Typology now: homology and developmental constraints explain evolvability

Ingo Brigandt

Abstract By linking the concepts of homology and morphological organization to evolvability, this paper attempts to (1) bridge the gap between developmental and phylogenetic approaches to homology and to (2) show that developmental constraints and natural selection are compatible and in fact complementary. I conceive of a homologue as a unit of morphological evolvability, i.e., as a part of an organism that can exhibit heritable phenotypic variation independently of the organism's other homologues. An account of homology therefore consists in explaining how an organism's developmental constitution results in different homologues/characters as units that can evolve independently of each other. The explanans of an account of homology is developmental, yet the very explanandum is an evolutionary phenomenon: evolvability in a character-by-character fashion, which manifests itself in phylogenetic patterns as recognized by phylogenetic approaches to homology. While developmental constraints and selection have often been viewed as antagonistic forces, I argue that both are complementary as they concern different parts of the evolutionary process. Developmental constraints, conceived of as the presence of the same set of homologues across phenotypic change, pertain to how heritable variation can be generated in the first place (evolvability), while natural selection operates subsequently on the produced variation.

Introduction

One of the major trends in recent evolutionary biology is the rise of developmental approaches to evolution in the last two decades, nowadays referred to as evolutionary developmental biology (evo-devo). This development has been accompanied by advocacy of developmental

I. Brigandt (✉)
Department of Philosophy, University of Alberta, 4-115 Humanities Centre, Edmonton, AB T6G 2E5, Canada
e-mail: brigandt@ualberta.ca

accounts of homology (Brigandt 2003). While a traditional *phylogenetic* account defines homology in terms of common ancestry (or synapomorphy), *developmental* approaches attempt to construe homology in terms of developmental features (such as shared developmental constraints). These two accounts have been seen as rivals. Proponents of developmental accounts have argued that common ancestry does not yield a complete account of homology (Wagner 1994). Yet developmental accounts have often been unclear how a developmental approach to homology relates to phylogeny—a pertinent issue given that homologies have always been identified by comparative and nowadays phylogenetic analysis. As a result, proponents of a phylogenetic understanding of homology have wondered about the intelligibility and relevance of a developmental account (Cracraft 2005).

One aim of this paper is to bridge the current gap between phylogenetic and developmental approaches to homology. The evo-devo term 'evolvability' refers to the capacity of organisms to generate heritable phenotypic variation (heritable phenotypic variation is a precondition for evolutionary change due to selection). Following the work of Günter Wagner and his collaborators on the character concept, I conceive of a homologue as a *unit of morphological evolvability*, i.e., as a part of an organism that can exhibit heritable phenotypic variation independently of the variation that the organism's other homologues can undergo. From this perspective, homology is a property of morphological organization, which actually consists in an evolutionary potential. Namely, homology is the phenomenon of an organism being composed of several homologues/characters, where one such character can phenotypically vary and evolve independently of the others (evolvability on a character-by-character basis). This evolutionary potential manifests itself in phylogeny, resulting in homologies across species, character distributions across taxa, and synapomorphies (features shared due to common ancestry). These are the phylogenetic patterns recognized by phylogenetic approaches to homology. A developmental approach attempts to understand how an organism's internal constitution and developmental processes result in distinct homologues as different dimensions of phenotypic evolvability. Thus, the *explanans* of an account of homology is developmental, yet the *explanandum* is an evolutionary phenomenon (evolvability in a character-by-character fashion), which manifests itself in phylogenetic patterns.

My account will link homology not only to evolvability, but also to the notion of *developmental constraints*. Natural selection—as emphasized by neo-Darwinism—and developmental constraints—as stressed by developmental approaches to evolution—have often been viewed as antithetical phenomena. In general, it has been unclear how to combine population genetics and evolutionary developmental biology, and even whether the approaches taken by these two disciplines can be reconciled at all (Amundson 2005; Wagner 2007a). The second aim of this paper is to show that explanations focusing on constraints and on selection are compatible and in fact complementary. I explain that there is a sense in which developmental constraints and morphological evolvability are two sides of one coin, both of which are explained by a developmental account of homology. As a result, while neo-Darwinians have viewed morphology with its notions of homology and morphological type as being under the spell of inadequate 'typological thinking' (Amundson 2005), the present perspective entails that homology, morphological organization / type, and developmental constraints are part of the explanation of evolution, in that they help to explain evolvability. The modes of explanation favored by evo-devo and neo-Darwinism are complementary as they address *different parts* of the evolutionary process: how heritable phenotypic variation is generated (evolvability) and how subsequently directed or lasting phenotypic modification takes place due to natural selection (adaptation). Thus, in the study of evolutionary change there are *different relevant explananda*

(evolvability as well as adaptation), so that there can be *different legitimate explanantia* (homology/developmental constraints as well as natural selection). Finally, the discussion uses the fact that homologues exist on different levels of organization to point to open empirical challenges for evo-devo, and to emphasize that an account of evolvability must address entities on several levels of organization and their interaction.

