FEATURE ARTICLE

Evolution Makes More Sense in the Light of Development

KOSTAS KAMPOURAKIS, ALESSANDRO MINELLI

Abstract

We highlight some important conceptual issues that biologists should take into account when teaching evolutionary biology or communicating it to the public. We first present conclusions from conceptual development research on how particular human intuitions, namely design teleology and psychological essentialism, influence the understanding of evolution. We argue that these two intuitions form important conceptual obstacles to understanding evolution that should be explicitly addressed during instruction and public communication. Given that a major issue in evolution is understanding how very different forms may share common ancestry – antievolutionists have argued that this is inconceivable – we suggest that evolutionary developmental biology (evo-devo), which provides concepts and evidence that large morphological change is possible, could be used to address the intuitions that organisms have fixed essences (psychological essentialism) and that their structure indicates some kind of intentional design (design teleology).

Key Words: Evolutionary developmental biology; preconceptions about evolution; design teleology; psychological essentialism; evo-devo

In 1973, in this journal, Theodosius Dobzhansky published the now famous and much cited article titled "Nothing in biology

makes sense except in the light of evolution." He explained that without evolution, biology is a pile of facts that make no sense as a whole. Here, in a similar vein, we argue that evolution makes more sense to students and the public if it is taught or explained alongside development. Biologists should realize that the idea of evolution is rather counterintuitive, psychologically speaking. Conceptual development research has shown that particular human intuitions, namely design teleology and psychological essentialism, influence the understanding of evolution. Research suggests that humans tend to think of organisms as if they were artifacts, intentionally

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obstacles that should be explicitly addressed during the teaching and public communication of evolution. In both cases, the aim should be to achieve a thorough understanding of the relevant scientific concepts.

Given that a major issue in evolution is understanding how very different forms may share common ancestry - antievolutionists often contend that this is inconceivable - we argue that evolutionary developmental biology (hereafter "evo-devo"), which provides concepts and evidence that large morphological change is possible, could be used to address the intuition that organisms have fixed essences (psychological essentialism), as well as that the adaptation of organisms requires some kind of design (design teleology). Evo-devo is considered here as an important educational tool that can be used to help students and the public understand why organismal properties are not fixed (because there is plasticity, novelty, and - eventually - evolution of form) as well as why organisms are not designed (because they exhibit peculiarities that are the product of the evolutionary history of their lineage and, often, of developmental reprogramming). Implications for the teaching and public communication of evolutionary theory are discussed.

Conceptual Obstacles to Understanding Evolution: Design Teleology & Psychological Essentialism

Science education research suggests that an accurate understanding of evolution is difficult to achieve (for a review, see Smith, 2010). For instance, it has been found that even an active-learning course with integrated evolution content, in which 90% of students have some natural-selection content knowledge and all have completed an undergraduate introduc-

designed with essences fixed for an intended use. Design teleology and psychological essentialism thus form important conceptual tory biology course, may have moderate learning outcomes. In this case, 70% of students employed more than four key evolutionary

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concepts in their responses but, most importantly, only 30% of them employed no misconceptions (Nehm & Reilly, 2007). In another study (Kampourakis & Zogza, 2009), secondary students provided different explanations for the same process in different problemcontexts. In particular, they gave explanations based on natural selection for a process when told the initial state, the final state, and information about predator–prey relations, but purpose-based explanations for a process when they knew only the final state. Why is it so? Evidently, there are important conceptual issues at stake that make evolution seem to be a counterintuitive idea.

Conceptual development research suggests that particular intuitions generate misconceptions, which arise during early childhood and persist into adulthood (Bloom & Weisberg, 2007). It is important to note that these intuitions seem to be deeply rooted and strongly held, so that they are not completely overwritten even by expert knowledge. Such intuitions make the idea of evolution seem entirely counterintuitive and, consequently, difficult to understand. Two important conceptual obstacles to understanding evolution are design teleology and psychological essentialism. It seems that humans tend to intuitively explain the characters of organisms as those of artifacts: being intentionally designed for a role (design teleology) and remaining fixed and determined by the role they serve (psychological essentialism). Teleology and essentialism are considered two major obstacles to understanding evolution (Shtulman, 2006; Kampourakis & Zogza, 2008, 2009; Shtulman & Schulz, 2008; Gelman & Rhodes, 2012; Kelemen, 2012; Kampourakis, 2014).

