THE ROLE OF TYPOLOGICAL THINKING IN EVOLUTIONARY DEVELOPMENTAL BIOLOGY

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Submitted to
Central European University
Department of Philosophy

In partial fulfilment of the requirements for the degree of Masters of Arts.

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Budapest, Hungary
2010

Abstract:

My aim in this thesis is to address the question about the role of typological thinking in evolutionary developmental biology (evo-devo). Evo-devo is a research programme that combines several fields in biology and that still needs to be fully integrated into the theoretical framework of evolutionary theory. The use of typological thinking in evo-devo has been emphasized as a possible problem for this theoretical integration since typological thinking is perceived as committed to essentialist ontology that is incompatible with the findings of evolutionary theory. In the light of these problems with typological thinking in evolutionary biology, I want to examine if typological thinking in evo-devo is just a useful heuristic in scientific research, or if it is grounded in the theory of evo-devo. My aim is to show that typological thinking in evo-devo is theoretically grounded and that it does not have to be conceived as incompatible with evolutionary theory. While I agree that typological thinking is committed to some form of essentialism, I argue that it is only a weaker form of essentialism (relational essentialism) that does not have to be incompatible with evolutionary theory.

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INTRODUCTION

The aim of the thesis is to examine what is the role, if any, of the typological thinking in evolutionary developmental biology (evo-devo). The main question that I will address is whether typological thinking is just a useful heuristic employed by evo-devo scientists or it is grounded in the theory of evo-devo. Evo-devo is a research programme that combines several fields of biology and therefore it is faced with problems of theoretical and conceptual unification of these diverse fields. One of the important issues for this theoretical integration of evo-devo is the possibility of achieving a synthesis with the theoretical framework of modern evolutionary biology (the so-called Modern Synthesis). While there seems to be a consensus that evo-devo and evolutionary biology should be theoretically integrated, there are differences in opinions as to how much conceptual and methodological accommodations are going to be necessary in order for this to happen.

I will focus on one specific explanatory strategy that is arguably used by evo-devo and that is in view of many authors (Richardson, Minelli, Coates, 1999; Amundson, 2005; Jenner 2006) incompatible with the theoretical framework of evolutionary biology. This explanatory strategy is typological thinking and the received view is that typological thinking is an essentialist and outdated view that was replaced by Darwin with population thinking. Typological thinking is conceived as a view that holds that there is a limited number of stable types which underlie and explain the observed patterns of diversity of form found in biological world (Lewens, 2009, p.355) As explained by Lewens, we can think of types as explanatory posits – some forms are frequent in nature because they are variations of an underlying type, while others are rare or non-existent because there is no corresponding type.

I will present two critiques that have been put forward against typological thinking by Mayr (1959) and Sober (1980) and try to show that while Mayr is attacking a straw man, Sober presents a relevant critique that typological thinking is committed to a view that there is

a natural tendency in biology towards some properties and structures, and this natural tendency underlies and explains similarities between organisms found in nature. Since typological thinking is conceived as a form of essentialism, I will try to explain what biological essentialism is and present Ereshefsky's (2010) distinction between two different types of essentialism, traditional and relational. After addressing the question whether typological thinking is used in evo-devo, my aim is to show that evo-devo uses typological thinking that only presupposes relational essentialism and not the traditional one. Furthermore I think that authors defending relational essentialism have shown that it does not have to be incompatible with evolutionary theory. This especially refers to the homeostatic property cluster version of relational essentialism according to which members of a kind are defined by a relatively stable cluster of properties that are caused by certain underlying mechanisms.

Three different accounts of how typological thinking is used in evo-devo will be examined (Amundson's (2005), Lewens' (2009) and Love's (2009)). Amundson (2005) thinks that typological thinking is incompatible with evolutionary theory. I will try to show that Amundson has a stronger claim about typological thinking which has some problematic implications and a weaker claim according to which typological thinking in evo-devo is not necessarily incompatible with the evolutionary theory. The weaker version corresponds to relational essentialism, more specifically homeostatic property cluster theory of biological kinds and I will argue that this is exactly the kind of typological thinking that is used in evo-devo. Lewens' (2009) account is something very similar to this homeostatic property cluster version of typological thinking but it seems like a bit more deflationary view since he emphasizes statistical regularities and probabilities and rejects Sober's (1980) claim that typological thinking is committed to assuming some natural tendencies that underlie shared properties and similarities. In my opinion, typological thinking (as used in evo-devo) is committed to this kind of view, however in a much less rigid form than Sober presents it. In

contrast to Amudson's and Lewens' suggestion, Love (2009) takes a different approach and accepts the critiques that typological thinking is implying an ontological view that is not compatible with evolutionary theory. However, he argues that it should be used as an explanatory strategy, a heuristic, without presupposing any ontological views.

This brings me to the main question of the thesis, is typological thinking just a useful heuristic employed by scientists or is it justified by the evo-devo theory. In connection with Love's claim that typological thinking is just a useful heuristic I will examine if this is so because typological thinking is grounded in our cognitive abilities. My aim is to explore if typological thinking corresponds to psychological essentialism that is supposed to be our reasoning bias. It seems that typological thinking corresponds to some forms of psychological essentialism, even this homeostatic property cluster version of typological thinking that is used in evo-devo. I address different views on the consequences of the possibility that typological thinking is a reasoning bias on its value as a scientific tactic, but I conclude that in the case of evo-devo, typological thinking is more than a reasoning bias or a useful heuristic, and that it is really supported by the theory of evo-devo. I offer some support to this claim by showing that in some areas in biology typological thinking is just a heuristic that is possibly grounded in our reasoning bias and has no theoretical support, while in evo-devo there are theoretical grounds for using typological thinking.

CHAPTER 1: EVOLUTIONARY DEVELOPMENTAL BIOLOGY (EVO-DEVO)

Evolutionary developmental biology is a research field that explores and links "two fundamental processes of life: development of individual organisms (ontogeny) and evolutionary transformation in the course of the history of life (phylogeny)." (Laubichler, 2007, p. 342). The starting point of evo-devo research is the presupposition that there is a causal relation between the processes of individual development and evolutionary change and the aim of evo-devo is to explore that relationship. I will present a general framework of the emergence of evo-devo in the context of the modern evolutionary theory since this is important for understanding in what way is evo-devo different from the standard evolutionary biology and why is there a need for a conceptual integration of the two fields.

Evo-devo emerged as a distinct field of research in the early 1980s and has since then evolved into a mature discipline (Muller, 2008, p.3). The development of evo-devo is a consequence two main factors: the fact that the prevailing theoretical framework in evolutionary biology – Modern Synthesis could not explain many characteristics of phenotypic evolution, and due to some important methodological advances that led to some interesting new discoveries. Modern Synthesis represents the theoretical integration of several fields of evolutionary thought and it developed as a consequence of the development of population genetics, as it was shown that Mendelian genetics was consistent with natural selection and gradual evolution. The only mechanisms of evolutionary change that were acceptable within the Synthesis were those that could be expressed in terms of (Mendelian) population genetics. However, some branches of biology were left out of the Synthesis, such as embryology and developmental biology, and this omission led to the accumulation of concern in 1970s and 1980s about the difficulties of Modern Synthesis to account for many

characteristics of phenotypic evolution[1] (Müller, 2008, p.5). The main concern was the fact that Modern Synthesis explanations neglect the processes that relate genotype to phenotype and ignore developmental constraints that are seen as a limitation to a possible phenotypic variation (Laubichler, 2007, p.347).

Other than the explanatory deficits of the Modern Synthesis, there were some important methodological advances that led to the emergence of the new field of evo-devo. Among these advances were the discovery of the techniques for gene cloning and visualization of gene activity in embryonic tissues which allowed the comparison of developmental processes of different taxa at the molecular level (Müller, 2007, p.943) According to Arthur (2002, p.758), the most important factor was the discovery of homeobox-containing genes[2] since they reveal the existence of a general mechanism that underlies the development of organisms that are morphologically diverse. Similarities in gene regulation among distantly related species were found and it became clear that relatively few genetic regulators are implicated in the embryonic foundations of all animal body plans (Müller, 2008, p.6) So, these discoveries led to the new research field now known as evolutionary developmental biology.