Characters and character states

The term 'character' is often used in two ways. It can denote either characters (properly speaking) or character states. A character is a part of an organism, such as a type of morphological structure, that can be present in several individuals and species. A character state is a property or set of properties that a character in a particular individual has. *One character* may be in *different states* in different individuals. For example, an eye is a character with the character states blue, green, brown, etc. This distinction is important for the present perspective, because homology is not similarity of character states, but sameness of characters, as expressed by Owen's original definition:

> HOMOLOGUE ... The same organ in different animals under every variety of form and function. (Owen 1843: 379)

As this definition makes plain, a homologue can be present in different species with a different shape (form) or function; in other words, a homologue is a *character* occurring in different species, where the *state* of this character may vary across species. Homologous characters in closely related species are often similar (in a similar state) due to common ancestry, yet homologous features can in fact be quite dissimilar as a character can undergo substantial evolutionary modification. Furthermore, similar features (states) in two species need not be homologous if they are homoplasies or analogies resulting from convergent evolution. Thus, two structures in different species are homologous if they are *the same character, not if they are in similar character states*.

So-called 'transformational' accounts of homology in recent evolutionary biology are aware of this point to some extent. A transformational account focuses on how a character is inherited across generations and species, typically undergoing gradual transformation in the course of evolution, resulting in a transformation series from ancestor to descendant (Donoghue 1992). Though this focuses on a transformation series as a series of different character *states*, it is recognized that these different states belong together as transformations of the same character, i.e., that there exists a homologue across species undergoing change. So-called 'taxic' accounts of homology in systematics and phylogeny, which define homology as synapomorphy (Cracraft 2005; Donoghue 1992; Patterson 1982), focus more strongly on character *states*. For taxa can be distinguished by noticeably different characters states being present in different taxa. A plesiomorphy (the ancestral condition) and an apomorphy (the derived condition) are two distinct character states. While transformational approaches focus on a fairly gradual series of character states in a single lineage, a taxic approach focuses on a split in a lineage (formation of different taxa) and the resulting marked differences between extant species of different taxa. Of particular interest is the situation where the apomorphic condition is noticeably different from the plesiomorphic condition (despite the former resulting by gradual modification from the latter), so that the apomorphy is characteristic of a taxon (synapomorphy), distinguishing the species of this taxon from all other species of the encompassing higher taxon. In principle, a taxic approach recognizes the notion of a character (as opposed to a character state), yet an

apomorphy and thus a synapomorphy is a character state, which explains why traditional morphological and modern developmental approaches to homology reject the taxic definition that identifies homology [same character] with synapomorphy [same character state] (Wagner 1989b; Müller 2003).

Thus a definition stating that that "Homology is resemblance due to inheritance from a common ancestry" (Simpson 1961: 78) is ambiguous. It does not distinguish between the *same character* being present in different individuals—homology in Owen's and my sense—and a character being in *similar states* in two individuals (due to them being closely related). Conflating the notion of character and character state may lead to what Ron Amundson (2005) calls a 'residual concept of homology'. This is the idea that homology consists in those ancestral features [character states] that have not (yet) been modified by natural selection and thus show up as shared features of two extant species (homology assumed to be the residue of evolutionary change). Such a conception fails to recognize the phenomenon of homology, which consists in the presence of characters as structural units being present across species and evolutionary modification. For the residual conception perceives homology only where there are similar character states in ancestor and descendant—and further evolution may even dissolve this similarity—failing to realize that even distinct character states may be states of the same character/homologue. On the residual conception, homology always decays over time, whereas on a proper understanding, homology is a *property of morphological organization* (the presence of homologues as organismal parts) that is often *stable over long periods of evolutionary time*.

Homology as evolvability in a character-by-character fashion

I conceive of a homologue as a character that can undergo evolutionary modification by taking on different character states in different generations, or varying in form and function, as Owen put it. More precisely, phenotypic evolution proceeds in each generation first by the occurrence of *heritable phenotypic variation* (accounted for by features within organisms), and then by natural selection acting on this variation so as bring about *directed or lasting phenotypic change* (accounted for by environmental demands external to organisms). Homology as a property of morphological organization is only about the first, variation component. A homologue is a unit of heritable phenotypic variability—a structural unit being able to phenotypically vary in response to genetic variation. Evolutionary change due to natural selection presupposes such variability. Since in contemporary evolutionary developmental biology (evo-devo) the notion of 'evolvability' refers to an organism's capacity to generate heritable phenotypic variation (Gerhart and Kirschner 1998), a homologue is a *unit of phenotypic evolvability*. Evolvability is a disposition that an organism and its homologues can possess, even though this disposition can manifest itself only in subsequent generations by actual variation being produced.

A more precise characterization of what makes a certain part of a body a homologue is needed. Many accounts of homology focus on how to determine which part of one organism (or species) is homologous to which part of another organism (or species). Such accounts spell out criteria of homology or define homology in terms of phylogeny. I agree that homologues can be established by phylogenetic analysis, yet a precise account of the nature of homology has to address what makes one homologue distinct from homologues that occur in the same organism. In other words, as well as asking what makes two structures in two organisms the same character we should ask what makes two structures in one organism different characters. I suggest that what makes two homologues distinct

characters is that *one homologue can vary independently of the other*. This independence of characters need not be absolute, yet different characters can and do vary largely independently of each other. An organism consists of many homologues as quasi-*independent* units of phenotypic variation. Thereby each homologue/character yields a fairly distinct *dimension* of morphological variability, where heritable phenotypic variation can occur along any of these dimensions. If subsequent natural selection selects for change along only one of these dimensions, the resulting phenotypic change along this dimension consists in only one homologue undergoing evolutionary modification (namely, the homologue that made the variation in this dimension possible), while the other homologues do not change (they exhibited variation that was not selected for). When construed in this way, the homologues an individual organism is composed of are units of *morphological evolvability*, making heritable variation (in the next generation) possible. As this variation is the basis for subsequent phenotypic evolution, homologues viewed as characters across generations are also units of *morphological evolution*.

