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Haeckel's ABC of evolution and development

MICHAEL K. RICHARDSON[1] and GERHARD KEUCK[2]

[1] *Section of Integrative Zoology, Institute of Evolutionary and Ecological Sciences, University of Leiden, Kaiserstraat* 63, 2311 *GP Leiden, The Netherlands* (Fax: (international: 31) (0) 715 274 900. Tel: (international: 31) (0) 715 275 215. e-mail: richardson@rulsfb.leidenuniv.nl)
[2] *Biologist, R & D Documentation, Aventis CropScience GmbH, Industriepark Höchst, K*607, 65926 *Frankfurt a.M., Germany* (e-mail: Gerhard.Keuck@aventis.com)

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ABSTRACT

One of the central, unresolved controversies in biology concerns the distribution of primitive *versus* advanced characters at different stages of vertebrate development. This controversy has major implications for evolutionary developmental biology and phylogenetics. Ernst Haeckel addressed the issue with his Biogenetic Law, and his embryo drawings functioned as supporting data. We re-examine Haeckel's work and its significance for modern efforts to develop a rigorous comparative framework for developmental studies. Haeckel's comparative embryology was evolutionary but non-quantitative. It was based on developmental sequences, and treated heterochrony as a sequence change. It is not always clear whether he believed in recapitulation of single characters or entire stages. The Biogenetic Law is supported by several recent studies – if applied to single characters only. Haeckel's important but overlooked alphabetical analogy of evolution and development is an advance on von Baer. Haeckel recognized the evolutionary diversity in early embryonic stages, in line with modern thinking. He did not necessarily advocate the strict form of recapitulation and terminal addition commonly attributed to him. Haeckel's much-criticized embryo drawings are important as phylogenetic hypotheses, teaching aids, and evidence for evolution. While some criticisms of the drawings are legitimate, others are more tendentious. In opposition to Haeckel and his embryo drawings, Wilhelm His made major advances towards developing a quantitative comparative embryology based on morphometrics. Unfortunately His's work in this area is largely forgotten. Despite his obvious flaws, Haeckel can be seen as the father of a sequence-based phylogenetic embryology.

Key words: Biogenetic Law, development, vertebrate embryo, embryology, Ernst Haeckel, evolution, phylogeny, recapitulation, scientific fraud, scientific illustration.

CONTENTS

I. INTRODUCTION

(1) Haeckel's importance to biology

Ernst Heinrich Haeckel (1834–1919) was a Professor of Zoology at Jena University in eastern Germany (Bölsche, 1900, 1906; Haeckel, 1923; Uschmann, 1954, 1960; Heberer, 1968; Gasman, 1971, 1998; Keitel-Holz, 1984; Krauße, 1984; Weindling, 1989; Nyhart, 1995; See Heberer, 1968 pp. 15–22 for a list of Haeckel's publications). He promoted his scientific views through a number of influential popular science books (e.g. Haeckel, 1868, 1874a). Less widely known are his important and magnificently illustrated zoological monographs, and his many scientific innovations, including his suggestion (Haeckel, 1866: pp. 287–289) that the nucleus was an agency of heredity (see also Heberer, 1968: p. 131).

Haeckel influenced many disciplines in science (Uschmann, 1985). His major contributions to evolutionary biology were his drive to integrate different disciplines, including taxonomy and embryology, into the new Darwinian framework, and to use the data for phylogeny reconstruction (Haeckel, 1866, 1894, 1896*a*). His Fundamental Biogenetic Law described parallels between individual development or 'ontogeny', and evolutionary history or 'phylogeny' (reviewed by Gould, 1977; Rieppel, 1988). He drew up family trees of the animal kingdom (Kemp, 1998) which, unlike the Linnean scheme, implied that animals were related by descent. He trained or mentored an impressive number of scientists, including Anton Dohrn, Richard and Oscar Hertwig, Wilhelm Roux, and Hans Driesch (Walzl, 1998: p. 137).

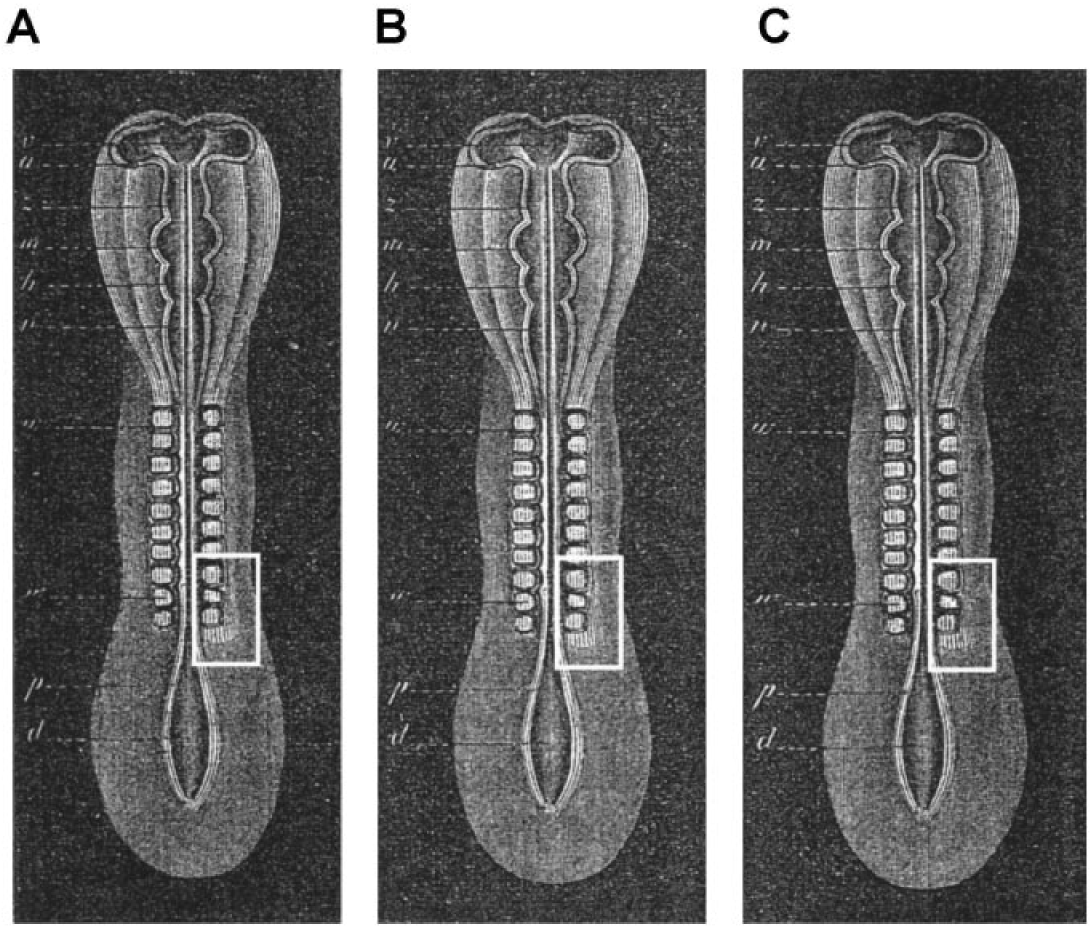

Fig. 1. Drawings from the first edition of *Natürliche Schöpfungsgeschichte* (Haeckel, 1868). Mid-somite embryos, supposedly of dog (A), chicken (B) and turtle (C) Figs 9–11, respectively, in the original. The woodcuts are identical, sharing the same irregularities in the somite series (e.g. boxed area, added by us). See Rütimeyer (1868), Gursch (1981), Rager (1986). Digital scan courtesy of Kurt Stüber, Köln.

(2) The need for re-examination of Haeckel's work in evolutionary developmental biology

It might be asked why there is a need for another discussion of Haeckel's biology. After all, Alberch (1985: p. 57) has warned against recapitulating the debates of the late 19th and early 20th centuries, and Kluge & Straus (1985: p. 247) argue that modern scientists may be trying to read too much into the work of pioneers. It is sometimes complained that the debates about Haeckel's work are anachronistic and irrelevant (e.g. de Pinna, 1994). We believe that there are good reasons for another discussion of Haeckel's work. In general terms, it is scientifically important, and continues to be relevant to comparative embryology.

More specifically, molecular studies of embryonic pattern formation re-awakened interest in issues such as the conservation of early development (Slack, Holland and Graham, 1993), and the evolution of developmental mechanisms. For these and other reasons, Haeckel's theories, and his embryo drawings (Figures 1–3), have come to be used in many influential developmental biology texts and articles (e.g. Duboule, 1994; Alberts *et al.*, 1994; Gerhart and Kirschner, 1997).

Comparative embryology has been greatly handicapped by its lack of a quantitative framework, and its failure to embrace phylogenetic methodology. However, this is changing with the advent of methodologies such as event-pairing (Smith, 1996; Mabee & Trendler, 1996; Velhagen 1997; Jeffery *et al.*, 2002*a*, 2002*b*; reviewed by Smith, 2001) which analyse developmental sequences within a phylogenetic framework. Haeckel is important in this context because his work, together with that of Karl von Baer and Wilhelm His (1831–1904) provides part of the foundation of phylogenetic embryology.

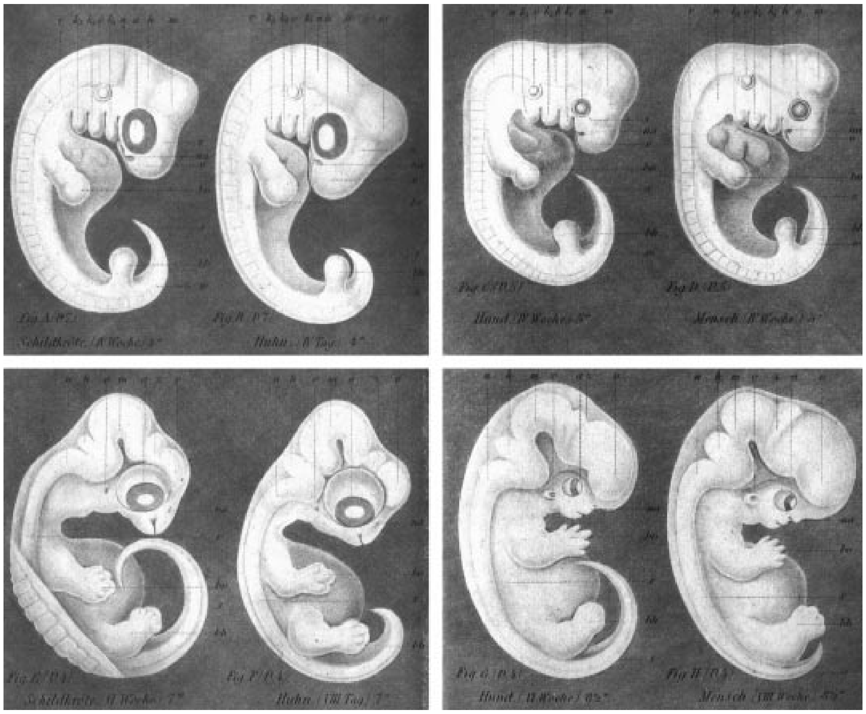

Fig. 2. Plate of four species at two stages from the fifth German edition *of Natürliche Schöpfungsgeschichte* (Haeckel, 1874*c*: plate II, III). Left to right: tortoise, chick, dog, man. The early chick embryo is possibly copied from Erdl (1845*a*: plate. XII Fig. 6) and resembles the chick in the middle row of Haeckel's (1874*a*) *Anthropogenie* plate IV (Fig. 3 here).

(3) Our approach in this article

We shall treat Haeckel's Biogenetic Law and embryo drawings as hypotheses about a key controversy in biology: the sequence of appearance of primitive *versus* advanced characters during development. We argue that this pattern provides a unifying theme for many major, but seemingly disparate, biological hypotheses. These include von Baer's laws, Darwin's 'late modification' of developmental stages, the phylotypic stage, the ontogenetic polarity criterion, and the zootype. We will discuss some of these models in detail.

Throughout the article, we consider how Haeckel's work has influenced modern scientific ideas about evolution and development, and examine Haeckel's theories in the light of contemporary and recent work. We identify criticisms of Haeckel's work based on legitimate scientific concerns, and try to distinguish them from confusion and ambivalence arising from a misunderstanding of the primary sources or scientific issues.

This paper is divided into three sections. First, we review the Biogenetic Law, and its applications, as Haeckel outlines them in the original texts. Second, we present a scientific analysis of those ideas, and describe how Haeckel's theories and methods have been received by other scientists. Third, we present a scientific analysis of Haeckel's embryo drawings and the scientific controversies surrounding them. Throughout, we try to compare old ideas and approaches with those used in modern biology. (Note: Where English translations of the German works have been read by us, we have cited these as separate references. A number of Haeckel's works ran to several editions, and we have cited the one known to us; this is not necessarily the first edition.)

II. HAECKEL'S BIOGENETIC LAW, AND ITS APPLICATIONS, AS DESCRIBED IN THE ORIGINAL TEXTS

In this section, we discuss Haeckel's formulation of the Biogenetic Law, and examine how he applied it to various problems in evolution and development, including phylogeny reconstruction and comparative embryology. We show that his views were more complex than is sometimes appreciated.

Fig. 3. Plates of eight species compared at three stages of development. Left to right: fish, salamander, turtle, chicken, pig, cow, rabbit and human. The pictures contain many anomalies. For instance, note that in HII and TII, the forelimb bud appears to be growing from the caudal part of the pharyngeal arch series. Plates IV and V from the second edition of *Anthropogenie* (Haeckel, 1874*a*: plates IV and V).

