Homology and Heterochrony:

The Evolutionary Embryologist

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Abstract

The evolutionary embryologist Gavin Rylands de Beer can be viewed as one of the forerunners of modern evolutionary developmental biology in that he posed crucial questions and proposed relevant answers about the causal relationship between ontogeny and phylogeny. In his developmental approach to the phylogenetic phenomenon of homology, he emphasized that homology of morphological structures is to be identified neither with the sameness of the underlying developmental processes nor with the homology of the genes that are in involved in the development of the structures. De Beer's work on developmental evolution focused on the notion of heterochrony, arguing that paedomorphosis increases morphological evolvability and is thereby an important mode of evolution that accounts for the origin of many taxa, including higher taxa.

Gavin Rylands de Beer (Fig. 1) was born in England in 1899, but spent the first 13 years of his life in France, where his father worked as a correspondent of a telegraph company. After returning to England, he went to Harrow School, where he became interested in zoology. In 1917 he entered Magdalen College at Oxford, graduating in 1922 after a leave for serving in the British Army during World War I. Upon graduation, he remained in Oxford as a fellow of Merton College, teaching and researching in zoology.[1]

The zoologists that exerted the largest influence on de Beer at Oxford were Edwin S. Goodrich (1868–1946), Julian S. Huxley (1899–1980), and J. B. S. Haldane (1892–1964). Gavin de Beer's early research focused on experimental embryology. Accordingly, he visited the Stazione Zoologica at Naples and Hans Spemann in Freiburg. De Beer's first two books—*Growth* ('24) and *An Introduction to Experimental Embryology* ('26a)—presented the methods of experimental zoology and discussed induction and the regulation of embryonic differentiation. During this early phase, he collaborated extensively with Julian Huxley, who likewise focused in the 1920s on the experimental study of development. The culmination of their joint work was *The Elements of Experimental Embryology* (Huxley and de Beer, '34). Though this book largely relied on established notions used to explain development, its approach was novel in that Huxley and de Beer tried to integrate Spemann's notion of organizers and Child's concept of axial gradients—in spite of the fact the Spemann was very critical of Child's theory.

But soon de Beer and Huxley were to abandon the study of experimental embryology. Mark Ridley ('86) interprets this as an important event in a broader historical development. Ridley views the history of embryology in Great Britain before World War II as proceeding in four main phases. The first phase started in the 1870s with the theory of recapitulation gaining popularity in the UK due to the work of E. Ray Lankester, which furthered developmentally based phylogenetic reconstructions and evolutionary studies. While Francis Balfour's school in

Cambridge was the focus of research in this first stage,[2] soon the center shifted from Cambridge to Oxford, with experimental embryology and developmental mechanics replacing the older phylogenetic embryology. J. W. Jenkinson was the main figure of this phase. The third phase started after World War I with a diversification of the causal approach to embryology. For example, Jenkinson's student Julian Huxley continued the experimental tradition, integrating new ideas such as Mendelian genes and how they influence rates of development. On Ridley's account, the fourth phase took place towards the end of the 1920s, when Huxley and de Beer finally began to react against experimental embryology, turning their attention back to traditional zoological and evolutionary questions (Huxley becoming in fact one of the founders of the Modern Synthesis).

In the case of de Beer, experimental embryology was abandoned in favor of descriptive and comparative embryology as well as evolutionary embryology and evolutionary biology. In this respect, de Beer returned to the interests of his teacher Edwin Goodrich, whose approach influenced de Beer in this domain. A student of Ray Lankester, Goodrich conducted research in comparative anatomy and phylogeny of both vertebrates and invertebrates. His prime method in phylogeny was the comparative study of development. Goodrich also paid attention to advances in genetics (de Beer, '47a), an interest de Beer pursued by integrating Mendelian genetics into his developmental account of evolution (as we shall see below). De Beer's reorientation away from experimental embryology took place in the second half of the 1920s (several years before he and Huxley wrote the important book on experimental embryology). He started with studies of the embryological relations of somites, gill slits and cranial nerves in elasmobranch fish and published several papers on the developmental of the head of fish. Extensive studies on the pituitary gland (partially in collaboration with L. T. Hogben) led to the publication of *The Comparative Anatomy, Histology and Development of the Pituitary Body* ('26b). De Beer's

