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Development and natural kinds

Some lessons from biology

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Abstract While philosophers tend to consider a single type of causal history, biologists distinguish between two kinds of causal history: *evolutionary history* and *developmental history*. This essay studies the peculiarity of development as a criterion for the individuation of biological traits and its relation to form, function, and evolution. By focusing on examples involving serial homologies and genetic reprogramming, we argue that morphology (form) and function, even when supplemented with evolutionary history, are sometimes insufficient to individuate traits. Developmental mechanisms bring in a novel aspect to the business of classification—*identity of process-type*—according to which entities are type-identical across individuals and natural kinds in virtue of the fact that they form and develop through similar processes. These considerations bear important metaphysical implications and have potential applications in several areas of philosophy.

Keywords Natural kinds · Developmental biology · Causal history

1 Introduction

In metaphysics it is typical to classify individuals and natural kinds in terms of form, function, and causal history. Attention to the natural sciences, however, suggests a

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finer-grained picture. While philosophers consider a single type of causal history—a sequence of events, closed under causal dependence, which includes and terminates with an event under scrutiny (Lewis 1986a)—biologists commonly distinguish between two types of causal history: *evolutionary history* and *developmental history*.[1] Evolutionary history, which traces an individual (species, organism, or trait) back to its ancestors, fits in well with traditional metaphysical discussions of causal history. In contrast, developmental history—which specifies the processes and mechanisms that are responsible for the ontogeny of an individual—brings in novel aspects to the business of part-identification.

Despite its prominence in the biological sciences, the significance of developmental history for the metaphysics of individuals and kinds is still awaiting appraisal. The goal of this essay is to study the peculiarity of development as a criterion of classification, as well as its relation to form, function, and evolution. In the following section, we present some biological examples showing that morphology and function, even when supplemented by evolutionary history, are sometimes insufficient to ground the classification of traits. In these cases the individuation of parts of organisms requires attention to the type of processes by which the trait is formed. In the second part of the article, we spell out some metaphysical implications of the biological discussion, and suggest further applications.

2 Biological criteria of classification

The individuation of organisms and traits as members of natural kinds plays a central role in the life sciences. Important biological endeavors—including phylogenetic classification, comparative anatomy, and evolutionary explanation—crucially hinge on our capacity to subsume individuals under general categories and identify them as members of species or types. The nature of kinds constitutes a long-standing philosophical debate that cannot be adequately addressed here. Throughout the article, we remain neutral regarding what kinds are and what—if anything—makes them "natural." Following standard scientific practice, we assume that individuals are sorted out into different types, depending on some characteristic features that distinguish them from other types, and focus on particular *criteria of classification*. We begin by asking: what criteria do scientists employ to classify biological traits as type-identical? The second part of the essay, draws some metaphysical implications of these biological considerations.

2.1 Form, function, evolution, and development

For a long time, and until recently, judgments of type-identity across organisms were formulated on the basis of overall similarity, largely appealing to functional and mor-

[1] While philosophers have extensively debated the nature of causation and causal dependence, the notion of *causal history* has received much less attention. In what follows, we remain neutral with respect to what causes are and how to identify them, and focus instead on distinguishing between different types of causal history.

phological criteria. Consider, for example, mammalian hearts. In spite of species-specific differences in size and shape, the heart is considered the same organ in all mammals, in virtue of anatomical and functional similarities: all hearts are structurally similar and, more importantly, they perform the same role, viz. pumping blood through vessels.

However—and perhaps unsurprisingly—form and function constitute an incomplete set of criteria for trait-individuation in biology; attributions of type-identity are often grounded in evolutionary considerations. Chiropteran and Avian wings provide a clear illustration. Wings are part of the same morphological type (vertebrate forelimbs) in birds and bats, they perform the same function (flying) and their shape is similar in relevant respects. Thus, if traits were classified solely on the basis of functional and morphological considerations, wings of bats and birds would always be treated as the same trait; structural differences could be abstracted away as we do with the wings of different birds.[2] Yet, phylogenetic considerations suggest that Avian and Chiropteran wings are not type-identical, after all: the two traits have a different evolutionary history, they do not descend from a single trait in a common ancestor.[3] In standard biological jargon, they are *analogous*, not *homologous*.[4] Thus, while based on functional considerations bat wings and bird wings can be treated as type-identical, evolutionary considerations suggest a different conclusion, according to which vertebrate forelimbs instantiate different (non-homologous) "types."[5] In short, not all current biological classifications can be understood in functional and morphological terms alone.

The example above shows that phylogenetic analysis sometimes leads researchers to distinguish traits that are functionally and morphologically type-identical. At the same time, there are different scenarios where evolutionary considerations pressure us to classify as type-identical traits that are functionally and morphologically distinct. An intriguing example (borrowed from Carroll 2005) is provided by the superficial simplicity of arthropod legs. For a long time, scientists believed that the jointed, unbranched limbs of insects, centipedes, millipedes, and *Onychophorans* was a sure

[2] A popular way to capture these structural differences is to say that birds "fly with their forearms," while bats "fly with their fingers." The reason is that bird wings are constituted by their entire forelimb, while bat wings are a prolongation of their digits, which are extremely long and connected by a thin membrane.

