of its representatives too optimistically believe themselves already to be near to generating living beings in the test-tube” (Franz Keibel, *Über experimentelle Entwicklungsgeschichte: Rede, gehalten am 27. Januar 1917 zur Feier des Geburtstages Sr. Majestät des Kaisers in der Aula der Kaiser Wilhelms-Universität Straßburg* (Strasbourg, 1917), 26). Keibel greatly admired

Ross Harrison: "His works are of the very greatest importance; I wish we had such a good man in Germany" (Keibel to Franklin P. Mall, 16 December 1907, Alan Mason Chesney Medical Archives, Johns Hopkins Medical Institutions, Baltimore: Carnegie Institution of Washington Department of Embryology Papers, record group 1, series 1, box 10, folder 33).

62. Keibel, "Das biogenetische Grundgesetz" (ref. 18), 758 (emphasis here and elsewhere in the originals), reviewing *idem*, "Entwicklungsgeschichte des Schweines. II" (ref. 57), 18. Keibel derived this stance from a review by Roux's former colleague and his own predecessor as a prosector in Freiburg, the Swiss anatomist Hans Strasser.
63. NT 1 (i.e., the first volume in Keibel's series; see Table 1), 1–9.
64. His, *Aufgaben und Zielpunkte* (ref. 46), 9.
65. G. Schwalbe, "Über Variation", *Verhandlungen der Anatomischen Gesellschaft*, xii (1898), 2–15. The classic work is William Bateson, *Materials for the study of variation treated with especial regard to discontinuity in the origin of species* (London, 1894). For (Berlin) anthropologists' caution towards Darwinism, see Zimmerman, *Anthropology and antihumanism* (ref. 2).
66. G. Schwalbe and W. Pfitzner, "Varietätenstatistik und Anthropologie", *Anatomischer Anzeiger*, iv (1889), 705–14; W. Pfitzner, "Beiträge zur Kenntniss des menschlichen Extremitätenskelets: Erster Beitrag", *Morphologische Arbeiten*, i (1891), 1–17, p. 6 (quote); Ernst Mehnert, "Bericht über die Leichenmessungen am Strassburger anatomischen Institute", *ibid*., iv (1894), 1–29. On Mehnert and Pfitzner, see G. Schwalbe, "Wilhelm Pfitzner †", *Zeitschrift für Morphologie und Anthropologie*, v, no. 3 (1903), pp. v–xii, also in *Anatomischer Anzeiger*, xxii (1903), 481–7; and *idem*, "Ernst Mehnert †", *ibid*., 387–92.
67. Ernst Mehnert, "Die individuelle Variation des Wirbelthierembryo: Eine Zusammenstellung", *Morphologische Arbeiten*, v (1895), 386–444, pp. 399, 430.
68. Gould, *Ontogeny and phylogeny* (ref. 11), 174–5.
69. NT 1, 80–81 (quote); Ernst Mehnert, "Allgemeine Entwicklungsgeschichte: II. Variation, Heredität. A. Variation", *Jahresberichte über die Fortschritte der Anatomie und Entwicklungsgeschichte*, n. s., iii (1898), 327–36, pp. 331–2; Franz Keibel, "Das biogenetische Grundgesetz" (ref. 18), 759–68; Mehnert, "Bemerkungen zu Keibels Kritiken und Referaten", *Anatomische Hefte*, xii (1899), 549–65; Keibel, "Zu Mehnerts Bemerkungen über meine Kritiken und Referate", *ibid*., 567–73; Mehnert, "K. E. v. Baer als Begründer der Erkenntnis der individuellen Variation im Embryonalleben", *Biologisches Centralblatt*, xix (1899), 443–55; Keibel, "Bemerkungen zu Mehnert's Aufsatz: K. E. v. Baer als Begründer der Erkenntnis der individuellen Variation im Embryonalleben", *ibid*., 744–6; NT 2, 13.
70. Ernst Mehnert, "Kainogenese: Eine gesetzmässige Abänderung der embryonalen Entfaltung in Folge von erblicher Uebertragung in der Phylogenese erworbener Eigenthümlichkeiten. Eine biologische Studie", *Morphologische Arbeiten*, vii (1897), 1–156; *idem*, *Biomechanik erschlossen aus dem Principe der Organogenese* (Jena, 1898); Keibel, "Das biogenetische Grundgesetz" (ref. 18), 776–81, 787–91. Grateful by this time for any specialist support, Haeckel praised Mehnert (Haeckel, *Anthropogenie oder Entwickelungsgeschichte des Menschen: Keimes- und Stammesgeschichte*, 5th edn (2 vols, Leipzig, 1903), i, 12–13), but accused Keibel, although "he has himself in very careful descriptive-embryological works provided a great number of supports for the Biogenetic Law", of failing to understand it or to grasp "even the important distinction between palingenesis and cenogenesis" (Haeckel, *Die Lebenswunder: Gemeinverständliche Studien über Biologische Philosophie. Ergänzungsband zu dem Buche über die Welträthsel* (Stuttgart, 1904), 439). Haeckel's secretary reckoned Keibel "one of the most zealous opponents of the Biogenetic Law". "In his embryological investigations he sees only the cenogenetic alteration of the germinal form; and when contemplating the B. L. he has eyes only for undisturbed palingenesis." There was nothing new about the extreme cenogenesis of mammalian development; Haeckel himself had pointed it out (Heinrich Schmidt, *Haeckels Biogenetisches Grundgesetz und seine Gegner*

