



Serial Homology

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Abstract

Serial homology, i.e., homology between repetitive structures in the same individual organism, is a debated concept in evolutionary developmental biology. The central question is the evolutionary interpretation of “sameness” in the context of the same body. This essay provides a synthetic analysis of the main issues involved in the debate, connecting conceptual problems with current experimental research. It is argued that a concept of serial homology that is not of the all-or-nothing kind can smooth several theoretical inconsistencies, while being more in line with what we know about evolutionary change and the way we investigate it.

Keywords Development · Evolution · Gene regulatory network · Sameness · Segmentation

Introduction and History of the Concept

A first, operational definition of serial homology will serve as a basis for the following discussion. *Serial homology* is homology between repetitive structures in the same individual (Minelli and Fusco 2013). The repetitive structures need not be arranged along an axis of the body (as the vertebrae of a mouse), but can also exhibit a different symmetry (like the petals of a rose), or even be sparsely distributed (like the setae of a fruit fly). *Homology*, in turn, can be defined as a relation of *sameness* between two or more traits, either in the same individual organism or in different individuals of the same or different species (Minelli and Fusco 2013). Homology is a complex, articulated concept. Intricacy mainly stems from different possible interpretations of what it means to be “the same thing,” and the scope of this understanding depending on where the traits under consideration are found, e.g., in different places of the body of the same individual, in the two sexes of the same species, or in the body plan of different species. This is why the term “homology” is usually accompanied by an adjective for specification.

In the literature, serial homology is often contrasted to *special homology*, where these two terms approximately

stand for within-individual homology and between-species homology, respectively. Special homology is also used to indicate homology between individuals of the same species, when it is not replaced by more specific terms (like “sexual homology,” for the relationship between the reproductive organs in the two sexes; Ghiselin 1976). This is the convention that will be followed here; however, the reader is alerted to other possible meanings of the two terms. For instance, special homology (based on the identity of features of a body structure) has been contrasted with “positional homology” (based on the location of a structure in the body) (e.g., Minelli 1998); or serial homology may not cover “antimeric homology,” i.e., homology between the left and right parts of structures with bilateral symmetry (Ghiselin 1976).

As a kind of homology, several questions related to the concept of serial homology derive from issues related to the more inclusive concept of homology, although serial homology also presents its own, as we will see.

The concept of serial homology, and that of homology in general, are pillars of comparative developmental and evolutionary biology. However, these concepts have witnessed considerable transformations and diversification since their first introduction in the biological literature, accompanied by animated debates, controversies, and some confusion (Wagner 2014).

Without the aim of affording a historical account of the evolution of these concepts (for which we refer to Panchen 1994, 1999; Hoßfeld and Olsson 2005; Minelli and Fusco 2013, and references therein), I will provide instead

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an analytical description of their articulation, which only loosely corresponds to a chronological sequence. Most of the examples and case studies are about animals, but the main arguments can be applied to other organisms as well (e.g., for the flowering plants, see Minelli 2018).

