
Concept of Burden in Evo-Devo

Diego Rasskin-Gutman and Borja Esteve-Altava

Abstract

The concept of burden was developed around the 1970s by Austrian zoologist Rupert Riedl, based on morphological insights rooted in Karl Ernst von Baer’s embryological tradition. Burden’s main tenet is that as a morphological character evolves, it develops more relationships with other characters, becoming more and more interconnected. Through this process, the morphological character acquires more biological “responsibilities” within the organism. Two main consequences of the burden hypothesis are that (1) a character’s evolvability will be limited by these responsibilities and (2) a set of heavily burdened characters could be considered as part of the body plan of a taxonomic group. The concept of burden is intimately related to that of developmental constraint, and as such, it is central to evo-devo.

Keywords

Morphology • Philosophy of biology • Rupert Riedl • Developmental constraints

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D. Rasskin-Gutman (✉)

Theoretical Biology Research Group, Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Valencia, Spain

e-mail: diego.rasskin@uv.es

B. Esteve-Altava

Structure and Motion Lab, Department of Comparative Biomedical Sciences, The Royal Veterinary College, Hatfield, UK

e-mail: boresal@gmail.com

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Introduction

The interplay between development and evolution forms the central issue of evo-devo. This apparently trivial statement harbors a very complex suite of concepts and associated problems, especially with regard to causality. As a fundamental part of the phenotype, developmental processes can be viewed as a series of intermingled characters shaped by evolutionary forces, including, but not limited to, the action of natural selection. Thus, development, as any other character, is a complex product of evolution. The converse statement – that evolution is shaped by development – has been less apparent throughout the history of biology and, to say the least, is more controversial. The problem at hand is, then, how the dynamics of development can shape (cause) evolution. This relationship is captured by a family of concepts that more or less have settled under the encompassing umbrella of “constraints,” to which the concept of “burden” owes its existence. Several authors have contributed to putting forward these concepts and although it is tempting to draw a linear conceptual genealogy starting with Ernest Haeckel’s biogenetic principle, Gavin de Beer’s heterochrony, and Stephen J. Gould’s and allied ideas on developmental constraints (including the likes of Pere Alberch, John Maynard-Smith, and several architects of the famous 1981 Dahlem Conference), the story is a bit more convoluted. Indeed, other important authors have contributed with additional concepts, such as von Baer’s embryological laws; Thompsons’ emphasis on the physical underpinning of growth and form; Waddington’s genetic assimilation, canalization, and epigenetic landscape; Goldschmidt’s “hopeful monsters”; and even Jacob’s evolutionary tinkering (von Baer 1828; Haeckel 1874; Thompson 1917; de Beer 1940; Goldschmidt 1940; Waddington 1956; Gould 1977; Jacob 1977; Bonner 1982; Maynard Smith et al. 1985).

Thus, the concept of burden belongs within this solid but disparate family of related ideas which, in essence, form the nucleus of modern evo-devo. Burden appeared originally in Rupert Riedl’s book, *Order in Living Organisms* (Riedl 1978), which was first published in German as *Die Ordnung des Lebendigen* in 1975. Riedl, an Austrian morphologist of the second half of the past century, devised the concept of burden with the clear goal of linking the morphological organization (Bauplan) of species with their evolvability in the broad framework of a particular idea of selection, namely that of “internal selection” (Schoch 2010, and see the chapter on “► [Rupert Riedl](#)” as well as the chapter on “► [Internal Selection](#)”). His good morphological intuition, rooted in German Idealist Morphology school, made him lean naturally on several classical nineteenth century ideas: von Baer’s embryological laws, Geoffroy’s principle of connections, and Cuvier’s conditions of existence. It is also worth mentioning that the concept of burden shows many

parallelisms to Wimsatt's concept of entrenchment, developed independently almost at the same time (Wimsatt 1986) but which will not be discussed here (see the chapter on "► [Generative Entrenchment](#)" and Wimsatt's own work on the issue, Wimsatt 2007). Wallace Arthur, whose idea of developmental bias is also close to the concept of constraint, is somewhat more neo-Darwinian in his account of internal factors in evolution, taking them as cases of selection: "in addition to directional selection for adaptation to particular environments, there would always be stabilizing selection for internal integration." Thus, burden, just like entrenchment, constraint, and developmental bias, would all be consequences of internal selection, whose weight would "fall disproportionately on early developmental stages" (Arthur 2015).