> The genetic determinism of the early Synthesis evolutionists had made development seem irrelevant to evolution. If genes directly caused phenotypic traits, evolution could be seen as the mere shuffling of genes. But if genes cause phenotypic traits only indirectly, by complex interactions with other developmental factors, then the core doctrine is vindicated. To understand evolution, we must understand how ontogeny can be changed. With the erosion of genetic determinism, the way was cleared for development again to be seen as a factor in evolution. (Amundson, 2008, p.10[3])

So, according to evo-devo, the evolution of organisms cannot be reduced to population genetics. Evolution affects not only genes and genotypes but it also affects and alters developmental processes thereby creating novel structures in organisms. That means that it is

[1] ''Such phenomena included biased variation (…), rapid changes of form (…), the occurrence of non-adaptive traits (…) and the origination of higher-level phenotypic organization such as homology and body plans (…)'' (Muller, 2010, p.5)

[2] Homeobox is a DNA sequence that was found in genes which are involved in determining which groups of genes are expresses during embryonic development.

[3] This refers to the page of the pre-print of Amundson's article in the Routledge Encyclopedia of Philosophy Online

not sufficient to study how genetic variation caused phenotypic variation, since developmental processes and mechanisms influence and determine that variation on the level of phenotypes. An important part of evo-devo is the study of how those developmental processes and mechanisms evolve. Furthermore, an area of interest is the study of how non-genetic factors produce changes in gene expressions, for instance epigenetics - molecular, cell and tissue interactions that affect evolutionary change, but are not directly genetically determined and phenotypic plasticity – the phenomenon that the same genotype can produce different phenotypes due to some environmental factors and external conditions.

1.1 What are the theoretical implications of evo-devo for evolutionary biology?

As was already mentioned, evo-devo introduced explanations about the phenotypic evolution that were not available in the theoretical framework of Modern Synthesis prior to evo-devo. This is because evo-devo represents the integration of several biological disciplines which means that it represents the integration of different research paradigms and theoretical frameworks. The main issue that arises with this integration of diverse theoretical approaches is the question of how evo-devo relates to the theoretical framework of the standard evolutionary theory, that is, with the framework of Modern Synthesis. The methodology and the explanatory strategies of evo-devo seem to significantly differ from standard theory of evolution, since the standard theory of evolution is based on searching for correlations between phenotypic characters and statistical gene frequencies in populations while evo-devo offers a causal mechanical approach to understanding of phenotypic change (Müller, 2007, p.945) Furthermore, the main goal of the Modern Synthesis was to explain adaptive change, but evo-devo is not so interested in whether the changes are adaptive or not, but wants to explain how developmental mechanisms influence phenotypic variations.

There seems to be a relative consensus among biologists and philosophers of biology (Callebaut, 2010; Laubichler, 2007; Müller, 2000) that evo-devo can and should be incorporated into the theoretical framework of Modern Synthesis, thereby creating a new, extended synthesis of different research fields in biology. The idea is that evo-devo expands on the explanatory power of Modern Synthesis framework since it encompasses the question of the influence of development on phenotypic evolution and evolution of development. The only question that is still not decided upon is the question of how different is the conceptual framework of evo-devo from the Modern Synthesis framework and how much effort will it require to achieve this theoretical integration. For instance, authors like Hall (2000) argue that there is no real conflict between evo-devo and the Modern Synthesis framework. On the other hand, authors like Laubichler (2007) and Callebaut (2010) think that the integration will require serious theoretical advances on the part of evo-devo and some "major conceptual reshuffling" (Callebaut, 2010, p.473).

The difference in the explanatory strategies of evo-devo and Modern Synthesis, and the possible need for theoretical integration is the main topic of this thesis. However, I will focus on one specific explanatory strategy that is supposedly used by evo-devo and try to address this more general problem by examining at it in a more concrete and specific way. This specific explanatory strategy is typological thinking which is usually contrasted with population thinking. The standard view in the Modern Synthesis is that typological thinking is incompatible with the theory of evolution and represents an outdated, pre-Darwinian explanatory strategy, while population thinking is the favored explanatory strategy.

In connection with this, there are several questions that need to be addressed: how is typological thinking used in evo-devo, is typological thinking incompatible with the framework of modern evolutionary theory, and depending on the answers to these questions, how does this influence the possible accommodation of evo-devo in the framework of Modern

Synthesis. Trough the paper I my aim is to show that typological thinking is a relevant explanatory strategy in evo-devo, and that if it is properly conceived typological thinking does not have to be incompatible with evolutionary theory.

As a first step it is necessary to clarify what typological thinking is, and how it relates to population thinking. For this reason the next section tries to give an account of typological thinking, mostly through the critique that has been put forward against it by the proponents of Modern Synthesis and population thinking.

CHAPTER 2: TYPOLOGICAL VS. POPULATION THINKING

The demise of typological thinking in biology is mostly due to Ernst Mayr (1959) who popularized the distinction between typological and population thinking. I will present Mayr's view and show that he is attacking a straw man with his criticism of typological thinking. However, as shown by Sober (1980), the difference between typological and population thinking is still relevant and it remains to be shown whether typological thinking of evo-devo can be integrated with the population thinking of evolutionary biology. In the last part of the section I will present Sober's criticism of typological thinking which I find convincing, since this is the main problem that needs to be solved if typological thinking used in evo-devo is to be integrated in the framework of evolutionary biology.

According to Mayr, typological thinking has its origins in the philosophy of Plato, and population thinking was introduced by Darwin, and replaced typological thinking in biology. Mayr describes typological thinking as the view that holds (influenced by Platonism) that there is a limited number of "fixed, unchangeable "ideas" underlying the observed variability" (Mayr, 1959) and these ideas (types) are the only things that are fixed and real, while this observed variability is not real. Furthermore, the gaps in nature are explained by the discontinuities between these ideas or types. From this follows Mayr's main critique that typological thinking is incompatible with evolutionary theory:

> Since there is no gradation between types, gradual evolution is basically a logical impossibility for the typologist. Evolution, if it occurs at all, has to proceed in steps or jumps. (Mayr, 1959, p.2)

On the other hand, population thinking as described by Mayr represents a view that is opposite to typological thinking. Population thinking "stresses the uniqueness of everything in the organic world" (Mayr, 1959, p.2) and the main claim is that no two individuals are alike. That is why all organisms and organic phenomena can collectively be described only statistically, and these statistics are merely averages that are abstractions and do not have any

reality. Mayr's conclusion is that typological thinking is incompatible with the evolutionary theory and it presupposes an erroneous ontological view according to which only the type is real and variability is not real.

However, I agree with authors (Amundson, 2005; Sober, 1980; Winsor, 2006) who have argued that Mayr's description of typological thinking is oversimplified and it does not apply to the practice of most biologists who have used typological thinking throughout the history of biology and those still using it. I will present his claims separately and try to show why thy do not represent a convincing view of typological thinking.

1) Only individuals have reality while types are not real

This claim was first criticized by Sober (1980) since it implies that much of the population biology should be dismissed[4]. He argues that population thinking must allow that there is something over and above individual organisms and he thinks that population thinking in fact deals with both individual organisms and populations, which both exist. Furthermore, it is questionable how Mayr's distinction between reality and abstraction is to be understood. If we are to interpret it as existence then Mayr's claims are simply not true since Winsor (2006) has shown that most of the pre-Darwinian naturalists (that were the target of Mayr's critique) were neither Platonists nor essentialists. Even the description of typological thinking is not correct if interpreted this way since population thinkers do not deny the existence of such things as averages. "Individual and group properties are equally "out there" to be discovered." (Sober, 1980)

However, there is one way of interpreting Mayr that seems to make sense that was proposed by Sober (1980) and that is to say that "being real" means "having causal efficiency". In that sense, in population thinking, individual differences are not the effect of interfering forces that confound the expression of a prototype, but rather they are causes of the

[4] For example Lotke-Volterra equations that describe the relations between predator and prey populations.

events that are central to the history of evolution (Sober, 1980). I find this claim well supported as the description of typological thinking and this kind of view will be at the basis of Sober's critique of typological thinking which I find relevant for typological thinking in general, and especially in evo-devo. Before continuing with Sober's criticism, I will address second Mayr's claim that was supposed to show the incompatibility of typological thinking with the evolutionary theory.