Teleology is the idea that characters or properties exist for a contribution to some role. Design teleology is the idea that this contribution is the outcome of intention or design (Lennox & Kampourakis, 2013). A large body of research suggests that people tend to intuitively provide teleological explanations of this kind for the characters and properties of organisms from very early in childhood. There is some disagreement on how exactly they do this. One body of research suggests that children provide teleological explanations for organisms and artifacts, but they do so in a different manner because they are able to perceive the differences between them (e.g., the thorns of a rose exist in order to protect it, whereas the barbs of barbed wire exist in order to protect something that is valuable to humans). Another body of research suggests that children provide teleological explanations in a nondiscriminative manner for organisms, artifacts, and nonliving natural objects (e.g., pets exist for loving; clocks exist for telling the hour; clouds exist for raining; for an overview, see Kelemen [1999] and chapter 3 in Kampourakis [2014]). Whatever the answer, there is a general agreement that children tend to intuitively provide teleological explanations for the characters of organisms.

Essentialism is the idea that entities have essences, or underlying properties that are characteristic of them (Wilkins, 2013). Psychological essentialism is the intuition that organisms have essences that are fixed and unchanging. Several research findings support this conclusion. First, children seem to believe that organisms that belong to the same taxonomic group share some underlying, nonvisible properties, and they rely on these properties to draw inferences about the characteristics of organisms. Second, children tend to think that the kind or category to which an organism belongs does not change, whatever changes may occur in the appearance of that organism. Third, children seem to consider internal, invisible features and properties more important than external ones. Fourth, children believe that organisms can undergo radical developmental changes without a change in their identity (for an overview, see Gelman [2003] and chapter 3 in Kampourakis [2014]). Thus, children seem to believe that organisms are characterized by underlying distinctive properties that form their "essence" and thereby make them what they are. These "essences" are unchangeable, so they characterize organisms despite any superficial changes they may undergo.

Given these findings, we consider evo-devo an important educational tool that can help students and the public understand why essences are not fixed (because there is plasticity, accommodation, and eventually evolution of form) and why organisms are not designed (because they exhibit peculiarities that are the product of the evolutionary history of their lineage). This is the topic of the next section.

Evo-Devo as a Tool to Overcome Conceptual Obstacles to Understanding Evolution

Problems with accepting evolution are usually related to explanations of major evolutionary transitions and the origin of complex organs in the absence of design. Such explanations make necessary appeal to a dimension of time we cannot directly experience. However, simply mentioning that earth sciences credit our planet with an age of thousands of millions of years does not make people understand how the human brain or a rose's flower may have evolved. The important point here is that biological forms, including those with the most complex architectures and sophisticated functions, are also the products of development - a process anyone can experience in a variety of different organisms, including humans. Not only is development easier for people to understand than evolution, but any evolutionary change in the mature, adult form of animals and plants is somehow related to modifications of developmental processes. Understanding how a developmental process can be modified, and what the consequences can be, could therefore be a starting point for presenting evolutionary explanations of living forms. Here, we argue that this approach, founded in evo-devo, is a conceptually sound and potentially effective strategy for overcoming people's difficulties in understanding the evolutionary origin of complex organismal traits.

Gilbert (2003b) has made a similar suggestion, stressing the concept of evolutionary novelty, and noted that teaching evolution solely from a population genetics perspective makes it very difficult to explain the origins of traits such as feathers, teeth, and eyes. Paleontology sometimes helps address this kind of question; for example, fossils can be used for the reconstruction of the origin of the stapes, a little bone in the ear of mammals, from a bone (the hyomandibular) of fishes, despite their very different form and completely different function (Brazeau & Ahlberg, 2006; Boisvert, 2013). However, even in well-documented cases, reconstructions of major transitions may remain unclear. The explanation becomes clearer if we can demonstrate that a large morphological change in some character can be the product of a relatively minor change in the expression of one or a few genes implicated in its development.

By shifting attention from the large differences between adult phenotypes to the eventually minor differences between the underlying developmental processes, we diverge from the popular view of evolution that strictly focuses on natural selection (i.e. on the survival



of the fittest). A solid place in the picture is now reserved for the *arrival* of the fittest by way of mechanisms that produce the phenotypic variation on which selection can operate. Development is more than the simple, invariant, and uniquely determined expression of the genotype. In addition, the variation that can be produced in a population is (probably always) not entirely random, but developmentally biased in favor of some alternatives (Arthur, 2004).