What Is Burden?

Since pre-evolutionary days, comparative anatomists have been noting that large groups of animals and plants share similar features; the suite of all these most characteristic features is what forms the Bauplan or "body plan" (see the chapter on "► [Body Plan](#)"). For example, the vertebral column is one of the most salient features of the vertebrate body plan, consisting of a repetitive series of bony elements, the vertebrae, that not only protect the spinal cord, but also anchor other bones and muscles, giving shape to the main anatomical arrangement of the body axis. During embryonic development, many transient features are also shared, such as the formation of a morula or a gastrula, or more specifically for vertebrates, the formation of the notochord. Thus, within the body plan, features are at some level constrained and invariable for large taxonomic groups: they are always present. The study of developmental constraints attempts to answer how these features come about and how they stay constant in diverse groups for hundreds of millions of years.

More specifically the question asked by the concept of burden is: do characters vary in their possibilities to transform during evolution? And, if so, are there any that can change more likely than others? In essence, Riedl's concept of burden represents a way of trying to explain the origination and maintenance of the body plan (Wagner and Laubichler 2004). In other words, how do groups of organisms acquire a set of characters and how do they retain them in the face of strong tendencies for change through natural selection. The question of origination cannot be answered directly, but the question of maintenance can. To answer this question, Riedl proposed that some characters are strongly constrained (so much so that they might become invariable during evolution, and hence become a part of the body plan), while others can change more freely (i.e., they are more evolvable).

According to Riedl, the source of these constraints or biological burden takes two forms: one is based on their embryological generality and another on their functional and developmental interdependencies. Raff (1996) refers to these two aspects as vertical and horizontal constraints. To him, while the former has been dispensed with by the embryological evidence (although not completely, see below), it is the latter that gives the concept of burden such a central place in modern evo-devo. In the next section, we will examine the value of embryological generality. The subsequent

section looks at the merits of biological dependencies. In the final section, we will present the notion of “burden rank” along with a metric based on anatomical networks, which allows a precise quantification of burden that can be tested in a phylogenetic context.

The Question of Embryological Generality

When embryos develop, processes follow one after another in a rather rigorous and precise way. Every morphogenetic process is followed by subsequent ones, beginning with general features such as the formation of a morula or the process of gastrulation followed by neurulation that will form typical gastrulas and neurulas. These embryological features are very general, insofar as they can be found in most triploblastic animals: any perturbation to their formation would cause severe consequences for the future organism. This was noted by Karl Ernst von Baer at the beginning of the nineteenth century, in pre-evolutionary times (see the chapter on the “► [History of Evo-Devo](#)”). His careful observations were encapsulated in several generalizations that came to be known as von Baer’s laws (Gilbert 2013):

1. The more general characters of a large group of animals appear earlier in their embryos than the more special characters.
2. From the most general forms, the less general are developed, and so on, until finally the most special arise.
3. Every embryo of a given animal form, instead of passing through the other forms, becomes separate from them.
4. Fundamentally, therefore, the embryo of a higher form never resembles any other form but only its embryo.

Von Baer’s laws have been revisited in the concept of phylotypic stage, which is most relevant to the discussion of burden (see the chapter on “► [Phylotypic Stage](#)”). Indeed, embryologists have realized that, in contrast to Von Baer’s laws, embryos can present a great variety of ways to go through their first stages, especially those concerning early cleavage and gastrulation. However, they all have to pass through some sort of middle stage, called the phylotypic stage, which is constrained by the multiple interactions of the early developmental processes (Slack et al. 1993). In vertebrates, the phylotypic stage corresponds to the late neurula. Following the phylotypic stage, embryos unleash variation in their morphogenetic processes that are species specific. This has been captured by the metaphor “phylogenetic hourglass” starting with early stages at which many evolutionary changes are possible and ending up with late stages where, again, many changes are possible. In the middle part, the phylotypic stages that characterize each phylum, there exist periods of highly constrained, less alterable interactions.