2) For the typological thinker evolution is a logical impossibility because there can be no gradation between types.

This claim also seems to be incorrect since the example of the discovery of the transmutation of elements in chemistry did not undermine the belief in the existence of chemical elements. The possibility of types changing one into another does not imply that those types do not exist. As explained by Lewens (2009), the existence of stable forms is perfectly compatible with an evolutionary process that explores the limits of, and transitions between such stable forms.

2.1 Natural State Model

That typological thinking is committed to an ontological view that is incompatible with the evolutionary theory and that is called Natural State Model is a criticism of typological thinking that was presented by Sober (1980). I find this criticism relevant and convincing and a good description of at least some forms of typological thinking. I will present this criticism because it is going to be relevant for the next sections of this paper where typological thinking in evo-devo is described and it is examined if typological thinking is committed to this ontological view that was called Natural State Model.

. Sober thinks that the main difference between typologists and populationists is in the way they try to explain variation. Typologists, according to Sober, use the essentialist explanatory strategy which was already formulated by Aristotle, and was widely used by 17th and 18th century biologists. This explanatory strategy relies on Aristotle's Natural State Model and according to Sober, 20th century population genetics showed that this model cannot be applied in the ways that essentialist requires. However, it seems that it can have some application in specific parts of biology. According to Aristotle's Natural State Model, there are states of an object which are natural and those which are not, and these unnatural states are produced by subjecting the object to an interfering force. So, variability in nature is regarded as a deviation from a natural state.

According to Sober typologists and populationists agree that averages exist and that variation exists, but they disagree on the explanatory character of these. For the typologists variation does not explain anything, rather it is something that should be explained away. In contrast to Mayr, Sober thinks that both populationists and typologists want to get past the individual variation in order to identify properties of groups which remain constant. According to a typologist, individual organisms must all posses some invariant properties – that is why typological thinking is considered a form of essentialism since all the members of a biological kind must share some common characteristics, and these common characteristics define the given kind. Sober characterizes typological thinking as a form of essentialist thinking where variation is understood as arising through a process of deviation from a type. All members of a species must posses some natural tendency "property that an organism is supposed to have regardless of what environment it might be in".

To summarize Sober's criticism - the main idea is that typological thinking is committed to essentialist metaphysics, and this kind of explanatory strategy is not compatible with evidence from evolutionary theory. In the section that describes different accounts of

evo-dvo I will try to show that this essentialist metaphysics that presupposes Natural State Model does not necessarily need to be in conflict with evolutionary theory, if we understand essentialism in a weaker sense.

In the next section I will try to briefly explain what biological essentialism is and how it is perceived in modern evolutionary biology in order to clarify why this view is conceived as incompatible with the evolutionary theory. It is important to notice that essentialism in biology is a term with a very wide use. Basically any account of kinds in biology (as opposed to individuals) is conceived as essentialist in that sense. That is why typological thinking is usually associated with essentialism, since types function as kinds in biology – there are some characteristics that are typical of a given kind, and these characteristics should have some underlying explanation (and when we invoke types, their explanatory power is based on that underlying explanation of typical traits or characteristics). Consequently, different kinds of biological essentialism are parallel to different kinds of typological thinking.

2.2 Biological essentialism

Biological essentialism is most often discussed as a view about biological species as kinds according to which there is some property that all and only members of a species share and this property – the essence is what explains all other properties of species members. Ereshefsky distinguishes two different kinds of essentialism: traditional essentialism and relational essentialism. According to the traditional essentialism, "all and only the members of a kind have a common essence. ... ( ) the essence of a kind is responsible for the traits typically associated with the members of that kind... ( ) knowing a kind's essence helps us explain and predict those properties typically associated with a kind" (Ereshefsky,2010). The consensus is that this view is incompatible with evolutionary theory since from this theory

follows that there is no such property among members of a species that could fulfill these conditions "Darwin made it very clear that no amount of difference between organisms due to various degrees of modification could impact our decisions about genealogy (…) The potential for indefinite change of individuals is at the very core of Darwinian metaphysics." (Jenner, 2005, p. 387). This is a reason why many evolutionary biologists and philosophers of biology support a view that is supposed to be the opposite ontological view on species[5] – that species are individuals (they are spatio-temporally restricted and causally interrelated). If typological thinking is conceived as a form of traditional essentialism, that would mean that type represents the sum of the properties that all and only species share. Type is an example of the class, and it is an abstraction that contains only the essential properties of the members of the class (properties that all and only members of that class share) and the members share these properties due to the common essence that is something intrinsic to members of the class and causes these shared essential properties.

There is also a weaker version of essentialism, what Ereshefsky has called relational essentialism according to which certain relations among organisms and the environment are necessary and sufficient for being a member of species. The most common version of this relational essentialism is homeostatic property cluster theory according to which it is enough that members of species share a stable property cluster that is caused by some homeostatic mechanisms and that this stable property cluster allows us to make better than chance predictions in our theories about species. The kind of typological thinking that reflects the homeostatic property cluster theory is represented by the strategy of using types as exemplars (types than function as the property clusters - they reflect the most common properties of a given kind), where the members of a kind should be sufficiently similar to the given exemplar (but members do not have to share all the properties of a type, and there could be members

[5] This is the opposite ontological view if we assume the basic dichotomy between individuals and classes. Essentialism presupposes that species are classes that have defining properties.

that do not have common properties among each other, but are in some properties similar to the type). However, as was already mentioned, this is not just an explanatory heuristic that uses exemplars, there are some ontological commitments involved in the sense that it is assumed that there are some underlying mechanisms that cause these clusters of properties.

After describing typological thinking and the different ways in which it can be conceived, it needs to be examined if evo-devo uses typological thinking as a relevant explanatory strategy. If typological thinking is used in evo-devo, then the question is what form of typological thinking is used (the one connected with traditional essentialism or the one connected with relational essentialism) and if this form that is used by evo-devo is incompatible with the theoretical framework of evolutionary theory. A further issue that will be raised in this paper is if we even have to consider typological thinking as implying some ontological commitments (essentialism) or if we can just perceive it as a useful heuristic that makes successful predictions and generalizations without presupposing any ontology. I will argue that typological thinking is used in evo-devo as a relevant explanatory strategy, and that evo-devo uses typological thinking that presupposes relational essentialism (homeostatic property cluster theory).The question of typological thinking as heuristic used by scientists will be addressed, however, I will try to show that while some fields in biology use typological thinking merely as a heuristic, in evo-devo this use is theoretically justified and comes with certain ontological commitments.

CHAPTER 3: TYPOLOGICAL THINKING IN EVOLUTIONARY DEVELOPMENTAL BIOLOGY

Before examining the explanatory strategies of evo-devo in order to see if they make use of typological thinking, I will present Amundson's (2005) interpretation of evo-devo and the use of typological thinking in evo-devo since he offers a rather detailed analysis of the way typological thinking is used and concludes that this explanatory strategy is widely used in evo-devo and is incompatible with the theoretical framework of the Modern Synthesis.

Amundson offers an illustration of the use of types in evo-devo by explaining that biologists interested in development study the vertebrate limb and not particular chick's wings (Amundson, 2005, p.230). So, the theory about the vertebrate limb should apply to all vertebrate limbs. In connection to this, he argues that developmental biologists make a distinction between "permitted" and "prohibited" morphologies, and base this distinction on the facts about mechanisms of limb development across the vertebrate lineage and from observed interspecies variation (Amundson, 2005, p.230) Depending on the developmental mechanisms, some modifications are more likely, some less likely and some impossible. Amundson examines another example of theorizing about the urodele limb, and argues that the urodele limb is conceived as an abstract theoretical construct which expresses shared patterns of development. The main point that Amundson wants to make is that modern developmental biologists talk about entities that he calls developmental types (entities like urodele limb and neural crest). As developmental types Amundson characterizes different concepts that are used in evo-devo such as body plans, homologies, life stages. Before continuing with Amundson's exact account of these developmental types and his opinion about the incompatibility of evo-devo with the theoretical framework of Modern Synthesis, I will try to address some of the concepts and strategies used in evo-devo and try to examine if they really rely on typological thinking.