An Outline of the Different Concepts of Homology

An analytical scheme of the more inclusive concept of homology will be useful for the following analysis of the concept of serial homology. Minelli and Fusco (2013) distinguished four main concepts of homology, which partially reflect the (much more complex) semantic evolution of the term. (1) A *nonhistorical* (or *idealistic*) *concept of homology* is one not committed to evolutionary thinking. “Sameness” in this context is intended with reference to an idealized (archetypical), or essentialist concept of body plan. The roots of this conception (although under different names) are deep, but the formalization of the term “homology” is attributed to Owen (1843, p. 379): “the same organ in different animals under every variety of form and function” (Boyden 1943; Panchen 1999). (2) A *historical* (or *evolutionary*, or *phylogenetic*) *concept of homology* accompanies the advent of evolutionary thinking; accordingly, “sameness” is interpreted as common ancestry (Lankester 1870; Mayr 1969; Bock 1974). In parallel, the subject shifts from organs to more inclusive characters (or features) (see Minelli 2021). As exemplified by Mayr’s (1969, p. 85) definition: “homologous features (or states of features) in two or more organisms are those that can be traced back to the same feature (or states) in the common ancestor of those organisms.” (3) A *proximal-cause* (or *biological*) *concept of homology* construes “sameness” as a relation between traits that share the same developmental causes, or generative mechanisms, e.g., the same genetic basis (Osche 1973; Van Valen 1982; Roth 1984, 1988; Müller 2003). For Wagner (1989, p. 62), “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.” (4) Finally, somewhat crosscutting with respect to the latter two comes a *factorial* (or *combinatorial*) *concept of homology* (Minelli 1998). This formalizes the idea that homology cannot be an all-or-nothing relation, such that two structures are either homologous or not homologous (Roth 1984). Since in evolution nothing stays precisely the same and evolutionary change can modify a feature, including its developmental control, to any degree, up to the point of affecting sameness itself, as a matter of fact homology can be partial (Minelli and Peruffo 1991; Abouheif 1999).

The last three modern concepts of homology are evidently not mutually exclusive, but because of the occurrence

of evolutionary processes like gene co-option (the involvement of existing genes in new functions; True and Carroll 2002) and developmental system drift (the change in the morphogenetic or gene-regulatory underpinnings of a conserved trait; True and Haag 2001) they are also logically independent and non-coextensive, i.e., the same traits can count as homologous or not under the different views.

Evolution of the Concept of Serial Homology

The concept of serial homology has undergone transformations and semantic divergence no less extensive and complex than the more inclusive concept of homology. Here we sketch its semantic evolution, highlighting some key passages that will be important for the following discussion. For a more comprehensive, historical account see Schmitt (2017).

Serial homology has pre-Darwinian, idealistic roots in the idea of a “correspondence” between repetitive parts of the body of the same individual, like the vertebrae of a trout, or the leg-pairs of a scolopender. Owen himself, in relation to the vertebrate endoskeleton, defined serial homology as a “repetition or representative relation in the segments of the same skeleton” (Owen 1848, pp. 7–8). Idealistic conceptions of serial homology are historically linked to several “theories” of the modular organization of the organism’s body plan. Developed between the 18th and the 19th century, these theories see the organism as “made of” a collection of archetypical-organ units, which can exhibit a variable degree of differentiation. Among these theories are, for example, Goethe’s (1790) theory of plant metamorphosis and Dugès’s (1832) theory of zoonites (Schmitt 2017). Interestingly, this idea has partially survived in the subsequent development of the concept of serial homology in the evolutionary assumption that the repeated parts, which can present any degree of differentiation, originally were essentially identical to each other, a question to which we will return later.

With the advent of evolutionary thinking, while special homology quite naturally found a new interpretation of sameness based on common ancestry, this was not so for serial homology. As noted by Schmitt (2017, p. 318), “From the moment that the notion of homology became intimately associated with that of phylogeny, the case of serial homology created problems that were altogether specific.” Central to the question is the problematic significance of being “the same by descent” in the context of the same body.

Opinions started diverging. As summarized by Moment (1945), some argued that serial and special homology have an almost totally unlike significance, since they are the results of different causal factors (e.g., Lankester, 1870; Boyden 1943), while others (e.g., Bateson 1894; Hubbs

1944) contended that serial and special homology are different aspects of the same thing. On another front, the historical interpretation of a serial-homology relationship fit quite naturally into Haeckel's view of the connection between ontogeny and phylogeny (Haeckel 1866; Schmitt 2017), while Bateson (1894) and Boyden (1943) argued that serial homology cannot truly have a historical/evolutionary definition (Siomava et al. 2020).