(Odenkirchen, 1902), 78–81). In Strasbourg, by contrast, Schwalbe regretted that Mehnert had rushed into speculation instead of completing his empirical work (Schwalbe, “Mehnert” (ref. 68), 390–1); the essay on what Mehnert insisted on calling ‘Kainogenesis’ “almost led to my resignation from my position here” (see, also for his health and writing, Mehnert to Haeckel, 14 May 1898, Ernst-Haeckel-Haus Jena: Best. A, Abt. I). In 1898 Mehnert had nevertheless been hired as an associate professor of anatomy under Roux at Halle.

71. Schwalbe, “Variation” (ref. 65), 8.
72. NT 2, 2–3, 13. Fischel concluded conventionally that the range of variation declined as development proceeded, presumably as a result of correlation; see Alfred Fischel, “Über Variabilität und Wachsthum des embryonalen Körpers”, *Morphologisches Jahrbuch*, xxiv (1896), 369–404; and Keibel, “Das biogenetische Grundgesetz” (ref. 18), 764–8.
73. Keibel, “Normentafeln” (ref. 59). There was not even an honorarium; see Annelise von Lucius (Fischer-Verlag) to Friedrich Kopsch, 26 May 1952, Thüringisches Hauptstaatsarchiv Weimar: Archiv Verlagshaus Gustav Fischer Jena, Korrespondenzakte 1952, Kl–Lat. I am grateful for the limited access I was granted to this collection, but I was not permitted to consult several possibly-relevant files.
74. Keibel received support from the Prussian Academy of Sciences (NT 1, 10), and Otto Grosser and Julius Tandler from the Academy of Sciences in Vienna (NT 9, preface).
75. Ewing Taylor (NT 5) described the work as making his brain feel “rather stale”; see Taylor to Minot, 30 July 1904, Harvard Medical Library in the Francis A. Countway Library of Medicine, Boston, Mass.: H MS c21.2. On Minot’s embryology, see Frederic T. Lewis, “Charles Sedgwick Minot”, *The anatomical record*, x (1916), 133–64.
76. F. R. L[illie], review of NT 11, *The anatomical record*, v (1911), 186.
77. Roy MacLeod drew attention to the relations between embryology and empire; see Roy MacLeod, “Embryology and empire: The Balfour Students and the quest for intermediate forms in the laboratory of the Pacific”, in *idem* and Philip F. Rehbock (eds), *Darwin’s laboratory: Evolutionary theory and natural history in the Pacific* (Honolulu, 1994), 140–65. I stress the intellectual and material transformations that scientists’ appropriations worked, and their limits.
78. Adele E. Clarke, “Research materials and reproductive science in the United States, 1910–1940”, in Gerald L. Geison (ed.), *Physiology in the American context, 1850–1940* (Bethesda, Md., 1987), 323–50, pp. 332–4.
79. NT 4, 2.
80. Keibel, “Entwicklungsgeschichte des Schweines” (ref. 56), 10–11; NT 6, preface; Fick, “Gedächtnisrede” (ref. 52), p. cxiii; NT 12, 1.
81. NT 9, preface, 1–2; http://www.fonyod.hu/, accessed 21 May 2004.
82. Albert C. Eycleshymer, “The habits of *Necturus maculosus*”, *The American naturalist*, xl (1906), 123–36, p. 132 (quote); NT 11, preface, 1; L[illie], review of NT 11 (ref. 76).
83. MacLeod, “Embryology and empire” (ref. 77).
84. George W. Corner, *Ourselves unborn: An embryologist’s essay on man* (New Haven, 1944), 28.
85. Semon, *Im australischen Busch* (ref. 17); John Graham Kerr, *A naturalist in the Gran Chaco* (Cambridge, 1950); Edward Hindle, “John Graham Kerr, 1869–1957”, *Biographical memoirs of Fellows of the Royal Society*, iv (1958), 155–66.
86. J. Graham Kerr, “The development of *Lepidosiren paradoxa*: Part II. With a note upon the corresponding stages in the development of *Protopterus annectens*”, *Quarterly journal of microscopical science*, xlv (1901), 1–40 (p. 3 suggests that the *Protopterus* embryos for the normal plate also came from Budgett); J. Graham Kerr (ed.), *The work of John Samuel Budgett, Balfour Student of the University of Cambridge ...* (Cambridge, 1907); Brian K. Hall, “John Samuel Budgett (1872–1904): In pursuit of *Polypterus*”, *BioScience*, li (2001), 399–407.