[3] Talk about "traits descending from traits" is controversial: some scholars argue that it would be more accurate to talk of lineages constituted by organisms (as opposed to traits). Throughout this article, we remain neutral with respect to this controversial issue regarding the units of selection. For the sake of simplicity, following standard cladistic practice, we shall talk freely of traits lineages; however, the same considerations could be rephrased in terms of organismal lineages.

[4] Biologists define "analogies" as structurally similar traits in organisms which are unrelated from a phylogenetic perspective (e.g. the eyes of vertebrates and arthropods). These structural similarities are typically explained as the result of convergent evolution. "Homologies," in contrast, are traits whose similarity can be attributed to a common ancestry.

[5] Whether (and when) functional-morphological classifications should be replaced by phylogenetic ones raises substantial issues that lie beyond the scope of this article. The important point, for present purposes, is simply that different biological considerations yield different and incompatible classifications. To emphasize, our claim is not that phylogenetic classifications are necessarily superior to morphological ones, but rather that evolutionary considerations provide an alternative systematization that classifies traits differently from functional and morphological criteria.

clue indicating that all these creatures belonged to a monophyletic group that evolved independently of crustaceans, trilobites, scorpions, and horseshoe crabs. The rationale for this inference was straightforward: compared to the simple tubular legs of arthropods, all other organisms have more complex forked appendages. Nevertheless, from a phylogenetic perspective, morphological and functional differences between arthropod limbs turned out to be a red herring that led researchers astray. Deeper analysis revealed that the grouping of the limbs of insects, centipedes, millipedes, and *Onychophorans*, on the one hand, and crustaceans, trilobites, scorpions, and horseshoe crabs, on the other, as different and independent structures that evolved independently is inaccurate. Compelling evidence from the fossil record (Gould 1989), subsequently corroborated by genetic analysis (Panganiban et al. 1995, 1997), indicated that the biramous limb evolved from simpler tubelike lobopods of lobopodians. This example shows, once again, that morphological and functional considerations sometimes diverge from phylogenetic analyses. Based on their shape and function, tubular and biramous legs of arthropods should be classified as belonging to different types. An evolutionary analysis, however, suggests the opposite conclusion: the fact that both kinds of limbs evolved from the same ancestral trait provides compelling reasons for classifying them as type-identical.[6]

Additional examples of the varying criteria governing classifications can be found within botany—a subfield of biology that, until recently, has been unduly neglected by the philosophical community. The taxonomic classification of plants rests on an intricate weighing of evolutionary, morphological, and developmental considerations. Consider, for instance, the genus *Solanum*, which includes a variety of plants, such as tomatoes, eggplants, and potatoes. While all these plants are relatively close from an evolutionary perspective, they are quite different with respect to both morphology and ontogeny.[7] In contrast, nuts, raise classificatory questions that, so far, have been addressed by focusing on function. To wit, the identification of walnuts as nuts and pseudo-drupes is based on the function of the covering husk (which in turn depends on its developmental trajectory); in such case, function takes precedence over competing considerations.[8]

Two significant philosophical conclusions can be drawn from the above discussion. First, the fact that anatomic simplicity can disguise and obscure phylogenetic classification suggests that morphological and functional criteria, by themselves, are sometimes insufficient for conclusively establishing the type-identity of traits: insofar

[6] To be sure, in the above example, the phylogenetic classification is not necessarily *inconsistent* with the functional-morphological one. To wit, if biramous limbs characterize a monophyletic group, then, on a cladistic analysis, one could still consider them as a distinct trait from tubular legs. The details of biological systematics need not concern us here. The relevant observation is simply that evolutionary considerations can sometimes lead to a different classification of traits from functional and morphological data.

[7] Indeed, the morphological difference between these plants is so evident that, for a long time, various species of tomato plants used to be considered part of a separate genus and only recently they have come to be regarded as a subgenus of *Solanum*.

[8] As Stuppy and Kesseler (2008, p. 73) recently expressed it, "Many of the fruits that we have just classed as proper nuts qualify only if nothing but the qualities of the mature ovaries are taken into account. For example, fresh walnuts look more like drupes. They are covered by a freshly green husk that peels off easily when the fruits are ripe. (...) This may seem to be a rather exceptional case but pseudo-drupes are also typical of members of the oleaster family (*Elaeocarpaceae*) such as sea buckthorn (*Hippophae rhamnoides*.)"

as we want our taxonomies to reflect the phylogeny of organisms and traits, a systematic analysis based on form and function alone sometimes need to be supplemented with the evolutionary history of a species. We should make it very clear that it does *not* follow from these examples that functional and morphological classification must always be replaced by a phylogenetic taxonomy. After all, there might be strong reasons to classify tubular and biramous legs as belonging to different types, based on significant structural differences. The point is rather that functional and morphological considerations, on the one hand, and evolutionary considerations, on the other, provide distinct criteria that may sometimes lead to incompatible classifications of traits. Whether or not there is an ultimate fact of the matter determining the type-identity of traits is an important issue, albeit one that shall not concern us here.

The second conclusion to be drawn is the importance of evolutionary history as an independent criterion of type-identity. Discovering the ancestral origin and the evolutionary trajectory of a trait, organism, or species provides valuable data for phylogenetic and anatomic classification. As noted, this information is sometimes inconsistent with preliminary identifications based solely on morphological and functional considerations. When this happens, we must decide which set of criteria to follow, and contemporary systematics tends to privilege phylogenetic history over form and function.