detailed comparative and studies of chordate development can be found in *Vertebrate Zoology* (’28). Due to its clarity and organization it proved to be very successful as a textbook. De Beer combined chapters on the morphology and development of the main chordate groups with chapters that discussed particular organ systems in a comparative fashion. The account embodied a phylogenetic perspective—as it was understood in these days. For when discussing a single extant species in detail to illustrate the morphology and development of a larger taxon, de Beer chose such an instance of a more ancestral type that its morphology and mode of development helps to explain the evolutionary emergence of the morphology and ontogeny of a more derived type. To be sure, this approach falls short of a genuine phylogenetic analysis as understood nowadays, which consists in studying how the features of an actual ancestor gave rise to those of its actual descendant, presupposing the explicit use of a phylogenetic tree and a valid character polarity assessment of the species involved. Finally, de Beer’s *Vertebrate Zoology* included several chapters on the evolution of vertebrates. From an evolutionary point of view, de Beer’s most interesting work is his account of developmental evolution, which was published in his 1930 book *Embryology and Evolution*. Subsequent and revised editions were published from 1940 onwards under the more popular title *Embryos and Ancestors*. I will discuss this important and influential work of de Beer in detail below. A further (yet evolutionarily less central) study is *The Development of the Vertebrate Skull* (’37), a landmark in comparative embryology.

In 1938 de Beer moved to the University College of London as a reader in embryology; and in 1940 he was elected Fellow of the Royal Society. After serving again in the British Army during World War II, he returned to University College as a professor of embryology and served as a president of the Linnean Society of London. In 1950 he became Director of the British Museum of Natural History; and in 1954 de Beer was knighted. In 1958 he held the presidency of the Fifteenth International Congress of Zoology, and thus was responsible for preparing the

centennial of Darwin's publication of the *Origin of Species*. After his retirement from the British Museum and from full-time academic work in 1960, de Beer's publications focused on the life and work of Charles Darwin and popular expositions of evolutionary theory. He edited Darwin's notebooks on the transmutation of species (which appeared in the 1960–61 issues of the *Bulletin of the British Museum of Natural History*). De Beer joined the London publisher Thomas Nelson and Sons, where among other things he personally published popular accounts and defenses of the theory of evolution by natural selection, emphasizing the bearing of Mendelian genetics on modern theories of selection (de Beer, '62b, '63, '64). After spending a few years in Switzerland, Sir Gavin de Beer returned to England in 1972, where he died.

Heterochrony and macroevolution

A central notion in de Beer's work was the idea of heterochrony. It is pivotal because heterochrony provides a causal link between ontogeny and phylogeny. Most of de Beer's developmental theory of evolution was already contained in his 1930 book *Embryology and Evolution*. Later editions (under the name *Embryos and Ancestors*) offered more examples and empirical detail but only minor theoretical additions or modifications. Given that de Beer rejected the theory of recapitulation, let me mention the relevant historical background. In Great Britain from 1870 onwards, the increasing popularity of the idea that ontogeny recapitulates phylogeny proved to be scientifically productive by spurring phylogenetic reconstruction using embryological evidence, leading to a general increase in embryological research and its evolutionary interpretation. Over the decades the phylogenetic interpretation of developmental evidence increased in sophistication. Not every researcher assumed like Haeckel (and Lankester in his early career) that early ontogenetic stages of higher animals simply reflected the adult forms of ancestors; and some (such as Balfour) were aware of the fact that features of early

ontogeny could reflect secondary adaptations rather than inheritance of ancestral characters (Hall 2000; Ridley ’86). When de Beer wrote *Embryology and Evolution*, recapitulationism was not generally accepted any longer, in spite of the prominent recapitulationist Ernest W. MacBride. De Beer’s teacher Goodrich himself rejected the doctrine of recapitulation (not in his publications, but in his lectures; see Ridley ’86), and apparently influenced de Beer’s views on these matters.

An important critique of recapitulation stemmed from the work of the marine biologist Walter Garstang (1868–1949), who coined the term ‘paedomorphosis’. Garstang wrote only a few papers on this issue, which did not attract wide recognition in his life-time, but his ideas prove to be important for the history of evolutionary developmental biology (Hall, 2000). As discussed below, de Beer strongly built on Garstang’s work on paedomorphosis. Garstang viewed many marine larval forms as adaptations rather than recapitulations of ancestral adult forms; and he was clearly aware of the fact that selection can act particularly on early ontogeny, leading to adaptive change in larval forms that may have a strong impact on adult structure and future morphological evolution. Garstang (’22) directly criticized Haeckel’s biogenetic law, challenging various items of alleged paleontological support for recapitulation from the animal kingdom, including paleontological examples. Suggesting that “The real Phylogeny of Metazoa has never been a direct succession of adult forms, but a succession of ontogenies or life-cycles” (p 32), Garstang argued against Haeckel that “Ontogeny does not recapitulate Phylogeny: it creates it” (p 32). A later essay on tunicate morphology and chordate evolution (Garstang, ’29) offered a prominent discussion of paedomorphosis—the idea that the ancestral metamorphosis and adult form can be lost so that the adult descendant corresponds to the ancestral larva. Garstang’s central target was the assumption that hemi- and urochordates are degenerate vertebrates. Instead, he took a tunicate-like ancestor to have played a prominent role in the origin of vertebrates. In a sessile ascidian-like ancestor, selection favored the motile condition of its planktonic larva. This