3.1 Theoretical themes in evolutionary developmental biology that can be related to typological thinking

3.1.1 Modularity (modular architecture of developmental systems)

Modularity is defined as an attempt to understand systems as integrations of partially independent and interacting units (Callebaut, Rasskin-Gutman, 2009). "Modular organization is pervasive at all levels of biological organization, from the genetic to the developmental, anatomical and behavioural." (Müller, 2007, p.944) There are two main approaches to the study of modularity. One is to study the correspondence between genetic and phenotypic variation in order to see if this variation can be decomposed into relatively independent units. Another way to study modularity and its role in evolution is by examining the mechanistic relationship between developmental modules and units of phenotypic construction (Müller, 2007, p.944). Here, modules are conceived as subsets of anatomical architecture that can vary and adapt independently of each other. According to Müller, such units have been called homologues in the morphological tradition. One could expect that there will be a correspondence between genetic and anatomical modules, but this is not necessary (there are cases when developmental pathways change, and homologues (anatomical modules) remain the same. Evo.devo biologists from this conclude that the evolution of anatomical homology cannot be explained only by continuities of gene regulation (as it would be suggested by the modularity approach).

Homology is an interesting topic in evo-devo that is according to Amudson explained with the use of typological thinking. I will try to see how homology is explained in evo-devo and if typological thinking really is the main strategy of explaining homologies. The standard definition of homology is that it is similarity between structures of organisms that belong to different taxa which is due to their shared ancestry. The classical definition of homology that

predated evolutionary theory was Owens's (1843), who defines a homologue as "the same organ in different animals under every variety of form and function"(Owen, 1843, p.379). For instance, examples of homologies are patterns of bones in bat's wing and those of porpoise's flipper.

Developmental account of homology (accepted in evo-devo) is usually taken to be an alternative to the historical account (widely accepted in the theoretical framework of Modern Synthesis). According to the historical concept of homology, only common history constitutes homology, and homologies are merely residues of ancestry. According to the developmental account of homology, common ancestry does not offer a complete explanation of homology, and an important factor is the fact that homologies reflect shared developmental processes. An articulated version of the developmental account of homology is Wagner's (1989) biological concept of homology. Wagner assumes that the stability of homologues can be explained by the properties of developmental processes that create them. He does not offer a direct definition of homology but rather broadly characterizes the kind of epigenetic organization that can produce well-individuated characters that persist through evolutionary time.

So far this account of homology can be viewed as a form of typological thinking in its weaker form – the one that is endorsed by the homeostatic property cluster theory. We have homologues among members of distant taxa and these homologues are defined as a structural similarity due to shared developmental processes. So, they are classes of similar structures that can be represented by a generalized type. However, many authors (Müller, 2003; Brigandt, 2007) disagree that homology is about similarity, and they invoke sameness: "homology is properly a statement about sameness, not about similarity" (Müller, 2003, p.54). This view has the potential of being interpreted as the strong version of typological thinking, the kind that Mayr attacked since it sounds like a Platonic view of homology as a universal being instantiated in particular organisms. But it seems that this is not how these authors

conceive of homology since Brigandt for example, explicitly claims that homologies are homeostatic property kinds and says that certain genetic developmental properties of the homologous character allow for it to be inherited across generations and undergo change of state while remaining the same morphological unit. Assis and Brigandt (2009) cite Wagner (2007) who presents evidence which shows that this identity or sameness of character is established by certain gene regulatory networks that remain stable across evolutionary change. So, I would interpret sameness as the constancy (stability) of properties that is caused by some underlying genetic properties.

In this interpretation of homology is accepted, we have a class of characters and these characters are present across reproductively isolated species that share some stable properties, and these shared stable properties can be generalized by using a type (it is still typological thinking even if there are no explicit uses of types since typological thinking is conceived as presupposing a more general ontological view of biological kinds as classes rather then individuals). The fact that there are certain genetic developmental properties that cause some constant properties justifies the use of types, and the explanatory power of types lies in this existence of some underlying causes.

3.1.2 Innovation (evolutionary origin of novelties)

Innovation is an important part of evo-devo, this is the problem of explaining phenotypic novelties. Examples of novelties are the evolution of the vertebrate jaw, feathers for flight in birds, turtle carapace, etc.

Evo-devo is interested in the mechanisms of epigenetic[6] causation in morphological innovations. Epigenetic causation is the idea that "developmental systems do not merely transform genetic change into phenotypic change but also represent a generative component

[6] Epigenetics are changes in the gene expressions which are not the result of changes in a gene's DNA sequence

in phenotypic evolution." (Muller, 2008, p.10) So, there are some non-genetic factors that cause genes' expression. This mechanisms can give rise to "generic forms" that are products of material cell aggregates and not deterministic genetic programmes.

According to Brigandt (forthcoming), the crucial question that needs to be answered is how genotypic variation translates into phenotypic variation (since it is mostly known what mechanisms produce genotypic variation). The term "evolvability" has been used in evo-devo for the capacity of developmental systems to produce heritable phenotypic variation (Brigandt, forthcoming, p.10). An important aspect of phenotypic variation is that some phenotypic variants are developmentally impossible; some variants are more likely to occur than others and there seems to be a "developmentally grounded bias" (Brigandt, forthcoming, p.10) in the direction of phenotypic variation that is produced. This means that unlike genetic variation, which is mostly random and unbiased, phenotypic variation is constrained by these developmental biases. According to Müller and Wagner (2003) developmental systems are governed by developmental constraints and the appearance of novelties is caused by breaking of those developmental constraints. Müller (2007) explains how evo-devo makes use of the mechanisms of epigenetic causation in order to explain morphological novelties:

> Developmental systems utilize several basic chemicophysical mechanisms that are common to non-living and living materials (…) In the context of evolving development, such mechanisms can give rise to "generic forms" that are products not of deterministic genetic programmes, but of the properties of the material cell aggregates, resulting in tissue layering, lumen formation, segmentation, and other forms of three-dimensional patterning. These simple morphogenetic templates, which can be exploited by further evolution, are thought to have an important in the evolutionary origination and innovation of phenotypic characters. (Müller, 2007, p.4)

From this we can see that mechanisms used by developmental systems give rise to some patterns of generic form[7]. So, there are some forms that are "preferred" by the developmental systems – some groups of properties have a higher chance of clustering together due to some underlying mechanisms. This is in accordance with Sober's characterization of typological thinking as presupposing some natural tendency that underlies the properties of members of

[7] "Generic form – biological forms that result from the autonomous interactions within and among cell aggregates, based on their physical properties, without a programme-like genetic control." (Müller, 2007, p.4)

some class. It seems that according to evo-devo some types of morphological form are more likely to appear due to underlying developmental mechanisms. So, the possible range of evolutionary novelties is in some way constrained and the possible and likely novelties can be grouped in classes that are exemplified by types.

3.1.3. Body plans

A body plan is a model of how an organism is laid out. It is an important feature of organism's morphology and it includes aspects such as symmetry, number of body segments, number of limbs, etc. There is a consensus that there are approximately 30 basic body plans (Raff, 1996) According to Hall (1999) evo-devo treats body plans as "fundamental, structural, phylogenetic organization that is constantly being maintained because of how ontogeny is structured'' (Hall, 1999, p.98, 99) This seems to be a standard example of typological thinking, there are some characteristic body types that are caused by the mechanisms of development and they appear in wide range of organisms.