In light of this hourglass pattern of variation, as discussed in Raff (1996), the concept of burden shows its deficiencies. The question of the generality of characters according to their temporal embryological position is the weakest part of the concept

of burden. Indeed, Raff presents counter examples showing that early entrenchment does not necessarily mean less variation. For example, the varied ways in which different early embryos start development show that variation can occur very early. This is more in line with the hourglass model, which dictates that variation will be greater both before and after the phylotypic stage. From the phylotypic stage onwards, every single downstream process becomes more and more specific for each species, both in morphogenetic process and in gene expression. Thus, the first aspect of burden can only be vindicated by the variation that occurs after the embryo has reached the phylotypic stage.

The Question of Dependencies

As we have just seen, of the two major tenets of the concept of burden, the question of dependencies is the stronger one, making burden a major research agenda for evo-devo. Indeed, biological dependencies resonate with other associated fields and concepts such as morphological integration, which was originally initiated by Olson and Miller (1958) in the context of morphometric analysis, as well as with modern ideas about the hierarchical nature of gene regulation during development (Gene Regulatory Networks or GRNs) as posited by Davidson and others (see, for example, Erwin and Davidson 2009). Both areas, morphological integration and GRNs, are very active on their own and often intermingled in evo-devo research.

Dependencies are understood as relations among parts of anatomical or functional systems that are in place during embryological development. As such, burden can be understood as “a direct measure of the organismal integration of a trait” (Schoch 2010). These dependences operate at all scales, from GNRs to articulations among bones (as we will see in the next section) and from cell-to-cell transport to hormone-regulated concerted growth of organs. In the context of burden, the more relations a part has with others, the more burden it will hold. This “burdened” part will then be constrained by the summary load of these dependences. In turn, the heavier the constraint, the less evolvable the part will be (see the chapter on “► [Evolvability](#)”). But evolvable in which sense?

Evolvability has been defined in population genetics as the ability to generate adaptive genetic diversity that is susceptible to natural selection. This definition, as is often the case with evolutionary definitions that are suitable for population dynamics, asks a different question from the one evo-devo is interested in. In evo-devo, unlike the population genetic definition just given, the question of evolvability has to do with the ability of an anatomical element to change under any kind of evolutionary influence, most importantly, during embryogenesis. And this is where the concept of burden has a lot to say: the more dependencies to other elements, the more constrained a trait will be. In other words, the concept of burden speaks directly to the problem of phenotypic evolvability, Riedl’s cornerstone (Fig. 1). Furthermore, there is an explicit connection between evolvability, burden, and genotype-phenotype mapping (see the chapter on the “► [Genotype-Phenotype Map](#)”) in the ways in which it constrains the possibility for the appearance of novelties since,

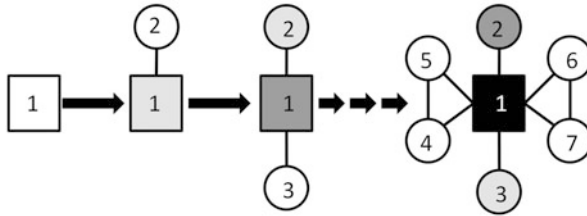


Fig. 1 Schema of the origination of a body plan through increasing burden. As evolution proceeds, character **1** develops more and more dependencies to new characters, eventually becoming so “burdened” that any changes will have big consequences. Eventually, **1** becomes part of the body plan and because of this high rank burden, it loses evolvability or capacity to change (Modified from Wagner and Laubichler 2004)

“newly arising variation is structured by development and presented to selection in a nonrandom way.” Thus, “(b)y conceptualizing the organisms in terms of patterns of variation, Riedl also created the much needed connection between organismal comparative biology and the variation based Neo-Darwinian theory of evolution” (Pavlicev and Wagner 2012).

Quantifying Burden Using Anatomical Network Analysis

The use of network theory to study anatomy has been implemented in the past decade (see Rasskin-Gutman and Esteve-Altava 2014, and the chapter on “► [Anatomical Network Analysis for Evo-Devo](#)” for an overview). This new methodology, called anatomical network analysis (AnNA), explores the connectivity relations among anatomical elements. Anatomical parts, such as the skull, are analyzed by looking at all the patterns of articulations among bones. What is important in this method is the neighborhood of each bone as it connects to others by sutures and joints, thus providing a natural way to quantify burden. When bones are taken as units of developmental or evolutionary change, a direct measure of burden is the degree of connectedness of a bone, that is, the number of its connections. Other measures, such as the betweenness centrality or the clustering coefficient, could also be used as proxies for burden. For example, a typical human skull has 21 bones. Each bone has a specific pattern of connections that can be quantified using AnNA. Some bones have many connections, such as the sphenoid, the ethmoid, and the frontal, whereas most of them have few connections, such as the nasals and the lacrimals. In addition, these connectivity patterns organize into two modules, the facial and the cranial. To explain the observed relationship between the number of contacts that a bone has and the importance of this bone within the organization of the entire skull, Esteve-Altava and co-workers (2013a) proposed “the burden-rank hypothesis,” (Fig. 2) based on Schoch’s analysis of the concept of burden (Schoch 2010).