> The fact that phenotypic evolution can be studied on a character by character basis suggests that the body is composed of locally integrated units. These units can be considered as modular parts of the body which integrate functionally related characters into units of evolutionary transformations. (Wagner 1996: 36; see also Laubichler 2000: 783)

In sum, what makes a structure a homologue in the first place is the fact that it can exhibit heritable morphological variability that is largely independent from the variability of any other homologue composing the organism.

The notion of a *morphological type* has often been used to express the idea that an organism is a set of homologues (Amundson 2005; Wagner and Stadler 2003). From the present perspective, a type is a partition of an organism into different homologues as units of morphological evolvability, i.e. different dimensions of heritable phenotypic variability. As homologues are reliably inherited over generations, the overall set of homologues reappears across generations and possibly species, so that the type is phylogenetically stable. Individual characters change—their *states* change—but the overall set of characters remains the same. Change occurs along certain dimensions, but the number of dimensions is constant. To be sure, the type itself may changes over evolutionary time when homologues are lost or novel homologues evolve. The evolutionary origin of a 'novelty' in the sense of Müller and Wagner (1991) is precisely the addition of a new homologue to a type. While the terms 'type' and 'typology' have occasionally been defined such that a type cannot evolve, this is not how type is conceived of in contemporary evolutionary developmental biology, as it is clear empirically that the set of organisms' morphological parts (the type) does change in phylogenetic lineages. The presence of a type (set of particular homologues) is due to the morphological-developmental make-up of organisms, and if the latter evolves in fundamental ways, the type can change. However, the present discussion focuses on those cases where the number of characters is constant, discussing 'evolvability' in the context of the change of existing homologues, rather than the advent of totally novel homologues (evolutionary novelties *sensu* Müller and Wagner).

Furthermore, in practice a neat partition of an organism into distinct homologues is not always possible, as the requirement that homologues vary independently of one another is only met to a degree and not absolutely. Still, different homologues can be found whose variability is largely independent, which is the reason why homologues could be discovered and distinguished in 19th century comparative anatomy. In sum, phenotypic evolution proceeds in a character-by-character fashion, and the notion of a type refers to the

underlying morphological basis of this phenomenon. Morphological organization into homologues—the type—constitutes *evolvability in a character-by-character fashion*, i.e., the capacity of existing characters to exhibit heritable phenotypic variation independently of each other. Each of the homologues composing the type is a distinct unit or dimension of morphological evolvability.[1]

The perspective proposed here is in line with recent developmental approaches to homology, at least insofar as they emphasize the fact that what has to be developmentally explained is why evolution proceeds on a character-by-character basis and how homologues are reliably inherited over generations so as to function as units of evolution (Roth 1988; Wagner 1989a; Laubichler 2000).[2] In fact, the present approach is strongly influenced by the recent account of Günter Wagner and his collaborators, who have worked towards a mathematical account of homologues as units of evolution, explicating the concept of a character (Wagner and Laubichler 2000; Stadler et al. 2001; Wagner and Stadler 2003). On this theory, possible phenotypes are modeled as elements of a topological space H, the particular structure of which is induced by the underlying genotype space and the genotype-phenotype map, reflecting the way in which genotypic variation (such as random mutation) results in phenotypic variation. Given its topological structure, the phenotype space H can be factorized into different components, where the number of factors (the dimension of H) is the numbers of characters. This approach explicitly views different homologues/characters as independent dimensions of phenotypic variation (the topological space H being what I call a type). In particular, this formal account is clear about the fact that homology is about sameness of characters not about similarity of characters states: homology is about which phenotypic dimensions are present, not about whether individuals have similar values in some dimensions. Furthermore, a central feature of this model is that the topological structure of the phenotype space (and thus which dimensions obtain) is essentially dependent on the genotype-phenotype map, i.e. development. Thus, an organism's development determines the number of characters that this organism has, yielding the dimensions along which evolutionary change may occur.

Bridging developmental and phylogenetic approaches to homology

My construal of homology bridges the gap between developmental and phylogenetic approaches to homology as follows. On the present account, homology is a phenomenon of morphological organization, yet one that consists in an evolutionary potential: homology *is* the property of an organism being organized into several homologues (partially developmentally dissociated structures) such that any such homologue can undergo heritable phenotypic variation independently of the other homologues. Because each homologue is a distinct unit of morphological evolvability, homology is a property of morphological organization *consisting in* phenotypic evolvability along several dimensions. The *causal basis* of homology as evolvability in a character-by-character fashion is the internal-developmental constitution of an organism. Homology *manifests* itself in phylogeny: a causal consequence of this capacity to generate heritable phenotypic variation (combined

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[1] As will become clear below, I assume that homologues exist on several levels of organization (also genes and developmental processes can be homologous). Therefore my notions of 'morphological' organization and 'morphological' structure/unit have a wide scope, including homologues on several levels.