(1) The Biogenetic Law and its formulation

the rapid and brief ontogeny is a summary of the slow and long phylogeny (Haeckel, 1903: p. 437)

It is well-known that Haeckel's *Fundamental Biogenetic Law* (Haeckel, 1866, 1872) describes the parallelism between embryonic development on the one hand, and phylogenetic history on the other. The word 'recapitulation' can be applied to the Biogenetic Law because Haeckel used it himself in its formal definition (Heberer, 1968: p. 210). It states that embryonic development is a short and rapid re-run, or recapitulation, of evolution (reviewed in Gould, 1977).

(*a*) *Caenogenesis and the alphabetical analogy*

Caenogenesis – the blurring of ancestral resemblances in development – was explained by Haeckel using an alphabetical analogy (commented on by His, 1874: p. 168, Lillie, 1952: pp. 4–6). This gives us perhaps the clearest statement of the Biogenetic Law to be found in all his writings. It reveals a more complicated view than is often appreciated:

[evolution in a given lineage] may be represented by the letters of the Alphabet A, B, C, D, E, etc., down to Z, in their alphabetical order. In apparent contradiction to this, the history of the individual evolution, or the Ontogeny of most organisms show us only a fragment of this series of forms, so that the interrupted chain of embryonic forms would be represented by something like: A, B, F, H, I, K, L, etc.; or, in other cases, thus: B, D, H, L, M, N, etc. ... In many cases also ... one or more letters, representing ancestral forms, are replaced in the corresponding places among the embryonic forms by equivalent letters of another alphabet. Thus, for example, in place of the Latin B or D, a Greek [β] or Δ is often found. (Haeckel, 1896*a*: 1, pp. 7–8).

Haeckel appears to be describing two types of caenogenesis: the deletion of whole stages (so that letters are missing); and the transformation of whole stages (e.g. D changing to Δ). The dropping out of stages was the law of simplified or abridged heredity (Haeckel, 1896*b*: 1: p. 408). He says he regards these processes as affecting individual developmental characters; in modern terms, the embryo was viewed as a mosaic of primitive (palingenetic) and advanced (caenogenetic) characters. Strangely, he does not have letters of the alphabet (stages) changing place – which would reflect sequence heterochrony – even though this was part of his model.

In the embryos of 'higher' vertebrates, Haeckel cites the notochord, pharyngeal arches and clefts, pronephros and neural tube, as examples of conserved features; and yolk sac, extra-embryonic membranes, egg membranes, endocardial tube and others as caenogenetic (Haeckel, 1903). Caenogenetic features are stated to be the result of adaptations to embryonic life, and palingenetic ones the result of heredity (Haeckel, 1903).

(*b*) *Heterochrony and developmental sequences*

Haeckel's caenogenetic processes were said to manifest themselves as shifts in organ location (heterotopy) or in the order in which organs appear (heterochrony). He viewed heterochrony as a gradual disarrangement in the original phylogenetic sequence, caused by embryonic adaptation (Haeckel, 1896*b*: 1, p. 13). Heterochrony can lead to an earlier or later formation of organs (ontogenetic acceleration or retardation, respectively):

> We have to consider as an earlier formation or 'ontogenetic acceleration' the following examples in human embryonic development: the early appearance of the heart, pharyngeal slits, brain, eyes, etc. These organs, in relation to others, form much earlier than originally in the phylogeny. The contrary happens with the delayed formation of the gut tube, coelom and genital organs. (Haeckel, 1903: p. 12).

Haeckel's alphabetical analogy shows that he was approaching heterochrony from the point of view of developmental sequences (i.e. sequences of characters or stages) and not rates of growth; this is in contrast to the morphometric approach to comparative embryology adopted by Wilhelm His (see Section IV.4*b*). Modern studies of ontogeny and phylogeny also show a division between morphometric approaches (e.g. Gould, 1977) and those based on developmental sequences (e.g. Smith, 1996; reviewed by Smith, 2001).

(2) **Applications of the Biogenetic Law**

Haeckel believed that the Biogenetic Law had implications for many different branches of biology. We shall now discuss some of those implications.

(*a*) *Phylogeny reconstruction*

To Haeckel, the Biogenetic Law was a tool for phylogeny reconstruction. He believed that conserved (i.e. palingenetic) features alone were useful for this purpose. Thus, he argues that conserved features 'permit a direct conclusion about the corresponding processes in the phylogenetic history of the developed predecessors' whereas derived (caenogenetic) features do not because they 'falsify and obscure' the record of the chain of ancestors. He states that, where the correspondence between ontogeny and phylogeny is not complete, phylogeny reconstruction has to rely on comparative anatomy and palaeontology:

> If [recapitulation] was always complete, it would be a very easy task to construct the whole phylogeny on the basis of ontogeny. If one would like to know the ancestors of each higher organism, including man, and from which forms this species developed as a whole, one would only need to follow the chain of forms of his individual development from the egg onwards; then one could consider each of the existing morphological stages as representative of an extinct ancient ancestral form. But the unconstrained direct transfer from ontogenetic facts to phylogenetic concepts is allowed only in a very small number of animals. There is certainly, even now, a number of lower invertebrate animals (e.g. some Anthozoa and Vermes) where we are authorised to interpret each embryological form directly as the historical repetition or the portrait-like silhouette of an extinct ancestral form. But in the great majority of animals, including man, this is not possible because the infinitely varied conditions of existence have led the embryonal forms themselves to be changed and to partly lose their original condition (Haeckel, 1903: pp. 435–436).

(*b*) *Comparative Embryology*

(i) *The embryonic portrait gallery*. Haeckel used the analogy of development giving a portrait gallery of ancestors (Haeckel, 1896*b*: 1, p. 407). But he says that the embryo only provides a portrait of an extinct ancestral form in a few cases because, as he acknowledges, embryos can differ among species:

> [Caenogenesis] ... obscures the original figure of the individual development by the introduction of new and foreign shapes, which did not exist in the earlier forms,

and were acquired by the embryo only by adaptation to the peculiar conditions of the individual development (Haeckel, 1892: 1, pp. 397–398)

In stressing that embryonic variation is due to adaptations to the embryonic environment, he differs from His (1874: p. 206) and Richardson (1999) who see some embryonic differences as the precursors of adult differences. Of course, the virtually identical appearance of embryos in some of Haeckel's pictures (Fig. 3), is in direct conflict with Haeckel's own statements on the variability among embryos (for further discussions of the external appearance of embryos in different vertebrates see: His, 1874: p. 192; Keibel, 1906; Kerr, 1919: pp. 429–454; Korschelt & Heider, 1936: pp. 1191–1210; Gerber, 1944).

(ii) *The 'gill slits'*. The presence of what appear to be transient gills slits, in the embryos of air-breathing vertebrates, was noted long ago by Rathke and von Baer (Oppenheimer, 1986: p. 229). Gould (1977: p. 7) remarks that: '... in Haeckel's evolutionary reading, the human gills slits *are* (literally) the adult features of an ancestor.' [original emphasis]. By contrast, Mayr (1994: p. 225) sees in Haeckel's *Generelle Morphologie* a belief only in the recapitulation of major evolutionary innovations.

In some writings, Haeckel is ambiguous on this matter. For instance, he says:

Certain very early and low stages in the development of man, and the other vertebrate animals in general, correspond completely in many points of structure with the conditions which last for life in the lower fishes. (Haeckel, 1892, 1: p. 355).

The correspondence is only in 'many points of structure', and he makes it clear later that he does not believe the pharyngeal apparatus in amniote embryos to represent adult fish gills:

we never meet with a Reptile, Bird or Mammal which at any period of actual life breathes through gills, and the gill-arches and openings which do exist in the embryos are, during the course of their ontogeny, changed into entirely different structures, viz. into parts of the jaw-apparatus and the organ of hearing ... (Haeckel, 1892: 2, p. 303).

He further acknowledges that:

We have to consider as one of the most prominent characters of all amniotes the total loss of respiratory gills ... in the embryos of amniotes there is never even a trace of gill lamellae, of real respiratory organs, on the gill arches (Haeckel, 1903: p. 628).

(iii) *Blastaea and Gastraea*. Haeckel described a series of conserved embryonic stages in the metazoa including a blastula stage or blastosphaera (Haeckel, 1903: pp. 546–547). In his *Gastraea-Theorie* (Haeckel, 1872, 1874*b*, 1875, 1877) he argued that all metazoa share a gastrula stage. Okudshawa & Josseliani (1985) argue that Kowalewsky's experimental studies on embryonic development in several animal phyla constituted the basis of Haeckel's theory. Lankester's similar *Planula Theory* was developed around the same time, although priority probably belongs with Haeckel (discussed by Lankester, 1877).

III. SCIENTIFIC ASSESSMENTS OF THE BIOGENETIC LAW AND ITS APPLICATIONS

In this section, we discuss scientific opinion of the Biogenetic law, and examine its relevance to the fields of phylogenetics and comparative embryology (i.e. the two components of phylogenetic embryology). We have focussed on the more recent literature and have tried to avoid duplicating material covered in previous accounts (e.g. Gould, 1977).

(1) Biogenetic Law

(*a*) *Modern support for the Biogenetic Law*

A common view is that, although Haeckelian views have been rejected, there is nonetheless some degree of parallelism between ontogeny and phylogeny (Alberch & Blanco, 1996; Langille & Hall, 1989; Mayr, 1998). One explanation for this parallelism is the selective pressure to retain transient embryonic structures which are needed for the development of other organs (e.g. Mayr, 1994). Khazen (1993) states that ontogeny is obliged to repeat the main stages of phylogeny, and for Rautian (1993), the reproduction of ancestral patterns of development in descendant ontogenies is a key aspect of biological systems. Maze (1998) discusses a possible causal relationship between ontogeny and phylogeny – an echo of Haeckel's idea that phylogeny causes ontogeny. On the other hand, Siewing (1982*c*) acknowledges the similarity of embryos in different species, and the laws of von Baer, but warns that no comparison of embryos with adult stages should be made.

Over-reaction against Haeckel should not lead us

Table 1. *Recent studies describing possible evidence in favour of the Biogenetic Law. Most refer to individual characters, although Miyazaki and Mickevich, 1982 provide a notable exception in which whole suites of characters show recapitulation*

Example	Reference
Plants	
Spore characters of Gigasporaceae	Bentivenga & Morton, 1996
Stamen development in Magnoliophytina	Decraene & Smets, 1998
Invertebrates	
Bivalve molluscs	Miyazaki & Mickevich, 1982
Engrailed expression in the freshwater crayfish *Cherax destructor*	Scholtz, 1995
Brain development in the Clitellata	Hessling & Westheide, 1999
Shell ontogeny and phylogeny in brachiopods	Cohen *et al.*, 1998
Ontogeny and phylogeny of giant clams	Schneider, 1998
Vertebrates	
Vomer development in salmonid fishes	Alexeev, 1993
Coelomocyte ontogeny	Munoz-Chapuli *et al.*, 1999
Haemopoietic system	Galindez & Aggio, 1997
Retinal histogenesis	Harris & Perron, 1998
Glial development	Balslev *et al.*, 1997
Auditory ossicles	Rowe, 1996
Tooth development	Peterkova *et al.*, 1993
Early mammalian development	Betteridge, 1995
African elephant ontogeny	Gaeth *et al.*, 1999
Ontogeny and phylogeny in whales and dolphins	Kemp & Oelschläger 1997
Cetacean hind limb development	Sedmera *et al.*, 1997
Pelvic traits in *Australopithecus* and neonatal *Homo*	Berge 1998

to overlook parallels between ontogeny and phylogeny, according to Gould (1992). Fischer (1997) points out that cladistics and developmental genetics, two fundamental innovations in biology since Haeckel's time, may force biologists to reconsider the Biogenetic Law. I. Müller (1998) believes that the theory of recapitulation is unprovable. Nonetheless, he thinks it was significant because attempts to test the theory gave rise to new discoveries, a fact also recognised by Walzl (1998). Indeed, we show below that Wilhelm His developed new approaches to comparative embryology in opposition to Haeckel's.

In addition to many examples cited by Gould (1977), parallels between ontogeny and phylogeny have recently been studied at the biochemical level (Altesor, Ezcurra & Silva, 1992; Boyer *et al.*, 1993; Irvine and Seyfried, 1994; Burnstock, 1996; Hoshita, 1996; Ozernyuk *et al.*, 1993), the behavioural level (Rial *et al.*, 1993; Baum, 1996) and even in the context of cancer (Johnston, Pai & Pai, 1992). A number of workers discuss the Biogenetic Law in terms of developmental genetics (Delsol & Flatin, 1992; Ohno, 1995; Theissen and Saedler, 1995). Recent work has identified numerous transformations consistent with the Biogenetic Law (Table 1). These apparent recapitulations all relate to single character transformations and not to entire stages (although see Miyazaki & Mickevich, 1982, where whole suties of characters show recapitulation).

(*b*) *Confusion surrounding the Biogenetic Law*

The Biogenetic Law and recapitulation are perhaps the sources of more confusion than any other ideas in evolutionary biology. It is not uncommon for the Biogenetic Law to be completely misattributed – to von Baer, for example (e.g. Simpson & Beck, 1965: p. 240). A more common and significant problem is failure to distinguish recapitulation from mere embryonic similarity (the latter is more easily encompassed by von Baer's laws than by Haeckel's; see de Beer, 1930: p. 46; Gould, 1977: p. 4). Thus, Guttman (1999: p. 718) gives an unusual form of recapitulation which envisages ontogeny as a series of recapitulated ancestral embryonic forms: 'As a mammal develops it first looks like a fish *embryo*, then like an amphibian *embryo*' [original italics]. Other fundamental errors in this debate include a failure to understand the relationship between developmental stages, developmental characters and heterochrony (Section III. 1*g*).