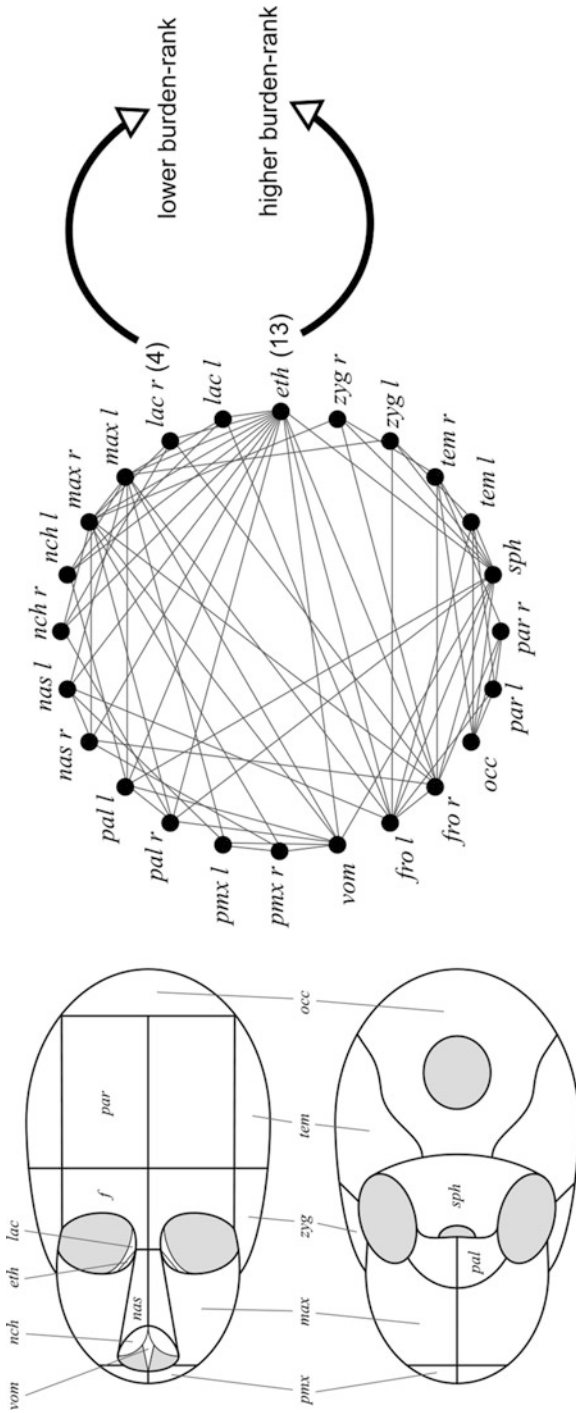


Fig. 2 Schema of the human skull and its corresponding network model highlighting the different number of connections or burden rank between the ethmoid and the lacrimal bones

In light of the concept of burden, this hypothesis states that the number of contacts that a bone has increases the number of developmental and functional co-dependences constraining its variation, which in turn would favor the conservation of this bone during evolution (Rasskin-Gutman and Esteve-Altava 2014). Thus, the more interconnected a bone is, the less likely it is to change over evolutionary time. Moreover, many bones have fused during the evolutionary history of mammals; thus, fusion can be seen as the ultimate fate of heavily burdened bones. In fact, fused bones could lead to an entirely new skull architecture, which could be said to have emerged from the “forces” exerted by the burden of the individual bones of the ancestor.