led to the production of a muscular tadpole-like tail and accelerated sexual development (neoteny). Due to paedomorphosis, its descendant became a free-swimming adult which provided the basis for the evolution of derived chordates and vertebrates. Based on his earlier observations, Garstang discussed in detail how a generalized protochordate can be derived by paedomorphosis from an echinoderm larva (the auricularia larva), where the protochordate neural folds are derived from the auricularia cilial bands and the endostyle is derived from the adoral band. Furthermore, Garstang showed that within the urochordates, the free-swimming Larvacea are derived by paedomorphosis from the larval form of the metamorphosing and sessile doliolids.

De Beer went beyond Garstang's account by offering a classification and systematic consideration of different types of *heterochrony* and according heterochrony a central role in morphological evolution, in particular in the contexts of macroevolution and evolvability. Furthermore, de Beer proposed a genetic mechanism for heterochrony, using Goldschmidt's physiological genetics. *Embryology and Evolution* started out with criticizing Haeckel's biogenetic law on two counts. Haeckel's causal claim that phylogeny is the mechanical cause of ontogeny is rejected. Instead, de Beer maintained that phylogeny is a succession of ontogenies, and that causal factors internal and external to the egg determine ontogeny. In addition, de Beer criticized Haeckel's descriptive claim that descendant ontogenies usually recapitulate ancestral ontogenies in an abbreviated and condensed fashion and that evolutionary modification occur only among adult characters as terminal additions to the ontogenetic sequence. In contrast, de Beer emphasized that novelties can occur at any stage of development. In the case of neoteny (an instance of paedomorphosis) an anti-recapitulatory pattern results as it is the *adult* descendant that reflects the *juvenile* ancestor. De Beer viewed evolution by neoteny as an important mode of evolution, and dubbed it in his popular presentations 'Peter Pan evolution' ('62a), since in the descendant development is arrested and it does not grow any further compared to the ancestor.

One reason to stress the importance of neoteny was that it helps to reconcile the theory of gradual evolution with discontinuities in the fossil record. If modifications and substantial novelties gradually evolve but occur primarily at early stages of development, then they are unlikely to be preserved in the fossil record. If, however, neoteny occurs in a second step, then these juvenile novelties will suddenly become adult characters and thus show up in the fossil record. De Beer called this mode of developmental evolution *clandestine evolution*.[3]

De Beer gave a classification of eight ways in which ancestral and descendant ontogenies can differ (Fig. 2). All of these patterns occurred throughout evolutionary history and account for the origin of lower as well as higher taxa. Even though de Beer presented all of these eight modes of evolution as different types of 'heterochrony', four of them refer to the introduction of novelties in early or late stages of development, but they are not types of *heterochrony* as understood nowadays—changes in relative timing of developmental processes. Among the other four, two of de Beer's morphological modes of evolution, *acceleration* and *hypermorphosis* yield a recapitulatory pattern in that the ancestral ontogeny is repeated by the descendant, though possibly in an accelerated form (Haeckel's condensation) or with terminal additions or prolonged development. Two further modes of heterochrony, *neoteny* and *retardation* refer to the quite different situation where the descendant recapitulates only a certain part of the ancestral ontogeny. I focus on neoteny, due to its overarching importance for de Beer's theory. De Beer argued that numerous taxa have originated by neoteny. This includes the origin of many lower taxa. A prominent example is humans, who have many adult characters that correspond to the fetal or juvenile condition in other primates. But neoteny also accounts for the origin of several higher taxa. As already mentioned, de Beer endorsed Garstang's ('29) theory that Larvacea are neotenous doliolids, and more importantly, that chordates are derived from ancestral echinoderms

by means of neoteny (Fig. 3). In addition, de Beer discussed evidence according to which Ctenophora are derived from Polycladida due to neoteny, as are Insecta from Myriapoda.

De Beer suggested a mechanism for heterochrony as an evolutionary process by pointing to contemporary studies on rate genes. A rate gene is a Mendelian gene that controls the speed of a particular developmental process. Richard Goldschmidt's research in physiological genetics addressed gene action, quantitative rates of gene activity and their influence on development, investigating for instance the gypsy moth *Lymantria* (Goldschmidt, '27). Another prominent example was the work on the shrimp *Gammarus* by E. B. Ford and J. S. Huxley ('27), who showed that differences in eye-color are due to genetically based differences in the speed and onset of pigment deposition processes. Huxley ('32) gave a comprehensive discussion showing that growth rates are biological characters in that the stay fairly constant during ontogeny, vary between species or individuals, and can be under the control of Mendelian factors. De Beer made essential use of these ideas, since rate genes provided a mechanism for how heterochrony and phylogenetic changes of developmental processes take place (Ridley, '86).