(*c*) *Ambiguities in Haeckel's formulation of the Biogenetic Law*

Could some of this confusion be due to flaws in Haeckel's own formulation of the law? We think so. It is not always clear whether he was advocating the repetition of entire developmental stages or of individual characters only. Furthermore, he is not consistent when describing the extent of parallelism between evolution and development. Consider these phrases from *Evolution of Man* (Haeckel, 1896*b*; volume 1):

> Indeed there is always complete parallelism between [evolution and development] (p. 8);
>
> In fact, in most cases the epitome is very incomplete, and greatly altered and perverted … (p. 8);
>
> But notwithstanding these numerous and sometimes very considerable gaps, there is, on the whole, complete agreement between the two series of evolution [and development] (p. 9);
>
> Indeed it will be one of my principal objects to prove the deep harmony and original parallelism between the two series (pp. 9–10);
>
> it is true that if the ontogenetic, and the phylogenetic stages (in Tables VII and XXII) are carefully compared, a complete agreement between the two is not observable; on the contrary, there are many divergences (p. 401).

This type of ambiguity makes it difficult to gain a clear understanding of Haeckel's views.

(*d*) *Caenogenesis*

The embryologist Wilhelm His criticised the concept of caenogenesis on the grounds that a fundamental law should not have exceptions (His, 1874: p. 167). Haeckel saw caenogenesis as resulting from adaptations to embryonic needs alone, and he has been followed in this assumption by other workers. Thus, Wolpert (1994) described the concept of a 'privileged embryo', whose principal selective pressure, at least in amniotes, was for the reliability and economy of developmental mechanisms.

These views have been criticised by Richardson (1999) who points out that embryonic stages may show significant variation among species, and that these variations may be driven by selection for adult characters – not just selection for the pressures of embryonic life. Wilhelm His made a similar point, noting for example that the large eye of the chick embryo may be related to adult needs (His, 1874: p. 206).

Equally, Delsol and Tinnant (1971) point out that Haeckel's caenogenetic changes may have no effect on adult morphology; they therefore concluded that Haeckel's scheme takes no account of embryonic modifications leading to divergence in adult form. Caenogenesis is often forgotten by scientists criticising the Biogenetic Law. For example, de Beer (1951: p. 7) gave the following argument against recapitulation: 'Sedgwick showed that the earlier stages of development of quite closely related animals (such as the hen and the duck) could be distinguished …' In this example, de Beer has overlooked the facts that the Biogenetic Law allowed for embryonic variation under its caenogenetic exceptions; and that embryonic resemblance is not the same thing as recapitulation.

Pennisi & Roush (1997) analyse the downfall of Haeckel's theories, and state that: 'if birds descended from reptiles, their embryos should show signs of developing scales before feathers, but that's not so'. This argument assumes a strict recapitulation; in fact, Haeckel allowed for embryonic character transformations (as in his letter D changing to a Greek Δ).

(*e*) *Terminal addition and the 'telescoping' of stages*

The idea that new adult stages are added terminally, then telescoped or pushed-back into the embryonic stages of descendants, is assumed to be part of the Haeckelian package (Gould, 1977: pp. 74–75; de Beer, 1951: p. 5; Lehman, 1987: p. 206; Richardson, 1999: p. 605; Miyazaki and Mickevich, 1982: p. 394) and can reasonably be inferred from his alphabetical analogy and some of his writings. Indeed, if the Biogenetic Law does depend on terminal addition, this requires changes in developmental timing to prevent development taking too long (Gould, 1977; although see Mayr, 1994: p. 225, who denies a central role for heterochrony in recapitulation).

Our modern understanding of pattern formation is difficult to reconcile with terminal addition and telescoping. Embryonic primordia are small, morphologically simple, consist of undifferentiated cells and may be undergoing positional specification under the influence of morphogens (Wolpert *et al.*, 1998). Adult organs, by contrast, are large, morphologically complex, consist of terminally differentiated cells, and are not undergoing pattern formation. It is not easy to see how the latter could become transformed into the former, during evolution, by means of a timing shift, because the number of transformations required would be so high.

Another argument against terminal addition leading to recapitulation is that any addition of a character to the end of development can only be produced by changes in patterns of gene expression and cell behaviour at earlier stages (Richardson, 1999). Apparent 'terminal additions' of gene expression patterns may be possible within the embryonic period itself. For example, early embryonic *Hoxd* gene expression patterns in the paired appendages are similar in tetrapods and the zebrafish *Danio* (*Brachydanio*) *rerio*; but they become divergent later when tetrapods show expression of a specialized pattern not seen in the fish (Sordino, van der Hoeven & Duboule, 1995; Shubin, Tabin & Carroll, 1997). Of course, this new pattern of Hox gene expression has not been added terminally, but intercalated within the total developmental sequence which leads to the adult. [See Kluge (1988: pp. 69–71) for a discussion of substitutions, deletions and additions in developmental sequences.]

(*f*) *Heterochrony*

Heterochrony is recognized as an important factor in evolution by many recent workers (e.g. Gould, 1977; McKinney & McNamara, 1991; Berge, 1998; David & Laurin, 1996; Delsol & Flatin, 1992; Duboule, 1994; Friedman & Carmichael, 1998; Peterkova *et al.*, 1993; Raff & Wray, 1989; Richardson, 1995; Richardson *et al.*, 1997; Zelditch & Fink, 1996; McNamara, 1999). Only rarely is Haeckel's original contribution to the topic acknowledged (e.g. Gould, 1977: p. 82). A distinction has to be drawn between heterochrony *sensu* Haeckel, which is a change in the sequence of discrete events; and heterochrony *sensu* Gould (1977), which leads to growth and shape changes measured as continuous variables (Klingenberg, 1998; Kim, Kerr & Min, 2000; reviewed by Smith, 2001).

(*g*) *Distinction between ancestral stages and ancestral characters*

The relationship between stage, character, sequence and heterochrony is modelled by Richardson (1999, 2000*b*) in the form of 'abacus' diagrams. Developmental stages are clusters of characters in a developmental sequence that are arbitrarily forced by the observer to be simultaneous. A developmental sequence of characters can therefore be used to define a series of stages (semaphoronts, *sensu* Hennig, 1966). Single 'key' characters may also be used, as in 'tailbud' stage (Slack *et al.*, 1993). Heterochrony alters developmental sequences – and, as a consequence, stages – making cross-species comparisons of stages difficult or impossible (Richardson, 1995). For these and other reasons, it is useful to distinguish between characters and stages when discussing recapitulation (see Wheeler, 1990, for discussion of the relationship between stages and characters in phylogenetics).

Gould (1977: p. 173 ff.) argues that Haeckel compared embryos with entire ancestors. Lehman (1987) states that Haeckel's Recapitulation Theory 'compares adults of lower species to embryonic stages of higher species'. Miyazaki & Mickevich (1982: p. 371) state that '… Haeckel applied the concept of terminal additions to the whole phenotype.' But other authors apply the term 'recapitulation' to single characters, not whole stages. For example, Siewing (1982*a*: p. 108 fig. 35) cites as an example of recapitulation the branchial slits in chicken embryos (p. 108 fig. 35); and some workers (Nelson, 1978; Osche, 1985) consider that the Biogenetic Law can make valid predictions about individual character transformations. As we showed above (Section III. 1*c*) Haeckel was not clear on this point.

Looking at his drawings (Fig. 3), we see that he found the strongest resemblance among embryos of different species, not between ancestral adults and descendant embryos. The exceptional cases, where he equates embryonic stages with total adult ancestors, are very early stages like the 'gastraea' or 'coelomula'.

(2) **Applications of the Biogenetic Law**

(*a*) *Phylogeny reconstruction and biological systematics*

Haeckel used his systematic knowledge to develop general phylogenetic conclusions (Heberer, 1968; Knorre, 1985), and to draw up family trees (discussed by Ermisch, 1985). Corliss (1998) calls Haeckel the 'Father of Protistology' because of his creation of Protista as the third Kingdom in a 'Tree of life'. Knorre (1985) evaluates Haeckel's merits in special systematic zoology, and considers the highlights to be his monographs on Medusae (including Haeckel, 1881) and Radiolaria (Haeckel, 1862, 1887); indeed, in the latter work, Haeckel describes 3508 new species. Goldschmidt (1956: p. 32) was less enthusiastic, calling these monographs 'almost the only factual contributions Haeckel made to zoology.'

Haeckel believed that only conserved characters, and not derived ones, were useful in phylogeny reconstruction. This is a major difference between Haeckel's ideas and modern cladistic methodology, which sees synapomorphies as being informative (Hennig, 1966; see also the important discussions of ontogeny and systematics in Humphries, 1988). Indeed, it may be possible to reconstruct phylogeny using not conserved developmental sequences, *sensu* Haeckel, but using the differences between developmental sequences (de Pinna, 1994; Jeffery *et al.*, 2002*a*, *b*).

An important debate in modern cladistics has centred on the ontogenetic polarity criterion, i.e. using the sequence of appearance of characters in development to polarize phylogenetic character transformations (Nelson, 1973; Hibbett, Murakami & Tsuneda, 1993; Mabee, 1993; Wenzel 1993; Meier, 1997; Mcdade & Turner, 1997). This debate represents, in part, an attempt to reconcile two fundamentally different approaches to phylogenetic embryology: in one, ontogeny provides a polarised sequence of characters (as in Haeckel's alphabetical analogy); and in the other, embryological characters are seen as more amenable to phenetic, than cladistic analysis (as represented, for example, by Haeckel's embryo pictures; see Richardson *et al.*, 2002).

Carroll (1988) points out that development can be used to establish affinities, especially if the adult is so specialised that its systematic position is not easily recognized. As an example he cites the relationship of tunicates (urochordates) with vertebrates, as deduced from larval structure. Haeckel had also recognized this fact (e.g. Haeckel, 1868: chapters 17 and 18). However, as Mayr (1994) points out, the usefulness of the Biogenetic Law in phylogeny reconstruction is diminished in animals that undergo metamorphosis.

Ontogenetic criteria can help clarify the systematic position of a group in order to obtain a 'natural' classification (for examples from botany, see Erbar & Leins, 1996; Roels & Smets, 1996; Letrouit-Galinou, 1966; Henssen & Jahns, 1974; Henssen *et al.*, 1981; Keuck, 1977, 1979, 1981). There are numerous other examples of the use of developmental characters in phylogeny reconstruction (e.g. Boxshall & Huys, 1998; Caldwell, 1996; Israelsson, 1999; Theilade & Theilade, 1996; Douglas & Tucker, 1996; Tucker, Douglas and Liang, 1993; Friedman & Carmichael, 1998; Jeffery *et al.*, 2002*a*, 2002*b*). Betteridge (1995) argues that early embryonic stages in mammals may contain phylogenetic information.

We do not have space to describe how Haeckel's classifications of the living world have been accepted or revised. But as examples, we note that Hou *et al.*, (1999) consider the most primitive birds or Saururae, a systematic category created by Haeckel, to be still valid (compare Haeckel, 1866, 1902, 1903). On the other hand, Zettler, Sogin & Caron (1997) used molecular data to argue for a separate origin of Acantharea and Polycistinea, once included in Haeckel's Radiolaria.

(*b*) *Comparative embryology*

A key controversy in biology concerns the difference in rank of plesiomorphies, as compared to apomorphies, in a developmental sequence. One reason why this difference is important is that it provides an explanation for phenotypic divergence [de Beer's (1930: p. 45) 'deviation'] – the changing degree of resemblance among embryos of different species as they develop; it may inform our understanding of the evolution of developmental mechanisms; and it may have consequences for phylogeny reconstruction.

The controversy is unresolved because phylogenetic embryology demands extremely complicated, quantitative analyses. A fundamental principle of such analyses – and, we suggest, a cornerstone of comparative embryology itself – is that a character has to be defined in terms of (i) its distribution on a phylogeny; and also (ii) its rank in the developmental sequence of each species on that phylogeny. Comparative embryology has only recently begun to develop a quantitative methodology (Smith, 2001) and so its conceptual framework is still strongly influenced by previous workers including von Baer (von Baer, 1828; for partial English translation see Blyakher, 1982; Richards, 1992: 106 cites a partial English translation by Huxley), and Haeckel (Fischer, 1997; reviewed in Gould, 1977; Patterson, 1983; Rieppel, 1988; Richards, 1992; Richardson, 1999; Smith, 2001).

(*c*) '*Haeckelian*' *versus* '*Von Baerian*' *approach*

K. E. von Baer (1792–1876) and Haeckel both struggled to model an immensely complex problem: the distribution of general and special characters during development in different animals. They had limited data and no computers, but both came up with predictions that are valid at some levels. So, when we ask: 'was von Baer right, or was Haeckel', the answer is that it depends on the character, stage and phylogeny in question.

Haeckel's law was recapitulationary and evolutionary. Von Baer's laws were neither, and his third and fourth laws are specific rejections of recapitulation (Gould, 1977). He did acknowledge variations on a theme or type, and flirted with evolutionary explanations later in life (Kluge & Strauss, 1985). Together, von Baer's first two laws propose that 'general' characters appear earlier in development than 'special' characters – because the former undergo transformation into the latter during ontogeny (Blyakher, 1982: pp. 352–354; Klug & Strauss, 1985; Kluge, 1988). This, of course, begs the question of whether we should interpret 'general' to mean 'ancestral' or simply 'more common' (reviewed by Kluge & Strauss, 1985; Kluge, 1988).