Budgett's sacrifice for evolutionary embryology rivals the gathering of emperor-penguin eggs on the 'winter journey' of Scott's Antarctic expedition; see Rudolf A. Raff, *The shape of life: Genes, development, and the evolution of animal form* (Chicago, 1996), 1–4.

87. A. A. W. Hubrecht, "Studies from the Zoological Laboratory in the University of Utrecht: IV. Spolia nemoris", *Quarterly journal of microscopical science*, xxxvi (1894), 77–125; Ric[hard] Assheton, "Dr Ambrosius Arnold Willem Hubrecht", *Proceedings of the Linnean Society of London*, cxxvii (1915), 28–31; Franz Keibel, "A. A. W. Hubrecht: Ein Nachruf", *Anatomischer Anzeiger*, xlviii (1915), 201–8; J. Faber, "Hubrecht, Ambrosius Arnold Willem", in *Dictionary of scientific biography*, vi, 535–6; Bowler, *Life's splendid drama* (ref. 28), 181–3, 295–6.
88. Semon, *Im australischen Busch* (ref. 17); Kerr, *Naturalist in the Gran Chaco* (ref. 85), 173–5.
89. For complaints of ignorance, see Eduard Seidel, "19. Jahrhundert: Zur Vorgeschichte des Paragraphen 218", in Robert Jütte (ed.), *Geschichte der Abtreibung: Von der Antike bis zur Gegenwart* (Munich, 1993), 120–39; for reframing, Hopwood, "Producing development" (ref. 8), 38–40; and *idem*, "Embryonen" (ref. 8), 240–1, 267–72.
90. NT 12, 1.
91. Kerr, *Naturalist in the Gran Chaco* (ref. 85), 175, 179, 180–1.
92. J. S. Budgett, "On the breeding-habits of some West-African fishes, with an account of the external features in development of *Protopterus annectens*, and a description of the larva of *Polypterus lapradei*", *Transactions of the Zoological Society of London*, xvi (1901), 115–36, p. 120.
93. NT 7, 35. Hubrecht probably means a belief he reported earlier that the loris skeleton is "most efficacious in bringing about death and destruction among the unfortunate inhabitants of a house in front of which it has been buried overnight". This generated "high demand among the wealthier natives who have family quarrels to settle, and I have known exorbitant prices, with which a collecting embryologist could not possibly compete, to be stealthily paid for one specimen, for this unfriendly though perhaps harmless purpose" (Hubrecht, "Spolia nemoris" (ref. 87), 90–91).
94. Kerr, *Naturalist in the Gran Chaco* (ref. 85), 179.
95. Keibel, "Normentafeln" (ref. 59), 231, 233; *idem*, "Mitteilungen" (ref. 59), 594.
96. The two prewar exceptions are Semon, who used a cheaper half-tone process because his figures had already been published in excellent lithographs (NT 3, iii), and Grosser and Tandler, who probably favoured photomechanical reproduction because they began with photographs that an artist retouched and made more detailed (NT 9, 2–3). Keibel, finding the retouched photograms "somewhat *dull*", preferred lithographs, but left the decision to Tandler and Fischer; see Keibel to Tandler, 19 March 1906, and Fischer to Keibel, 28 August 1908, Institut für Geschichte der Medizin der Medizinischen Universität Wien: HS 4508/3 and 4066/4. Peter had drawings done after photographs, but mostly not directly onto them (NT 4, 3–4).
97. NT 3, 2; NT 4, 3.
98. Daston and Galison, "Image of objectivity" (ref. 4); Hopwood, "Producing development" (ref. 8), 73–74.
99. Kerr, "Development of *Lepidosiren*" (ref. 86), 36–37; NT 10.
100. NT 5, 1; NT 12, 1. On reconstructions, see also Frederic T. Lewis, review of NT 8, *Science*, xxix (1909), 939–40. To get to grips with complex structures wax models were sometimes reconstructed from the serial sections and occasionally even depicted on normal plates (NT 1, 11, pl. II–III), an indication of the centrality of modelling in vertebrate embryology, on which see Hopwood, "'Giving body'" (ref. 5); and *idem*, *Embryos in wax* (ref. 8).
101. NT 12, 70.
102. NT 8; Hopwood, "Producing development" (ref. 8), 74–76.
103. NT 12, 70–78; Balfour, *Development of elasmobranch fishes* (ref. 10), 71–80, pl. VI–VII.

