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Review article

Development is an evolutionary phenomenon

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Abstract. EvoDevo called homeotic genes "architect genes" because they "control" "body plans". The first metaphor involves purposefulness and brings finalism; the second one is cybernetic; the third one is idealistic/platonic. These are three ways of thinking that are incompatible with today's evolutionary theory. Using such ordering causal factors, EvoDevo partly stayed outside biology—and evolution as well—because in biology, order is not causal: it is a consequence that we need to explain. Natural selection is one of the concepts explaining the rise of apparent short-term biological order, or regularities. We no longer need the verb "to control" [Nijhout, *Prog. Biophys. Mol. Biol.*, 169–170 (2022)]. Since genes are controlled [Noble, *Interface Focus*, 7 (2017)], just as much as they control, the notion of control in this context is not appropriate. It would be better to speak of "contribution". *Natural selection* and *descent with modification*, the two pillars of the Darwinian approach to life [Gayon, *C. R. Palevol*, 8 (2009)], are entering the soma. They are not restricted to the functioning of the adult soma, but also to the entire developing soma, avoiding "adultocentrism" [Minelli, *Toward a Theory of Development* (2014)]. The first pillar, natural selection within the body, anticipated by [Roux, *Der Kampf der Teile im Organismus: Ein Beitrag zur Vervollständigung der Mechanischen Zweckmässigkeitslehre* (1881); Roux, *La lutte des parties dans l'organisme* (2013)], but occulted during the past century [Heams, *La lutte des parties dans l'organisme* (2013b)], is now helping to explain cancer dynamics, aging, neurogenesis, etc. With the second pillar, it is now possible to construct the phylogeny of cells of a single developing organism, or to perform a phylogenetic analysis of metastases from a single patient. Ontogenesis and phylogenesis are no more two distinct processes: *natural selection* and *descent with modification* both contribute to explain both the developing individual and its stability, as well as the regularity of individuals of a same population from which we name species. The two pillars of evolutionary theory—descent with modification and natural selection—do occur within the developing organism itself and the resulting phenomenon is ontophylogenesis [Kupiec, *L'ontophylogenèse. Évolution des espèces et développement de l'individu* (2012)], which is actually studied by EvoDevo.

Keywords. Descent with modification, EvoDevo, Genetic program, Natural selection, Ontogenesis, Ontophylogenesis, Phylogenesis.

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This paper is dedicated to André Adoutte (1947–2002), who developed a true passion for phylogenetics and development.

If we define living organisms by their abilities to reproduce, develop and evolve, the discovery of developmental genes has permitted to associate these three phenomena and incorporate them into the evolutionary theory. However, the corresponding field of research called "EvoDevo" adopted into its deserving and fruitful research program idealistic views where order (things are at the "right place")

and instruction (the order to come is already written) are the causes of biological phenomena. Genetic control, genetic program, architect genes, phylotypic stages, body plans do ensure order. The point we would like to raise here is that these platonic ideas have prevented development from being fully viewed as an evolutionary phenomenon. It seems to be useful because, although EvoDevo is not a homogeneous field, these ideas are still in use in most of today's Evo-Devo practitioners in their most visible papers. Last but not the least, EvoDevo did not develop those ideas, but rather borrowed them from the classical comparative anatomy of the early 19th century (e.g. body plan, see Schmitt, 2006) and the history of molecular biology, rooted in Erwin Schrödinger's *What is life* (1944), (Fox-Keller, 2000; Fox-Keller, 2002; Morange, 2003; Kremer-Lecointre and Lecointre, 2023, p. 197).