2.2 Homology: developmental and phylogenetic

The discussion above emphasizes how phylogenetic considerations play an important role in biological taxonomy. Yet, an appeal to evolutionary history is not always decisive for the individuation and classification of organisms and their parts. As biologists have known for a long time, under particular circumstances, a different sort of causal history is required: *developmental history*.

The importance of distinguishing between evolution and development as grounding different types of causal history is supported both by historical considerations and contemporary scientific practice. Historically, the fact that some biological classifications are established over and above form and function was accepted before and independently of evolution. Over fifteen years before the publication of Darwin's *Origin* (1859), Richard Owen recognized the possibility of traits and structures being type-identical across organisms and species without sharing any common ancestors, as in the case of arthropod and vertebrate legs (Raff 1996).[9] Still, once descent with modification became an established fact, the term "homology" began to be associated with *synapomorphies*: shared features that originate in a common ancestor. Consequently,

[9] The relationship between Owen's definition of homology as "the same organ in different animals under a variety of form and function" (1843, p. 379) and evolution is controversial. According to some authors, in a somewhat Platonic fashion, Owen conceived of two structures as homologous whenever they are concrete and imperfect instantiations of an abstract perfect archetype (Brigandt 2003). Other scholars have challenged the explicitly anti-evolutionary nature of Owen's argument (Rupke 2009). (See also the introductory essays collected in Owen 2007). Here we need not enter into the dispute. The important point is simply that Owen's definition predates Darwin's seminal publication by over a decade, and is independent of Darwinian evolutionary theory.

a historical notion of homology became available to biologists as a further and independent criterion of classification. Traits and organs across organisms and species could be said to be type-identical not just because of morphological or functional similarity, but also in virtue of their evolutionary history.

Over the last few decades, however, some biologists began to notice that the historical–phylogenetic (H–P) notion of homology is insufficient for establishing all kinds of biological identities.[10] The pioneers of this insight (Roth 1984, 1988; Wagner 1989, 1994, 1999) argued that the traditional H–P conception of homology is incomplete because it fails to identify the causal mechanisms that underlie the development of the trait. They suggested that the H–P account be replaced by a "developmental" homology concept, which makes a direct contribution to understanding the causal mechanisms by which evolution occurs. Since then, biologists and philosophers have quarreled over whether there is a single "correct" definition of homology, and what this definition might be.[11]

The debate over the definition of homology, and whether a single correct definition exists, is tangential to the present discussion and needs not concern us here. The relevant point is that the two competing notions of homology—developmental and phylogenetic—reflect the distinction between the two types of causal history isolated above: developmental and evolutionary. The conclusion that two traits have the same structure in virtue of a similar evolutionary history or a common ancestry is independent of developmental processes by which these traits are produced. Now, surely, the two causal histories are often overlapping, in the sense that developmental similarities are sometimes explained by the homology of two traits. For instance, going back to the examples above, structural and anatomical similarities in the forelimbs of bats and birds, and in the biramous limbs of trilobites and horseshoe crabs are grounded in the fact that these organisms descend from the same distant ancestor. Yet, the evolutionary and developmental trajectories of organisms and species need not necessarily coincide. As emphasized above, we can sometimes classify traits as type-identical in spite of the fact that the species in question do not belong to the same monophyletic group; and, vice versa, a coincidence in developmental processes does not necessarily indicate a shared evolutionary origin. The traits in question could be *homoplasies*: a correspondence between parts or organs acquired as the result of parallel evolution or convergence.

A similar point can also be phrased as a distinction between *homology of process* and *homology of structure* (Gilbert et al. 1996). The difference is that while classic homology looks at similarities between traits, homology of process concerns the similarities of dynamic interactions by which these traits are produced. As a result,

[10] The expression "historical-phylogenetic" homology is borrowed from Cracraft (2005).

[11] The center of the dispute has focused over whether homologous traits are synapomorphies—traits that derive from a common ancestor—or traits that are developmentally individualized. In short, while Wagner argues in favor of developmental homology, others (e.g. Cracraft 2005) reply that homology is essentially a phylogenetic notion. In a somewhat conciliatory fashion, some philosophers (Brigandt 2007; Griffiths 2007) have defended a pluralistic approach according to which there is no single "correct" homology concept. On this view, far from being mutually exclusive alternatives, "the kind of developmental constraint brought about by the phenomenon of homology and morphological evolvability in a character-by-character fashion are *two sides of one coin*." (Brigandt 2007, p. 717).

there are organs (such as the eyes and legs of vertebrates and arthropods) that are structurally analogous but may be formed by processes that are actually homologous. In order for these distinctions to be meaningfully drawn, the two kinds of causal histories—developmental history and evolutionary history—must be kept separated.