[2] My account also broadly accords with Müller's (2003) approach to homology and morphological organization, though Müller focuses more on the developmental rather than evolutionary role of homologues.

with natural selection acting on the generated variation and the occurrence of phylogenetic branching) is the occurrence of well-known phylogenetic patterns: character state distributions across species for several independent characters, homologies across species, and synapomorphies of monophyletic groups.

When homology is construed in this manner it is not the case that homology is synapomorphy (or similarity of traits due to common ancestry)—as phylogenetic definitions of homology may have it—instead, homology *manifests* itself in synapomorphies. This is not to belittle the relevance of phylogenetic approaches to homology. Phylogenetics still yields the most effective criteria for establishing homologies, namely the congruence tests of cladistic analysis. The establishment of homologies based on phylogenetic analysis is scientifically significant for the purposes of phylogeny and taxonomy. Furthermore, the analysis of phylogenetic patterns shows that there is evolution in a character-by-character fashion, whose underlying basis is evolvability in a character-by-character fashion ('homology' on my account); and a developmental approach attempts to understand the developmental processes that account for this. In other words, the phylogenetic study of homology yields a certain *explanandum*—evolution on a character-by-character basis as a manifest fact in need of explanation (see Griffiths, this issue). A developmental approach to homology attempts to give the *explanans*—an explanation of how an organism's developmental-morphological constitution results in evolvability along several dimensions.

One of the central items on the agenda of evolutionary developmental biology is the explanation of evolvability (Gerhart and Kirschner 1998; Kirschner and Gerhart 2005). Traditional evolutionary biology could take evolvability for granted—phenotypic variation occurs and the extent of this variation can be studied—and proceed to explain evolutionary change through natural selection acting on variation without attempting to explain why that variation occurs. For several decades it has been well-understood how *genotypic* variation occurs, yet this alone does not explain why the genotypic variation translates into *phenotypic* variation the way it does (=evolvability). Evo-devo biologists consider evolvability as the general capacity to produce heritable phenotypic variation.[3] My account links evolvability to homology and morphological organization by pointing out that *evolvability has a structure*: there are different units of phenotypic evolvability, i.e. *different dimensions* along which variation can be produced. This is a particular feature of evolvability in need of explanation. Somewhat imprecise talk about developmental 'definitions' of homology has led to the misleading assumption that a developmental homology 'concept' is being introduced that refers to a developmental phenomenon, and thus to something different than the traditional phylogenetic homology concept. My discussion clarifies this by pointing out that evolutionary developmental biology aims at putting forward a developmental *account* of homology, and how the latter relates to phylogeny. The explanandum for a 'developmental' account of homology is an *evolutionary* phenomenon (evolvability of different characters); the account is called 'developmental' because the explanans involves development.

Some of the existing evo-devo literature bears on how evolvability on a character-by-character basis is generated. In particular the literature on *modularity* aims at understanding how the developmental relations across different developmental-structural units that are internally highly integrated (modules) can be so weak that the interconnections among modules can be reorganized, thereby facilitating the generation of evolutionary

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[3] 'Evolvability' as commonly used includes the origin of novelties, possibly even in the strong sense of Müller and Wagner (1991), i.e. the addition of distinct homologues to a type. However, as mentioned above my account of homology as evolvability focuses on 'evolvability' in the sense of the possibility of the morphological change of *given* characters.

novelty (Bolker 2000; Kirschner and Gerhart 2005; Schlosser and Wagner 2004; von Dassow and Munro 1999; Winther 2001). Wagner (2007b) recently suggested based on concrete cases that there exist gene regulation networks which he terms 'character identity networks' (ChINs). These are present in any instance of a character across species, whereas other genes that are not part of the ChIN vary so as to lead to different states of this character in different species. Thus, there seem to be developmental features characterizing a character/homologue (e.g. ChINs), which have a dual role. They are reliably inherited across generations and hard to modify, so that the homologue reappears across generations and species. At the same time, these developmental features determining character identity provide the very basis for this homologue undergoing evolutionary change by permitting other developmental properties to change without resulting in the loss of this character. Still, despite these empirical advances, a genuine explanation of homology as evolvability is to be achieved by future empirical and conceptual research.

Advocates of a phylogenetic (taxic) account of homology, such as Joel Cracraft (2005), have objected to developmental approaches. One source of misunderstanding among the different camps is terminological. As a remedy, I have explicitly distinguished three features, while emphasizing that they are different parts of an overall phenomenon: (1) the causal-developmental basis of evolvability in a character-by-character fashion, (2) evolvability of independent characters, (3) the phylogenetic manifestation of this evolvability. Phylogenetic approaches use the term 'homology' to refer to feature 3, while some developmental accounts of homology rather refer to feature 1. I use 'homology' to refer to feature 2, so as to bridge phylogenetic and developmental approaches. Yet which of the three features is to be called 'homology' is nothing but a terminological issue. The context usually makes quite clear whether 'homology' is used to talk about homologies across species and synapomorphies, or whether it refers to the developmental basis of an organism's organization into different homologues.