1. Background

When is a theory called "Darwinian"? Two pillars are classically required (Gayon, 2009): natural selection and descent with modification. Natural selection occurs when three conditions are met among the entities considered (individuals, cells, viruses, behaviors, etc.). First, these entities spontaneously vary at random. "Random" means (1) that we don't focus on the cause of the variation; and (2) that the new version of the trait where variation just occurred can be disadvantageous to the entity, or neutral or else advantageous in terms of its transmission to other entities of the same kind. Second, this new version is subject to transmission to other entities, whatever the process of transmission (mitosis, infection of a cell where copies will be produced, sexual reproduction, mimicking, learning, etc.). It is heritability, and the spectrum of properties involved strongly widened during the last 25 years (Danchin and R. H. Wagner, 2010; Danchin, Charmantier, et al., 2011; Laland et al., 2015; Laland, 2022; Danchin, 2022; Danchin, 2023). Both the "inclusive evolutionary synthesis" (Danchin, 2013; Danchin, 2022) and the "extended evolutionary synthesis" (Laland et al., 2015) consider that variance heritability with evolutionary effects extends far beyond DNA sequences. At this step, if no constraining conditions are met, frequencies of different variants will fluctuate at random in the illimited population: this is called drift. In the presence of constraining conditions, only variations that favor the number of its copies among descendants will have an increasing frequency; possibly reaching 100% if differences among competing variants at the same trait are maintained all along the process. Indeed, a fourth condition has sometimes been put forward (e.g. Danchin, 2022, p. 39): for natural selection to occur, heritability of the variant is required, for sure, but it is not sufficient: there must be heritability of differences among variants.

The second pillar is descent with modification. Traits that are shared by entities which do not mix in any way must have been inherited from past ancestors, dating back to the times when the new trait appeared and increased within a single mixing population. Since then, generations have followed each other, possibly through two diverging genealogies leading to the two extant separated entities. Modifications continued to occur all along the two genealogies (*modification*), explaining why entities are different today. But they still share some traits in common (explained by descent). This principle allows the reconstruction of phylogenies. Genealogies being empirically inaccessible (ancestors have disappeared), the search of ancestor-descendant relationships is an epistemological dead-end. But global genealogies can be partly inferred through the search for sister-group relationships, a methodology brought by Hennig (1950) and Hennig (1966). Therefore, producing a hierarchy of shared traits among entities (under the mathematical form of a "tree") reflects phylogenetic relationships. In certain circumstances, horizontal transfers or fusion of organisms seem to challenge the form of that "tree"; however, it does dot. We must see the mathematical form of a "tree" as a tool to depict a hierarchy of properties, or "relationships", even when these relationships are not phylogenetic. Horizontal transfers can be represented using several such trees.

Considering these general principles, it is obvious that everything that biology has to deal with begins with *variation* (e.g. with neither instructions nor order). Charles Darwin dedicated an entire book to it (Darwin, 1868). It is the concept embedded at the very core of natural selection, drift, and descent with modification. Biology is the science of variation. Not in the sense where one should explain the causes of each variation taken separately. Physics and chemistry already have theories and methods to

take it in charge. Biology is biology because it focuses on the global consequences of such variations at the population level, whatever their individual tiniest causes.

2. Where is variation when order is causal?

"Genetic control" and "genetic program" come from cybernetics (Fox-Keller, 2000; Fox-Keller, 2002; Peluffo, 2015), not biology (Segal, 2011; Heams, 2013a; Nijhout, 2022; Kremer-Lecointre and Lecointre, 2023, p. 197). "Architect genes" is a finalistic, DNA-centered metaphor (Kremer-Lecointre and Lecointre, 2023, p. 228), as used for instance in Philippidou and Dasen (2013). The notion of "Phylotypic stage" comes from circular reasoning (Hejnol and Dunn, 2016) which maintains an essentialist view of animal phyla (taxonomic realism Lecointre, 2021, pp. 147–148). "Body plan" is a platonic, idealistic concept (Kremer-Lecointre and Lecointre, 2023, p. 184) that should be replaced by phylogenetic mosaics (Takhtajan, 1959)'s and Hennig (1965) and Hennig (1966)'s heterobathmy of characters). These concepts all use the notion of instruction: the order (biological organization, regularities to come) is already written somewhere and development is the unfolding of a program. These concepts were all ignoring biological variation as the fundamental biological phenomenon. Nijhout (1990) diagnosed:

> The concepts that genes control development and morphology, that genomes contain developmental information, and that development follows a genetic program pervade modern thinking in molecular, developmental, and evolutionary biology. The genome is assumed to encode higher levels of organization. Genes and their products are seen as the causative agents of differentiation, and controlled gene expression is seen as the driving force of progressive change in development. The crucial regulatory role attributed to genes is emphasized by the widespread acceptance of the notion that a substantial number of genes are specifically concerned with the orderly progression of events during development. As a consequence, it is assumed that an understanding of the mechanisms of gene regulation and of the detailed structure of the genome are not only fundamental to an understanding of development but virtually sufficient for this understanding.

Several decades later, in a remarkable critical analysis of genetic control and genetic program, Nijhout (2022) confirmed:

> Genes code for the sequence of nucleotides in RNA. That's it. Everything else about an organism plays out at higher levels of organization, where RNAs make essential but circumscribed contributions, mostly through the production of proteins. This basic fact has been known for a very long time and is codified as the Central Dogma of molecular biology. Yet, research published in technical journals regularly ascribes special properties to genes and genomes that greatly exceed their actual mandate of coding for proteins. Among other things, they are said regularly said to 'control' various biological parts and processes, ranging from other genes to complex morphologies. Similarly, genes and genomes are also said to contain 'programs' and 'blueprints' for cells, tissues, organs, behaviors, and even entire organisms. These claims have been commonplace for decades (...), yet authors who appeal to genetic control, programs, and blueprints seldom—if ever—define what exactly they mean by these terms. It has long been recognized that these terms are actually metaphors that, perhaps, need no definition because they describe processes that need no definition because they are commonly used in day-to-day life (...). In particular, the idea that genes control development is now widely accepted, and often simply taken for granted. This understanding of what genes do has regularly been called into question, but research practices have seldom changed as a result. One reason why criticisms of the genetic control paradigm have been ineffective is that efforts to dethrone genes from their seat of causal primacy have often been accompanied by calls to install some other purported controller in their place (Waggoner and Uller, 2015). This simply trades one king for another. An alternative way to approach the problem is to reject the notions of control and master regulation entirely.

Genes are partners, not "controllers". The ideas rejected by Nijhout have their deep roots in the idealistic morphology of the German nineteenth century and preformationist thinking of the seventeenth century (Tort, 1998): the phenotypic order is sufficiently

explained by a microscopic order where the homunculus is replaced by the "genetic program" (Kupiec and Sonigo, 2000; Heams, 2013a). The fact is, such ideas are not compatible with evolutionary biology. In modern biology, order does not explain anything; it is what we need to understand based on disorder and changes at the chemical scale that produce variations. If the explanation of the regularity of forms between adult cats and their offspring is "because there is a cat genetic program", we have explained nothing at all. Vignaux (1977, p. 15) already pointed out the circularity of Lwoff's claim (1969):

> La seule source d'ordre biologique est l'ordre biologique.

Development is not the unfolding of a program (Heams, 2013a; Moczek, 2014, p. 224; Kampourakis, 2017, pp. 172–173), it is a construction (Laland et al., 2015).

Charles Darwin (1859) revolutionized biology precisely because, with the principle of natural selection, he explained apparent order (regularity of forms in a same species and fit between forms and functions) from disorder (random variation), ignorantly importing Moreau de Maupertuis (1751, p. 15)'s intuitions into science. During the twentieth century, biochemistry, molecular biology (molecular genetics included), molecular physiology, medical research, and EvoDevo were non-Darwinian, in that sense. These disciplines tried to explain biological order from biological order, ignoring that natural selection was a concept already available to explain an apparent order (or regularity) at a given scale of space and (short) time from disorder at a lower scale. Indeed, natural selection eliminates extreme variations, then ending up with an impression of regularity to our eyes. Unfortunately, the Nobel laureates Lwoff, Monod and Jacob tried to explain macroscopic order as a consequence of a sufficient microscopic order (instructions from a program). Mayr (1961) did the same by introducing the "program" and the associated concept of teleonomy to eradicate suspicion of teleology in biology, in order to explain the apparent purposefulness of organisms and their characteristics. In a less sophisticated manner, Jacob (1970, p. 17) did not mention teleonomy but confessed:

> Longtemps le biologiste s'est trouvé devant la téléologie comme auprès d'une femme dont il ne peut se passer, mais en compagnie de qui il ne veut pas être vu en public. À cette liaison cachée, le concept de programme donne maintenant un statut légal.

When biology makes a causative use of order (e.g. by using a genetic upward causation), biology thinks outside its own theory. Put in another way, evolution and above all, evolutionary thinking, must fully enter the soma and its development. EvoDevo is just starting this mutation four decades after its birth.

3. Order and regularity: causes, or consequences?

During the last third of the 20th century, the genetic program accounted for the regularity and repeatability of developments. Other processes, such as self-organization and the stabilizing effects of intricat networks of genetic influences, have been evoked to account for their stability (Guo and Amir, 2021) and repeatability (i.e. robustness). Later on, robustness was better explained by homeostatic mechanisms, which dynamically maintain forms and functions against varying environments and genetic variation (Nijhout et al., 2019; Nijhout, 2025). In developing organisms, such homeostatic mechanisms "make the progression of morphogenesis relatively insensitive to genetic and environmental variation so that the outcomes vary little, even in the presence of severe mutational and environmental stress. Accordingly, developmental systems give the appearance of being goal-oriented" (Nijhout et al., 2019).

In parallel, natural selection was taught as a factor of change. Natural selection was supposed to explain how a species changes over time. To account for a repeatable developing organism, researchers did not need a factor of change, but factors of stability and robust repeatability. The genetic program played that role. Then, during half a century, we were taught that the regularity of species was ensured by the genetic program and the change of species by natural selection. This view is a consequence of species realism, maintained, among others, by Ernst Mayr. Mayr gave priority to understanding what a species is, here and now in synchrony, privileging processes over patterns, leading to its "biological concept" of species. Species being the given (Table 1), so one has to explain how the given species changes. Other authors like Georges Simpson gave priority to understanding species in diachrony, privileging patterns

Table 1. Effects of Mayr's species realism, and the present "coming back" to the original Darwin, after Lecointre (2015a) and Lecointre (2015b)

Century		What explains	What is to be explained	The given
18th	Linnaeus	God	Regularity	Species
19th	Darwin	Natural selection	Regularity and change	Individuals
20th	Mayr	Natural selection	Change	Species
21st		Natural selection	Regularity and change	Individuals

over processes. The first approach tends to species realism (the given is species), the second favors a perception of species as a linguistic convention. In this second approach, the given being varying individuals, then one has to explain how a species does not change: this was Darwin's approach. Today, the theoretical phylogenetic definition of species is a set of individuals being members of the same genealogy as long as this genealogy is not split. If there is a split, whatever the reason, another species name must be given to subsequent daughter branches. Empirically speaking, a species here and now is just a hypothesis made by taxonomists. It is the hypothesis that all known members are parts of a same isolated genealogical lineage. This hypothesis is supported by several criteria, the most common being similarity and interbreeding, and is made to facilitate language and communication. The modern phylogenetic concept of species is nominalist: what does exist are individuals.