3.1.4 Study of ontogeny

Study of ontogeny presents a standard example of typological thinking. Love (2010) examines an example of the form of typological thinking that operates through idealization. He examines idealization found in some evo-devo investigations and uses the example of the study of ontogeny which is usually executed by "establishing a set of normal stages for embryonic development, which enables researchers in different laboratory contexts to have standardized comparisons of experimental results." (Love, 2010, p. 679) He describes these normal stages as idealizations since they intentionally ignore known variation that occurs in development.

> This is a tension between the phenomenon of developmental plasticity and the practice of developmental staging. The tension has consequences for evo-devo investigation because specific kinds

> of variation in developmental features that might be relevant to evolution are downplayed in the process of rendering ontogeny experimentally tractable. (Love, 2010, p.280)

The study of ontogeny works with "developmental staging" – establishing of stages of "normal" embryonic development (these stages help getting standardized experimental results that can be compared). "The developmental trajectory from fertilized zygote to fully formed adult is broken down into distinct temporal periods by reference to the occurrence of major events such as fertilization, gastrulation or metamorphosis"(Love, 2010, p. 681). According to Love, these stages ignore variation that is associated with phenotypic plasticity. In connection to these normal stages are the assumptions about the causal processes that underlie these stages. This kind of idealization is explanatorily very useful and yields good results. However, there is a lack of sensitivity to environmental conditions and influences. This is how Love describes the tension between the practice of idealization by postulating developmental stages and discovering the phenomenon of plasticity:

> (1)Variation due to phenotypic plasticity is a normal feature of ontogeny. (2) The developmental staging of model organisms intentionally downplays variation in ontogeny associated with the effects of environmental variables (e.g. phenotypic plasticity) by strictly limiting the range of values for environmental variables and by removing variation in characters used to establish the comprehensive periodization. (3) Therefore, using model organisms with specified developmental stages will make it difficult, if not impossible, to observe patterns of variation due to phenotypic plasticity. (Love, 2010, p. 683)

Love's main claim is that the explanatory strategies such as idealization are necessary for the successful investigation of ontogeny in evo-devo, but that there should be some tactics that compensate the fact that much of the variation is being ignored. What characterizes this strategy as typological thinking of the homeostatic property cluster kind is the fact that there is the assumption about the causal processes that underlie these stages represented by types.

In this section my aim was to show that evo-devo uses typological thinking in explaining some phenomena and that it uses the homeostatic property cluster version of typological thinking. In some cases there is more explicit use of the types and in some types or kinds are presupposed on the grounds of shared properties and underlying mechanisms that cause these properties. It seems to me that Amundson was right when he characterized evo-

devo biologists as interested in the study of the development of the vertebrate limb and not particular chick's wing. The interest lies in the general process of development and not particular instances. This means that important parts of study in evo-devo are classes of characters that share similarities due to underlying mechanisms that cause these similarities. However, this strategy would not be theoretically justified if there were not some facts about development that allow us to presuppose those underlying mechanisms. These are facts like the developmental system being governed by developmental constraints, that there are shared patterns of development among distantly related species, that developmental mechanisms make some phenotypic variations more likely, some less likely and some impossible, etc.

CHAPTER 4: DIFFERENT ACCOUNTS OF TYPOLOGICAL THINKING IN EVOLUTIONARY DEVELOPMENTAL BIOLOGY

4.1 Amundson's account – typological thinking is incompatible with evolutionary theory

As it was already mentioned, Amundson thinks that typological thinking is incompatible with evolutionary biology. I will try to show that Amundson's view of typological thinking can be interpreted in two different ways, one of which really is incompatible with evolutionary theory while the other does not have to be. I think that two claims can be can be extracted from Amundson: a stronger claim that types have causal power and a weaker claim that there is some underlying causal structure that is responsible for the occurrence of similarities we subsume under a type. Stronger claim about types is apparent when he talks about downward causation where types influence phenotypic variations.

> Thus conceived, the urodele limb preexisted even the selective processes that produced the modified limb of a particular urodele species. From this perspective, development (or its set of possibilities, as expressed in the limb) is more ultimate even than natural selection, because selection can act only on the variation allowed by the limb! (...) Adaptationists see structure as a mere consequence of previous adaptations; structuralists see adaptation as merely making adjustments on preexisting structure. (Amundson, 2005, p.232)

> Developmental types (bauplans, the urodele limb, the neural crest) are conceived to exert lawlike, causal influences over populations that have been reproductively isolated from each other, sometimes for hundreds of millions of years. (Amundson, 2005, p.237)

So, according to the stronger claim, types preexist particular structures that are instances of those types and they have causal influences over reproductively isolated populations. This stronger claim seems very unconvincing and sounds like Mayr's characterization of typological thinking. The position that some abstract, preexisting structure causes and produces particular instances of that structure is a view that seems incompatible with the framework of modern biology. It is not clear how evo-devo could account for types conceived as abstract entities having causal power over organisms that are instances of these types. This stronger claim about typological thinking leads Amundson to conclude that typological

thinking is incompatible with evolutionary biology since evolutionary biology cannot account for types causally affecting reproductively isolated populations. I do not see how any biological theory could account for this kind of causality, so I think this criticism of typological thinking in evo-devo is not relevant. Lewens (2009) tries to show that we do not have to interpret types in this way and says that that Amundson has assumed that the evo-devo biologist is committed "to a metaphysically rich notion of a single entity multiply instantiated in distinct species, something akin to universal" (Lewens, 2009, p. 364). It is not necessary to believe that a single entity is shared by different species. For instance, it can be said that each species has limbs that resemble the limbs of some other species (because they descended from the common ancestor and they share similar developmental mechanisms).

Nevertheless, I think that Amundson also offers a weaker claim concerning typological thinking. The weaker claim would be that types are not merely idealizations or abstractions, but that there is something that underlies and causes the grouping into types. This kind of view seems to be supported by some of Amundson's claims:

> (...) it is assumed by everyone that developmental types such as bauplans and vertebrate limbs are causally involved in the evolutionary process in three ways. First, such a type shows a real unity that calls for a specific causal explanation (i.e., they are not mere coincidences, or epiphenomena). Second, the observed unities are to be understood in terms of developmental processes (even though no simple association between ontogeny and adult form exists; the biogenetic law is false). Third, once these unities are understood at the developmental level, we will have a much richer understanding of other evolutionary phenomena. (Amundson, 2005, p.234)

This weaker claim sounds like a homeostatic property cluster theory of types according to which there are causal homeostatic mechanisms that underlie the similarities found in various instances of the type. This theory was first proposed by Richard Boyd (1991) who thinks that a kind (in this case a type that represents a kind) is projectable (or natural) if we have some theoretical grounds to assume that there is a causal explanation for the observed properties. The causal homeostatic mechanism is "something that causally explains the maintenance of the same property correlations throughout the set of instances of the kind" (Griffiths, 1999, p.218) and it corresponds to a traditional essence of a natural kind. This causal mechanism

does not need to be a set of intrinsic properties possessed by organisms. This is how Griffiths explains that kinds (or types) in biology are needed for induction and explanation:

> They represent theoretical categories that we judge to be projectable, which requires them to enter into lawlike, counterfactual supporting generalizations. It does not require that these generalizations be universal, deterministic laws: lawlike generalizations of more limited scope and force are enough. Finally, kinds are defined by the processes that generate their instances, and for many domains of objects these processes are extrinsic rather than intrinsic to the instances of the kind. (Griffiths, 1999, p.219)

Griffiths cites Darwin's law of Unity of Type (fundamental agreement in structure in organisms of the same class) in order to show that there is a "well-known Darwinian ground for expecting groups defined by common descent to share morphological and physiological characters" (Griffiths, 1999, p.219). He explains that this principle maintains organisms in their existing form, acting like inertial force, until some adaptive force changes that form. Griffith calls this phylogenetic inertia and argues that this is what licenses induction and explanation of a wide range of properties (morphological, physiological and behavioral). As I already mentioned, the homeostatic property cluster version of typological thinking can be seen as the way that typological thinking is used in evo-devo, and can be viewed as compatible with evolutionary theory as Griffiths shows. However, the question is whether this homeostatic property cluster account of typological thinking is still committed to what Sober calls a Natural State Model, which is arguably incompatible with evolutionary theory. That is why in the next section I will examine Lewens' account of typological thinking since he seems to defend a form of typological thinking that is very similar to the homeostatic property cluster version, but he argues that typological thinking is not committed to the Natural State Model.