104. Gould, *Ontogeny and phylogeny* (ref. 11), 174.
105. E.g., NT 7, 28–34, 48–61; NT 8, 152–62; NT 9, 43. Bruno Henneberg, believing his penultimate volume likely to be the last, attempted to summarize the relative rates at which different organs developed among the amniotes in the series, and concluded that there was considerable agreement (NT 15, 110–60).
106. Gould, *Ontogeny and phylogeny* (ref. 11), 174; Bowler, *Life's splendid drama* (ref. 28). Keibel's own position changed little; see Franz Keibel, "Die Entwicklungsgeschichte der Wirbeltiere", in Paul Hinneberg (ed.), *Die Kultur der Gegenwart: Ihre Entwicklung und ihre Ziele*, part iii, section iv, vol. ii: *Zellen- und Gewebelehre, Morphologie und Entwicklungsgeschichte*, part 2: O. Hertwig (ed.), *Zoologischer Teil* (Leipzig, 1913), 333–98.
107. Wilhelm Pfühl, "Karl Peter †", *Anatomischer Anzeiger*, cii (1955), 224–44.
108. Keibel, "Das biogenetische Grundgesetz" (ref. 18), 758.
109. J. Graham Kerr, *Text-book of embryology*, ii: *Vertebrata with the exception of Mammalia* (London, 1919), 575. See also Anon., review of NT 1, *Revue scientifique*, 1898; C. A. K., review of NT 2, *Journal of applied microscopy and laboratory methods*, both consulted as clippings in the Fischer Archiv (ref. 73), Rezensionsarchiv, Karton 40; and W[ilhelm] Waldeyer, "Anatomie: X. Lehr- und Handbücher", *Ergebnisse der Anatomie und Entwicklungsgeschichte*, xii (1903), 652–742, p. 715, judging NT 1–3 "indispensable for all further investigations".
110. For the standard run, see von Lucius to Kopsch, 26 May 1952 (ref. 73). The prices (from the wrappers of NT 10–12) range from 7.50 marks for NT 9 to 36 marks for NT 8; as a comparison, Oscar Hertwig's textbook cost 13 and his 6-volume handbook 135 marks.
111. On Tandler, see Karl Sablik, *Julius Tandler, Mediziner und Sozialreformer: Eine Biographie* (Vienna, 1983); and for the suggestion that Abraham, the leading figure in German psychoanalysis, "never lost" the interest in embryology gained in work on NT 2 and his dissertation on budgerigar development, Hilda C. Abraham, "Karl Abraham: An unfinished biography", *International review of psychoanalysis*, i (1974), 17–72, p. 22; see also Richard E. Scammon and Leroy A. Calkins, *The development and growth of the external dimensions of the human body in the fœtal period* (Minneapolis, 1929).
112. Gursch, *Die Illustrationen Ernst Haeckels* (ref. 43), 84–136; Andreas W. Daum, *Wissenschaftspopularisierung im 19. Jahrhundert: Bürgerliche Kultur, naturwissenschaftliche Bildung und die deutsche Öffentlichkeit, 1848–1914* (Munich, 1998), 210–35; Franz Keibel, "Haeckel und Brass", *Deutsche medizinische Wochenschrift*, xxxv (1909), no. ii, 350–1.
113. Franklin P. Mall, review of NT 8, *The anatomical record*, ii (1908), 368–71, p. 371; see also Lewis, review of NT 8 (ref. 100). Keibel had the book sent to Mall and asked for a review; see Keibel to Mall, 23 July 1908, Carnegie Department Papers (ref. 61), record group I, series 1, box 10, folder 34.
114. Ernst Haeckel, "Die Grenzen der Naturwissenschaft", *Deutsche medizinische Wochenschrift*, xxxvi (1910), no. ii, 1855–7, p. 1857 (quotes); *idem*, *Anthropogenie*, 5th edn (ref. 70), i, 380; Heinrich Schmidt, *Haeckels Embryonenbilder: Dokumente zum Kampf um die Weltanschauung in der Gegenwart* (Frankfurt am Main, 1909), 81–87.
115. On Keibel's career, see especially Nauck, *Keibel* (ref. 52), 18–25; and on the anatomical job market, Nyhart, *Biology takes form* (ref. 11), 278–305.
116. Wilhelm His, "Antrag der Königlich Sächsischen Gesellschaft der Wissenschaften auf Bestellung einer Fachcommission für menschliche und thierische Entwickelungsgeschichte und für Anatomie des Gehirnes, vorgelegt der Generalversammlung der Internationalen Association der Akademien am 16. April 1901 zu Paris", *Berichte über die Verhandlungen der Königlich Sächsischen Gesellschaft der Wissenschaften zu Leipzig, Mathematisch-physische Classe*, liii (1901), 77–82. The Association (on which see Frank Greenaway, *Science international: A history of the International Council of Scientific Unions* (Cambridge, 1996), 6–18) decided