De Beer offered two reasons why he viewed neoteny as such an important mode of developmental evolution. First, several types of heterochrony allow for large phenotypic changes and thus for the origin of higher taxa, which applies in particular to clandestine evolution based on neoteny. Second, even after the evolution of higher taxa, further evolution and diversification on lower taxonomic levels occurred. De Beer called the capacity for further morphological evolution after the emergence of a higher taxon *plasticity* ('30, p 91) or *evolutionary plasticity* ('58, p 116). A fundamental idea of de Beer's was that neoteny can explain why macroevolution can occur without obstructing further microevolution. For neoteny is an instance of what he called *paedomorphosis*,[4] in contrast to *gerontomorphosis*, which is a mode of evolution that assumes recapitulation and terminal additions to late stages of development (the above mentioned

modes of acceleration and hypermorphosis). Gerontomorphosis leads to racial senescence in that morphologically overspecialized evolutionary lineages emerge that are developmentally incapable of offering adaptively necessary novelties. According to de Beer's earlier account ('30), paedomorphosis supports evolutionary plasticity for histological reasons. Once neoteny has taken place, the new adult corresponds to the ancestral embryo and is thus composed of relatively undifferentiated cells. This enables further differentiation and increase of complexity in an evolutionarily flexible way. De Beer's later writings ('58) favored another, a genetic explanation, making use of a quite modern way of thinking about genes and their impact on development and evolution. Given that neoteny results in the loss of the former adult characters, the genes that used to be involved in the development of these characters are not employed any longer, so that a large number of genes is available for new variation and the adoption of several novel functions. Whichever scenario is the more probable one, de Beer was convinced that paedomorphosis is a crucial mode of evolution, making evolutionary plasticity (morphological evolvability) possible.

Homology, development, and genes

De Beer's discussions of homology were a small part of his overall scientific work, and not necessarily the most visible and influential aspect of his theories. But his views on this topic can be viewed as setting the stage for current debates of homology in that his conclusions are still valid and set the framework in which investigations into the nature of homology have to take place (Hall, 2000; Laubichler, 2000). De Beer approached homology from a developmental point of view and discussed the bearing of findings from embryology and genetics on the criteria of homology. De Beer stated his views on homology for the first time in the 1938 essay "Embryology and Evolution", dedicated to his teacher E. S. Goodrich. This early account already contains most of de Beer's arguments and conclusions about the homology concept. His position

is briefly restated in *Embryos and Ancestors* (de Beer, ’58), but this discussion is overshadowed by de Beer’s account of heterochrony and his theory of developmental evolution. The essay *Homology, An Unsolved Problem* from 1971—actually one of the last publications of de Beer—offers a succinct account of de Beer’s position.

Before discussing de Beer’s developmental approach to homology, I want to mention Hans Spemann’s (’15) critique of the homology concept, because Spemann’s essay foreshadowed some points that de Beer was to make later (Laubichler, 2000). Spemann has to be viewed as belonging to the tradition of developmental mechanics, which rejected the evolutionary morphology of Gegenbaur and in particular Haeckel, considering the reconstruction of phylogenetic trees and postulation of ancestors as speculative business. Homology was the main concept and tool of phylogenetic morphology, and thus Spemann takes a critical stance towards this notion. His critique centers on what he calls the *genetic conception* of homology, which defines two structures as being homologous in case they have a common origin. It is important to recall that 19th century biologist did not conceive of ontogeny and phylogeny as distinct as we do nowadays. Based on prevailing ideas of recapitulation, common origin of structures was often viewed as the idea that two structures have the same developmental precursor or are derived from the same developmental precursor in the common ancestor. Spemann criticized the genetic-historical concept of homology from the point of view of causal embryology, claiming that the homology concept was based on assumptions that turn out to be wrong given recent findings about the development of organisms. His main example was the regeneration of experimentally removed lenses in amphibians. The regenerated lens is obviously homologous to the old one; however, the regenerated lens develops from a different source than the original, normally developed one. Thus it has a different origin and cannot count as homologous on the genetic definition of homology. In addition, the genetic conception requires one to trace homologous

structures back to its origin in the parent. However, while one can trace an adult structure back to a developmental precursor, it does not correspond to a structure in the egg. As the adult character is not structurally preformed in the egg, it appears to exist only in potentiality in the egg. Thus on a genetic conception that emphasizes derivation from the parent, one is forced to assume that the structure of the offspring is only 'ideally' related to the parental structure. In conclusion, from the perspective of experimental embryology, the homology concept appears to raise more problems than it solves.