2.3 Serial homology

The distinction between evolutionary history and developmental history becomes especially salient in cases where phylogeny, function, and morphology, by themselves, are insufficient for the individuation and classification of biological traits. Well over a century ago, Bateson (1892) noted that establishing correlations across species is problematic in cases of *serial homologies*: homologous traits, such as ribs, teeth, and vertebrae, which have been serially duplicated throughout evolutionary history. To illustrate, consider the following example. Human beings have twelve pairs of ribs, that arose as the product of genetic duplications over long periods of time. If we compare *Homo sapiens* with a distant ancestor who had fewer ribs, some ribs will correspond—in the sense of being type-identical—to the ribs of the ancestor. In contrast, other ribs, namely those that are present in the descendant but not in the ancestor, will be evolutionary novelties. The question raised by Bateson is: how do we establish which descendant traits are correlated with the ancestral traits and which are evolutionary novelties, i.e. duplicates? Morphology and function do not provide a clear answer, since both descendant traits could share the same form and function as the ancestral trait, or, where there are differences, these differences could be the result of subsequent specialization. An appeal to evolutionary history is also unlike to solve the puzzle. The problem, succinctly put, is that whenever a trait is duplicated, both traits trace back to the same ancestor. As a result, we cannot address Bateson's question by distinguishing between traits in terms of evolutionary history, morphology, or function.

At this point, one might argue that there is no definitive answer to the problem. When an amoeba divides in two, it is meaningless to ask which amoeba is the "original" one and which one is the product of a duplication event. Likewise, the objection runs, there is no fact of the matter as to which rib corresponds to the ancestral trait and which one constitutes an evolutionary novelty. Indeed, there are cases in which Bateson's question is left without an answer. For instance, if different homology criteria lead persistently to incompatible results, it is not possible to classify one of many serially duplicated traits as type-identical with its distant ancestor, and other ones as subsequent duplications. When the evidence is conflicting, competing hypotheses regarding trait-correspondences cannot be adjudicated—at least not without further evidence.[12] However, it would be a mistake to conclude, from the observation that these identity-questions are sometimes undecidable (based on current evidence), that

[12] To wit, consider the following example, borrowed from Wagner (1989). The evolutionary history of amphibians displays a reduction in the number of digits, due to size-related re-patterning of chondrogenic condensations (the conjunction of cartilaginous traits). Imagine comparing two hands with different numbers of phalanxes, and asking whether it was a terminal or preterminal element that got lost. If we focus on shape, we may note that the terminal element (the phalanx that constitutes the tip of the finger) is identical in both

an answer can never be found. Under particular circumstances, Bateson's puzzle *can* be solved. This occurs when the traits have acquired *developmental individuality*, that is, when they autonomously express characteristic features through similar developmental processes.[13]

In sum, developmental history provides the means to solve puzzles regarding the individuation and classification of traits that cannot be addressed in terms of evolutionary history alone. We should emphasize that developmental individuality is not just of historical or philosophical significance, but is also employed to resolve contemporary biological problems. As a concrete example, consider the phenomenon of limb reduction in amphibians: the loss of phalanxes, digits, or both, frequently occurring in vertebrate evolution. Both anurans (frogs) and urodeles (salamanders) have experienced hindlimb reduction throughout their evolutionary history. Interestingly, the process by which the traits gets lost is different in the two orders: while frogs began by losing the first (anteriormost) digit, salamanders lost the posteriormost digits (4 or 5) first. In both groups, the first digit to be lost is the last (or one of the last) to be formed during normal ontogeny (Alberch and Gale 1985). The biological significance of this discovery is that certain propensities for change occur as a result of inherent propensities (e.g. the genetic potential of the organism) that, while having a significant impact on the evolutionary trajectory of the species, are seemingly independent of evolutionary history (Wake 1991). A different example of developmental individuality can be found in the comparison of the development of short-germ and long-germ insects. While short-germ insects lay down most of their body segments one after the other, dipterans (long-germ insects) produce the totality of body segments—more or less—at once (Sander 1983). As Wagner (1989, p. 59) emphasizes: "The main body regions of short-germ and long-germ developers are undoubtedly homologous [in the H–P sense], but the way they are made is not."

In conclusion, developmental processes, biases, and constraints provide a criterion for individuating traits by focusing on the processes by which these traits are formed. It is developmental mechanisms that permit the individuation and classification of serially homologous traits. In such cases, the diagnostic feature for identifying duplicated parts across species is the characteristic processes through which they are formed. This individuation criteria is independent of morphological, functional, and evolutionary considerations; it is based on a different kind of relation: the type-identity of developmental process, *identity of process*, for short.

Footnote 12 continued
the longer and shorter finger. This may lead us to conclude that it was the preterminal element that was lost. However, if we focus on the proximo-distal position of the new terminal element, we may note an analogy with a former preterminal element, suggesting the opposite conclusion, viz. that it is the terminal element that was lost in the descendant.

[13] Providing a precise definition of "developmental individuality" and "developmental homology" is a substantial problem for the philosophy of biology. (Wagner 1989, p. 62) offers the following preliminary definition of developmental homology: "Structures from two individuals or from the same individual are homologous if they share a set of developmental constraints, caused by locally acting self-regulatory mechanisms of organ differentiation. These structures are thus developmentally individualized parts of the phenotype." To avoid complications that transcend our present concerns, here we simply assume that a trait or organ is developmentally individualized if it reacts to stimuli as an individualized whole.