to constitute a special commission for brain anatomy, but for the moment to leave the smaller and more divided field of embryology to the subject societies; the Anatomische Gesellschaft created a commission of Wilhelm Waldeyer, Carl Rabl, Keibel and His (His, "Wissenschaftliche Centralanstalten" (ref. 59), 414).

117. P. D. Nieuwkoop, "'L'Institut International d'Embryologie' (1911–1961)", *General embryological information service*, ix (1961), 265–9. For a record of the first two meetings, see [Franz] Keibel, [Richard] Assheton and [A. A. W.] Hubrecht, "Institut International d'Embryologie: Session de 1912", *Bibliographie anatomique*, xxii, no. 3, offprint numbered 1–12, in Carnegie Department Papers (ref. 61), record group I, series 1, box 9, folder 27. The Institut was also interested in supporting the International Commission on Embryological Nomenclature. Of the 11 men at the founding meeting, eight were among Keibel's actual or prospective authors. Nieuwkoop's and other accounts name Hubrecht, Keibel and the British embryologist Richard Assheton as the initiators of the Institut, but Bonnet was in fact the third signatory of the call, was (unlike Assheton) at the founding meeting, and was even the first president. He may have been written out of the history for unclear reasons associated with the resignation of his membership by the following year.

118. Nieuwkoop, "'L'Institut International'" (ref. 117), 265–6; Patricia Faasse, Job Faber and Jenny Narraway, "A brief history of the Hubrecht Laboratory", *International journal of developmental biology*, xliii (1999), 583–90; Michael K. Richardson and Jennifer Narraway, "A treasure house of comparative embryology", *ibid.*, 591–602. Patricia Faasse, *Zuiver om de wetenschap: De Akademie en haar levenswetenschappelijke instituten* (Amsterdam, 1999), 27–30, makes clear that the idea of a central embryological collection went back to His's proposals.

119. On the early years of the Carnegie Department, see Florence Rena Sabin, *Franklin Paine Mall: The story of a mind* (Baltimore, 1934); O'Rahilly, "One hundred years" (ref. 10); and Lynn M. Morgan, "'Properly disposed of': A history of embryo disposal and the changing claims on fetal remains", *Medical anthropology*, xxi (2002), 247–74. For Mall's extensive discussions with Keibel over founding what became the *Contributions to embryology*, see their correspondence in Carnegie Department Papers (ref. 61), record group 1, series 1, box 10; and on the money, specifically Keibel to Mall, 23 February, 10 April and 18 June 1914, *ibid.*, folder 37.

120. Peter, "Keibel" (ref. 52), 202–4; Fick, "Gedächtnisrede" (ref. 52), pp. cix–cxi; Weindling, *Darwinism* (ref. 26), 250.

121. Keibel to Fischer, 10 and 15 March 1922, Fischer Archiv (ref. 73), Korrespondenzakten.

122. Keibel to Fischer, 24 January 1929, *ibid.*

123. Fischer to Keibel, 9 December 1922, *ibid.*; Keibel to George L. Streeter, 13 December 1922 and 25 March 1924, Carnegie Department Papers (ref. 61), record group I, series 2, box 26, folder 24.

124. Glaesner had also been an assistant at the Berlin oceanography museum; see Lynn K. Nyhart, "Science, art, and authenticity in natural history displays", in de Chadarevian and Hopwood (eds), *Models* (ref. 8), 307–35, pp. 323–7.

125. Dan. de Lange, Jr, and H. F. Nierstrasz, *Tabellarische Uebersicht der Entwicklung von* Tupaia javanica *Horsf.* (Utrecht, 1932); F. J. Huisman and Dan. de Lange, *Tabellarische Uebersicht der Entwicklung von* Manis javanica *Desm.* (Utrecht, 1937). These volumes are smaller than Keibel's. On the revival of the I. I. d'E., negotiations over and promotion of the plates, see the German, English and French introduction to the de Lange and Nierstrasz plate; and correspondence of the I. I. d'E. with Warren H. Lewis, American Philosophical Society, Philadelphia: B L586; and with Streeter, 1931–8, Carnegie Department Papers (ref. 61), record group I, series 2, box 24, folders 25–26.