Cracraft (2005) also criticizes pluralistic approaches, such as my previous discussion distinguishing a phylogenetic and a developmental homology concept (Brigandt 2003). A pluralistic approach is legitimate (and consistent with the present account) for the following reason. Two different *accounts* of homology (or different *approaches* to homology) are needed in that two aspects of a phenomenon are addressed that are both scientifically important and significantly different: an account of phylogenetic analysis, on the one hand, and a developmental-morphological account, on the other hand. Furthermore, each of these accounts serves distinct biological aims: the establishment of phylogenies/taxonomies vs. the explanation of the developmental basis of evolvability. Yet in addition to a pluralist approach to homology, it is necessary to explain how the different accounts relate to each other. I provided an answer here by explaining how the phylogenetic and the developmental conception focus on different aspects of *one phenomenon*. On my construal, *homology is developmentally based morphological evolvability in a character-by-character fashion, which manifests itself in phylogenetic patterns*. Developmental and phylogenetic approaches are compatible as they focus on different aspects of this overall phenomenon: the developmental basis of homology as evolvability, and the phylogenetic manifestation of homology as evolvability.[4]

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[4] In Brigandt (in press) I construe a homologue as a homeostatic property cluster (HPC) natural kind. The HPC view of natural kinds additionally clarifies how the two approaches to homology are related: an HPC kind consists in (1) a cluster of properties that tend to co-occur and (2) homeostatic mechanisms that are the causal basis of the properties' clustering. Phylogenetic approaches focus on the cluster of properties that are diagnostic of a natural kind (synapomorphies shared among most instances of a homologue), while developmental approaches focus on the homeostatic mechanisms that form the causal basis of the cluster properties' correlation.

Finally, Cracraft stresses that developmental accounts do not have any operational criteria to identify homologies—unlike the taxic approach. However, a developmental account does not attempt to replace the traditional criteria of identifying homologies based on phylogenetic analysis; rather, the aim is to develop an explanation of the developmental basis of evolvability. Some scientific ideas are associated with effective criteria (as the taxic homology concept is), or actually support scientific explanations (e.g., the molecular gene concept explains how a protein with a certain amino acid sequence is produced). Yet there are also ideas whose primary value is as the locus of an explanatory agenda; i.e., the idea points to a phenomenon to be explained, even if at this point the desired explanation is not yet available. The homology concept as used by a developmental approach is such an idea (Griffiths, this issue). This conception of homology aims at explaining evolvability on a character-by-character basis. This explanandum is legitimate—it is a phenomenon whose reality was established by phylogenetic analysis—but the explanans can only be provided in the future by a mature developmental account of homology. While there is currently no genuine developmental account of homology, as Cracraft points out, this does not entail that such an explanation is not to be sought (Rieppel 2006).

Reconciling selection and developmental constraints

Natural selection and developmental constraints[5] have often been viewed as opposing forces in evolution—favored by neo-Darwinists and developmental evolutionists, respectively—the assumption being that while selection generates phenotypic change, constraints prevent evolutionary change and adaptation (Amundson 1994, 2005; Gould and Lewontin 1979). The present perspective that ties homology to evolvability provides a way to view selection and constraints as compatible, and in fact as complementary. The phenomenon of homology consists in a *particular kind of developmental constraint*: given that an organism is composed of several homologues that are distinct dimensions of morphological evolvability, variation and subsequent phenotypic evolution can only proceed along these given dimensions, but not along others. A morphological type—the fact that an organism has a certain number of homologues—thereby embodies both developmental constraints and evolvability. Unless some homologues are lost or added, the type and the number of characters is fixed across evolutionary change—a kind of developmental constraint that is in need of explanation. The flip-side of this stable number of characters is that any of these characters can undergo evolutionary modification, so that the type also embodies evolvability. Thus, the kind of developmental constraint brought about by the phenomenon of homology and morphological evolvability in a character-by-character fashion are *two sides of one coin*. (It is in this sense that the title of my paper claims that 'homology and developmental constraints explain evolvability'.) Viewing constraint and evolvability as related is in line with the current evo-devo literature. While developmental approaches to evolution of the 1980s focused strongly on the notion of constraint, the recent literature came to center on evolvability, using notions such as developmental 'opportunities',

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[5] "A developmental constraint is a bias on the production of variant phenotypes or a limitation on phenotypic variability caused by the structure, character, composition, or dynamics of the developmental system" (Maynard Smith et al. 1985: 266).

'potentials' or 'deconstraints'. Despite this shift in focus, it is assumed that development creates both constraints and deconstraints on evolvability (Kirschner and Gerhart 2005).[6]

The selection-based explanations favored by neo-Darwinists and the development-based explanations favored by evo-devo biologists are both legitimate as they address two distinct explananda. Apart from explaining speciation, the main aim of neo-Darwinism is to account for *adaptation*, and adaptation is explained by natural selection using the models of population and quantitative genetics. One of the explanatory aims of evo-devo is to account for *evolvability*, and features of the developmental make-up of organisms (how genetic variation translates into phenotypic variation) provide the explanation. *Different explananda require different kinds of explanantia*, so that different modes of explanation may be perfectly legitimate. In his previous discussions, Ron Amundson has been very clear about the difference between traditional adaptation-oriented explanations and more recent developmental approaches to evolution, discussing why each approach insists on the relevance of its mode of explanation. Yet Amundson's (1994) account relied too much on traditional terms, e.g., non-adaptationist approaches were viewed as relying on the notion of 'developmental constraints' as constraints on the generation of form. In particular one may wonder in which sense the *developmental* accounts Amundson described are actually explanations of *evolutionary* phenomena, so that they can be relevant in addition to selection-based explanations. My account helps to clarify this, in that developmental approaches attempt to account for *evolvability* as a genuine evolutionary explanandum, with developmental constraints being part of the explanans. More importantly, while Amundson (2005) is inclined to view neo-Darwinian and evo-devo accounts as incommensurable and maybe impossible to reconcile, this is a highly unsatisfactory view. In addition to saying that both kinds of approaches are different yet legitimate (because they address different explananda), it is essential to explain why they are in fact compatible and how they can be *integrated*.