A common feature of the laws of Haeckel and von Baer is that they are not laws at all: they only apply to certain characters at certain stages and levels of phylogenetic inclusiveness. Von Baer's first two laws are violated by numerous instances where early developmental pathways differ across a phylogeny, even though later pathways appear to be conserved (Wagner & Misof, 1993; Raff, 1996; Goldstein, Frisse & Thomas, 1988). This is one reason for being cautious when using developmental sequences to polarise character transformations (but see de Pinna, 1994, for counter-arguments).

In terms of outcome, Haeckelian and von Baerian models both yield embryonic similarity – not necessarily at the same stages – followed by divergence. Here is an example of Haeckel's sequence of conserved stages: Chordula, Acraniate, Cyclostome, Ichthyode, Amniote etc. (Haeckel, 1903: Table 37, pp. 681, 683). Haeckel describes phenotypic divergence as follows: '... the embryo must necessarily (especially in the later stages of development) deviate more or less from the original figure of the corresponding primary form, and, indeed, the more so the more highly developed the organism is' (Haeckel, 1892: p. 357). Haeckel (1892: 1, p. 361) acknowledges that individual ontogeny is a linear parallel of phylogeny only with respect to the ancestors in the immediate line of descent, and that the true pattern of phylogeny of a group is not linear but 'branching or tree-shaped'. He is therefore seeing the recapitulation of a series of common ancestors. No series of conserved stages, embryonic or adult, is possible with von Baer: it is precluded by the principle of progressive deviation or third law (see Fig. 1 in Richardson *et al.*, 2002).

A further key difference between Haeckelian and von Baerian schemes, in modern practice, is their relation to developmental timing. Haeckel's scheme is tied to developmental stages, each defined by particular characters in the developmental sequence. Gould (1977: p. 3) notes that recapitulation involves heterochrony (because ancestral adult characters become juvenile) whereas von Baer's scheme need not.

Løvtrup (1978) recognizes similarities in the Haeckelian and von Baerian approaches, but confusingly describes 'von Baerian recapitulation' (p. 351) as being seen when the ancestral stages repeated are embryonic ones; and 'Haeckelian recapitulation' as the 'occurrence of ancestral adult stages in the course of ontogeny'. However, Løvtrup's 'von Baerian recapitulation' is not recapitulation at all under Gould's (1977) definition, because it does not involve heterochrony. According to de Beer (1930: p. 56) von Baer's laws differ from recapitulation because the latter assumes that developmental characters provide evidence of what an ancestral adult looked like. Alberch (1985: pp. 46, 52, 56) writes of a 'Haeckelian approach' in which adult and embryonic stages are compared so as to establish homologies. Gould (1977: p. 174) prefers von Baer's view of phenotypic divergence in development over Haeckel's, arguing that Haeckel compared embryos of 'higher' animals with adults of 'lower' ones.

Haeckel's model is often said to be based on terminal addition, whereas von Baer's reflects terminal and sub-terminal modification (because general characters are transformed into special ones during ontogeny). But this distinction is not a complete explanation, in view of the subterminal modifications in Haeckel's own alphabetical analogy (e.g. the letter D changing to Δ). In fact, as we mentioned above, Haeckel repeatedly discusses the differences between embryos of different species introduced by adaptation; these embryonic modifications will tend to produce progressive divergence, yielding an outcome identical to von Baer's.

(i) *The phylotypic stage and developmental hourglass.* Modern approaches to phenotypic divergence are based on the concept of the phylotypic stage. This is said to be a period of reduced phenotypic diversity in several higher taxa (reviewed by Hall, 1997). It is derived in part from the *typus* concept of von Baer (Fischer, 1997), and in part from Haeckel's *Anthropogenie* plates (Fig. 3) which are used as evidence for this theory in several works (e.g. Duboule, 1994; Alberts *et al.*, 1994). The phylotypic stage is said to lie between divergent earlier and later stages, giving an hourglass pattern of phenotypic divergence (Raff, 1996). The early divergence, which violates some of von Baer's laws, is due to differences in egg size and patterns of cleavage and gastrulation among species. Recent explanations of the conservation of mid-embryonic stages, despite variations in early development, include the idea that they are subject to strong stabilizing forces (e.g. selection, pleiotropy; see Wagner & Misof, 1993; Raff, 1996; Wagner, 1996).

Haeckel was aware of these early differences, and they were included among his caenogenetic exceptions. With regard to egg size for example, he noted that ova of different species look very similar at early stages of maturation (although he did acknowledge that they must show molecular differences; see Haeckel, 1896*b*: 1, p. 137). He commented that: 'If a very young egg from the ovary of a hen is examined, it is found to be exactly like the young egg-cells of Mammals and other animals. But it afterwards grows so considerably that it expands to the well-known ball of yelk (*sic*)' (Haeckel, 1896*b*, 1, p. 137). He also recognised that ova may subsequently become divergent, during cleavage and gastrulation, before reaching a stage of greater resemblance:

> The particular form which egg-cleavage and the formation of the germ-layers assume in the case of Mammals, is, however, by no means the original, simple, and palingenetic form of germination. On the contrary it has been very much changed, vitiated, and kenogenetically modified in consequence of numerous embryonic adaptations (Haeckel, 1896*b*: 1, p. 187).

Haeckel clearly distinguishes holoblastic and meroblastic eggs and illustrates their different patterns of cleavage and gastrulation in Tables II and III of *Anthropogenie* (Haeckel, 1903). This is further detailed in three following text tables and the whole chapter IX dedicated to this issue. In summary, piecing together Haeckel's views as revealed in his figures and text, he apparently saw similarity in ova, followed by divergence at maturation, cleavage and gastrulation stages, then convergence on a conserved stage, and, finally, divergence to the adult form. His view is therefore more complex than are von Baer's laws, or the developmental hourglass.

(ii) *Blastaea and Gastraea*. Xiao, Xiang & Knoll (1998) describe Doushantuo fossils which may represent Precambrian metazoan embryos. They say that these fossils might be broadly equivalent to blastaea or planuloids, *sensu* Haeckel. Gould (1998) notes the similarity of these fossils to some of Haeckel's hypothetical ancestors. Finnerty (1998: p. 217) confirms the phylogenetic importance which Haeckel attributed to *Amphioxus*. Haeckel's (1902) views on the monophyly of animals (p. 498 ff), his inclusion of sponges in this group, and his 'monophyletic tree of the animal kingdom' (p. 513), are all supported by molecular evidence (reviewed by W. E. G. Müller, 1998).

Nielsen (1998) identifies a holopelagic ancestor (blastaea), which may have given rise to sponges; and a eumetazoan ancestor, consistent with Haeckel's gastraea. He acknowledges Haeckel's identification (Haeckel, 1902: pp. 543–544) of the trochophore as a type of the Trochozoa, the putative ancestors of several animal phyla. Siewing (1982*b*: p. 192) sees the discovery of Placozoa (the simplest metazoa) as a strong confirmation of Haeckel's gastraea theory. On the other hand, Salvini-Plawen (1998: p. 147) denies the usefulness of Haeckel's gastraea theory and sees the importance of Haeckel's work after 1866 as mainly in pioneering an multidisciplinary approach to phylogenetics.

(3) Other opinions of Haeckel's science

Opinions on Haeckel have always been divided. For example, Heberer (1968) gives a positive appraisal of Haeckel's life and work and identifies Haeckel's merits as the development of evolutionary theories in opposition to creationism. On the other hand, Oppenheimer (1967: p. 254) gives a more mixed assessment:

> Haeckelianism had its progressive side, by inspiring so many young men to enter biology and embryology … But Haeckel had his retrogressive influence in embryology, also. So powerfully dogmatic was his teaching of the outworn law of recapitulation that for years embryos were investigated primarily for what they might reveal of their ancestry; and the development of analytical and physiological embryology had to await the subsidence of his surge of ideas.

(*a*) *Haeckel's total evidence approach*

Haeckel believed that many different sciences could provide evidence for phylogeny reconstruction – including palaeontology, ontogeny, comparative anatomy and ecology (Haeckel, 1902: pp. 790–4; Haeckel, 1903: pp. 94–101). The first three of these were the most important to him, although he recognised that none alone could give a complete explanation of phylogeny. Nelson (1978: p. 326) provides a lively discussion on the extent to which embryology informed Haeckel's phylogeny reconstruction. Haeckel's use of phylogenetic information from a variety of disparate sources is paralleled in some ways by the development of 'total evidence' and supertree theory in phylogenetic analyses (Kluge, 1989; Sanderson, Purvis & Henze, 1998; Bininda-Emonds, Gittleman & Purvis, 1999). Bayer & Appel (1996), in their analysis of angiosperm families, represent one of many examples of how a combination of morphological and ontogenetic evidence can provide informative characters in modern phylogeny reconstruction.

(*b*) *Haeckel's speculations and missing links*

Haeckel's speculative approach often drew criticisms, and he was accused of trying too hard to make the data fit the theory (Semper, 1877). Nonetheless, Haeckel's speculations sometimes led to conclusions that later proved correct. Gould (1998) argues that Haeckel was 'outstandingly right far more often than random guesswork would allow'.

Haeckel speculated that the allantois was formed in man in exactly the same way as it was in other mammals. However, this had not been directly observed at that time, and Wilhelm His (1874: p. 170) accused Haeckel of playing fast and loose with the facts (reviewed by Hopwood, 2000). Haeckel was therefore pleased to record (Haeckel, 1896*b*: 1, p. 383) that the allantois had now been discovered and illustrated in a human embryo by Krause (1875, 1876). Haeckel was ultimately proved right about the allantois; unfortunately, though, Krause's embryo was probably a fake, bearing more resemblance to a bird embryo than to a human one (His, 1880: pp. 68–72; Hopwood, 2000).

Kirchengast (1998: p. 176) argues that Haeckel's speculation about a 'missing link' in human evolution, which he named *Pithecanthropus*, led to the discovery of human fossils by E. Dubois in Java. This is a famous example of a generic name being created before the discovery of the corresponding fossil. He adopted this name in honour of Haeckel, who had given a lecture that inspired Dubois to begin his research. Haeckel's theory of south-east Asia as the cradle of mankind was, however, overturned by later discoveries of fossil hominids in Africa (Cann, Stoneking & Wilson, 1987).

Gould (1977: p. 173) stated that Haeckel's method of creating hypothetical ancestors from ontogenetic stages had few successes. He criticises Haeckel's phylogenetic trees from 1866 because they do not show the actual diversity of animal groups but conform to the traditional principle of increasing diversity and perfection, giving the impression of linear evolution (Gould, 1994: pp. 292–298). Kemp (1998) also criticises the tree of vertebrate evolution taken from the *Natürliche Schöpfungsgeschichte* (1874*c*) because of its implicit hierarchy. Gaps in Haeckel's scheme were sometimes filled with hypothetical ancestors, a move which drew criticisms from some scientists (Semper, 1877).

(*c*) *Charges of unoriginality*

Fischer (1997) has recently suggested that Haeckel adapted his 'blastaea' theory from von Baer without acknowledgement. As Fischer notes, von Baer had described an early, vesicular stage of development shared by all animals, and this was probably the origin of the blastaea theory: 'the simple form of the vesicle is the general basic form, by which all animals develop, not only in idea, but also historically' (von Baer, quoted in Blyakher, 1982: p. 354). However, Haeckel (1902: p. 502) does acknowledge that: 'The high significance of the blastula, as an ancient common ancestral form of the animal kingdom, was already foreseen by the brilliant embryologist Baer 74 years ago …'

(*d*) *Typologism*

Haeckel has been criticised for drawing too sharp a distinction between form and function, and his emphasis on laws of evolution and development have been criticised for being too typological (Breidbach, 1997; Oppenheimer, 1959). Similar observations have been made of modern biology (Breidbach, 1997; Richardson, Minelli & Coates, 1999). Alberch (1985) has cautioned that 'evolutionists must avoid repeating Haeckel's errors that caused the downfall of the whole field. By erecting a rigid and artificial taxonomy of patterns, the real insights will be obscured.' We believe that a major cause of Haeckel's downfall was the controversy surrounding his embryo drawings.