2.4 Induced pluripotent stem cells

The above discussion concerning "identity of process" might suggest that developmental history is only relevant to the individuation of organisms and their traits. This is not the case: the notion of developmental history is applicable in many other areas of science, where the relata are neither biological species nor biological organisms. To illustrate, consider an example from contemporary stem cell research, a field that plays a prominent role in both molecular biology and clinical research. Embryonic Stem Cells (ESCs) are *pluripotent*, meaning that their developmental fate in not yet committed: they have the potential to differentiate into virtually any other kind of embryonic cell. In nature, once ESCs commit to a certain fate (e.g. to become neural stem cells), eventually turning into a specific kind of neural cells (e.g. striatus neurons), they gradually and permanently lose their potency. A neural stem cell can only generate neural cells, and once a cell has developed into a striatus neuron, its developmental fate is fully committed and irreversible. However, a group of researchers led by Shinya Yamanaka (Takahashi and Yamanaka 2006; Okita et al. 2007) successfully isolated a way to reprogram a fully committed cell into a multipotent stem cell, in a sense reversing the cell's life cycle. The key to this process of genetic reprogramming is the discovery of a small set of genes that govern the specification of cells: when these genes are (re)activated, the cell regresses to a previous stem cell stage. The products of this remarkable experiment are called *induced pluripotent stem cells*, *iPSs* for short.

Setting aside the clinical and biological significance of these remarkable experiments, let us focus on the philosophical implications for the classification of cells as members of particular kinds. In virtue of what can we distinguish between "normal" ESCs and reprogrammed iPSs? In principle,[14] an ESC and its iPS counterpart may have the same morphological, functional, and evolutionary features while counting as different. Indeed, it is the process from which iPSs develop, the reprogramming engineering, that gives iPSs their characteristic identity that distinguishes it from ESCs. What is relevant to the classification of a cell as an iPS or an ESC is the cell's developmental history, not its morphology, function, or evolutionary origin.

At this point, we should address a potential worry. Some readers may object that presenting the case of iPSs in the context of a discussion of *natural* kinds is misleading since iPS are modified cells engineered in a lab and thus are, in some sense, artificial. In other words, to wonder whether an iPSs is type-identical as an ESC, is like wondering whether a piece of paper that has been printed without the approval of the U.S. mint (e.g. money from a board game, or from a different country) may count as official U.S. currency. What is at stake in both cases, the objection runs, is whether a certain entity—a cell or a banknote—counts as a genuine or counterfeit token of a *social* kind. While answering such a question may be far from trivial (as witnessed by the constantly growing philosophical literature on forgery) it is irrelevant

[14] The "in principle" qualification is required because, at the current state of research, there still are some structural and functional differences between ESC and iPS. For instance, in order to reprogram an adult cell into an iPS, it is not necessary to restore the whole genome, but only to reactivate (at most) four key genes. Consequently, one could distinguish between an iPS and an ESC by identifying certain parts of the genome that are still activated in the former but not the latter. However, in principle these differences could (and perhaps in the future will) be washed away.

for our understanding of natural kinds.[15] We recognize that the example of iPSs deals with kinds obtained, at least in part, through human intervention, yet we maintain that iPSs instantiate a particular variety of natural kinds and, consequently, are relevant to the present discussion. Rather than comparing the case of iPS to counterfeited currency, a better analogy is with the domestication of species and varieties of plants and animals. As we see it, studying how the artificial selection of cats, walnuts, or beans affects their taxonomic classification is no less instructive for our understanding of natural kinds than the classification of bats and birds. Now, surely, just as there is an important distinction between artificial selection and natural selection, there is also a significant difference between kinds that are produced through direct human intervention and kinds that are not. This, however, does not imply that natural kinds cannot be artificially produced or modified. In the context of the present example, the fact that human intervention drastically changes the developmental history of iPSs, making them developmentally different from ESCs, does not affect the fact that we have a natural kind whose type-identity depends, at least in part, on its developmental history, any more than the identity of the natural kind *canis familiaris* depends on evolutionary trajectory, which is affected by both natural and artificial selection.[16] In sum, we are not claiming that diversity of process *necessarily* entails diversity of kind; our point is simply that it might—and, in several cases, it does.

2.5 Conclusion

Developmental and evolutionary processes fill in for different facets of causal history and thus must not be conflated. As illustrated by the examples above, under certain circumstances, we distinguish between traits and characters that share the same evolutionary history, or group together traits with divergent evolutionary histories. Furthermore, in the case of stem cells, development has no relation at all to evolution. The significance of distinguishing between two types of causal history becomes even more evident once we recognize that development and evolution range over different sorts of causal sequences: evolutionary processes pertain to populations, while developmental processes concern individual organisms. Consequently, focusing on the evolutionary history of an organism or species provides a partial description of its causal history, which also includes the details of its ontogeny, its developmental history.

[15] We would like to thank an anonymous referee for raising this objection.

[16] Here one may also consider various case studies provided by chemistry. For instance, while vanillin was originally extracted from the fruits of orchids of the genus *Vanilla*, it may now be synthesized from substances such as clove oil or lignin, or biosynthetically produced from the ferulic acid in rice bran. While sharing the same molecular formula ($C_8H_8O_3$), natural, synthetic, and biosynthetic vanillin are regarded as distinct kinds in the food industry. In addition, one may also consider counterfactual or hypothetical scenarios. Suppose that scientists discovered a method for producing gold in a lab through a nuclear bombardment process: even granting that samples of "artificial" gold have the same chemical structure as the "natural" ones, there are good reasons for regarding them as distinct kinds—as witnessed by the fact that a customer buying a "natural gold" ring who discovers that the ring is actually made of "artificial gold" seems, intuitively, entitled to a refund. (We are grateful to an anonymous referee for bringing up this last example.) Of course, the way in which kinds are devised is sometimes accidental (see LaPorte 1996, for further examples from mineralogy).