Natural selection and developmental constraints have often been viewed as two forces pulling in opposite directions. Therefore the question has been which force is the larger one, with adaptationists denying the relevance of developmental constraints, and developmentalists using the notion of constraints to argue against adaptationism. In contrast, I claim that that *constraints and selection are fully compatible as they operate at different steps of the evolutionary process*. In each generation, the first step consists in how genotypic variation within a species results in phenotypic variation (developmental constraints/evolvability operate here), the second step is which of the generated phenotypic

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[6] My focus on developmental constraints as those features that determine the type as the set of homologues aligns with the account of novelty by Müller and Wagner (1991, 2003). On their position, a morphological 'novelty' is a character that is not homologous to any ancestral structure; and the evolution of a novelty involves "a breaking up of developmental or functional constraints that prevailed in the ancestral lineage", as the transitions from ancestral states to novelties "require developmental modifications that are not within the mutational reach of the ancestral character state" (2003: 220). In my terminology, their account says that the ancestral type embodies constraints determining a set of characters as the dimensions along which *regular* heritable phenotypic variation can occur (changes 'within the mutational reach' of the ancestral state), ensuring evolvability as change in given characters. The origin of a novel character consists in the ancestral type ceding to a reorganized type characterized by a different set of constraints. While a novelty emerges after rounds of mutation and selection, these notions do not carry the explanatory force when accounting for the evolution of a novelty, as in this case the *regular* phenotypic variation does not lead to the novel character (and the novelty may be an epigenetic *side-effect* of changes in overall development caused by selection; Müller 1991). Instead, any such explanation has to specify how the developmental system could be reorganized such that the new character could evolve after all. Thus, in the explanation of the evolution of novelties—as in the explanation of evolvability—features of *development* make up the explanans (Wagner 2000).

variation is selected by natural selection (adaptation).[7] The existence of developmental constraints—understood as the presence of certain dimensions of variation—does not challenge the fact that adaptation occurs. An account explaining adaptation can simply take the existing developmental constraints / dimensions of evolvability for granted. To be sure, in the past *some* adaptationists have in their putative explanations simply ignored the presence of developmental constraints, but these were accounts that erroneously ignored that evolvability and phylogeny occurs on a character-by-character basis, where several features may evolve together and thus count as only one character. Nowadays it is more commonly accepted that evolutionary explanations have to be based on previous phylogenetic analysis that informs about the relevant characters and the character state transitions under consideration (Griffiths 1996; Amundson 2005). As long as homology and the dimensions of morphological variation are actually taken into account, adaptation explanations are valid. The explanation of adaptation has to recognize the presence of developmental constraints, yet the actual explaining is done by the notion of natural selection, so that the notion of selection carries the explanatory force for adaptation explanations.

Developmental accounts stressing constraints are similarly valid as they concern a different explanatory problem. Evo-devo differs from more traditional evolutionary biology in its methods and theories, in particular its inclusion of ideas from developmental biology. But the most fundamental difference is that evo-devo addresses new *explananda*—it attempts to explain features about evolution that have not systematically been pursued previously. While traditional neo-Darwinian biology used to focus on two basic explananda—the explanation of adaptation and the explanation of speciation—one of the central items on the evo-devo agenda is the *explanation of evolvability*. Other important items are the explanation of the evolutionary origin of novelties and of total body plans. In the explanation of evolvability the explanatory force resides in considerations about developmental features, such as morphological organization and the resulting developmental constraints. Neo-Darwinists such as Ernst Mayr (1959, 1994) and Bruce Wallace (1986) have argued that developmental biology cannot contribute to the explanation of evolution by drawing a distinction between ultimate and proximate causes of organismal form. Adaptation is one of the ultimate causes, whereas development is one of the proximate causes. This distinction may be valuable when analyzing explanations of adaptation, but it obscures the fact that explaining evolvability is also part of explaining evolution. Furthermore, the neo-Darwinian critique of the notion of a morphological type and the related distinction between (inadequate) 'typological thinking' and (adequate) 'population thinking' is based on the neo-Darwinian concern with adaptation and speciation proceeding from variation *in populations* (Mayr 1982). Yet the notion of a type advocated here recognizes both features shared between organisms (same set of characters across individuals) and phenotypic variation (change in character states across individuals). Construing the type and its developmental constraints as consisting in several dimensions of morphological evolvability removes any tension that may have existed between the idea of type and 'population thinking'.

In sum, to reconcile constraints and selection, what is needed is first the recognition that different explananda may be pursued (so that different explanantia are legitimate). Second, it has to be understood how the different modes of explanation *combine*, namely, the fact

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[7] Some proponents of the notion of developmental constraints were aware of this point (e.g. Oster and Alberch 1982), but it has often been forgotten in the ensuing debate that set up selection and constraints against each other (Amundson 1994).

that developmental constraints/evolvability and natural selection operate at two stages of one overall process: (1) the generation of heritable phenotypic variation, and (2) the selection of given phenotypic variation resulting in phenotypic change. To be sure, biologists still have to develop models that actually integrate both evolvability (developmental constraints) and selection.