More importantly, evolution often seems to offer examples of discontinuities that cannot be explained as the result of a long series of individually small and regularly adaptive changes. Examples (cf. Frazzetta, 2012) are the apparently sudden transition from bilateral symmetry to directional asymmetry in the lineage of flatfishes; the advent of visceral torsion at the base of the gastropod lineage; the displacement of the pectoral girdle from the usual external position to the unique condition in the turtles, in which the pectoral girdle is encased within the ribs (a saltational change according to Gilbert et al. [2001]; a change "not compatible with scenarios of gradualistic, stepwise transformation" according to Rieppel [2001]); or the also unique condition of the two snake species (Bolyeria multocarinata and Casarea dussumieri) endemic to the small Round Island in the Indian Ocean, in which the mandible is represented by two distinct and articulated pieces (a proximal and a distal one), rather than by a single piece as in all other tetrapods. These are exactly the evolutionary changes that, claim antievolutionists, evolutionary theory cannot explain. As Gilbert (2003b, p. 735) said, "creationists are not concerned about antibiotic-sensitive bacteria becoming antibiotic-resistant or about the beak-shape changes of Galapagos finch species," two usual, welldocumented examples of microevolution. These are also the evolutionary changes, and their underlying processes, that students and the public need to understand.

We know how macroevolution is possible: smaller and larger steps are likely mixed along the evolutionary history of life (e.g., Orr, 1998). Through evo-devo, we are becoming increasingly aware of the likely developmental genetic changes responsible for major evolutionary transitions or for the evolution of even the most complex structures. In particular, we can now address the otherwise intractable problem of the origin of major body plans (e.g., the vertebrate, the arthropod, the mollusk) and, thus, of the higher taxa (e.g., Carroll, 1995, 2005; Kemp, 2007). An evo-devo perspective leads us to address these questions in terms of *evolvability* of the concerned structure. There are several, only partly congruent notions of evolvability; we adopt here Hendrikse et al.'s (2007, p. 394) definition of this term as "the capacity of a developmental system to evolve," which depends on the potential of the developmental system to generate variation.

The concept of evolvability applies to single organismal characters that often come out as distinct *modules* (e.g., Schlosser, 2002; Schlosser & Wagner, 2004; Callebaut & Rasskin-Gutman, 2005), either as the domains of individualized developmental processes (*developmental modules*) or as focal targets of natural or sexual selection (*evolutionary modules*). Analyzing the development or evolution of a strictly circumscribed module is certainly easier than trying to understand the development or the evolution of the whole organism, but it is also sensible to ask whether we can ignore the unavoidable *integration* of the individual phenotypic characters, which interact functionally with one another in specifically determined ways. However, modularity does not account for the existence of evolvability, because many of the different interacting parts and processes of an organism lack modularity and because there is no one-to-one correspondence between recognized developmental and phenotypic modules. In addition, natural selection operates on organisms as wholes and not exclusively on single characters (Kemp, 2007).

This suggests that the evolution of the different parts of the body is subjected to correlated progression (Lee, 1996; Budd, 1998; Kemp, 1999, 2007). This process can best be understood if approached from the perspective of the evolution of development. As noted by Klingenberg (2008), development produces covariation between characters that can have substantial implications for understanding genetic variation and the potential for evolutionary change. A nice example is the coevolution of human hands and feet studied by Rolian et al. (2010). By addressing evolution from an evo-devo perspective, it is vital to avoid a simplistic (and unwarranted) view of the relationships between genes and bodily organization, the so-called "genotype→phenotype" map (e.g., West-Eberhard, 2003). The important phenomenon here is pleiotropy, the multiple phenotypic effects of the expression of individual genes.

Two other phenomena deserve attention in this context. The first is phenotypic plasticity, the fact that genetically identical individuals may develop specifically different phenotypes according to the environmental conditions to which they are exposed during development. Examples are the solitary versus gregarious morphs of migratory grasshoppers, the worker versus soldier casts of many ants, and even the female versus male of the alligator and other reptiles. This means that development is not uniquely determined by genes. However, these environmentally controlled alternative phenotypes eventually fall under genetic control, as the case of the pea aphid (Acyrthosiphon pisum) may demonstrate (Brisson, 2010). In this insect, males are either winged or wingless, depending on a singlegene genetic polymorphism (Braendle et al., 2005a), but the gene locus (aphicarus) responsible for male wing type is also involved in the polyphenic response to varying environmental cues that causes presence versus absence of wings in the females (Braendle et al., 2005b).