IV. EMBRYO DRAWINGS

Haeckel illustrated his popular works with plates supposedly showing vertebrate embryos at different stages of development (Figs 1–3). These images are important for two reasons. First, they are widely

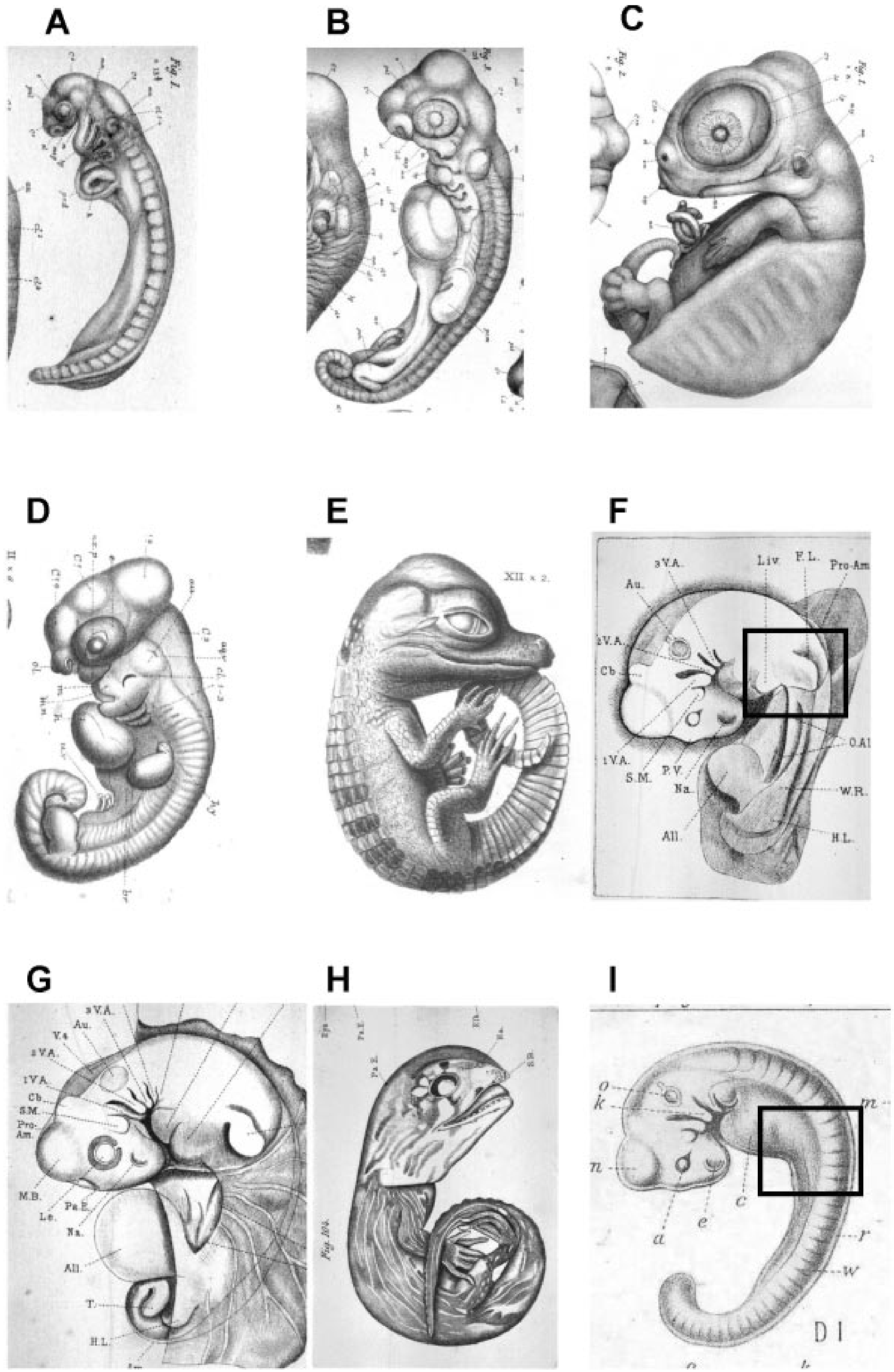

Fig. 4. Possible original sources for Haeckel's embryo drawings. These are our suggestions based on the similarity of the illustrations; Haeckel did not give his sources. Where necessary, the original pictures have been rotated so that the cranial end of the embryo is at the top of the picture. See Table 2 for full details of sources. (A–C) Turtle *Chelone viridis* [*Chelonia mydas*] (Parker, 1880); (D, E) *Alligator mississipensis* [*mississipiensis*] and *Crocodilus* [*Crocodylus*] *palustris*, respectively (Parker, 1883). (F–H) *Sphenodon punctatus* (Dendy, 1899). (I) *Sphenodon* embryo, Fig. DI, from plate X in *Anthropogenie*, fifth edition (Haeckel, 1903). Comparison of boxed region with G shows that the limb buds have been removed.

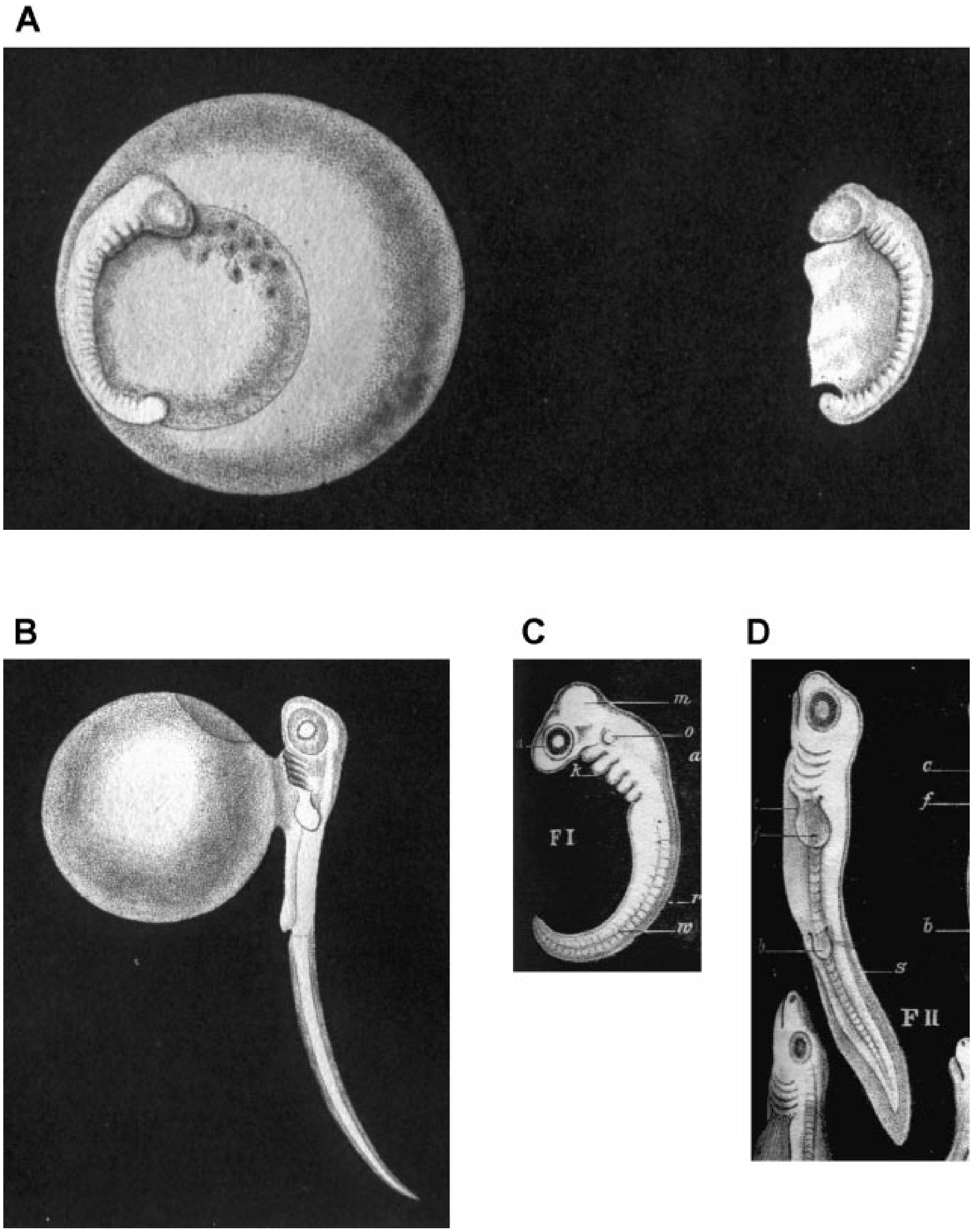

Fig. 5. Rathke's (1833) figures of the blenny *Blennius* [*Zoarces*] *viviparus* is a likely source for Haeckel's early fish embryos in the famous *Anthropogenie* (Haeckel, 1874*a*) figures. (A) Rathke's Figs 1 (left) and 2 (right) from plate I. (B) Fig. 8 from the same plate. (C, D) Haeckel's (1874*a*) Figs FI and FII, respectively, (details taken from Fig. 3 in this review). Note the strong resemblance to the Rathke figures. Furthermore, the cloaca in B has been misinterpreted as a pelvic fin in D.

used as teaching aids in biology; and second, they are influential phylogenetic hypotheses. Our aims in this section are: to examine how the drawings are used as scientific evidence by Haeckel and by modern workers; to see what hypotheses can legitimately be derived from them; to identify potential original sources for the drawings; and to examine the scientific arguments about the pictures. We also discuss their influence on some important, but overlooked, aspects of the work of W. His.

(1) Original context and interpretation

Haeckel's drawings were used to illustrate three phenomena: embryonic resemblance as proof of evolution, recapitulation as proof of the Biogenetic

Table 2. *Some examples of criticisms of Haeckel's embryo drawings. ¶It is not clear to us if Agassiz's are original criticisms; similar charges were made by Rütimeyer (1868)*

Author	Drawings criticised	Charge	Reference
Ludwig Rütimeyer	*Natürliche Schöpfungsgeschichte* (Haeckel, 1868).	Same woodcut reprinted 3 times	Rütimeyer (1868)
Louis Agassiz (unpublished marginalia)	Various in *Natürliche Schöpfungsgeschichte*	Fabrication¶	Gould (2000)
Wilhelm His, Sr.	Set of three eggs (p. 242) and three embryos (p. 248) in first edition of *Natürliche Schöpfungsgeschichte* (Haeckel, 1868)	Same woodcut reprinted three times	His (1874: pp. 168–9)
	Set of eight embryos from the fifth edition of *Natürliche Schöpfungsgeschichte* (Haeckel, 1874*c*)	Changes in proportions of body parts	His (1874: pp. 169–70)
	Anthropogenie (first edition) set of 24 embryos (Haeckel, 1874*a*).	Fabrication	His (1874: pp. 170–171)
	Anthropogenie (first edition; Haeckel, 1874*a*) Fig. 42, sole-shaped embryo	Fabrication	His (1874: pp. 170)
Arnold Braß	Various in *Menschen-Problem* (Haeckel, 1907)	Species switched, fabrication, doctoring	Braß (1909); Gursch (1981)
Franz Keibel	Various in *Menschen-Problem*	Doctoring and fabrication; species switched (e.g. bats)	Keibel (1909)
Francis Balfour	*Die Gastrula* (Haeckel, 1875)	Changes in colouration to alter the meaning	Balfour (1876: p. 521 note 1)
Michael Richardson and colleagues	*Anthropogenie* various editions (embryo plate showing vertebrates at three different stages)	Doctoring, inaccuracy	Richardson (1995); Richardson *et al.*, (1997)

Law, and phenotypic divergence as proof of von Baer's laws. We give some examples, and suggest possible primary sources, in Figs 1–5 and Table 3. The set of 24 embryos from the early editions of *Anthropogenie* (Haeckel, 1874*a*; shown here as Fig. 3) is the most famous, and is the one reproduced in modern books. It shows different species arranged in columns, and different stages in rows. There are several ways of reading the picture. Reading horizontally we see embryonic resemblance in the first row, and phenotypic divergence between species in the lower two rows. Reading vertically we see the gradual appearance of specialised characters in each species. Reading diagonally we see some examples of recapitulation (e.g. fins of the advanced fish embryo are echoed by limb buds on the young mammals).

Haeckel shows only the recapitulation of certain adult characters and not of entire stages. Thus, his human embryo bears little resemblance to the adult fish *in toto*, but does have pharyngeal arches and limb buds which resemble the gill slits and fins, respectively, of the adult fish (Fig. 3). The embryos in the top row are shown as virtually identical for all species, including the human (described as a human embryo at the end of the 21st day: Haeckel, 1896*b*: 1, p. 367). He says of the top row: '... we are unable even to discover any distinction between the embryos of these higher Vertebrates and those of the lower, such as the Amphibia and Fishes' (Haeckel, 1896*b*: 1, p. 365).

In the second row, some differences are apparent. The human embryo at this stage is 28–30 days old (Haeckel, 1896*b*: 1, p. 369) and now has limb buds (p. 371). By the final stage of development (bottom row), each animal has acquired its own special characteristics, and looks very different from the

Table 3. *Possible sources of figures in Haeckel's plates of 24 embryos (from various editions of Anthropogenie e.g. Haeckel, 1874a, 1891, 1903; see Fig. 3)* Potential sources were identified by us after searching the classical comparative embryology literature. This table reflects our own subjective judgements about similarities in the appearances of drawings. In most case, we feel confident that Haeckel's figure is related to the proposed source. In some cases, however, question marks indicate that the Haeckel copy matches the presumed source closely, but not exactly. In general, the later two stages are often entirely accurate, but the earliest stage has often been modified during copying. A common modification is removal of the limb buds. In other cases, the earliest stage cannot be traced by us to any original source. Haeckel makes some changes which seem to us to be perfectly legitimate, such as removing extra-embryonic membranes and inverting the pictures so that the embryos all face the same way. Note that Haeckel's species are sometimes made up of drawings from more than one species (e.g. his alligator is based on drawings representing two different crocodilian genera). See Gursch (1981) for other possible sources of Haeckel's embryo pictures. In the column 'Suggested source' the nomenclature used by the original author is given in parentheses, and current nomenclature is indicated by square brackets.

Edition	Figure	Suggested source	Figures in present study	Notes
First and second (Haeckel 1874*a*)	Fish: plate IV, Figs FI–III	Rathke (1833) Blenny (*Blennius* [*Zoarces*] *viviparus*).	5	We are not certain of the identity of Haeckel's FII. His FI matches Rathke's plate I, Figs 1 and 2 closely. Source of FIII not identified (see criticism of FIII by Richardson, 1998).
	Turtle: plate IV, Figs TI–III	Agassiz (1857) TII? = plate XIV, Fig. 4; (*Chelydra serpentina*); TIII? = plate IXc, Fig. 22 (*Chrysemys picta*) or plate XIV, Fig. 1 (*Chelydra serpentina*).		Source of TI not identified
	Chick: plate IV, Figs HI–III	Erdl (1845*a*) HII? = plate XI, Fig. 6; HIII? = Plate III, Fig. 7.		HII: tail greatly lengthened. HI not identified.
	Human: plate V, Figs MI–II	Erdl (1845*b*) MIII? = plate XI, Fig. 2 or plate XII, centre image.		MI and MII not identified
Fourth (Haeckel, 1891)	Turtle: plate VII, Figs TI–III	Parker (1880) TI = plate I, Fig. 1; TII = plate I, Fig. 7; TIII = plate III, Fig. 1. *Chelone viridis* [*Chelonia mydas*]. Note: Two of these illustrations were copied, accurately, by Balfour (1881), Figs 132–3.	4A–C	TI: hindlimb, and possibly forelimbs as faintly discernible on original, have been removed. Branchial apparatus remodelled, nasal pit removed. TII: seems accurate. TIII: seems accurate except toes are free whereas they were webbed on the original.
	Dog: plate IX, Fig. HII	Bischoff (1845) HII = plate XI, Fig. 42B.	8C	Appears accurate. Sources of HI and HIII not identified.