Gould and Lewontin (1979) prominently argued that the 'adaptationist program' erroneously atomizes organisms by taking any feature as an adaptation and ignoring developmental constraints. From the present perspective, and consistent with Gould and Lewontin, an organism can be legitimately decomposed into units, provided that these are homologues as units of morphological variability. The explanation of evolvability actually requires that an organism is broken down into smaller structural units that are independent of each other in terms of the ability to undergo adaptive modification, so that in a sense these units can be studied independently. At the same time, understanding what makes these units evolutionarily independent and thus units in the first place requires investigating the *developmental relations between them*—even if only to explain why these units are largely developmentally dissociated such that they can undergo variation independently of each other. What makes a homologue a unit of evolvability may often not solely depend on the *internal* structure of this homologue, but on larger parts of the *overall* developmental system and its dynamics, governing how an organism is partitioned into semi-autonomous modules. A homologue can exhibit heritable variation independently of other homologues, but taken in isolation it need not be able to generate this variation. (In philosophical terms, the evolvability a homologue possesses is an extrinsic or relational property.) Thus, if the task is to understand why the material constitution of an organism is such that there are different dimensions of evolvability, breaking down an organism into units still requires studying any such unit in its organismal context. This suggests that an intermediate position is to be taken between reductionism and holism, the two opposites characterizing historical debates about the physiology and development of organisms (Gilbert and Sarkar 2000).

Further challenges: homologues on different organismal levels

Now I want to point to some open empirical and conceptual challenges for the explanation of homology/evolvability in particular, and evo-devo in general. My discussion has assumed that an organism is partitioned into several homologues. Yet homologues can exist on different levels of organization. One such level is adult morphology; in fact, when the homology concept emerged in 19th century comparative anatomy it was structures on this level that were recognized as being homologous across species. Nowadays it is well-known that homology among gross morphological structures is independent from sameness of developmental processes and homology among genes. There are many examples of homologous structures that develop by means of different developmental processes (Abouheif 1997; de Beer 1971; Hall 1995; Love and Raff 2006; Roth 1988; Wagner and Misof 1993). Likewise, homologous structures may develop based on non-homologous genes and homologous genes may be involved in the production of non-homologous structures in different species. As a result, sameness of gene expression patterns in two species is just a defeasible criterion for homology, not to be confused with homology itself (Abouheif et al 1997; Bolker and Raff 1996; de Beer 1971; Dickinson 1995; Müller and Wagner 1996; Newman 2006; Nielsen and Martinez 2003; Roth 1988). The conclusion that is commonly drawn from these facts is that homology among morphological structures

cannot be reduced to or defined in terms of developmental processes or the action of genes, and that homology is instead to be defined and empirically established based on phylogeny.

An additional implication I emphasize here is that *homologues exist on different levels of organismal organization*. For instance, genes and proteins can be homologous across species just like morphological structures. The account defended here yields a precise construal of what makes structures on intuitively different levels distinct homologues. On my account, what makes a structure a homologue in the first place is its being a distinct dimension of evolvability, i.e., the fact that the structure can exhibit heritable phenotypic variability that is independent from the variability of any other structure. So far I have used this criterion to distinguish different homologues on the same level of organization, but the same idea applies to structures on potentially different levels. The above mentioned empirical findings show that there are some morphological structures whose variability is independent (at least to a significant extent) of the variability of the genes that are involved in its development, so that evolution on the genetic level can be partially uncoupled from evolution on the morphological level (Müller 2003).

Another relevant level of organization is *development*. Some evo-devo practitioners have proposed 'process homology', the idea that developmental processes can be homologized across species (Gilbert and Bolker 2001; Gilbert et al 1996; Minelli 2003). Others are more cautious, as they fear that homologizing processes, which involve function, runs afoul of the traditional homology-analogy distinction. But as Alan Love (this issue) makes explicit, developmental processes involve 'function' not in the sense of adaptive function (which pertains to analogy), but in the sense of activity (or causal role). And the phylogeny of activity-functions can be studied and assessed for homology (Amundson and Lauder 1994; Griffiths 1996, 2006). From my perspective, developmental processes can be homologues provided that one such developmental process can phenotypically vary and evolve independently of some other developmental processes and some entities on lower or higher levels of organization; and whether a developmental process is a genuine unit of phenotypic evolution can be established by phylogenetic analysis. Some of the examples referred to above show that it is indeed possible for a developmental process to be evolutionarily decoupled from the structure(s) it generates in ontogeny. A further level of organization is *behavior*. Marc Ereshefsky (this issue) gives a detailed review of homology among behavioral patterns, the criteria used to establish it, and how a behavioral homologue can have distinct morphological bases in different species (and *vice versa* how homologous structures can form the basis of non-homologous behaviors). George Lauder (1986, 1994) has argued that behavioral homologies can be established by means of comparative study using phylogenetic trees, but that behavior cannot be reduced to certain morphological, neurological, or genetic features. From my perspective, this means that a behavioral pattern can be a distinct homologue, provided that it can phenotypically vary independently from other characters, in particular the genes, morphological structures, and neurological features that are involved in the production of this behavior.[8]

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[8] This does not mean that I assume that there is a fixed number of levels applying to all organisms or that for any organism there is a clear-cut number of levels into which all homologues can be neatly arranged. What an organism's homologues are depends on what the dimensions of variability are, which may differ from taxa to taxa. While for a given organism there are cases where a certain gross-morphological structure is a distinct homologue from a particular developmental process, another structure may vary only together with its developmental basis, so that both form a single homologue that cannot be assigned to one of the standard levels. Rather than being committed to a strong notion of organismal levels, my position is that there are genuinely distinct homologues (according to my account of homology) that occupy in some cases what are intuitively considered distinct levels.