The other phenomenon is saltational evolution. Contrary to Darwin's own views, and to the mainstream, neo-Darwinian perspective on evolution, rapid (nearly instantaneous) evolutionary leaps are indeed possible. For more than a century, to accept saltational evolution as a major explanation for macroevolutionary transitions was strictly banned as heretical. Things are different today, however, because of an appreciation of the nonlinear character of the genotype—phenotype map. A single-gene mutation was probably responsible for the change from radial to bilateral symmetry in the orchid flower (Theißen, 2009), and a similarly small genetic change may have caused a sudden duplication of the number of leg pairs in a lineage of scolopenders (Minelli et al., 2009).

Conclusions & Implications for Evolution Education

Defining evolution as "a change in gene frequencies due to natural selection of randomly occurring variations" is not sufficient for a conceptual understanding of evolution. The reason for this is that it is difficult to conceive how the accumulation of variations through selection can produce more complex or very different structures compared to those in the ancestors. By contrast, the integration of development with evolution that is advanced in evo-devo explains

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more sufficiently that small changes in the developmental processes can have significant effects on morphology, and so complex and functional structures do not emerge from the simple accumulations of variations but, rather, from the reorganization and reprogramming of extant structures and developmental modules (for detailed examples, see Arthur, 2011). Thus, what evo-devo adds is the idea that it is not adult phenotypes that evolve but their developmental trajectories. The question then asked is not how adult form A evolved to B, which may be difficult for students to conceive if A and B are morphologically very different. Rather, the question asked is how the developmental process that produced A evolved to one producing B. By realizing that some elements of these processes are common and that minor changes in molecular networks can have significant phenotypic effects, it would be easier for students to conceive of how evolution of complex forms takes place.

The concepts of evo-devo discussed here can be used as educational tools to help effectively address students' preconceptions about evolution, namely design teleology and psychological essentialism. If students tend to intuitively think that organismal properties are fixed and thus unchangeable, the concepts of plasticity and novelty could be crucial to explaining exactly how organismal properties (essential or not) may change in the course of evolution. Most importantly, if students tend to intuitively think that organismal parts are designed to serve a purpose, evo-devo helps explain that they are not designed, because they exhibit peculiarities that cannot be the product of design but, rather, are produced by the evolutionary history of their lineage. It would also explain that the apparently designed structures that effectively serve some function can evolve through minor changes in development that produce major changes in morphology - which, in turn, could be selected for the advantage they confer to their bearers. In short, if it is difficult to conceive how evolutionary change is possible because one cannot understand that changes in "essential" properties are possible or because structures seem to have been designed for some function but not for some other, evo-devo helps explain with concrete examples that organisms can change significantly through minor changes in their genomes and acquire new structures in the course of evolution.

If we accept that an evo-devo perspective on the diversity of life can be effective in reducing resistance to accepting evolution and, specifically, macroevolutionary change – we must acknowledge that a major change is required to the educational literature on this subject. Ten years ago, Arthur (2004, p. 193) lamented the chasm, in introductory undergraduate texts on evolution, between the treatments of microevolution and of evo-devo, respectively - provided, of course, that the latter topic was even covered in the text: "What you will probably find is that the evo-devo material is organized around homeobox genes and their developmental effects, with some speculations about their evolutionary significance." Exactly in the year this remark was published, the first paper was also published of what we might call a "popgen/devgen" (cf. Gilbert, 2003a) literature - that is, a study establishing a bridge between population genetics (and microevolution) and developmental genetics (and developmental evolution). Specifically, that study (Abzhanov et al., 2004; also see Abzhanov et al., 2006) illustrated the developmental genetic basis of the variation in bill size and shape in Darwin's finches, one of the most popular subjects of microevolutionary studies (e.g., Grant, 1986; Grant & Grant, 2008). Let's hope that science educators responsible for teaching evolution will soon be convinced of

the strategic importance of using this well-investigated case, and others that are progressively enriching the evo-devo literature, as an exemplary tool to help their students understand evolution. There are several introductory (Arthur, 2004; Carroll, 2005; Minelli, 2009; Bateson & Gluckman, 2011) and more advanced (Hall & Olson, 2003; Arthur, 2011; Stern, 2011) books that could be used by educators for this purpose.

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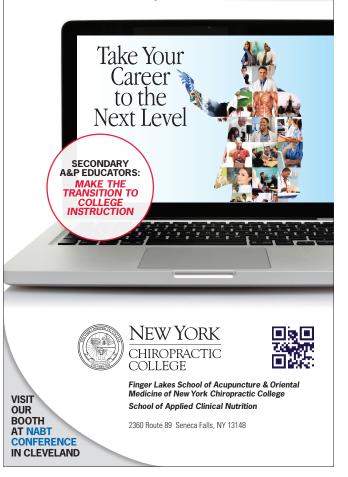
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