Fourth (Haeckel, 1891) (*cont.*)	Snake: plate VI, Figs AI–III	Rathke (1839) AI = plate I, Fig. 3; AII = plate II, Fig. 3; AIII = plate II, Fig. 9. *Coluber* [*natrix*] *natrix*.		Accurate for all stages. Rathke's Fig. 3 has been inverted.
	Alligator: plate VI, Figs KI–III	Parker (1883) KII = plate 62, Fig. I (*Alligator mississipensis* [*mississipiensis*]); KIII = plate 62, Fig. VIII (*Crocodilus* [*Crocodylus*] *palustris*).	4D, E	Haeckel's 'alligator' in this figure is in fact a composite of species from 2 different genera (*Alligator* and *Crocodylus*). In KII, somites appear to have been mistakenly rendered as scales; otherwise accurate. Source of KI not identified.
	Deer: plate VIII, Figs CI–III	Bischoff (1854) CI = plate IV, Fig. 30; CIII = plate VI, Fig 37.		CI appears accurate, except heart de-emphasised; CII inverted, otic vesicle added? Source of CIII not identified.
	Lizard: plate VI, Figs EI–III	Peter and Nicholas: mentioned, but not cited, in Keibel (1906). EIII is probably from Nicholas.		
Fifth (Haeckel, 1903)	Chick: plate IX, Figs GI–III	Erdl (1845*a*) GI? = plate X, Fig. 5 (*c*. 24 somites); GII? = Tab XI, Fig. 6; GIII? = plate III, Figs 6–8.		GI: pharyngeal arches added. GII: the extended tail of the Haeckel (1874*a*) Fig. HII has now been corrected, but the forelimb has been altered to make it resemble that of the neighbouring ostrich embryo (Fig. ZII).
	Kiwi: plate X, Figs YI–III	Parker (1891) YI–III = plate 3, Figs 1, 3 and 10, respectively (*Apteryx australis*).		YI: limbs de-emphasised and forelimb changed in shape. YII accurate. YIII: inverted and straightened.
	Tuatara: plate X, Figs DI–III	Dendy (1899) DI–III = Figs 92, 94, 104, respectively. *Sphenodon punctatus*.	4F–H	DI: limb buds removed (compare Fig. G and 4I in this paper). DII and DIII accurate; Dendy's Fig. 104 has been inverted.

Table 3 (*cont.*)

Edition	Figure	Suggested source	Figures in present study	Notes
	Turtle: plate X, Figs JI–III	Keibel (1906, from originals provided to him by Mitsukuri). JI–III = Figs 35f, g and i, respectively (*Trionyx japonicus* [*Pelodiscus sinensis*]).		JI: limb buds removed and tail straightened. JII–III accurate. Keibel's Fig. 35i has been inverted.
	Echidna: plate XI, Figs VI–III	Semon (1894) VI–III = plate X, Figs 40s, 43s, and plate XI, Fig. 51s, respectively (*Echidna* [*Tachyglossus*] *aculeata*).		VI: limb buds removed. VII–III accurate (see Richardson and Keuck, 2001).
	Dolphin: plate XI, Figs PI–III	Kükenthal (1893) PIII = plate XV, Fig. 16. 'Delphinenembryo'.		PIII appears accurate. PI and PII not identified.
	Opossum. Plate XII, Figs BI–III	Selenka (1887) BII = plate XXIII, Fig. 4; BIII = plate XXVII, Fig. 2. *Didelphis virginiana*.		BII: maxillary process misinterpreted, otherwise accurate. BIII: accurate. Source of BI not identified.

other species. According to Haeckel (1896*b*: 1, p. 373), the human is now different from 'lower' mammals but very close to those of apes. The early embryos all have a narrow, elongated trunk region, and this gives the appearance of a long tail, even in the human embryos. Haeckel's text suggests that the principal aim of these drawings was to demonstrate embryonic resemblance, and the retention by tetrapod embryos of fin-like structures and gill structures:

> The fact is that an examination of the human embryo in the third or fourth week of its evolution [i.e. development] shows it to be altogether different from the fully developed Man, and that it exactly corresponds to the undeveloped embryo-form presented by the Ape, the Dog, the Rabbit, and other Mammals, at the same stage of their Ontogeny. At this stage it is a bean-shaped body of very simple structure, with a tail behind, and two pairs of paddles, resembling the fins of a fish, and totally dissimilar to the limbs of Man and other mammals, at the sides. Nearly the whole of the front half of the body consists of a shapeless head without a face, on the sides of which are seen gill-fissures and gill arches as in Fishes. In this stage of evolution the human embryo differs in no essential way from the embryo of an Ape, Dog, Horse, Ox, etc., at a corresponding age. (Haeckel, 1896*b*: 1, p. 18).

In correspondence with the 'law of the ontogenetic connection of related forms', a part of the Biogenetic Law, and also a feature of von Baer's thinking, the drawings show embryonic resemblance among species (Haeckel, 1903: p. 377).

(2) **Evolution of the embryological drawings**

Haeckel's drawings, like some of his ideas, change through subsequent editions of his works. In later editions of *Anthropogenie*, Haeckel modifies and elaborates the set of eight species from 1874 – presumably in response to criticisms, and to accommodate new data. He takes more trouble to acknowledge, in text and pictures, that there are differences among embryos of different species. The plates in the fourth edition (Haeckel, 1891) show more species than those in the first and second editions, although anamniotes are no longer depicted.

In the fifth edition (Haeckel, 1903), a further six species are added making a total of six plates. He also takes more care to compare embryos at similar stages, citing for example the rapid developmental transformations in the region of the pharyngeal arches (Haeckel, 1910: pp. 35–36). Some elements of the 1874 plates are retained while others are modified. For example the chick embryo in Table IX of Haeckel (1903) uses the same advanced stage (GIII) as the Haeckel (1874*a*) Anthropogenie figure, but presents revised early stages (GI–II).

He says of those in the fifth edition (Haeckel, 1903: p. 377): 'The envelopes and appendices of the embryonal body (amnion, yolk sac, allantois) are omitted. All 60 figures are slightly enlarged, the upper ones more, the lower ones less. To facilitate comparison, all are reduced to nearly the same size in the drawing'. To the best of our knowledge, he never lists the sources of the pictures. However, he did claim in Haeckel (1874*a*) to have his own specimens.

(3) Modern influence

The embryo drawings are still widely printed in reference books and student texts, and have therefore been widely accepted as teaching devices (Gould, 2000). They are also used in technical scientific publications (Duboule, 1994; Butler and Juurlink, 1987). Their modern use is to illustrate one or more of the same three points that Haeckel intended, namely: embryonic resemblance as evidence of evolution; phenotypic divergence; and recapitulation. The eight embryos from *Natürliche Schöpfungsgeschichte* (Haeckel, 1874*c*) are redrawn in the modern text *Biology* (Arms and Camp, 1995), and were used to illustrate embryonic development in *The Study of Animal Life* (Thomson, 1917).

The most widely reproduced of Haeckel's embryo drawings are the set in the first edition of *Anthropogenie* (Haeckel, 1874*a*). In several text books, the drawings are used as scientific illustrations to show the reader what embryos look like (Wilson, 1886; Lull, 1927; Cole, 1933). They have been widely used in numerous standard works (e.g. Alberts *et al.*, 1994; Collins, 1995; Gilbert, 1997) and in countless student texts (e.g. Kardong, 1995; Gould, Keeton & Gould, 1996; Gerhart & Kirschner, 1997; Müller, 1997). Embryo plates from later *Anthropogenie* editions are copied by some authors (e.g. Platt and Reid, 1967; Leakey, 1986). These texts faithfully reproduce scientific errors in Haeckel's original (e.g. his depiction of the forelimb bud of the chick embryo, in the middle row of the plate, as being a caudal member of the pharyngeal arch series).

Some texts appear to have copied their drawings second-hand, rather than directly from Haeckel. The version in *Darwin and After Darwin* (Romanes, 1892) is the commonest secondary source (Fig. 6). Some books (e.g. Phillips, 1975; Minkoff, 1983) use other second-hand sources. The drawings in some textbooks have deteriorated in quality from Haeckel's originals, and anatomical errors have been introduced during copying. For example, the set in *Gray's Anatomy* (Collins, 1995) has eye and ear primordia in the wrong places.

(4) Scientific criticisms of the drawings

Haeckel presented the embryo drawings as data in support of his hypotheses. Therefore, scientists disagreeing with Haeckel's views have often challenged the accuracy of the drawings (Richardson *et al.*, 1997), and their interpretation. Other criticisms of the drawings, which will not be discussed here, are religious or political in motivation (e.g. Assmuth & Hull, 1915).

Wilhelm His was ideologically opposed to Haeckel's views (Gerber, 1944; Richardson & Keuck, 2001) and used an empirical, morphometric approach to challenge the embryonic resemblances depicted in Haeckel's drawings (see Section IV. 4*b*) below). Unfortunately, however, most scientists discussing embryonic similarity have done little more than make subjective judgements about overall appearances, and this approach to comparative embryology is essentially phenetic. For example, Yapp (1955: p. 673) claims that: '... a $5\frac{1}{2}$ day chick and a 13-day rabbit embryo are almost indistinguishable'. Dubious phenetic statements of this type reflect the lack of a rigorous approach to comparative embryology.

Scientific objections to Haeckel's drawings (Table 2) include charges of: (i) doctoring (the alteration of images during copying); (ii) fabrication (the invention of features not observed in nature); and (iii) selectivity (the use of a misleading phylogenetic sample). Various authors have made these charges, as reviewed by Gursch (1981), who concentrates on non-scientific aspects of the controversy.

(*a*) *Some contemporary scientific criticisms*

In a review of Haeckel's (1868) *Natürliche Schöpfungsgeschichte*, Ludwig Rütimeyer (1868) suggests that Haeckel had reprinted a single woodcut of a turtle embryo to give the impression that it represented the embryo or egg of three different species (Haeckel's Figs 9–11; reproduced here as Fig. 1). A recent examination of the drawings (Rager, 1986) supported this claim. His (1874: p. 169) made similar criticisms. The printing block for this figure is preserved in the archive of the Ernst-Haeckel-Haus,

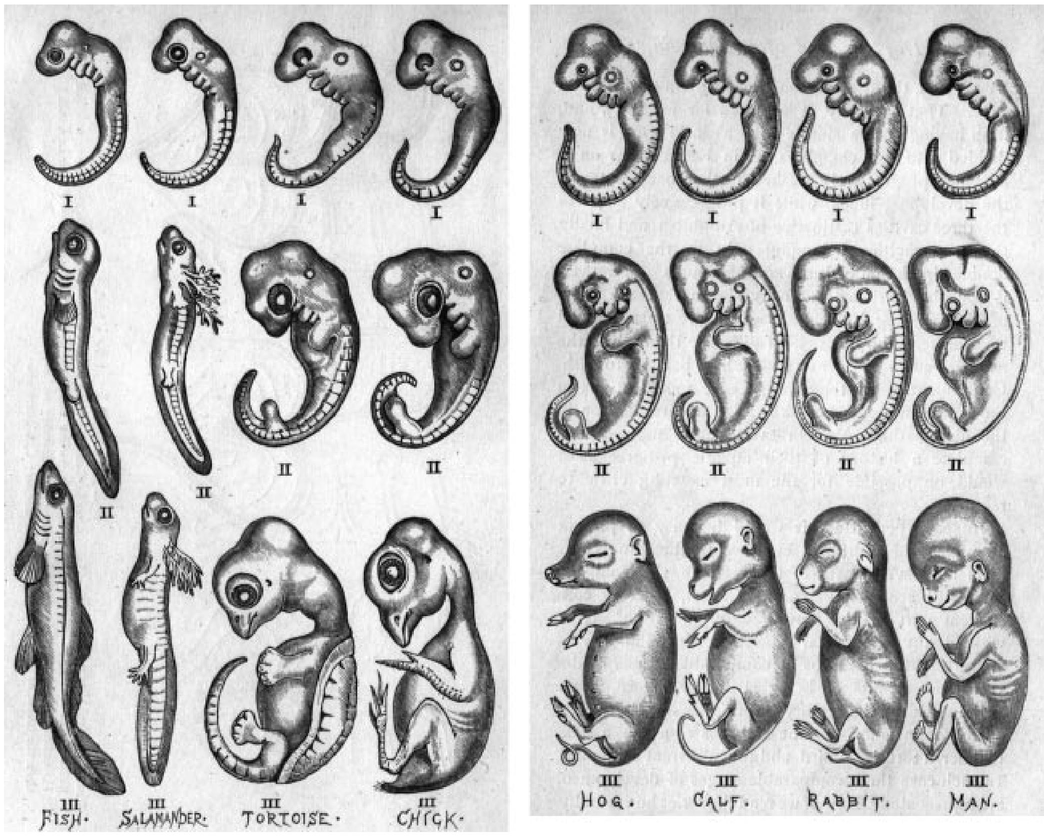

Fig. 6. The Romanes (1892: Figs 57–58) copy of the Haeckel drawing shown in Fig. 3. This copy is widely used in textbooks and is frequently attributed incorrectly to Haeckel.