Going back to Darwin (1859), species are conventions aimed to name a certain degree of similarity among individuals. What is given is not the species itself, but individuals (Table 1). This is the reason why he could pay attention to variations among them (contrary to Linnaeus, who explicitly neglected variation). Darwin offered a nominalist explanation of the origin of species by asking the question: given the variation among individuals that do interbreed, what is the cause of similarity among individuals? Natural selection, in the short term, explains similarity: each generation is pruned, with extreme variants being eliminated. From the resulting similarity, we do create species for the needs of our language. Thus, for Darwin, first of all natural selection acts as a stabilizing factor. We just have to consider the profound meaning of the subtitle of his main book, The origin of species by means of natural selection or the preservation of favoured races in the struggle for life. The words evolution, transformation or transmutation are absent. The word "preservation" is used to specify the permanence of something. Obviously, in the long term if the environment changes, the mean form of the species will change. But first of all, natural selection explains apparent stability and similarity, i.e. regularity across individuals. In other words, apparent order is the short-term consequence of natural selection.

This was neither fully understood nor taught during the last third of the last century because the genetic program replaced natural selection within the soma to account for its stability.

4. Natural selection within bodies

For many decades, the cause of regularity and "fine tuning" of somatic functioning has been thought as the result of a program. It is time to replace the notion of program with natural selection among cells, without excluding (1) the stabilizing effects of intricate consequences of many genetic impulses ("genetic networks"); (2) at certain molecular levels, self-organization; and (3) homeostatic mechanisms (Nijhout, 2025). Roux (1881) and Roux (2013) introduced natural selection within the organism. Darwin read the book a year before his death and declared in a letter to G. J. Romanes (Heams, 2013c):

> As far as I can imperfectly judge, it is the most important book on evolution which has appeared for some time.

A century later, the concept of natural selection was locally introduced into some somatic processes described by neuroscience (e.g. Edelman's "neural darwinism" in 1987, and his opposition to instructionist approaches, both in immunology and in neurocience). Immunology has also been one of the first biological fields to move away from

instructionist schemes of explanation, as early as 1966 (e.g. Brenner and C. Milstein used random somatic hypermutation of immunoglobulin genes to explain immunoglobulin diversity, G. Edelman and J. Gally used random somatic gene recombinations as a source of immunoglobulin diversity, MacFarlane Burnett's "clonal selection" being different than what we call here natural selection). Cancerology did it soon after (Nowell, 1976; Sonnenschein and Soto, 1999; Soto and Sonnenschein, 2005). Soto, Sonnenschein and Miquel (2008) summarized the role of physicalism and downward causation in developmental and cancer biology of the past century. Above all, at the very end of the last century, two major theoretical advances took place. First, variation (and not instruction) is at the source of any phenomenon occurring within and among cells—already anticipated by Edelman—was generalized when gene expression itself began to be understood as stochastic, culminating with the remarkable study of Elowitz et al. (Elowitz et al., 2002; Raj, 2008; Kupiec, Gandrillon, et al., 2013; Heams, 2013b). Second, Kupiec (1997) based his views on the fundamental stochasticity of gene expression to propose a Darwinian theory of cell differentiation (Kupiec, 2014). Today, the stochasticity of gene expression in cell populations, i.e. random variation among cells, appear to have a better explanatory power than instructionist models to understand the development and the functioning of an organism (Kupiec, 2012; Noble, 2017). As a result, studies of cancer and aging now fully adopt models involving natural selection (Nelson and Masel, 2017) and metastasis is considered an evolutionary process (Turajlic and Swanton, 2016). Grajzel et al. (2020) perfectly summarized the present state of the art by the formula:

> Cancer is a genetic disease fueled by somatic evolution.

Somatic evolution is not only for cancerous cells, but for all cells. Among them, we find somatic variation (indeed to a very high degree among tumoral cells), transmission (through mitosis) and constraints (nutrients, space, etc.). These are the three fundamental conditions to obtain natural selection of some cellular lineages over others. In the past decade, cancer and evolution made the front pages of the most visible journals (Willyard, 2016) and therapies based on evolutionary reasoning are developed and appear to be successful (Enriquez-Navas et al., 2016; Degregory and Gatenby, 2019a; Degregory and Gatenby, 2019b; Thomas, 2019).