4.2 Lewens' account – typological thinking is compatible with evolutionary theory

According to Lewens (2009), types are explanatory posits - some forms are frequent in nature because they are variations of an underlying type, while others are rare or non-existent because there is no corresponding type. The existence of types as stable forms is compatible with an evolutionary process that explores the limits of, and transitions between, such stable forms (Lewens, 2009). Typological and population thinking are not mutually exclusive if one accepts a somewhat weaker form of typological thinking according to which the nature of stable forms is itself something that can change over time. There might be underlying structural factors that limit the range of possible forms, whereas changing local demands then determine which of the possible forms are actual.

Lewens addresses Sober's (1980) critique and wants to show that typological thinking is not necessarily committed to Natural State Model. He describes "positions of organic stability" which are "sets of physical facts that dictate which organic forms are more or less likely to appear in a population, and which thereby explain constancy in observed patterns of variation over time." (Lewens, 2009). The main point is that these positions of organic stability which are assumed in typological thinking do not necessarily imply a Natural State Model view. In order to demonstrate his point, Lewens offers an analogy with a die that is loaded to land six up:

> For such a die, six is more stable, comparatively speaking, than other orientations. We should expect alternative numbers to come up with regularity, albeit less often than six. Indeed, the facts about the distribution of mass within the die, which make it the case that the die has a particularly high chance of landing six up, are the very same facts which make it the case that the die also has a good chance (a lower one, but still significant) of landing three up, or two up. Twos and threes are less likely than sixes, but their appearance is not anomalous. It is to be expected, just not so often as sixes. Finally, the sorts of causes that lead the die to land six up are of the same type as those which cause it to land two up, or three up. There are no characteristic 'error-inducing' causes which cause the die to land on three or two, nor is there any way of isolating a characteristic set of causes such that were those causes absent, the die would always land six up. A 'position of stability', understood as a set of physical facts determining which orientations of the die are more and less likely to appear, can therefore constitute a characteristically typological notion, which explains a series of varied events, and which demands no distinction between constant causes and the causes of error. (Lewens, 2009)

This is supposed to show that typologists do not conceive of variations as some sort of deviations from the Natural state model, they simply claim that some organic forms are more likely to appear than the other ones, and that this explains constancy in observed patterns of variation over time.

However, if Lewens is saying that the fact that some organic forms appear more often, this can be interpreted as only a fact about statistic regularity. But, there must be something more to typological thinking since according to Lewens' own definition of typological and population thinking, population thinkers do not object to "types" as statistical summaries of the average form, but they are committed to the view that these types do not explain why there is a tendency to that average. So, if there are some organic configurations that are stable and that are represented by types, there must be something that explains that stability, so that when we invoke types in scientific explanations, these types do some explanatory work.

In order to account for this, Lewens invokes "positions of stability" which are supposed to be physical facts that dictate which organic forms are more and less likely to appear in a population, and which thereby explain constancy in observed patterns of variation over time. The main difference between this view and Natural State model is the fact that here there are no different, error-inducing causes which cause deviation from the type; the same causes are responsible for typical and non-typical outcomes. The same way that the distribution of mass in a die causes it to land six up more often, it also causes it to land three or two up, but just not as often. Nevertheless, I am not sure whether Lewens' account really shows that typological thinking is not commited to a Natural State Model. It is true that less likely outcomes are not regarded as deviations or errors and that there are no separate error-inducing causes, but there seems to be a natural tendency of developmental systems to produce certain forms while some forms are impossible to produce. To me this still seems like

a Natural State Model, but I do not think that it should consequently mean that Natural State Model is necessarily incompatible with evolutionary theory.

Furthermore, if we know the set of physical facts that dictate the appearance of organic forms, why we should invoke types? It seems that invoking of the types oversimplifies the situation since it only covers the standard cases where typical organic forms occur, and do not apply to non-standard cases. The answer seems to be that in biology, this set of physical facts that dictate the appearance of organic forms changes so that there is always a degree of uncertainty about the set of physical facts that caused the organic form to occur:

> Development in any given organism is produced by the interaction of numerous resources of many different kinds. Large networks of genes act against complex environmental backgrounds. When the organism reproduces, it is conceivable that any of these elements might change, and with such a change, an altered phenotype may or may not be produced in the offspring generation. Different probabilities can be attached to these different phenotypic alterations. The probabilities we assign will be a function of the configuration of the entire developmental system. (Lewens, 2009, p.365)

So, the question is if typological thinking is just a useful heuristic due to complexity of biological influence, or if it is grounded in the theory of evo-devo. Even though Lewens insists on speaking in terms of probabilities and statistic regularity, he seems to think that typological thinking is justified since there are underlying factors that explain the distribution of properties.

Nevertheless, Lewens thinks that this still does not show that explanations in evo-devo in terms of typological thinking are compatible with evolutionary biology, since there really are major differences in explaining shared structures among reproductively isolated species from the perspective of evolutionary biology (only in terms of adaptations)[8] and from the perspective of evo-devo. The main difference is the fact that evolutionary biology explains conserved traits in terms of low fitness of alternative variants, while evo-devo explains them in terms of low probability of alternative variants. “The “developmental type” is posited as a

[8] One of the evolutionary (adaptationist) explanations of shared structures is known as generative entrenchment. Here shared structures are explained as having arisen early in evolutionary history and they served as a basis for the development of functional structures that arose later in evolutionary time.

structure shared across taxa, which determines which structures are more and less likely to arise in mutation, and hence which governs the probabilities of various evolutionary trajectories independently of the population-level "forces" (selection, drift and so forth) acting on species." (Lewens, 2009, p.365). According to Lewens, if ontogeny is reasonably conservative then developmental structures will remain shared across reproductively isolated groups just in virtue of descending from common ancestors. He goes on to give evidence that ontogeny really is conservative and that the description of developmental types is compatible with the population causation. So, the conclusion is that the fact that ontogeny is conservative and some other facts about developmental factors and processes justify the use of typological thinking in evo-devo and that typological thinking is not necessarily incompatible with evolutionary biology.

I think that these facts that Lewens enumerates that allow for typological thinking to be compatible with evolutionary theory commit him to some kind of Natural State Model view. Nevertheless, I think that this view is compatible with evolutionary theory since these "natural tendencies" really are facts about development and developmental mechanisms that are accepted in evo-devo and are not postulated for its heuristic value. While Natural State Model is not compatible with population genetics since genetic variation is mostly random and unbiased, phenotypic evolution is constrained by developmental biases, so here I do not see a problem in accepting this kind of ontological view. Furthermore, I think that Griffiths has shown that these facts about development being conservative and biased are not incompatible with evolutionary theory since they were already formulated in Darwin's law Unity of Type.

However, one does not need to be theoretically committed to such claims about ontogeny being conservative and about the mechanisms that underlie development. There are authors like Love who defend typological thinking even though they think that it implies an

ontological view that is incompatible with evolutionary biology. Love thinks that typological thinking is a useful heuristic for scientific research in evo-devo, and that we should not be discussing its ontological implications to evolutionary theory but rather focus on the usefulness of that strategy for scientific research. In the next section I will try to present some of Love's argument for this view.