Jena (catalogued as 'Bestand VA,004'; we thank the archivist, Dr. Thomas Bach, for this information).

As in some other cases, Haeckel admitted his mistake. In his 'Apologetisches Schlußwort' to *Anthropogenie* (Haeckel, 1891) he acknowledged the truth of this 'story of the three woodcuttings' saying that it was 'an imprudent folly' due to lack of time when preparing the few illustrations for the *Natürliche Schöpfungsgeschichte* (Haeckel, 1868). W. His (1874: pp. 169ff) attacks several of Haeckel's embryo pictures. Of the plates of eight embryos in the fifth edition of *Natürliche Schöpfungsgeschichte* (Haecekl 1874*c*, plates II & III) he says:

Copies (apart from the turtle figure) are illustrations allegedly of a 4 week old dog (compare Bischoff [1845] Taf XI 42b, dog embryo of 25 days) and that of the allegedly 4 week old man (compare Ecker [1851–9], Icones Physiologicae Taf XXXII, 2, there without age indicated). These are free copies made in a way that favours the desired identity. (His, 1874: pp. 169–170).

Of the plate (see Fig. 3) of 24 embryos in *Anthropogenie* (Haeckel, 1874*a*) His says: 'The majority of figures in embryo plates IV and V are invented. To mention only an example, the embryos of frog and fish are given the same brain flexure at the vertex seen in the turtle, chick and mammals'. His points out that Haeckel had used drawing prisms in earlier studies, and so he cannot be excused on lack of technical skill. He concludes (His, 1874: p. 171): 'The procedure of Professor Haeckel remains an irresponsible playing with the facts even more dangerous than the playing with words criticised earlier'.

In his well-informed and balanced critique, the embryologist Keibel (1909) writes:

Let us consider the illustrations in Haeckel's essay on 'Das Menschenproblem' as we find them on Plates II and III. The sandal-embryos of the pig are probably after my *Normal Table of the Development of the Pig* [Keibel, 1897] but they are strongly schematised and the third stage in particular is extensively modified. In the second column (rabbit) the first stage is definitely incorrect, being a slightly altered copy of the outdated figure 162 in Kölliker's *Handbuch* of 1879. In the third column (man) the first stage is a bad copy after an embryo described by Count Spee. However, it is possible to recognise the illustration. The second and third stages are figments of the imagination, in which embryos of *Tarsius* and *Semnopithecus* have been used to a greater or lesser extent … As in all figures, Haeckel has omitted the umbilical stalk and the yolk sac and here, as usual, has performed the removal, perhaps one could also say the suppression, of these structures carelessly, in so far as parts of the definitive body are also deleted. Presumably Haeckel has omitted these parts to facilitate comparison with anamniote embryos. I do not think these cuts are fortunate, though this is debatable; but in any case it would be good to explicitly point out such schematisings.

While Keibel supports Haeckel's practice of filling in gaps in the embryonic series by speculation, he criticises him for not making it clearer to the reader that he was presenting hypothetical forms. Even in popular works, says Keibel, this is 'unscientific'. Nonetheless he agrees with Haeckel to the extent that embryonic resemblance provides evidence for evolution. He also agrees that similarity in the appearance of the embryonic nervous system, tail and gill clefts is undoubtedly of great significance.

Speaking generally about embryonic similarity, Beard (1896) argued that there is a 'critical stage' in vertebrates when all organs are present in rudimentary form. But Beard suggests this is not a stage of maximal similarity, but a stage when each embryo has already developed characteristic features of its class. If so, then this finding conflicts with claims that there is a stage of maximum resemblance among vertebrate embryos when all the organs are present as undifferentiated rudiments (Minot, 1897: p. 278; Slack *et al.*, 1993). Others who criticised embryonic similarity in general, or Haeckel's drawings in particular, include Sedgwick (1894), Marshall (1893) and Lillie (1919: p. 4).

(*b*) *W. His's morphometric approach to comparative embryology*

Wilhelm His, Sr. (1874: pp. 201–203) made some highly important, but overlooked, observations – motivated by his opposition to Haeckel and his embryo drawings. His outlined a practical methodology for phylogenetic embryology which, we believe, contains fundamentally important statements about the nature of developmental characters. He acknowledged that embryos are simple in form, and lack the secondary characters which allow us to distinguish among the adults of different species. However, he noted that embryos are not identical, but show class, species, even individual and sex differences (see also Richardson & Keuck, 2001). He provided drawings intended to prove this claim (Fig. 7), although their accuracy has also been questioned (Richardson & Keuck, 2001).

We summarise His's other arguments as follows. Late-developing characters, such as feathers, teeth and claws, cannot be used to distinguish among embryos. Instead, he advocated the use of special embryonic characters (e.g. cell masses and epithelial thickenings). He believed that even an early embryo has an outline plan characteristic of its species; an experienced embryologist ought to be able to determine the species in the same way that an architect reads a building plan. The same level of detail used by Linnaeus to construct his taxonomic system should be applied to embryos.

He advocated a morphometric approach to comparative embryology; in a crude but effective experiment he traced pictures of embryos onto paper, cut round the outlines of various organs, weighed the cut-outs and showed that the embryo of each species has its own characteristic body proportions. Finally, he suggested that embryonic variations are linked with adult morphological differences, and that these in turn are correlated with differences in behaviour and other variables. In our view, His's methodology never reached fruition because he did not realise that the whole procedure is utterly dependent on rigorous developmental staging (see Richardson and Keuck, 2001, for an example of this oversight).

(*c*) *More recent scientific discussions of the drawings*

According to Goldschmidt (1956: p. 36): 'A real storm brewed when [Haeckel] was accused of having falsified pictures which were to prove the absence of differences in animal and human development. There was no doubt that the originals had been tampered with in the reproduction, although an exact copy would have been just as good for illustrating his argument.'

Richardson *et al.* (1997) compared Haeckel's drawings with photographs of real embryos at equivalent stages and concluded that Haeckel had exaggerated similarities, down-played resemblances, and excluded embryos from the figure which have atypical appearances. Hall (1997: p. 461) cites Haeckel's common embryological stages which he used to hypothesise metazoan ancestors. He concludes that 'Haeckel's famous and oft-reprinted figures of conserved stages were figments of idealism and imagination rather than a reality derived from observation'. See Collazo (2000) for further critical discussion of embryonic similarity.

The critiques by Richardson (1995) and Richardson *et al.*, (1997) provoked strong reactions, including press coverage and other discussions (for example *The Times* London: 12/8/1997, p. 14; *Süddeutsche*

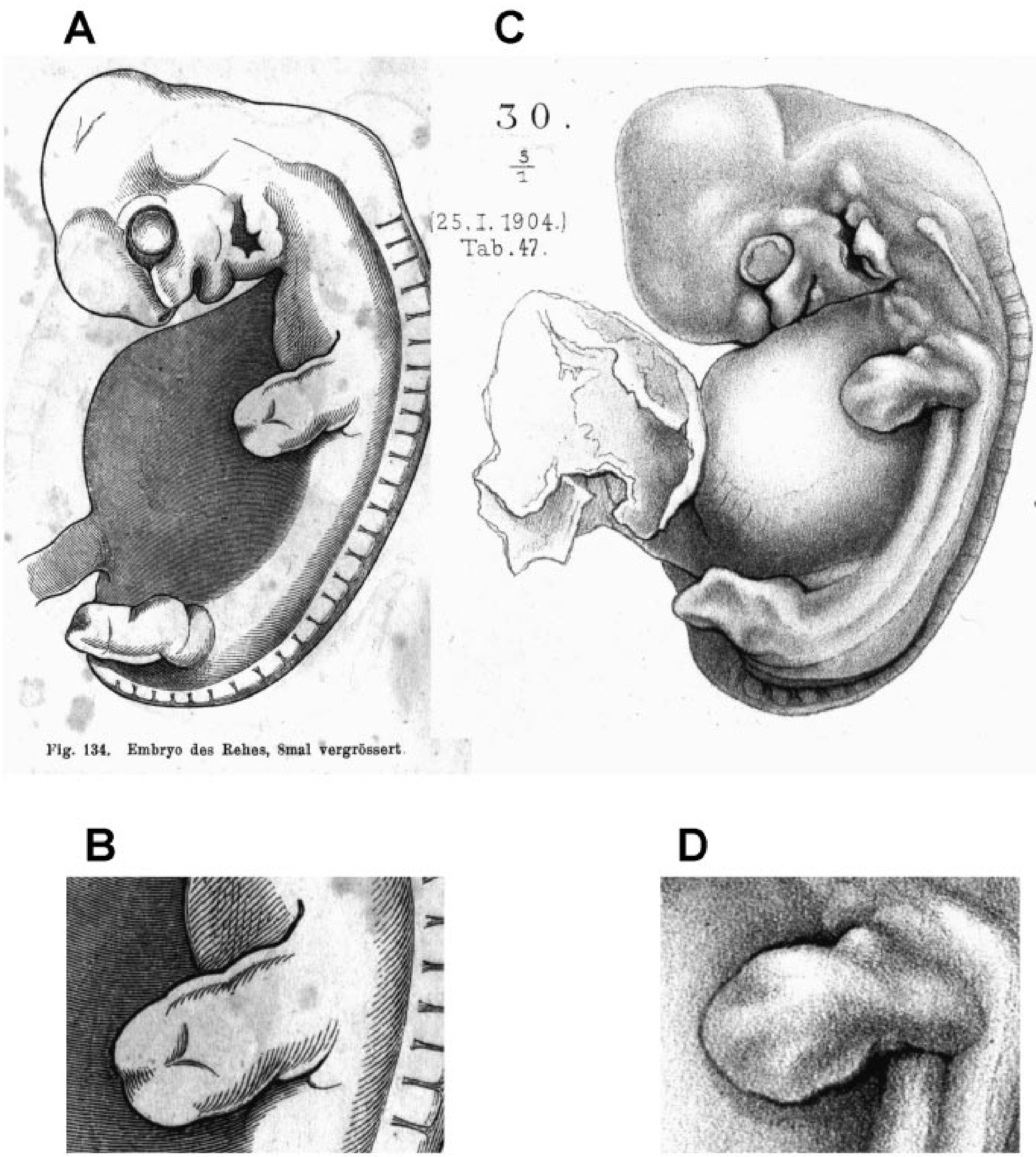

Fig. 7. (A, B) Drawings of a deer embryo (A) and a detail of its forelimb (B) taken from His (1874) who used them in a rebuttal of the concept of embryonic similarity. (C) Deer embryo of similar stage to (A), judging by the development of the auricular hillocks, and detail of its forelimb (D), from plate 1, Fig. 30 in Sakurai (1906). His's (1874: Figs 132–137) figures were intended to illustrate the individual differences in embryos of different vertebrates, in contrast to the arguments of Haeckel. Unfortunately His's embryos are mostly at later stages than the nearly identical early-stage embryos illustrated by Haeckel (see top row of Fig. 3). They thus do not inform the debate and indeed may themselves be disingenuous (Richardson & Keuck, 2001). For example, the deer embryo (A, B) is shown with cloven hooves; other studies (C, D) show that the hoof does not develop initially with a cleft, but as a digital plate with rays.

Zeitung: 18/8/1997, p. 34: *Focus* 34: 18/8/97, p. 128; *Frankfurter Allgemeine Zeitung*: 20/8/1997, p. N1; 6/9/1997, p. 23; Anonymous, 1997; Behe, 1998; Sander & Bender, 1998). Several textbooks added disclaimers to their use of Haeckel's figures (e.g. Guttman, 1999; Pennisi, 1997). Lewis (1997) reproduces what appears to be a copy of the Romanes' copy of the *Anthropogenie* set (see Fig. 6), while making the curious comment in the legend that: 'These sketches were drawn in 1901 and therefore have some inaccuracies'. Equally, in *Evolution* (Strickberger, 2000) copies of the *Anthropogenie* drawings (1874) carry the comment that while Haeckel 'took liberties' with them, the drawings are nonetheless helpful. It could be argued that these comments do not encourage students to regard comparative embryology as a rigorous scientific discipline.

Richardson's critiques were praised as 'good science' by Gould (2000), although they may also be criticised as weak history of science. They overlooked the extent of previous criticisms made against the drawings, and also perpetuated an old claim, apparently false, that Haeckel was convicted of fraud over the embryo drawings (Richardson, 1997, 1998; Sander and Bender, 1998). Clarifications were issued when the historical facts became clearer (Richardson, 1998, 2000*a*).

Gould (2000) concentrates his criticism on Haeckel's earlier published embryo figures (Haeckel, 1868) including the three identical woodcuts of the 'sandalion' stage (an archaic term for a neurula embryo). He criticises Haeckel's textbook illustrations in general, as well as those in *Kunstformen der Natur* (Haeckel, 1904) and *Die Radiolarien* (Haeckel, 1862), concluding that Haeckel had in some respects committed the 'academic equivalent of murder'.

(*d*) *A comparison of Haeckel's drawings with possible primary sources*

For this paper, we have searched the classical embryology literature in an attempt to identify plausible sources. Our aim was to determine whether there is evidence that the drawings were fraudulently altered (as defined by Richardson and Keuck, 2001). We summarise our findings in Table 3, and illustrate some examples in Figs 4–5. Our suggestions are tentative, and are based purely on our own subjective judgement of the similarity in appearance of the pictures. We have no objective, independent evidence confirming that these are indeed Haeckel's sources. Nonetheless, the early publication date of Haekel's drawings does mean that the number of likely sources is limited.