The fact that homologues exist on different levels raises an additional challenge for explaining evolvability (Brigandt 2006). Above I indicated that the central task for an account of homology as evolvability is to understand what makes it the case that an organism is composed of several homologues which can heritably vary independently of each other, even though the different parts of an organism are causally-developmentally connected. In the present context, the question is: 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 homologues on one level can evolve fairly independently of homologues on other levels? This is an additional empirical and conceptual challenge. Indeed, it is vital for evolutionary biology to understand the internal-developmental features of organisms that permit evolution on one level of organization to occur without obstructing evolution on other levels. While evo-devo is making progress on various details bearing on evolvability, the issue raised here is for the most part a task for future work. In fact, despite relevant new knowledge about empirical details, the very question as to what dissociates characters on different levels has to my knowledge hardly been addressed in an explicit and theoretical fashion. Although the growing empirical literature on modularity bears on this issue, Wagner and Misof (1993), Müller and Newman (1999), and Müller (2003) are some of the few publications that directly address the issue as a feature that is in need of explanation and provide general ideas as to how to solve the problem.

This challenge of accounting for dissociated evolvability on different levels is increased by the fact that in addition to structural organization as traditionally construed, there is also functional organization. As Love (this issue) discusses in detail, several biological fields (molecular developmental biology, functional morphology) appeal to homologous functions, where 'function' is for the most part understood as activity (see also Wouters 2003). Just as structural homologues are spatially related in a structural organization (where one structure can be the mereological part of a larger structure), functions are connected by procedural interdependencies (where a function can contribute to and be part of a larger system, which is itself a hierarchically organized activity-function). The existence of function parts that can be homologous across organisms and species implies that the phenomenon 'homology of function' has to be understood—including its different levels—and that function homologues have to be related to structural homologues.

In the previous section I pointed out that even though an account of morphological evolvability consists in breaking an organism down into independent units, explaining what makes such a unit autonomous requires studying the developmental relations to other units and how a unit figures in its overall organismal context. The same applies to homologues on different levels of organization. Even understanding why a single structure on one level can heritably vary independently of other structures presupposes explaining the developmental relations to structures on other levels that underwrite this partial dissociation of structures and levels. As a result, the explanation of phenotypic evolvability requires examining the *interaction of structures on several levels of organization*. Generally, studying several levels of organization at the same time is part of the methodology of evo-devo (Love 2006; Wagner 2000).

Conclusion

In this paper I suggested that homology as a phenomenon of morphological organization consists in an organism being composed of several homologues, such that each homologue

is a unit (or dimension) of morphological evolvability. 'Unit of morphological evolvability' means that a homologue is a character that can be subject to heritable phenotypic variation (in its character state) largely independently of the variation of other characters. I used this construal of homology to bridge previous developmental and phylogenetic accounts of homology. Evolutionary developmental biology aims at causally explaining the developmental basis of the process of morphological evolution; phylogenetic systematics studies the phylogenetic patterns that are the product of morphological evolution. These two biological tasks address different, but compatible aspects of homology, construed here as evolvability on a character-by-character basis. Developmental approaches to homology attempt to understand the causal-developmental basis of homology as morphological evolvability along several independent dimensions, while phylogenetic approaches detect and study homologies and synapomorphies, which are the phylogenetic manifestations of evolvability in a character-by-character fashion. The discussion used the fact that homologues exist on different levels of organization to point to open empirical challenges for evo-devo, and to emphasize that an account of evolvability must address entities on several levels of organization and their interaction.

Furthermore, I argued that this construal of homology points to a way of thinking about developmental 'constraints' that emphasizes how they actually enable evolution. Morphological organization—the set of homologues and dimensions of evolvability—is relatively stable across evolutionary change, reflecting developmental constraints. Yet this existence of stable dimensions of evolvability makes heritable phenotypic variation and subsequent phenotypic change based on natural selection possible. Therefore I suggested that constraints and selection should not be understood as two antithetical forces, because they are distinct parts of the evolutionary process and are thus compatible. The first part is the generation of heritable phenotypic variation, and its developmental basis (evolvability) is studied by evo-devo, using such notions as developmental constraints/deconstraints and modularity. The second part is natural selection acting on given heritable phenotypic variation, and this process of adaptation is explained by neo-Darwinian evolutionary theory using the models of population genetics. Thereby different perspectives on evolution pursue different relevant *explananda* (evolvability vs. adaptation) and thus make use of different modes of explanation, i.e. *explanantia* (features of development such as organization and constraints vs. natural selection and population genetics).

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