Gavin de Beer also discussed homology from a developmental perspective and made similar points, but he was much less hostile towards an evolutionary approach to biology and a phylogenetic understanding of the homology concept.[5] For instance, he recognized the very phenomenon of serial homology as the reduplication of a pattern, but stated that "serial homology is really a misnomer, because it is not concerned with tracing organs in different organisms to their representatives in a common ancestor" ('71, p 9). Despite the overall recognition that homology is a phylogenetic phenomenon, the facts of developmental biology and genetics have profound implications for standard criteria of homology. In fact, development offers substantial challenges for our understanding of the nature of homology. De Beer discussed several important ways in which the traditional embryological criterion of homology fails, i.e., the idea that homologous structures develop in a similar fashion. First, homologous structures need not develop from the same part of the egg or the same part of the embryo. De Beer discussed several descriptive and experimental studies that show this point. To give an example, a homologue such as the alimentary canal in different vertebrates can be formed from the roof of the embryonic gut cavity (as in sharks), the floor (lampreys), the roof and floor (amphibians), or from the embryonic disc (reptiles). Similarly, de Beer's own observations showed that homologous structures need not develop from the same germ layers (de Beer, '47b). Moreover, using the lens example of

Spemann and the experiments of Holtfreter, de Beer pointed out that homologous structures need not be induced by the same organizers or induction-processes. Thus, homologous structures can arise be means of quite different developmental processes, and substantial differences in early development of different species is compatible with homology between adult structures. De Beer's conclusion was that "comparative anatomy, not comparative embryology, is the primary standard for the study of homologies" ('71, p 14).

Homologous structures need not originate from the same part of the fertilized egg. Given that the cytoplasm does not help us any further, what about searching for homology in the genes? Appeal to the inheritance of genes could acknowledge Spemann's point that adult structures are not preformed in the egg without being forced to rely on the mysterious notion that structures of the offspring is only 'ideally' related to the parental characters. However, de Beer's claim was precisely that it is futile to try to pin down sameness of structure by the sameness of a limited set of genes. This is a quite remarkable insight, given that de Beer already stated it in his 1938 essay.[6] On the one hand, phenotypic characters that are controlled by identical genes can be non-homologous. De Beer supported this claim by several examples. The *antenna* gene in *Drosophila*, for instance, can control the production of an additional antenna instead of an eye, structures that are not homologous. In fowl, a particular gene controls the formation of crest feathers in some species, in other species it also causes a cerebral hernia, with upswelling of the skull. On the other hand, homologous characters can be controlled by non-identical genes. Phenocopies and the *eyeless* gene in *Drosophila* show this point. Other genes of a gene complex can apparently "deputize" and make up for the missing gene that normally controls the formation of the character ('71, p 15).

> "It is now clear that the pride with which it was assumed that the inheritance of homologous structures from a common ancestor explained homology was misplaced; for such inheritance cannot be ascribed to identity of genes." (de Beer, '71, p 16)

As de Beer was clearly aware, this fact raises puzzles about the nature of homology:

> "But if it is true that through the genetic code, genes code for enzymes that synthesize proteins which are responsible for the differentiation of the various parts in their normal manner, what mechanism can it be that results in the production of homologous organs, the same 'patterns', in spite of their *not* being controlled by the same genes? I asked this question in 1938, and it has not been answered." ('71, p 16)

The Reception and Significance of de Beer's Work

Gavin de Beer presented a large set of examples showing that homologous structures may develop from different precursors or by means of different developmental processes, and he was the first to emphasize the that sameness of genes and sameness of morphological structures do not map onto each other. His conclusion was that the only reliable method of establishing homologies is comparative anatomy, while developmental evidence is defeasible. While viewing homology as a phylogenetic phenomenon, de Beer like his contemporaries established the homology of two structures by standard morphological criteria, in particular their relative position to other structures and the morphological transformability of one homologue into another by intermediate forms.[7] These criteria provided a relatively reliable way of assessing homologies and forming phylogenetic hypothesis that did not presuppose a phylogenetic tree in the first place. However, for modern phylogenetic (cladistic) analysis the primary criterion is that homologies are to be established and re-assessed based on the distribution of a character across several species on a phylogenetic tree. A case similar to de Beer is the German evolutionary