A remark should be made here about the different words "regulation", "control" and "instruction". A multicellular organism is a colony, and we have to consider the fitness of the colony. In tumors, it can be argued that cells do not evolve anymore for the benefit of the colony, escaping coordination with their neighbors. So, this is the tumorous cell's own fitness (reproductive potential) that predominates in cancer cell competition, precisely because they have escaped most homeostatic phenomena. But normal development is not a mildly managed tumorigenesis. It is anti-tumorigenic, heavily constrained, as a whole and as a result of organismal selection. Regulation is predominant, in the sense that cells actively prevent the proliferation of their neighbors. We don't have open-ended evolution as in a population within an ecosystem. Not only that, but there is active elimination of extreme variants ("sick cells", see for instance Kajita et al. (2010)). One can argue that this is because cell populations in a given organ are strictly confined in numbers and volume at any stage of development, allowing for the evolution and predominance of homeostatic mechanisms. So, there is a component of "order" in selection at the level of the multicellular colony that predominates over the individual fitness of cells in the developing individual. However, here regularity could be better designated by "regulation" rather than by "control" or "instruction".

5. Descent with modification within (developing) bodies

It is now possible to reconstruct a phylogenetic tree of metastases from a single patient (Zhao et al., 2016). The comparison of transcriptomes of single cells made it possible to reconstruct the phylogeny of tissues of a developing zebrafish (Farrell et al., 2018; D. E. Wagner et al., 2018), or the phylogeny of tissues of the frog *Xenopus* (Briggs et al., 2018). Interestingly, the tissues that were traditionally considered to be homogeneous in origin (endoderm, mesoderm, ectoderm) actually are not. Surprisingly, there are several ways to develop a vertebrate: in the frog, ectoderm is paraphyletic and mesoderm is monophyletic, while in the zebrafish

Table 2. From the origins of biology, reification of species and individuals has led to separate two distinct phenomena: phylogenesis and ontogenesis

Reified entity	Components	What is to be explained	What explains
Individuals	Cells	Ontogenesis	Genetic program
Species	Individuals	Phylogenesis	Descent with modification
None	Cells and individuals	Ontophylogenesis	Natural selection and descent with modification

In the latter, the "genetic program" replaced the short-term stabilizing effects of natural selection (and other homeostatic mechanisms). Ontophylogenesis corrects this philosophical heritage (after Lecointre et al., 2020).

ectoderm is monophyletic and mesoderm is paraphyletic (mesoderm gives birth to endoderm). This is a strong experimental argument against the vertebrate body plan, and the notion of "body plan" in general (Kremer-Lecointre and Lecointre, 2023, p. 184); the true phylogenetic reasoning invites us to view patterns and processes as evolutionary mosaics. More recently, the lineage tracing of human development was obtained through the phylogenetic analysis of somatic mutations (Chapman et al., 2021), allowing to discover the hypoblastic origin of extra-embryonic mesoderm and primitive blood. Schmid-Siegert et al. (2017) could reconstruct the phylogeny of somatic mutations in a single oak. Actually, the view of a phylogeny reconstructed from parts of a single organism had been initiated long ago by Fitch (1970). By defining orthologous genes and paralogous genes among different copies within a multigenic family (e.g. globin genes), he already conceived that a phylogeny of different elements of an individual could be constructed.