126. For American demand for a rat *Normentafel*, see Streeter to Keibel, 5 March, 28 April and 11 June, and Keibel to Streeter, 25 March and 1 April 1924, Carnegie Department Papers (ref. 61), record group I, series 2, box 26, folder 24; on the much delayed production of the plate, which unusually

includes many figures of sections, see correspondence between Bruno Henneberg and Fischer, Fischer Archiv (ref. 73), Korrespondenzakten 1937, Hart–Hern; and for its status as Henneberg's "main scientific work", see Hans-Rainer Duncker, "Bruno Henneberg (1867–1941) / Anatom", in Hans Georg Gundel, Peter Moraw and Volker Press (eds), *Gießener Gelehrte in der ersten Hälfte des 20. Jahrhunderts* (2 parts, Marburg, 1982), Part 1, 378–86, p. 384.

127. Michael K. Richardson, "Heterochrony and the phylotypic period", *Developmental biology*, clxxii (1995), 412–21; Olaf R. P. Bininda-Emonds, Jonathan E. Jeffery, Michael I. Coates and Michael K. Richardson, "From Haeckel to event-pairing: The evolution of developmental sequences", *Theory in biosciences*, cxxi (2002), 297–320, pp. 301–3.
128. Benjamin H. Willier, Paul A. Weiss and Viktor Hamburger, *Analysis of development* (Philadelphia, 1955), p. v.
129. Jane M. Oppenheimer, "Problems, concepts and their history", *ibid.*, 1–24, p. 22; *idem*, "Methods and techniques", *ibid.*, 25–38.
130. *Idem*, "The normal stages of *Fundulus heteroclitus*", *The anatomical record*, lxviii (1937), 1–8; *idem*, "Fifty years of *Fundulus*", *The quarterly review of biology*, liv (1979), 385–95, p. 386. This was in a Yale tradition, which, as I am about to describe, went back (through John S. Nicholas) to Harrison.
131. Viktor Hamburger and Howard L. Hamilton, "A series of normal stages in the development of the chick embryo", *Journal of morphology*, lxxxviii (1951), 49–92, reprinted in *Developmental dynamics*, cxcv (1992), 231–72; Joshua R. Sanes, "On the republication of the Hamburger–Hamilton stage series", *ibid.*, 229–30.
132. John V. Pickstone, "Museological science? The place of the analytical/comparative in nineteenth-century science, technology and medicine", *History of science*, xxxii (1994), 111–38. On the literary control of variability in the laboratory, see Kohler, *Lords of the fly* (ref. 2), 71–77.
133. Karl Peter, "Der Grad der Beschleunigung tierischer Entwicklung durch erhöhte Temperatur", *Archiv für Entwicklungsmechanik der Organismen*, xx (1906), 130–54, p. 134.
134. Ross G. Harrison, "Experiments on the development of the fore limb of *Amblystoma*, a self-differentiating equipotential system", *The journal of experimental zoology*, xxv (1918), 413–59, p. 417; *idem*, *Organization and development of the embryo*, ed. by Sally Wilens (New Haven, 1969), 45. On Harrison, see especially Maienschein, *Transforming traditions* (ref. 11), 261–89.
135. Ross G. Harrison, "The development of the balancer in *Amblystoma*, studied by the method of transplantation and in relation to the connective-tissue problem", *The journal of experimental zoology*, xli (1925), 349–427, pp. 359, 361.
136. Harrison to the Chicago anatomist, C. Judson Herrick, 26 March 1937, Yale University Library, Manuscripts and Archives: Ross Granville Harrison Papers (MS 263), series I, box 12, folder 884.
137. Joseph L. Schwind and Victor C. Twitty to Harrison, 3 October 1927, *ibid.*, series III, box 38, folder 257.
138. Harrison, *Organization and development* (ref. 134), 44–66.
139. Quote from H. E. Lehman, "A memorial in embryology", *Science*, clxviii (1970), 724–5; see also Viktor Hamburger, review of Harrison, *Organization and development* (ref. 134), *American scientist*, lviii (1970), 321–2.
140. Arthur W. Pollister and John A. Moore, "Tables for the normal development of *Rana sylvatica*", *The anatomical record*, lxviii (1937), 489–96, p. 489.
141. For a distribution list, see Harrison Papers (ref. 136), series III, box 38, folder 258.
142. Francis H. Swett to Harrison, 21 November 1928, *ibid.*
143. Viktor Hamburger, *A manual of experimental embryology* (Chicago, 1942), 196–204. Compare Roberts Rugh, *Experimental embryology: A manual of techniques and procedures*, rev. edn

(Minneapolis, 1948), 56–101; Rugh to Harrison, 25 February and 28 March 1941, Harrison Papers (ref. 136), series I, box 23, folder 1727. To my knowledge, the stage descriptions were first published in Harrison's book.