morphologist Adolf Remane (1898–1976), who likewise used a largely pre-cladistic understanding of phylogeny and comparative analysis when putting forward detailed criteria of homology as a phylogenetic phenomenon (Remane, 1952).[8] Some years after de Beer, Remane ('61) also pointed out that the sameness of structures need not coincide with sameness of development or sameness of genes, arguing that homology is an essentially morphological phenomenon to be established by comparative analysis. These ideas did not immediately prove to be influential, but they became important with the rise of phylogenetic studies in the last two decades, especially developmental and genetic approaches to phylogeny. It is nowadays well-known—though not always respected in everyday biological practice—that similarity of developmental mechanisms and gene expression patterns is a fallible criterion of homology between structures, not to be confused with homology itself (Abouheif et al., '97; Bolker and Raff, '96; Dickinson, '95; Hall, '95; Müller and Wagner, '96; Nielsen and Martinez, 2003; Roth, '88). Consequently, in spite of the availability of genetic and developmental clues, homology among morphological structures is most reliably established by comparative analysis, nowadays understood as phylogenetic (cladistic) analysis.

Apart from the criteria of homology, de Beer's results have important implications for the nature of homology and the nature of organismal organization. Among contemporary evolutionary developmental biologists it is widely recognized that individuals are organized in a hierarchical fashion—though researchers have not always been clear about the reasons for this assumption and the scientific implications of this fact. Homologues exist on different levels of organization. The main reason why different levels of organismal organization are to be distinguished is the fact that structures on one level can sometimes evolve relatively independently from structures at other levels (Abouheif, '97; Müller, 2003; Striedter and Northcutt, '91). For—as de Beer's work supports—homology and evolutionary stability at one

level is compatible with evolutionary change and non-homology at other levels. This has far-reaching consequences for a *developmental homology concept*. Homologues are units of phenotypic variation in that a homologue (a character) can vary across individuals and species relatively independently from other characters. Homologues are the units of morphological evolution (Wagner ’96; Laubichler, 2000). The task of a developmental homology concept is to understand the developmental underpinning of an individual’s organization into homologues. Which features of an organism’s developmental-morphological constitution make it the case that there are distinct homologues where one homologue can phenotypically vary across individuals independently of variation in other characters? Given that different characters do not just exist on one level of organization, but on different levels, this raises an additional challenge (Wagner and Misof, ’93). In spite of the fact that structures on different levels are developmentally and functionally closely related (morphological structures develop based on developmental processes and the action of genes), what makes it the case that modules on one level can evolve fairly independently of homologues on other levels? In this sense, a developmental account of homology is part of an account of morphological evolvability; and the existence of homologues and evolvability on different levels of organismal organization has to be taken into account and to be explained—largely an empirical and conceptual challenge for future work.

The notion of *heterochrony* figured prominently in developmental approaches to evolution of the 1980s, fueled by discussion such as Alberch et al. (’79). De Beer’s own account of heterochrony was discussed and criticized in detail in Stephen Jay Gould’s seminal book *Ontogeny and Phylogeny* (1977). Gould argued that the above mentioned four types of heterochrony should better be reclassified according to whether acceleration or retardation of either somatic development or development of the reproductive organs, respectively, occurred. Both acceleration of somatic development and retardation of sexual maturation (acceleration and

hypermorphosis) yield a recapitulatory pattern, while the other two modes (neoteny and retardation) yield paedomorphosis. Gould's critique was that de Beer's classification is about evolutionary *pattern*s (the results of phylogenetic change in ontogenies), while a good account should rather refer to different *processes* of developmental evolution. Paedomorphosis as a pattern or evolutionary result can be brought about by retardation of somatic development (neoteny) as well as acceleration of sexual maturation (progenesis in Gould's terminology), but these are two different processes that need to be kept apart, because they occur for different evolutionary reasons. Gould agreed with de Beer's morphological argument that paedomorphosis occurred because it avoids racial senescence. However, he complained that this is a macroevolutionary argument that does not explain why there was an adaptive advantage of paedomorphosis at the time it occurred. Gould used ideas from life-history theory to explain the microevolutionary causes of paedomorphosis. He argued that r-selection favors progenesis (acceleration of sexual maturation), while K-selection favors neoteny (retardation of somatic development), underscoring the need to keep processes apart that yield the same evolutionary pattern.

In a similar vein, Rudy Raff ('96) distinguishes between heterochrony as a pattern and heterochrony as a process, arguing that a heterochronic pattern need not be caused by a heterochronic change in developmental processes. This is a case where a contemporary understanding of phylogeny offers conceptual clarity. The study of evolution based on phylogenetic trees uncovers character transitions such as heterochrony as a pattern. The explanation of such a phylogenetic pattern is a different question—whereas de Beer tended to conflate heterochrony as a pattern and as a process. Lately, the notion of heterochrony came to play a less central role for explanations in developmental evolution than in the 80s. For instance, de Beer's assumption that paedomorphosis accounts for the origin of a variety of taxa is not

generally shared any longer. Not even most structural novelties need to be due to changes in the relative timing of developmental processes (Müller and Wagner, ’91). Still, heterochrony—on which de Beer’s account of developmental evolution focused—is one of the relevant concepts of evolutionary developmental biology, as it is the cause of several developmental alterations and can bring about substantial structural changes (McKinney and McNamara, ’91; McNamara, ’95).