The burden-rank hypothesis predicts that modules with fewer interactions (i.e., contacts) will be more evolvable than modules with a greater number of interactions. In the context of AnNA, the fewer the number of contacts in a module, the greater the module’s capacity to exhibit phenotypic variation and, therefore, to evolve. A prediction from this study of the human skull is that the facial module should show more morphological evolvability than the cranial one, because the facial skull has fewer contacts among its bones than the neurocranium. Although classical morphometrics studies demonstrated that adjacency is a key factor in shape correlations, and more recent approaches vindicate the inclusion of topological considerations in shape analyses, translating these predictions of evolvability at the connectivity level to predictions of variability in the shape and size of the skull is a major challenge.

The burden-rank hypothesis explains the difference in evolutionary conservation between the facial and the cranial phenotypic modules as a consequence of differences in their complexity. By virtue of the greater richness of bone-to-bone interactions, more complex modules entail more developmental and functional codependences, which constrain module variation. In this context, the lower complexity and greater anisomerism of the facial module suggests specialization due to anatomical differentiation of bones in terms of number of contacts. Morphometrics studies in primates support the finding that regions with lower disparity of the cranial module are less evolutionarily plastic than parts of the facial region (Goswami and Polly 2010).

Criticisms

Riedl’s theory of burden is far from being a perfect account of the behavior of anatomical traits in a neo-Darwinian framework. However, it provides a solid departure point to bring back the importance of development to understanding how evolution shapes multicellular organisms. Thus, as so often happens when new theories are put forward, several criticisms have been raised against the concept of burden by different authors. We will just mention three of them, by Raff (1996), Schoch (2010), and Budd (2006):

Raff has questioned the validity of the theory of burden regarding the hierarchy of developmental processes (Raff 1996), a question that has been solved by the hourglass model of development. Only if we examine development from the phylotypic stage onwards, rather than from the beginning of embryo development, the process seems to conform to the notion that early morphogenetic events are less variable than later ones.

Budd has pointed out that, as it has been formulated, the concept of burden would entail that characters get more and more burdened to the point of irreversibility, which might lead to dead ends (Budd 2006). However, as we have noted in the precedent section, intimately connected elements that might end up fusing into one new element, as has happened repeatedly in the evolution of the skull, can overcome such irreversibility by changing the whole dynamics of the system (Esteve-Altava et al. 2013b and references therein).

Schoch has noted that developmental processes are full of pleiotropic effects, as well as nestedness among them, making the gradual and linear acquisition of burden for single characters unlikely (see the chapter on “► [Pleiotropy and Its Evolution: Connecting Evo-Evo and Population Genetics](#)”). Also, Schoch has criticized the use of burden ranking on the grounds of characters not being clearly linked causally, because the dynamics of morphogenesis is not linear but consists of a complex network of cause-effect relationships that involve genetic-epigenetic regulation of morphogenetic mechanisms (Schoch 2010). These two criticisms, the pleiotropy effect and the causal linkage, are the most compelling ones against the concept of burden as it was originally formulated.

Conclusions

The most interesting evolutionary aspect of burden is its dynamic properties: as characters change their dependencies to other characters (sometimes new ones), they increase their resilience towards change since more is at stake or, in Riedl's words, their “responsibility” towards the developing embryo is greater. Thus, characters are not fixed entities subject to change by natural selection. Rather, they are constrained by their burden, so that their evolvability would also be compromised. We have seen that the concept of burden relies on two types of mechanisms: the hierarchical importance of the time of appearance of a character and the biological dependencies. Of these two, the latter seems to resonate more strongly in modern evo-devo.

Beyond the mentioned criticisms, the concept of burden is central to evo-devo because it is a statement about organization and dynamics explained as the morphogenesis constraining the organization of the body plan. Conversely, we might also say that the concept of burden explains how the organization of the body plan constrains the dynamics of morphogenesis, and thus the possible innovations that might arise.