144. Viktor Hamburger, "Über den Einfluss des Nervensystems auf die Entwicklung der Extremitäten von *Rana fusca*", *Wilhelm Roux' Archiv für Entwicklungsmechanik der Organismen*, cv (1925), 149–201, pp. 157–8; *idem*, "Afterword: The stage series of the chick embryo", *Developmental dynamics*, cxcv (1992), 273–5, p. 273. Hamburger's own account suggests he was inspired by Harrison's work, and the Yale zoologist may have been more important to him than the Freiburg anatomical tradition, but he appears to have obtained photographs from Harrison only in 1929 (Hamburger to Harrison, 10 March 1929, Harrison Papers (ref. 136), series I, box 11, folder 828). On Hamburger, see his *The heritage of experimental embryology: Hans Spemann and the organizer* (New York, 1988); and "Viktor Hamburger virtual exhibit", http://library.wustl.edu/units/biology/vh/, accessed 24 May 2004.

145. Salome G. Waelsch, "The causal analysis of development in the past half century: A personal history", *Development*, 1992, supplement, 1–5, p. 1 (quotes); Salome Glücksohn, "Äussere Entwicklung der Extremitäten und Stadieneinteilung der Larvenperiode von *Triton taeniatus* Leyd. und *Triton cristatus* Laur.", *Wilhelm Roux' Archiv für Entwicklungsmechanik der Organismen*, cxxv (1931), 341–405; Hamburger, "Afterword" (ref. 144), 274; Peter E. Fäßler, *Hans Spemann 1869–1941: Experimentelle Forschung im Spannungsfeld von Empirie und Theorie. Ein Beitrag zur Geschichte der Entwicklungsphysiologie zu Beginn des 20. Jahrhunderts* (Berlin, 1997), 70–72 (on Spemann's treatment of female doctoral candidates). Hamburger sought Harrison's permission for Waelsch to refer to his stages; see Hamburger to Harrison, 21 November 1930 (quote), and Harrison to Hamburger, 27 June 1931, Harrison Papers (ref. 136), series I, box 11, folder 828.

146. Howard L. Hamilton, *Lillie's development of the chick: An introduction to embryology*, 3rd edn (New York, 1952), 74–91; Hamburger and Hamilton, "Normal stages" (ref. 131); Hamburger, "Afterword" (ref. 144).

147. For critical remarks on NT 2, see Hamburger and Hamilton, "Normal stages" (ref. 131), 50; and on NT 4, Jean J. Pasteels, "Une table analytique du développement des reptiles: 1. Stades de gastrulation chez les Chéloniens et les Lacertiliens", *Annales de la Société Royale Zoologique de Belgique*, lxxxvii (1957), 217–41, pp. 217–18. For Glücksohn's explanation why she followed Harrison's stages rather than Glaesner's (NT 14), see her "Äussere Entwicklung" (ref. 145), 353. See also Hamburger to Harrison, 21 November 1930, Harrison Papers (ref. 136), series I, box 11, folder 828.

148. See Hamburger and Hamilton, "Normal stages" (ref. 131), 50, for one of many claims that earlier controversies could have been avoided had proper stages been used.

149. Hamburger, "Afterword" (ref. 144), 275.

150. Hamburger and Hamilton, "Normal stages" (ref. 131), 52.

151. Fr[iedrich] Kopsch, *Die Entwicklung des braunen Grasfrosches* Rana fusca *Roesel, dargestellt in der Art der* Normentafeln zur Entwicklungsgeschichte der Wirbeltiere (Stuttgart, 1952), p. vi. Quote from Keibel to Gustav Fischer, [1922], Fischer Archiv (ref. 73), Korrespondenzakte 1922, Kla–Kly. Kopsch switched to a Stuttgart publisher because obtaining permission to publish the work with Fischer in Jena threatened to take too long. On Kopsch, see W. Richter, "Friedrich Kopsch und sein Beitrag zur Entwicklung der Berliner Anatomie im 19. und 20. Jahrhundert", *Charité-Annalen*, n. s., viii (1988), 237–42.

152. Nieuwkoop and Faber (eds), *Normal table* (ref. 1), 1; Gurdon and Hopwood, "Introduction of *Xenopus*" (ref. 1). Funding was obtained from various Dutch organizations and (for publication) from the International Council of Scientific Unions, successor to the International Association of Academies (Nieuwkoop and Faber (eds), *Normal table* (ref. 1), 3).