4.3 Turning from ontology to epistemology

Love thinks that the focus should be put on styles of explanatory reasoning, modes of representation, and methodological preferences. "Typology needs to be understood as a form of thinking or reasoning, as conceptual behavior – typological thinking involves representing and categorizing natural phenomena, including both grouping and distinguishing these phenomena according to different characteristics, as well as ignoring particular kinds of variation." (Love, 2009, p.53)

Typological thinking is a scientific tactic that involves representing natural phenomena using idealization and approximation. According to Love, stressing the link between typology and essentialism just keeps the epistemological roles of typology from receiving proper attention. "Typological thinking construed epistemologically is much more broad than metaphysically malfeasant typology of concern to Mayr and others."(Love, 2009, p.67)

> Representational typologies are constructed for the purpose of investigation, explanation and theorizing. Thus, the virtues and limits of strategies used to create these typologies can be assessed on the basis of how well they contribute to these explanatory goals. The appropriateness of an idealization that ignores variation of a particular kind to achieve a more abstract typology depends on the explanatory goals of the disciplinary context in which it is accomplished. (Love, 2009, p.65)

However, one can wonder whether we can we can separate epistemic practices from ontological assumptions. This view can be criticized if we accept Quine's (1948) claim that we are ontologically committed to those entities that are necessary for our scientific theory to be true. Also, Love does not even try to account for the fact that typological thinking is a so

successful strategy. He addresses this as a possible criticism; he refers specifically to Griffiths' (1999) claim that if we want to legitimately use typology in explanations, we need a causal basis of shared properties (metaphysics) since that gives typology its counterfactual force. Love's answer is that he does not argue for the removal of metaphysical questions related to ontology but he only wants to shift the attention to epistemological questions without worrying about ontology. Nevertheless it seems that he does more than that since he seems to say that ontological implications of typological thinking are incompatible with the evolutionary theory, but it is a successful explanatory strategy that should be kept and the ontological implications should be ignored.

If typological thinking is a useful epistemic practice, scientifically useful heuristic, an interesting question that arises is why it is so useful. Is it because of some characteristics of certain biological theories (like evo-devo) or is it maybe grounded in our cognitive abilities, i.e. do we have a reasoning bias to represent the world in the way that typological thinking implies.

CHAPTER 5: IS TYPOLOGICAL THINKING GROUNDED IN OUR COGNITIVE ABILITIES?

In his article against typological thinking in evo-devo, Jenner (2006) describes a situation where he tested the audience at the *Development and evolution of arthropods symposium* and he discovered that almost everybody in audience manifested typological thinking. He saw this as a serious problem: "If this manifestation of typological thinking is accepted as unproblematic, perhaps only implicitly, the door is wide open to serious misunderstandings of important issues in evolutionary biology." (Jenner, 2006, p.386) He thinks that this naïve view can lead to "unfortunate, but preventable errors in thinking".

Where this implicit tendency to typological thinking comes from and why it is still present in trained biologist if it is something so incompatible with the evolutionary theory? One possible answer would be that we have a reasoning bias to think that way. That is why I would like to examine a couple of theories that describe our reasoning about biological kinds. One is a theory by Scott Atran (1998) who claims that all people share a commonsense view of biology that is a product of a core domain of our brain being selected to deal with the living world. The other is a theory by Susan Gelman who describes psychological essentialism, which is supposed to be a persistent reasoning bias that affects our categorization. I will also briefly refer to Keil and Richardson's (1999) account of psychological essentialism.

5.1 Atran – folk biology is a cognitive universal that is still useful as a heuristic in science

Atran (1998) presents an interesting view on how "cognition constraints culture in producing science" (Atran, 1998, p. 574) He describes folk biology as "cognitive universal" – a view on biological taxonomies grouping in species that is shared across different cultures

and that seems to be common to all people. He calls this shared views “habits of our minds” (he supports the view that folk biology is a core domain of human knowledge evolutionarily selected for dealing with the living world). For instance, across different cultures people classify living organisms into something that Atran calls generic species. This generic species concept, according to Atran, provided a “pretheoretical basis for scientific explanation of the organic world” (Atran, 1998, p.575). People share a commonsense assumption that these generic species have an underlying causal nature or essence, and this common nature or essence is supposed to be responsible for the typical appearance, behavior and ecological preferences of that species. These species are also organized in hierarchies (higher and lower level groups) so that this folk biological knowledge is relatively well structured and organized. These groupings into generic species also provide “a powerful inductive framework for making systematic inferences about the likely distribution of organic and ecological properties among organisms” (Atran, 1998, p.575) Atran’s assumption is that folk biology evolved “to provide a generalized framework for understanding and properly responding to important and recurrent features in hominid ancestral environments” (Atran, 1998, p.576). In contrast to this, biology as a science has been developed to understand “an organization of life in which humans play only an incidental role no different from other species.” (Atran, 1998, p.576) However, regardless of these differences, Atran thinks that folk biology and scientific biology still interact, since systematic biology and common sense folk biology still share some core concepts such as the species, taxonomic ranking and teleological causality. However, scientists use these concepts more as heuristics than as ontological concepts.

5.2 Does typological thinking in evo-devo correspond to some form of folk biology?

I am interested in examining if typological thinking is something based in our cognitive abilities or folk biology (according to Atran) that has remained in use in some parts of biology. I am interested specifically in the typological thinking that is used in evo-devo. And if it turns out that it is a reasoning bias, what consequences should that have on the scientific status of typological thinking in evo-devo. However, essentialism in folk biology in the way that Atran describes it corresponds more to the typological thinking that presupposes traditional essentialism with intrinsic essences that cause properties that all and only members of a kind share. The accounts of typological thinking presented in this paper try to describe typological thinking used in evo-devo, and it seems that most authors in evo-devo who use typological thinking do not presuppose traditional essentialism, rather its weaker kind – the relational essentialism (homeostatic property cluster theory).

According to Atran, in folk biology an essence is conceived as an intrinsic physical property that causes all perceptible properties of species. This is the sort of thinking that was criticized by Mayr and Sober when referring to typological thinking. Amundson assumes that there is something that underlies and causes grouping into types[9], but that is not understood as a single physical essence but a whole network of developmental processes and external influences (it is not conceived as something necessarily intrinsic) so it seems that Amundson's view is not reflecting this folk-biological type of reasoning. It is even less plausible that this kind of folk-biological view can be discovered in Lewens' account of typological thinking, since in his view what underlies types and causes grouping into types also causes variations from these types which seems highly incompatible with folk-biological view on essences.

[9] I will not be referring to Amundson's stronger claim since it does not seem convincing that this kind of typological thinking is used in evo-devo

And Love's view is most obviously not a form of this folk-biology view since it does not presuppose any ontology whatsoever.

However, there are other views about how we categorize the world into natural and biological kinds, i.e. about psychological essentialism. For instance, authors like Gelman argue that psychological essentialism is a "pervasive, persistent reasoning bias that affects human categorization in profound ways. It is deeply ingrained in our conceptual systems, emerging at a very young age across highly variated cultural contexts."(Gelman, 2003). Gelman presents three components of psychological essentialism as an intuitive folk belief: 1) people believe that some categories are natural kinds which mean that they really exist in nature independently of us, 2) they believe that there is some unobservable property (the essence) that causes things to be the way they are, 3) they believe that everyday words reflect this kind of categorization (Gelman, 2003, p.7). Gelman defines a causal essence[10] as "the substance, power, quality, process, relationship, or entity that causes other category-typical properties to emerge and to be sustained, and that confers identity" (Gelman, 2007, p.9) Gelman argues that essentialism can be sketchy and implicit, she quotes Medin and Ortony (1989) who propose that people have an "essence placeholder" which stands in place of essence, people assume essence, even if they do not know anything about that essence. This sort of sketchy and implicit essentialism seems like it is similar to the typological thinking as described by Amundson and Lewens since they both assume that there are some underlying processes that cause grouping into types (however it is not similar to Love's views since he does not presuppose any ontological commitments for sorting phenomena into types). What is more important, this kind of essentialism corresponds to the homeostatic property cluster

[10] Gelman makes the distinction between sortal, causal and ideal essences: ''The sortal essence is the set of defining characteristics that all and only members of a category share.'' (…) ''Causal essence is the substance, power, quality, process, relationship or entity that causes other category typical properties to emerge and to be sustained, and that confers identity. (…) The ideal essence is assumed to have no actual instantiation in the world. For example, on this view the instance of ''goodness'' is some pure, abstract quality that is imperfectly realized in real-world instances of people performing good deeds.'' (Gelman, 2007, p. 8,9)

version of typological thinking which I have been assuming that is at the core of both Amundson's and Lewens' account, even though it is not always clear that this can be interpreted as their own view.