Cross-References

- ▶ [Anatomical Network Analysis in Evo-Devo](#)
- ▶ [Body Plan](#)
- ▶ [Evolvability](#)
- ▶ [Generative Entrenchment](#)
- ▶ [Genotype-Phenotype Map](#)
- ▶ [History of Evo-Devo](#)
- ▶ [Internal Selection](#)
- ▶ [Mechanisms of Pattern Formation, Morphogenesis and Evolution](#)
- ▶ [Modularity in Evo-Devo](#)
- ▶ [Phylogenic Stage](#)
- ▶ [Pleiotropy and Its Evolution: Connecting Evo-Devo and Population Genetics](#)
- ▶ [Rupert Riedl](#)

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References

- Arthur W (2015) Internal factors in evolution: the morphogenetic tree, developmental bias, and some thoughts on the conceptual structure of evo-devo. In: Love A (ed) *Conceptual change in biology*, Boston studies in the philosophy and history of science, vol 307. Springer, Dordrecht
- Bonner JT (ed) (1982) *Evolution and development*. Report of the Dahlem workshop on evolution and development Berlin 1981, May 10–15. Springer, Berlin
- Budd GE (2006) On the origin and evolution of major morphological characters. *Biol Rev* 81:609–628
- de Beer GR (1940) *Embryos and ancestors*. Clarendon Press, Oxford
- Erwin DH, Davidson EH (2009) The evolution of hierarchical gene regulatory networks. *Nat Rev Genet* 10:141–148
- Esteve-Altava B, Botella H, Marugán-Lobón J, Rasskin-Gutman D (2013a) Structural constraints in the evolution of the skull: Williston's law revisited. *Evol Biol* 40:209–219
- Esteve-Altava B, Marugán-Lobón J, Botella H, Bastir M, Rasskin-Gutman D (2013b) Grist for Riedl's mill: a network model perspective on the integration and modularity of the human skull. *JEZ Part B Mol Dev Evol* 320(8):489–500
- Gilbert S (2013) *Developmental biology*, 10th edn. Sinauer Associates, Inc., Sunderland
- Goldschmidt R (1940) *The material basis of evolution*. Yale University Press, New Haven
- Goswami A, Polly PD (2010) The influence of modularity on cranial morphological disparity in Carnivora and Primates (Mammalia). *PLoS One* 5:e9517
- Gould SJ (1977) *Ontogeny and phylogeny*. Harvard University Press, Cambridge, MA
- Haeckel E (1874) *Anthropogenie oder Entwicklungsgeschichte des Menschen*. Englemann, Leipzig
- Jacob E (1977) Evolution and tinkering. *Science* 196(4295):1161–1166
- Maynard Smith J, Burian R, Kauffman S, Alberch P, Campbell J, Goodwin B, Lande R, Raup D, Wolpert L (1985) Developmental constraints and evolution: a perspective from the Mountain Lake conference on development and evolution. *Q Rev Biol* 60(3):265–287
- Olson EC, Miller RL (1958) *Morphological integration*. The University of Chicago Press, Chicago
- Pavlicev M, Wagner GP (2012) Coming to grips with evolvability. *Evo Edu Outreach* 5:231–244

- Raff RA (1996) *The shape of life: genes, development, and the evolution of animal form*. University of Chicago Press, Chicago
- Rasskin-Gutman D, Esteve-Altava B (2014) Connecting the dots: anatomical network analysis in morphological EvoDevo. *Biol Theory* 9:178–193
- Riedl R (1978) *Order in living organisms: a systems analysis of evolution*. Wiley, New York
- Schoch RR (2010) Riedl's burden and the body plan: selection, constraint, and deep time. *J Exp Zool Mol Dev Evol* 314B:1–10
- Slack JMW, Holland PW, Graham CF (1993) The zootype and the phylotypic stage. *Nature* 361:490–492
- Thompson DW (1917) *On growth and form*. Cambridge University Press, Cambridge, UK
- von Baer KE (1828) *Entwicklungsgeschichte der Thiere: Beobachtung und Reflexion*. Königsberg, Bornträger
- Waddington CH (1956) Genetic assimilation. *Adv Genet* 10:257–290
- Wagner GP, Laubichler MD (2004) Rupert Riedl and the re-synthesis of evolutionary and developmental biology: body plans and evolvability. *J Exp Zool Mol Dev Evol* 302B:92–102
- Wimsatt WC (1986) Developmental constraints, generative entrenchment and the innate acquired distinction. In: Bechtel W (ed) *Integrating scientific disciplines*. Martinus Nijhoff, Dordrecht, pp 185–208
- Wimsatt WC (2007) Echoes of Haeckel? Reentrenching development in evolution. In: Laubichler MD, Maienschein J (eds) *From embryology to evo-devo: a history of developmental evolution*. MIT Press, Cambridge, pp 309–355