Comparison of the copies with our suggested sources reveals a number of interesting points (Table 3). We believe that many of the drawings in the bottom two rows of the *Anthropogenie* set (i.e. the later stages) have been copied entirely accurately. The same is not always true of the earlier stages, which often appear to have been modified to increase similarity among species. In several cases, we could find plausible sources for the later embryos, but not the earliest stage.

We note the remarkable resemblance between the two embryos on the left hand side in Haeckel's top row (Fig. 3), and the blenny embryos (Fig. 5) illustrated by Rathke (1833). If Rathke is indeed the source, this would be another example of a single picture being duplicated by Haeckel to represent different species. It would also rule out the claim by Richardson *et al.* (1997: p. 91) that Haeckel's early embryo is a stylised amniote embryo. We note that Haeckel removed limb buds from several early embryos in the *Anthropogenie* drawings (compare Fig. 4G, I; see also Gursch, 1981, and Richardson and Keuck, 2001, for further examples of limb removal). Sometimes, Haeckel has attempted to represent a single species by copying embryos from more than one species. Thus we find that his 'alligator' embryos (Haeckel, 1891: plate 6, Figs KI–III) are in fact a mixture of *Alligator* and *Crocodylus* species (Table 3). Similar charges, of mixing species, were made by Braß (1909) in relation to drawings in Haeckel's (1907) *Menschen-Problem*.

(5) In defence of Haeckel's drawings

(*a*) *The schematisation defence*

The principal defence of Haeckel's illustrations is that they are not intended to be technical scientific renderings; rather they are schematic drawings or reconstructions for a lay audience (Haeckel, 1910, 1911; see also his preface to the third edition of *Anthropogenie* (translation in: Haeckel, 1896*b*: 1, xxxiv).

The schematisation defence is not easy to reconcile with the observation that limb buds were removed by Haeckel from some early embryos (Richardson and Keuck, 2001). Indeed, one could argue that such selective schematisation is no different from fraud. However, many writers have defended Haeckel's methods (e.g. Schmidt, 1909), although they may admit that Haeckel sometimes blurred the distinction between the methods of technical zoology and popular science. For example, Gursch (1981) concluded that, while Haeckel's drawings were open to criticism, they were not falsifications. Rather they should be regarded as reconstructions – a valid scientific procedure in Haeckel's time. Gursch (1981) does think that Haeckel should have made this clearer to the reader. He felt that Haeckel's response to his critics was too general and failed to address the specific scientific questions. Ultimately, Gursch

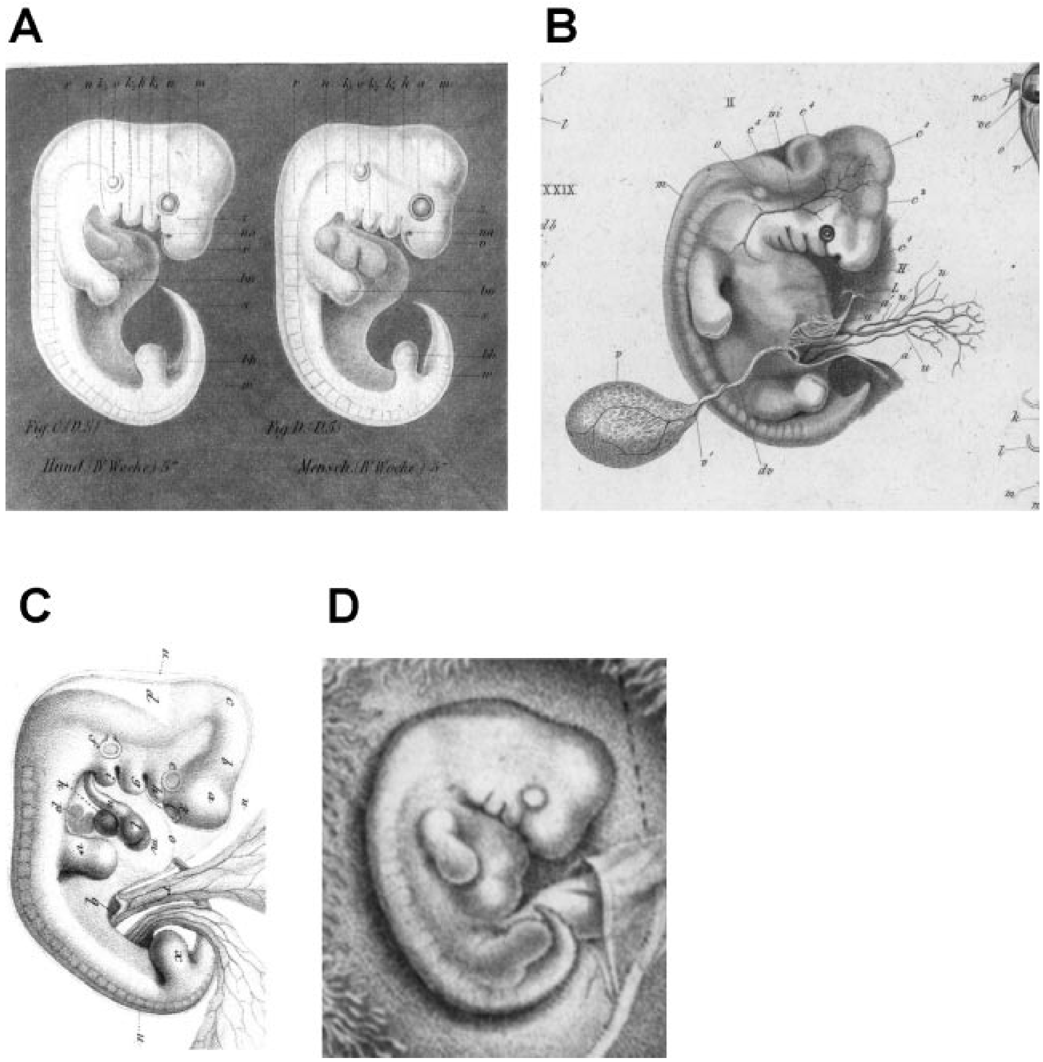

Fig. 8. The Bischoff-Ecker sources for Haeckel's human and dog embryos. (A) Dog (left) and human (right), both labelled: IVth week, 5‴. Figs C and D respectively from plate III in Haeckel (1874*c*; the complete plate is reproduced here as Fig. 2). (B) Plate XXX, fig II from Ecker (1851–9) labelled: 10‴ (no age given). (C) Plate XI, fig 42B from Bischoff (1845). Image rotated 90°. (D) Plate XXVI, Fig. VIII from Ecker (1851–9), labelled: 5 weeks, 5‴. Inverted horizontally and rotated for comparison with A. His claimed that Haeckel had copied the human embryo badly from Ecker (B) and that the eyes were enlarged and the tail lengthened in the process. But note that embryo D, from the same Ecker publication, is a more plausible source (its tail is longer, and its eyes larger, than those in B; furthermore, unlike B, it is the same size as the Haeckel copy, according to the measurements given in the legend). If this is the case, then at least some of His's objections to these particular Haeckel drawings are removed.

(1981) concludes that neither side in the debate was particularly rigorous with their scientific arguments.

Nordenskiöld (1929) states that Haeckel's drawings were inaccurate and not derived from real specimens, but considers charges of fraud unreasonable. Goldschmidt (1956: pp. 36–37) sees in Haeckel's art nothing more sinister than an attempt to improve on nature. Bender (1998) rejects His's claims about the fabrication of the sandalion stage, arguing that Haeckel's drawing is a faithful representation of a real stage, as shown by comparison with published embryos.

(*b*) *Haeckel's views on scientific illustration*

Haeckel's own views on art stressed the primacy of interpretation over pure observation, for example when he describes (Haeckel, 1995) the landscape paintings of Baron Hermann von Königsbrunn who had visited Ceylon in 1853. Breidbach (1998: p. 13) remarked: 'For Haeckel, the illustration is not a depiction of existing knowledge, but is itself the acquisition of knowledge of nature'. Referring to scientific illustrations in the introduction to his *Kunstformen der Natur* (1904), Haeckel states:

I have confined myself to a true reproduction of the really existing natural produce, refraining from stylistic modelling and decorative use; these I leave to the artists themselves.

And in *Die Natur als Künstlerin* (1913: pp. 13–14) he defends his pictures in *Kunstformen*:

Everybody who knows the corresponding literature and the sources from which I faithfully copied my figures can easily convince himself that I have strictly adhered to that principle of objective representation. This fact has been questioned some years ago. It was asserted that my drawings were stylised and that the forms I reproduced did not occur in nature … A trained eye would notice especially the unartistic appearance of the real forms [of Radiolaria and other protists] … Everybody who has even a little training in working with the microscope will recognise that these claims are totally erroneous … and if one would undertake the effort to compare Radiolaria preparations under the microscope with the drawings published by me, one would recognise without difficulty that the latter are objective reproductions of the real forms and there can be no question of reconstruction, trimming, schematisation or falsification.

This view is supported by Breidbach (1998: p. 9) in his notes to a recent edition of *Kunstformen*:

The individual forms are drawn with extreme delicacy, using … stylistic elements of that time … but with the aim of reproducing the natural forms as exactly as possible. A comparison of Haeckel's drawings, e.g. of Radiolaria, with the original preparations that still exist in the Ernst-Haeckel-Haus in Jena, demonstrates that Haeckel met this requirement. The reproach made against Haeckel by some scientific colleagues of having alienated the natural is not apt. Haeckel shows the nature of forms; he only shows it in a certain 'way' that also explains the high appeal of these Tables.

The scientific photographer Manfred Kage, who has studied Haeckel's work on Radiolaria, also aims to rehabilitate him. He compares Haeckel's drawings with modern light and electron micrographs and finds Haeckel's versions to be highly accurate (see George, 1996).

(*c*) *His's unreasonable accusations*

In addition to his legitimate criticisms of Haeckel's embryos (see Section IV.4*a*) His also made some quite unreasonable ones. He presented his own line drawings as counter-evidence (Fig. 7); their purpose was to show that the early embryos of different species were not identical, as Haeckel claimed, but could easily be identified. This is often cited in evidence against Haeckel: '… W. His … demonstrated its incorrectness [embryonic resemblance], by word and picture, as early as 1874.' (Assmuth & Hull, 1915: p. 65). However, we have noted (Richardson & Keuck, 2001) that the embryos His shows are late ones, and have already started to develop the differences illustrated by Haeckel in the bottom two rows of his plate (Fig. 3). In addition to these staging problems (see Fig. 7) His's drawings may contain tendentious errors (Richardson and Keuck, 2001).

In another famous episode, His (1874) criticises Haeckel for making a distorted copy of the drawing of a human embryo by Ecker (1851–9: plate XXX, Fig. 2). His's identification of Ecker (1851–9) as the source of Haeckel's figure has been used by anti-evolutionists in their attacks on Haeckel (e.g. Assmuth & Hull, 1915; Rusch, 1969). However Gursch (1981: p. 32) doubts that Ecker is the source and suggests that Haeckel may have modelled the human on his own figure of the dog on the same plate.

We suggest an alternative explanation for Haeckel's alleged distortion. There are other illustrations of human embryos in the Ecker plates which more closely match the Haeckel picture. We think it possible that Haeckel's 'distorted' human embryo may in fact be a rather faithful copy of one of these other pictures (see Fig. 8 here).

V. CONCLUSIONS

(1) Zoologist Ernst Haeckel is widely known for his influential popular science books, magnificent zoological monographs, and scientific innovations. He attempted to integrate taxonomy and embryology into the Darwinian framework and to use the data for phylogeny reconstruction. His work is historically and scientifically important, and has influenced modern thinking in evolutionary developmental biology and phylogenetics.

(2) Haeckel's Biogenetic Law makes predictions about the rank of primitive and advanced characters in developmental sequences. To Haeckel, heterochrony was a change in developmental sequence. Some modern methods in comparative embryology, such as event-pairing, also exploit sequence heterochronies. Haeckel's 'alphabetical analogy' shows

characters or stages (it is not always clear which) dropping out of a sequence, being added terminally, or undergoing transformation. Significantly, Haeckel's caenogenetic changes were all adaptations to embryonic life; he does not acknowledge the possibility that embryos could be affected by selection acting on adult characters. Haeckel believed that primitive characters alone are important in phylogeny reconstruction, in contrast to modern cladistic methodologies which employ synapomorphies. Haeckel is often accused of advocating absurd recapitulatory scenarios – such as fish gills in human embryos. However, we find that he explicitly rejected this scenario in some of his writings.

(3) Modern views on Haeckel are, typically, ambivalent. His early work is praised, but there is confusion about the Biogenetic Law and recapitulation (the latter being very often confused with embryonic resemblance). Some of this confusion can be blamed on ambiguities and logical flaws in Haeckel's writing. Several modern studies support the Biogenetic Law in the case of single character transformations. However, there is no evidence from vertebrates that entire stages are recapitulated. Haeckelian and von Baerian models both make the same prediction: that plesiomorphies are transformed into apomorphies during ontogeny. The principle differences between the two models are that Haeckel's scheme involves heterochrony as one of its mechanisms, and leads to a series of conserved stages.

(4) Haeckel's embryo drawings are important as phylogenetic hypotheses, teaching aids – even scientific evidence. They reflect a phenetic, non-quantitative, 'portrait gallery' approach to comparative embryology. This approach is still common today, although quantitative comparative methodologies are gaining ground. The drawings illustrate embryonic similarity, recapitulation, and phenotypic divergence. They have been criticized – not always fairly – on the grounds of inaccuracy and tendentiousness. We have identified potential sources for several of the drawings, and find some evidence of doctoring. In opposition to Haeckel and his drawings, Wilhelm His proposed a rational, morphometric approach for comparing embryos. His failed, however, because he overlooked the importance of rigorous developmental staging.

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