According to Keil and Richardson (1999) people have abstract and general ways of choosing explanations of biological phenomena. They examine the claims that the notion of essence had a limiting effect on thinking about species in evolutionary biology and that it is because of Aristotelian essentialism that it was assumed that species have fixed essences and this prevented the scientist from discovering the theory of evolution (Hull, 1965). Keil and Richardson argue that in this critique, the sortal essence (as defined by Gelman) is assumed to play the main role in reasoning about kinds, while for much of folk-biology, causal essences seem to play the main role. And, these causal essences are not on their own incompatible with the notions of species as a probabilistic concept, a distribution of types which is critical in understanding how evolution occurs through natural selection. They think that Boyd's notion of causal homeostasis might easily be a form of causal essence. However, in this case we would need to account for the illusion of fixedness of essence that people usually have. Boyd and Richardson think that this is a product of cognitive bias, where process like causal homeostasis is not appreciated because "processes in general are not preferred or because any probabilistic components to such processes are not allowed" (Keil and Richardson, 1999, p.272).

> A very general cognitive bias may be at work here as well: the tendency to focus on what are known in statistics as main effects and not on interactions. It may be simpler and more cognitively compelling to think of a kind being created by either intrinsic essential properties or environmental forces, rather by an interaction between the two. (Keil and Richardson, 1999, p.272)

According to Keil and Richardson, the question is whether people, when they see that patterns of causal homeostasis result in relative stability of property clusters, mistakenly assume that this is not caused by that homeostatic process but rather by a fixed physical source. They think that the cognitive bias towards essences "might consist of positing a stable property for

living kinds as a kind of simplifying heuristic." (Keil and Richardson, 1999, p. 275) In conclusion, Keil and Richardson seem to think that our reasoning about causal essences is compatible and can be justified by the homeostatic property cluster theory about kinds in biology, but that we might have a bias which leads us to think that causes are some fixed physical sources rather than a whole network of mechanisms and processes.

So, if typological thinking possibly reflects our persistent reasoning bias, what consequences should that have on the scientific status of typological thinking? We have already seen that Atran thinks that some concepts from folk biology can be useful as heuristics in scientific research. Keil and Richardson also seem to think that interpreting biological kinds in terms of causal essences does not necessarily need to be incompatible with the theories of evolutionary biology. On the other hand, authors like Shtulman and Schultz (in press) argue that in the case of species, essentialist beliefs were impediments to the discovery of natural selection and still represent an impediment to learning about and understanding natural selection (Shtulman, Schulz, in press). They try to offer evidence how a form of reasoning very similar to typological thinking prevents people from fully understanding evolution, even if they are well educated about it.

I want to argue that whether typological thinking represents a reasoning bias or not, its value for a scientific theory should be judged according to the criteria and evidence provided by that theory. In some cases and parts of biology it seems that this reasoning bias really is not in accordance with the theory and evidence provided by the theory, while in some other cases typological thinking seems to be grounded in the theory. I will try to demonstrate this by offering as an example the field of microbiology where typological thinking seems to be a reasoning bias that is not grounded in theoretical findings, and contrast it with evo-devo, where I think typological thinking is justified and supported by theoretical findings as a not only useful but also justified strategy.

5.2.1 Typological thinking in prokaryotic systematics

Typological thinking dominates the field of prokaryotic systematics. For instance, bacteriologists agree that species exist and they recognize that "bacterial diversity is organized into discrete phenotypic and genetic clusters" (Doolittle, 2009, p.3) and that species can be recognized as clusters of genotypes which are distinct from other such similar clusters. However there seems to be a consensus that almost no data support this belief.

> In short, no known or likely to be discovered law of Nature will constrain known processes working separately or together to always (or perhaps even often) produce "discrete phenotypic and genetic clusters, which are separated by large phenotypic and genetic gaps" (...), unless "discrete" and "large" are allowed to take a very wide range of values. (Doolittle, 2009, p.4)

Also, many molecular phylogeneticists believe that it is possible to construct a universal tree of life for all living organisms even though there is no evidence that such a thing is possible. Different genes and organismal parts (those which transmit hereditary characters and are thus relevant to evolutionary systematics) have different phylogenies. To obtain a single tree, one must select particular organism parts, such as genes, gene groups, or membranes, and construct a genealogy of these objects. But in order to do this, we must be willing to say that certain organismal parts are of greater importance then others or are essential to organism's identity, while there are no theoretical grounds for assuming their importance. Doolittle (2009) concludes from this that we as humans have a need to make classifications (because of our evolved psychology) but that scientists do not have to believe in these classifications. This seems like a good example of a psychological bias that affects scientific research and in this case I think that typological thinking should either be replaced, or it should be kept if it shows that it is pragmatic to use it for some goals of scientific research (maybe in the similar sense like Love suggests). In any case, scientist should keep in mind that there are no real theoretical grounds for their classifications, and that it is (perhaps) just pragmatic to use them. However, it seems to me that this is not the case with typological thinking in evo-devo.

5.2.2 Typological thinking in evo-devo has theoretical grounds

In the case of evo-devo there are some real theoretical grounds for using typological thinking. According to evo-devo there are developmental mechanisms that make some developmental modifications more likely, some less likely and some impossible, and types represent shared developmental processes and mechanisms. Also, evo-devo biologists claim that the body plan is constantly maintained because of how the ontogeny is structured. It seems that Lewens' claims that there are relatively few stable organic configurations because of underlying structural factors that limit the range of possible form really are based in the theory of evo-devo, so that representing those organic configurations in terms of types seems like a strategy that is well grounded in the theory of evo-devo.

CONCLUSION

The main research question of this paper was whether typological thinking in evolutionary biology is just a useful heuristic or it is grounded in the theory of evo-devo. I have tried to show that typological thinking really is justified by the theory of evo-devo. One of the main problems associated with evo-devo was the opinion that it presupposes essentialist ontology that is incompatible with the modern evolutionary theory. I have described two versions of essentialism and argued that typological thinking in evo-devo presupposes only the weaker kind of essentialism (the relational essentialism) which is not necessarily incompatible with evolutionary theory. Nevertheless, many authors argue that even this version of essentialism is incompatible with the evolutionary theory since it presupposes an ontological view that Sober calls Natural State Model and that does not fit into evolutionary theory. This is the reason why Lewens (2009) wants to show that his account of typological thinking does not presuppose this ontological commitment. I think that this Natural State Model does not fit into the population genetics part of evolutionary theory since genetic variation is mostly random and unbiased, but phenotypic variation is constrained by developmental biases, and some variations are likely to be caused by developmental mechanisms, some are not so likely, while some are impossible. I do not see a problem in saying that there are some natural tendencies[11] in the sense that some properties of developmental organisms are more likely to produce some forms. I think that Lewens (2009) and Griffiths (1999) make some good points about developmental biology being compatible with the evolutionary theory – Grifiths by invoking phylogenetic inertia and Darwin's law of the Unity of Type, and Lewens by relying on the fact that if ontogeny is conservative (which

[11] Perhaps the term natural is not so appropriate since it presupposes some normality in contrast to deviations or errors.

is something that evo-devo supports) then developmental biology is not in conflict with the evolutionary theory.

Nevertheless, the possibility that typological thinking is just a heuristic that makes no ontological commitments should not be excluded so easily, especially since there are some parts of biology that use it as a heuristic (without any theoretical grounds for that). An interesting example of this is prokaryotic systematics where typological thinking is used even though the scientific evidence suggests that there is no ground for that. That is why it was interesting to examine if typological thinking is grounded in our cognitive abilities. The comparison of typological thinking and psychological essentialism has shown that this is a real possibility since there are many similarities between these two types of reasoning. Some authors think that this means that typological thinking is constraining us in understanding evolutionary biology. While I think that this can be true for some parts of biology, I believe that I have shown that this is not the case for evo-devo.

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