The importance of Gavin de Beer for 20th century evolutionary biology has been portrayed in different ways. The medical scientist Steven Waisbren (’88) views de Beer’s work as an example showing how important morphology was for the Modern Synthesis. Despite some of Waisbren’s interesting points, this account is clearly too bold (Love, 2003). In spite of de Beer defending Darwinian selection and the novel insights of population genetics, in his actual research de Beer focused on comparative anatomy, phylogeny and the developmental and genetic underpinnings of morphological evolution, while not conducting active research on the core themes of the Modern Synthesis—change in population structure, adaptation, and speciation. The other extreme can be found in the discussion of de Beer and Julian Huxley by the prominent historian Frederick Churchill (’80). The upshot of Churchill’s account is that de Beer did not contribute to the Modern Synthesis because he could not have contributed to any causal study of evolution. Churchill investigates why de Beer—unlike Huxley—did not become a founder and main proponent of the Modern Synthesis, even though both originally worked together as experimental embryologists (Huxley and de Beer, ’34). Churchill explains the divergence of the two intellectual trajectories by arguing that Huxley was conceptually pre-adapted to think along the lines of population genetics, whereas de Beer was conceptually barred from addressing the mechanisms of the evolution of natural populations (Churchill, ’80, p 118). In fact, the claim is that while de Beer viewed embryology as an explanatory approach, he viewed the study of phylogeny as a merely descriptive enterprise. According to Churchill’s interpretation, the lesson

that de Beer took from the failure of Haeckel's biogenetic law—which causally linked phylogeny and ontogeny—was that the study of ontogeny and phylogeny should be kept separate. Churchill's claim is that for de Beer "biology possessed an irreconcilable dual nature" (p 120)—ontogeny is causal as opposed to phylogeny, and both should not be causally connected.[9]

Churchill's overall interpretative scheme is likely to shed light on the origin of the historical split between evolutionary and developmental biology (which took place around 1900). In the particular case of Huxley and de Beer, however, it is inadequate. Churchill's account makes de Beer look like one of the late 19th century proponents of developmental mechanics. Experimental embryologist such as Wilhelm Roux vehemently rejected Haeckel's idea that phylogeny causes ontogeny and moreover completely abandoned the study of phylogeny in favor of the study of development. This clearly does not hold for de Beer, who discontinued experimental embryology when starting to address evolution from the point of view of development. Churchill ignores that even though de Beer criticized the theory of recapitulation decades after many others had refuted it, de Beer's rejection of the biogenetic law set the stage for his own positive account of the causal relation between ontogeny and phylogeny (Ridley, '86). The main drawback of Churchill's ('80) interpretation of de Beer is that it is based on the notion of evolutionary causation that was prevailing in the 1970s. Churchill apparently assumes that a causal approach to evolution can only consist in using the methods of population genetics.[10] But despite Churchill's assertion that population genetics is "the causal connection between phylogeny and ontogeny" (p 121), in the meantime biologists have acquired a broader notion of evolutionary causation and explanation. Nowadays it is recognized that in addition to the explanation of adaptation and speciation there are other goals of evolutionary biology, such as the explanation of evolvability and the origin of structural novelties and body plans. The latter are

causal explanations that address the mechanisms of evolution without focusing primarily on population genetics (Wagner, 2000; Müller and Wagner, 2003).

De Beer did in fact have an explanatory approach to evolution (Hall, 2000; Ridley ’86), and he offered some suggestions as to the causal impact of development on phylogeny—as far the biological knowledge of his time permitted. One example is his model of clandestine evolution, which puts forward an explanation for patterns in the fossil record based on particular changes in ontogenies. In addition, even though de Beer introduced his modes of heterochrony as a classification of different *patterns* of evolution, as we saw above he also viewed heterochrony as an evolutionary *process*. This is particularly clear from his discussion of rate genes, which assumes that changes in genes controlling rates of development leads to heterochrony and thus to morphological change. As genes are a crucial link between ontogeny and phylogeny, de Beer’s account has a causal impact on evolutionary issues—even though he discusses the inheritance of genes not in the context of population genetics.[11] As detailed above the main reason why de Beer emphasized paedomorphosis is that it permits the formation of higher taxa without preventing further evolution and diversification on lower taxonomic levels.[12] De Beer suggested mechanistic answers to how this is possible, based on different developmental considerations such as cell-differentiation or changes in gene function. In this context, de Beer did not focus on factors such as natural selection which explain why a certain evolutionary change took place in a certain population. Instead, his discussions on ‘evolutionary plasticity’ offered a theory of what we would nowadays call evolvability—connecting both macro- and microevolvability. In sum, de Beer proposed and discussed causal factors that have a prima facie impact of evolution—even though it is not one of the causal factors that Churchill (’80) is looking for.