6. What EvoDevo is actually studying: ontophylogenesis

If natural selection and descent with modification—the two pillars of Darwinian evolution—are now fully considered as explanatory within the developing body, then development is understood as an evolutionary process. EvoDevo becomes EvoEvo, in a way. Moczek (2012) formulated this idea as an epistemological program: "*development should be nested within a theory of developmental evolution*". Kupiec (2009) and Kupiec (2012) already developed the idea that ontogenesis and phylogenesis are two facets of the same general process of life deployment and diversification called *ontophylogenesis* (Kupiec, 2009; Kupiec, 2012). As already mentioned above, there is no process of cell deployment in the individual development that is ontologically separated from the process of deployment of a species. Ontogeny and phylogeny are a single process of diversifying lineages of entities that are submitted to natural selection. In the absence of any platonic invariants, like "the genetic program" or "the body plan", and in the absence of reification of species, phyla or individuals, EvoDevo would already have achieved Moczek (2012) and Moczek (2014)'s program of "building a theory of developmental evolution", which is ontophylogenesis (Table 2).

7. Conclusion

By viewing development as an evolutionary phenomenon, we don't refer to the idea of "recapitulation" of Étienne Serres (1786–1868), Johann Friedrich Meckel (1781–1833) and Ernst Haeckel (1834–1919). For these authors, developmental stages reflect the past history of organisms and as such, are constructed as an argument in favor of transformism, soon called "la théorie de l'évolution des formes organiques", a remarkable modern expression brought by Gérard (1845, p. 212, 219) (Laurent, 1987, p. 384). The point here is that the developmental process involves basic phenomena that make a given transformation an example of *Darwinian evolution*. In development, natural selection among cells is at play, as well as homeostatic mechanisms (Nijhout, 2025), to explain functionality, regularity and robustness. Müller (2007) reviewed how EvoDevo's results "*take evolutionary theory beyond the boundaries of the Modern synthesis*", which is a way of promoting EvoDevo's scientific

Table 3. Replacement of cybernetic/idealistic/finalist metaphors by pre-cybernetic, truly biological terms in order to view genes as partners (not "controllers") and to make development as an evolutionary phenomenon

End-20th century metaphors	To be replaced with
Genetic control	Genetic contribution**
Architect genes	Upstream-effect genes*
Genetic program	None
Phylotypic stages	None
Body plan	Phylogenetic mosaic

* Or homeotic genes (in the sense of Bateson (1894)'s homeotic mutations).

** Or just "genic action" of H. J. Müller or T. H. Morgan.

fecundity, for good reasons (Minelli, 2014). But there is still a paradox: EvoDevo continues to publish papers full of instructionist and/or platonic metaphors. Sometimes metaphors are productive for a certain time span, and finish to become an obstacle later (Kremer-Lecointre and Lecointre, 2023). As nicely summarized by Peluffo (2015):

> However, metaphors that 'illuminate matters quickly and efficiently' may dim 'with time and frequent *usage*' (Wilkins, 2013) until they no longer capture the complexity of the field to which they belong.

EvoDevo should fully enter evolutionary thinking, to which, paradoxically, it contributes: contrary to Lwoff (1969), biological order does not come from biological order. Biology is neither physics nor chemistry. Biology is biology because its explanations do not deal with invariants like universals and laws, but with historical singulars and their variations (Gayon, 2003). To do so, EvoDevo should abandon the platonic metaphors of body plan, phylotypic stage, and the associated taxonomic realism, which are clearly potential sources of methodological bias (Levin et al., 2016; Hejnol and Dunn, 2016). They should be replaced by words embedded within a true phylogenetic way of thinking (Table 3). The diversity of organismal patterns unfolds through time as mosaics, not plans: this is what Takhtajan and Hennig called heterobathmy of characters, and EvoDevo has already introduced phylogeny into the soma to depict its development. EvoDevo should abandon the instructionist notions of genetic program and genetic control as well; natural selection and homeostatic mechanisms being stabilizing sources. EvoDevo is the right place to unify biology. There should not be two separate theories in biology, the one explaining the rise of the reified individual through the unfolding of an instructionist program, and the other explaining the rise of a reified species through natural selection. The achievement of the EvoDevo program should be ontophylogenesis, where descent with modification and natural selection enter into the somatic development from egg to death. This change is ongoing, better explaining cancers and aging, among other phenomena occurring within consortia of cells.

Declaration of interests

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