In conclusion, the natural sciences distinguish—even if only implicitly—between different sorts of causal processes that determine the identity of an organism and its parts. We contend that the same distinction should be preserved also in philosophical discussions. In the following section, we spell out some metaphysical implications of these biological examples.

Before moving on, two clarifications are in order. First, in claiming that developmental processes provide a different sort of causal history, we are not denying the obvious connection between development and evolution: the evolutionary trajectory of a population supervenes upon the developmental changes that occur in its members. Our point is rather that these causal histories are independent, and sometimes lead to different (and incompatible) classifications of traits. Second, we should make it clear that attention to developmental processes is not necessary for the classification of *all* biological traits; in many occasions morphology, function, or evolutionary history will be sufficient. The claim defended here is that under certain circumstances—e.g. when dealing with serial homologies and engineered cells—developmental conditions become necessary for the individuation and classification of individuals and kinds.[17]

3 Developmental processes: metaphysical implications

The fact that biological traits are sometimes classified on the basis of their developmental history raises an important metaphysical question: what is the relationship between developmental processes and the entities that employ them to develop? In this section we discuss some implications of developmental processes for a certain philosophical notion of identity of kinds and individuals. As a preliminary clarification, let us dispel a potential misunderstanding. It is important not to confuse the notion of type-identity that is discussed here with a notion of token-identity, or *indiscernibility*. Our focus here is on individuals which are regarded as kind-identical because they are classified within the same rank (e.g. species taxon or cell-type). From the fact that two individuals share similar process in their development, it would be a mistake to conclude that such individuals are token-identical, or indiscernible on all other grounds.

3.1 Kinds

Developmental conditions bring in a novel aspect to the business of identification: *identity of process-type*. One of the characteristic features of developmental processes is their diachronic character. What is relevant is not just that an entity evolves and persists across time; what determines its identity is the kind of processes through which the individual is produced and maintained. One can view this process either

[17] It is legitimate at this point to wonder about the nature of the causal sequence defining developmental processes. What holds together the different phases of a process? What type of causal link is required by this conception of kinds and individuals? The causal process in question will be identified in terms of two distinct aspects: its qualitative stages as well as its phylogenetic history. Developmental history serves to spell out the former; the latter is taken care of by evolutionary history (see Griffiths 1999, esp. pp. 219–222). Addressing these questions in full requires a solid understanding of the nature of biological traits, an important scientific and philosophical endeavor that, however, transcends the scope of this essay.

as a series of qualitatively different discrete stages that come in a specific order, or as a continuous event—somewhat metaphorically, we could say that a developmental process cannot be captured by a snapshot; something like a video is required. The important point is that the characteristic feature of the entity does not depend solely on the properties exhibited at any particular instant. What determines the identity of the trait—what makes a cell an iPS and what makes a serial trait type-identical to its ancestor—is the cross-temporal sequence of stages through which these entities are produced.

The significance of diachronic features for trait-identity is no news for biologists and philosophers of biology, who have long recognized the importance of adopting a historical or processual perspective in the study of both ontogeny and phylogeny (Oyama 1985; Griffiths and Gray 1994; Griffiths 1999). This attention to a cross-temporal perspective is clearly reflected in recent debates on natural kinds. According to traditional essentialism—as revived by Putnam (1975) and Kripke (1980)—a natural kind is defined by a set of necessary and sufficient conditions that fix its immutable essence. This perspective, however, is hard to apply to the biological sciences because of an obvious tension with the basic facts of evolution and with the the lack of uniformity among populations, species, or kinds (Mayr 1959; Sober 1980). In response to the shortcomings of traditional essentialism, authors such as Boyd (1999), Griffiths (1999), and Millikan (1999) have stressed the importance of developing a *dynamic* conception of natural kinds according to which the conditions for belonging to a kind are allowed to change in time. Instead of having fixed and immutable essences common to all and only their members, kinds themselves are a product of evolution and, as such, are allowed to change with the entities that satisfy them.

At the same time, the distinction between evolutionary and developmental history has, so far, been neglected within the philosophical debate on natural kinds. What has been generally overlooked is that, just as some individuals are type-identical in virtue of their evolutionary history (as in the case of species), individuals can also belong to a kind in virtue of their developmental history. As shown by the case studies presented above, there are some entities that fall under a kind not in virtue of their phylogenetic history, but rather because they have been generated by means of a specific type of process. These examples bring forth a novel dimension of the dynamic (historical) conception of natural kinds: *identity of process*. We should note that diachronicity and identity of process are neither necessary nor sufficient conditions for an entity to belong to a natural kind. The more modest—but by no means unimportant—moral to be drawn is that *some* kinds require a diachronic perspective with respect to developmental processes. Metaphysical tools and concepts thus need to be sharpened in order to accommodate this possibility.