De Beer’s developmental theory of evolution is surely incomplete and partially inadequate from a current point of view. But the extent to which the views of a past biologist

were correct is irrelevant when one tries to evaluate whether he or she can be viewed as an important forerunner of some current biological approach or discipline. Alan Love and Rudy Raff (2003) point out that the history of a biological field is often viewed in terms of the scientific *tools* it uses and inherited from former approaches, leading for instance to the idea that evolutionary developmental biology is nothing but a synthesis between neo-Darwinian evolutionary biology and developmental genetics. But they go on to argue that this leaves out the important question about the scientific *problems* that a discipline tries to answer and that define its historical identity as well. If we focus on the problems that evolutionary developmental biology addresses, then de Beer is of utmost relevance. De Beer asked important questions about the causal relationship between ontogeny and phylogeny, the origin of larger taxonomic groups, morphological evolvability and the relationship between macroevolution and microevolution, making him a true forerunner of evolutionary developmental biology. Gavin de Beer's work on homology, heterochrony and macroevolution remains significant for the contemporary research agenda of evolutionary developmental biology.

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Footnotes

[1] For more details on de Beer's biography see Barrington ('73).

[2] See Hall (2003) on the relevance of Balfour for the history of evolutionary developmental biology.

[3] J.B.S. Haldane ('32) is an early example of someone making use of de Beer's account of heterochrony and clandestine evolution.

[4] Another type of paedomorphosis on de Beer's usage is deviation, a phylogenetic change in early ontogeny that has impact on the adult condition, leading to a strong deviation of the ancestral and the descendant regards their adult features.

[5] "In conclusion, attention may be turned to a recent tendency in embryological work, which is of interest because it shows how the wheel has come round full circle since the early days of the theory of evolution. Then, it was common to neglect ontogenetic causes since phylogeny was supposed to explain everything; now, some authors who find ontogenetic causes for the formation and presence of structures, are for that reason inclined to deny those structures any phylogenetic significance!" (de Beer, '38, p 75)

[6] De Beer's claims about homology of genes are based on the perspective of Mendelian genetics, though. Two genes in different species were considered the same ones (homologous) only if they were the same Mendelian allele (which can be shown based on their phenotypic effect in hybridization experiments that transfer one gene into a different species). Nowadays, however, homology of genes is viewed as compatible with substantial dissimilarity in gene sequence and function. At the time de Beer was writing, geneticists still lacked our contemporary notion of

deep homology, i.e., homologous genes existing across higher taxa such as phyla (Brigandt, 2003).

[7] "It follows therefore, that the best criterion for homology is comparative anatomy, and it is still possible to hold as did Etienne Geoffroy St Hilaire more than a century ago: 'the only general principle which can be applied is given by the position, the relations, and the dependencies of the parts, that is to say, by what I name and include under the term of connexions.' These are now more usually referred to as morphological relations, and it is their general constancy which gives them their value." (de Beer, '38, p 70).

[8] However, Remane can be viewed as a transitional form between a traditional and a contemporary view of phylogeny (Laubichler, 2000).

[9] "Embryology for de Beer was a cause-directed field; it explained the mechanics and the physiology and the chemistry of form. On the other hand, the study of phylogeny for de Beer was a historical and descriptive endeavor that produced lineages. Haeckel's great mistake had been trying to connect these two very different domains of science. … Whereas the embryologist de Beer had become sensitized through Haeckel's failure to avoid connecting phylogeny and ontogeny in a causal manner, the eclectic biologist Huxley quickly saw that population genetics and the study of natural population filled the very same causal role vacated by the much discredited biogenetic law." (Churchill, '80, p 120–121)

[10] Churchill's ('80) approach is in fact an instance of what Ron Amundson (2005) calls 'Synthesis Historiography', i.e., the use of the explanatory goals and standards of neo-Darwinism to interpret and judge the history of biology.

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[11] "Evolution is brought about by the acquisition of qualitative novelties, and by the production of novel situations by quantitative alteration of the rate of action of the internal factors." (de Beer, '30, p 107–108)

[12] "But neoteny does not only contribute to the production of large structural change; it is also the cause of the retention of plasticity." (de Beer, '30, p 93)