153. Nieuwkoop and Faber (eds), *Normal table* (ref. 1); additional information from Faber to the author,

14 July 1999.

154. Emil Witschi, "Proposals for an international agreement on normal stages in vertebrate embryology", *XIV International Congress of Zoology, Copenhagen, 5.–12. August 1953, proceedings* (Copenhagen, 1956), 260–2. Ronan O'Rahilly of the Carnegie Department found the idea "attractive"; see O'Rahilly, *Developmental stages* (ref. 10), 7–8; and *idem* and Müller, *Developmental stages* (ref. 10), 8.
155. Jane M. Oppenheimer, "The growth and development of developmental biology", in Michael Locke (ed.), *Major problems in developmental biology* (New York, 1966), 1–27; Evelyn Fox Keller, *Refiguring life: Metaphors of twentieth-century biology* (New York, 1995); Hopwood, "Embryology" (ref. 3).
156. Gurdon and Hopwood, "Introduction of *Xenopus*" (ref. 1); for 'literary technology', see Steven Shapin, "Pump and circumstance: Robert Boyle's literary technology", *Social studies of science*, xiv (1984), 481–520.
157. In the late 1980s and 1990s, many laboratories switched to the zebrafish and consulted Charles B. Kimmel, William W. Ballard, Seth R. Kimmel, Bonnie Ullmann and Thomas F. Schilling, "Stages of embryonic development of the zebrafish", *Developmental dynamics*, cciii (1995), 253–310.
158. James Griesemer and Grant Yamashita, "Managing time in model systems: Illustrations from evolutionary biology", unpublished paper. Other aspects of the history of normal plates could be analysed in time management terms, such as Keibel's enlisting collaborators and the use of *Xenopus* to overcome seasonality.
159. O'Rahilly, "One hundred years" (ref. 10), 93.
160. On the Carnegie Department at mid-century and since, see Corner, *Ourselves unborn* (ref. 84); Loretta McLaughlin, *The pill, John Rock, and the Church: The biography of a revolution* (Boston, 1982), 58–71; Donald D. Brown, "The Department of Embryology of the Carnegie Institution of Washington", *BioEssays*, vi (1987), 92–96; and http://nmhm.washingtondc.museum/collections/hdac/index.htm, accessed 3 June 2004.
161. George L. Streeter, "Department of Embryology", *Carnegie Institution of Washington year book*, xxi (1922), 76–92, p. 76.
162. *Idem*, "Developmental horizons in human embryos: Description of age group XI, 13 to 20 somites, and age group XII, 21 to 29 somites", *Contributions to embryology*, xxx (1942), 211–45, pp. 213–14; Franklin P. Mall, "On stages in the development of human embryos from 2 to 25 mm long", *Anatomischer Anzeiger*, xlvi (1914), 78–84. On Streeter, see George W. Corner, "George Linius Streeter, 1873–1948", *Biographical memoirs of the National Academy of Sciences*, xxviii (1954), 260–87.
163. George L. Streeter, "Developmental horizons in human embryos: Description of age groups XV, XVI, XVII, and XVIII, being the third issue of a survey of the Carnegie Collection", *Contributions to embryology*, xxxii (1948), 133–203, p. 135.
164. *Idem*, "Developmental horizons in human embryos: Description of age groups XIX, XX, XXI, XXII, and XXIII, being the fifth issue of a survey of the Carnegie Collection", *ibid*., xxxiv (1951), 165–96, p. 169.
165. *Idem*, "Third issue of a survey" (ref. 163), 137.
166. *Idem*, "Archetypes and symbolism", *Science*, lxv (1927), 405–12.
167. O'Rahilly, *Developmental stages* (ref. 10), 4; *idem* and Müller, *Developmental stages* (ref. 10).
168. O'Rahilly, *Developmental stages* (ref. 10), 7–8. Carnegie stages are still in general use, but there are signs that they no longer meet all the demands of a human embryology that has been transformed in the last few decades (Patrick Barbet, "Une approche historique de l'étude des stades du développement de l'embryon humain", talk presented at workshop, "L'embryon humain face au temps de l'histoire, face au temps de la vie", Fribourg, Switzerland, 29 October 2004).

169. Galison, "Judgment against objectivity" (ref. 4).
170. *Ibid.*, 354; Daston, "Objectivity versus truth" (ref. 4).
171. Quotes from Corner, preface to Streeter's *Developmental horizons* (ref. 10).
172. During the First World War Mall obtained embryos of various species for Keibel; their letters illustrate the utility of normal plates in communicating with collectors. Keibel sometimes used the plates to describe stages he needed (Keibel to Mall, 7 November 1915 and 14 March 1916, Carnegie Department Papers (ref. 61), record group 1, series 1, box 10, folder 40), but Mall "could not get any standard plates on the turtle, so it was impossible for me to place the order with the collector in a more definite way" (Mall to Keibel, 24 January 1916, *ibid.*).