One way to bring forward the suggested amendment to a conception of natural kinds is to explicitly include an additional condition of diachronicity that defines a kind K as a diachronic network of properties N, where N can be viewed as a cluster of properties ordered under a temporal relation, which—depending on the constraints on the space-time manifold—will turn out to be anti-symmetric. The general idea is that an individual a falls under K if and only if, a instantiates N at some point of its life or existence. Schematically, we can represent this condition as follows:

$$N =_{df} (t_1\langle P_1, \ldots, Pn\rangle, \ldots, t_n\langle P'_1, \ldots, P'_n\rangle)$$

where $t_1, \ldots, t_n$ stand for temporal segments and $P_1, \ldots, P_n, P'_1, \ldots, P'_n$ stand for clusters of properties.

To sketch a concrete example, consider again the genetic reprogramming of cells. As noted, if we consider only the presence or structure of the four relevant genes, then it is legitimate to treat the ESC and the iPS as belonging to the same kind of cell since, after all, the relevant sequences of nucleotides correspond in both cells. Adopting a developmental perspective, however, allows us to distinguish the individuals as members of different kinds. To wit, consider four genes (call them A, B, C, D) that are responsible for the pluripotency of the cell. In a "normal" ESC, these genes are constantly activated (*), since pluripotency is a defining characteristic of ESCs (Table 1). In the case of iPSs, in contrast, the four relevant genes are not constantly expressed. Recall, an iPS begins as a fully committed cell, in which the pluripotency typical of ESC is then experimentally induced, effectively reverting its life-cycle, by reactivating the relevant genes (A, B, C, D). The developmental history underlying an iPS genome can be thus represented as a matrix like Table 2, where t_m is the point where the cell commits to its fate and t_n is the point at which the re-engineering process occurs.[18] In short, the network characterizing iPSs includes the different stages that are needed to ensue its developmental process. Of course, the large variety of developmental processes calls for a close study of their typical causal structures before the rough schema provided here can be fruitfully applied to concrete scenarios, yet this is a substantial task that transcends the scope of the present work.

Evidence for a dynamic conception of kinds—expressed by the above condition of diachronicity—based on developmental processes can also be found outside of biology, for example in sciences such as physics and chemistry. To illustrate, for a long time, elements belonging to Mendeleev's periodic table have been regarded as prime examples of natural kinds of the traditional essentialist sort. The reason is that we could seemingly point out a set of precise, necessary, and sufficient conditions for an element to be a member of a natural kind: two elements could both be said to be pieces of gold in virtue of having atomic number 79 (regardless of atomic weight). However, it turns out that even these paradigmatic instances of immutable essences are more problematic than philosophers have generally assumed. In particular, structural properties, such as atomic number, do not exhaust the relevant differences between chemical elements. As Needham (2008) has recently argued, there are important differences between isotopes concerning, for example, differences in rates of chemical reactions. The point is obviously not to challenge the conventional classification of isotopes as belonging to the same element-kind. The interesting claim is rather that further significant distinctions emerge as soon as we transcend traditional classificatory boundaries, such as atomic numbers. Another important class of examples that suggest a similar conclusion is constituted by chemical compounds, such as water, which cannot be identified simply in terms of its microstructure, i.e. H_2O. This is

[18] For the sake of simplicity, in this example, we are assuming that the genes responsible for pluripotency can be "reactivated" whereas, in a more realistic scenario, they would be reinserted into the cell's DNA. On this reading, we can interpret A^*, B^*, C^*, and D^* as the genes that are artificially inserted into the genome.

Table 1 The developmental history of an ESC genome

Time	Genome
t_1	$\ldots A^*, B^*, C^*, D^* \ldots$
t_2	$\ldots A^*, B^*, C^*, D^* \ldots$
t_3	$\ldots A^*, B^*, C^*, D^* \ldots$
t_4	$\ldots A^*, B^*, C^*, D^* \ldots$
$\ldots$	$\ldots$

Table 2 The developmental history of an iPS genome

Time	Genome
t_0	$\ldots A^*, B^*, C^*, D^* \ldots$
t_1	$\ldots A^*, B^*, C^*, D^* \ldots$
$\ldots$	$\ldots$
t_m	$\ldots A, B, C, D \ldots$
t_{m+1}	$\ldots A, B, C, D \ldots$
$\ldots$	$\ldots$
t_n	$\ldots A^*, B^*, C^*, D^* \ldots$
t_{n+1}	$\ldots A^*, B^*, C^*, D^* \ldots$
$\ldots$	$\ldots$

both because H_2O is never found in isolation (Hendry 2006) and because water has a dynamic structure: what we call "water" is an oligomer, that is, a chain of molecules constantly forming and breaking their bonds (Needham 2000; Brakel 2000).

In conclusion, even the classification of chemical elements and compounds depends on the processes by which they are produced and maintained. In this respect, isotopes of an element and compounds, such as water, are on a par with ribs and iPS: their membership to certain kinds depends—at least in part—on the processes by which they are created and maintained.

3.2 Individuals

Although kinds and individuals are, metaphysically speaking, cognate entities, our understanding of the latter has arguably been much less influenced by the perspective of the life sciences. Examples from recent biological findings rarely appear within the literature on foundational questions in ontology.[19] Nonetheless, developmental processes can play an important role in grounding the identity of individuals. While the literature on individuals is quite vast, we shall here limit ourselves to two issues where the condition of diachronicity spelled above becomes relevant.

[19] There are of course exceptions, such as Kripke (1980), who famously recognizes the importance of ancestral relations in fixing personal identity or van Inwagen (1990), who sees a crucial ontological divide between living and non-living organisms. However, it is fair to say that none of these arguments is grounded in biological evidence or directly supported by current biological research. In general, metaphysicians seem to regard the biological worldview as methodologically plausible, yet ontologically suspicious.

First, consider the *perdurantist* view, first labeled in Lewis (1986b) but already under discussion starting with Kripke (1980). Perdurantists emphasize the importance of a diachronic perspective on identity in order to solve metaphysical puzzles concerning persistence, such as the so-called problem of temporary intrinsics (Lewis 1986b, pp. 202–205) or the attribution of seemingly diachronic features to individuals, like being a singer or a dancer (Varzi 2003). We suggest that the perspective presented in the previous sections should be used to supplement the perdurantist view: the identity of some individuals depends on the adequate unfolding of precisely ordered patterns of development, rather than on a generic diachronic perspective. Thus, a perdurantist should explain the identity of a rib in terms of the specific process through which the trait is formed. Similar considerations hold for the examples brought forward by Varzi: an individual is a singer or a dancer only upon completing the appropriate sorts of processes that are distinctive of singers (or dancers).

The following considerations illustrate why this additional requirement is relevant to perdurantism. In his unpublished 1978 Cornell lectures on identity and time, Kripke criticizes the Holographic Theory of Time. This is fundamentally a perdurantist Neo-Humean view according to which a persisting individual is a four-dimensional spatiotemporal worm composed of individual-stages, and there is no property of the entire worm that cannot be explained in terms of the properties of its stages. Kripke contends that a Holographic Theory is problematic. For instance, it cannot distinguish between a world containing only a perfectly homogeneous disk at rest, and an analogous situation where the disk is spinning on its axis of symmetry. Without entering into the details of the dispute, Kripke's objection hinges on the diachronic nature of individuals. A number of authors (e.g. Sider 2001, pp. 226–236) have responded to Kripke's challenge but, to the best of our knowledge few—if any—have rebutted that the attribution of diachronicity is ill-taken. In order to distinguish the two scenarios of the disk at rest and in movement, the perdurantist could adopt a developmental perspective: different causal processes are embedded in the two cases.

4 Concluding remarks

In conclusion, diachronic features of individuals have been widely discussed in contemporary metaphysical literature and for different purposes; yet little attention has been paid to the question of how to ground an account of diachronic identity in the natural sciences and, more importantly, of how to blend such an account with a general theory of individuals and kinds. Individuals and kinds are commonly identified by means of form, function, and causal history; the latter, however, has generally been analyzed in terms of evolutionary history, thereby overlooking the possibility that some individuals might also be identical in virtue of the fact that they were formed and developed by means of analogous processes. Our goal in this essay was to show that developmental processes play a significant, albeit often overlooked, role in the identification of both individuals and kinds. By focusing on an array of biological examples, we argued that identity of process should be recognized as a metaphysical criterion, valid across the board, that provides a more fine-grained notion of causal history to supplement form and function.

Our conclusions can be extended far beyond the particular fields and examples discussed here: what holds for insect wings and iPSs also holds for a great number of other living an non-living entities. Hence, we surmise that the diachronic picture may be used to accommodate kinds other than natural ones. For instance, an area where a diachronic conception of individuals and kinds plays a central role is the literature on artifacts, where development becomes a major factor in the determination of identity.[20] Consider the well-known paradox of the Ship of Theseus. In the variant discussed by Hobbes, the example involves a ship all of whose original constituent planks are gradually replaced with new ones, until the ship is left with no more original parts. Meanwhile, the original planks are used to build a second ship, identical to the former. The problem is determining which of the two identical ships (if any) is the original Ship of Theseus. Metaphysicians traditionally tackled the paradox in terms of entities enduring as opposed to perduring across time. But a step towards the solution might reside in the type of process by which the ship is built. Leaving the details of the story to another occasion, it should be noted that the identity of the boat depends not just on the synchronic or diachronic relations between the various parts of the ship, but also on the process (or processes) that assembles them and keeps them together. In short, the identity of Theseus ship might depend, at least in part, on whether its planks have been assembled with the right kind of process and at the right time. What precisely is meant by "right kind of process" and "right time" is a question that deserves to be investigated independently of the issues at hand. Still, the developmental approach hints to an elegant (potential) solution that has so far lacked proper recognition and that our discussion tries to legitimize.

Other contexts in which developmental processes can be applied to determine the nature of (non-natural) kinds include art, architecture, sport, or political institutions. Consider, for example, a possible application of identity of process to aesthetics and the philosophy of art. It strikes us that the identity of a work of art depends at least partially on the process that led to its production. Only by taking processes into account can a distinction be drawn between forms of restoration that preserve originality from intrusive work that disrupts the authenticity of the piece. More needs to be said with respect to the nature and causal structure of various developmental processes. The goal of this essay was, more modestly, to bring attention to the importance of development as a criterion for identity and to sketch how such criterion fits in with traditional metaphysical discussions of individuals and kinds.

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[20] For an extensive discussion of artifacts, see Petroski (1992) and Thomasson (1999).

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