In more recent times, somewhat mirroring the modern evolution of the homology concept, two main concepts of serial homology have been forming in parallel: a *proximal-cause* (or *developmental*) *concept of serial homology*, mainly concentrated on the similarity in developmental mechanisms and their genetic control, and a *historical concept of serial homology*, mainly concerned with anatomical similarity and evolutionary continuity (Wagner 2014; Siomava et al. 2020; DiFrisco 2021). Despite further conceptual elaborations (e.g., Wagner 2014; with refinements in DiFrisco et al. 2020; McKenna et al. 2021), the two concepts remain separated in practice, and the interactions between the two are a matter of discussion (e.g., Diogo 2020; Kuznetsov 2020).

The State of the Art in the Concept of Serial Homology

How the concept of serial homology is put to work in practice may provide clues not only to what is commonly meant by the term, but also to what it is useful for and its scope.

Developmental and Evolutionary Serial Homology

Several operational definitions of serial homology can be found in recent experimental works. For instance, Tomoyasu et al. (2017, p. 3) defined serially homologous structures as being “orchestrated by the same developmental system,” while Lev and Chipman (2021, p. 8) adopted a definition of serial homology as the relationship between “structures in a single organism [that are] patterned by the same gene regulatory network.”

Not surprisingly, these are definitions of serial homology of the proximal-cause type, since, on a strict mechanistic basis, only a biological homology concept allows homology between parts of the same organism (Wagner 1989; Minelli and Fusco 2013; DiFrisco *in press*). Accordingly, support for serial homology hypotheses is mainly provided in terms of shared regulatory gene networks and/or contributing tissues. However, an examination of the current use of the concept of serial homology going beyond the terminological clarifications provided in the introduction of research papers shows that genuine historical questions are at stake.

For instance, Lev and Chipman (2021) questioned the serial homology of the three most anterior arthropod segments (the pre-gnathal) with all the following segments. Their argument is based on the observation that in a model species (the bug *Oncopeltus fasciatus*) these three segments do not share the same gene regulatory network with the following segments. In particular, segment-polarity genes are expressed (1) at different relative times, (2) in different relative positions, and (3) have different functional interactions among each other. This is clearly a developmental argument. However, also based on some fossil evidence, they conclude that the three pre-gnathal segments have an evolutionary history that is independent from the following segments and that they may represent the ancestral arthropod head. These conclusions are evidently of a historical type.

Another example is provided by recent investigations on so-called “wing serial homologs” in insects. These are structures that are not wings, but share with wings a common developmental basis, despite major morphological and functional divergence. The list of identified or putative wing serial homologs includes scarab beetle prothoracic horns, treehopper helmets, mayfly nymphal gills, and bristletail stylus (Tomoyasu et al. 2017; Linz et al. 2020). Evidence is largely based on gene expression and functional genetics analyses, and thus rooted in a developmental concept of serial homology. However, these studies are aimed at understanding the mechanisms that have implemented the diverging evolution of insect wings and their homologs. For instance, results support the idea of a “dual” evolutionary origin of insect wings, with the combined contribution of ancestral tergal expansions and proximal leg articles (Linz and Tomoyasu 2018). This responds to an evolutionary question.

Although hypotheses of developmental and historical homology are formulated and tested differently, the former mainly through experimental developmental biology (including developmental genetics), the latter through phylogenetic comparative methods (including data from fossils to bioinformatics), the two are intimately linked in the evolutionary inference. A factorial concept of sameness could solve the alleged inconsistency between them.

Serial Homology Dissection

When the analyses of serial homology hypotheses go deep into dissecting different aspects of the developmental process, the need to specify where homology lies, and to what degree, inescapably emerges. For instance, on the serial homology of tetrapod fore- and hind limbs, Sears et al. (2015, p. 2551) argued that, “although the muscles and at least some of the bones of each of these limbs were acquired independently and at different evolutionary times and cannot

therefore be considered serially homologous under a historical definition, some of them might be considered serially homologous under a developmental definition.” Based on the dual origin of insect wings, Hu and Moczek (2021, p. 8) claimed that scarab beetle prothoracic horns “may only represent partial wing serial homologues,” since they rely on a part of the wing gene regulatory network associated with tergal contribution.

Serial homology is probably the phenomenon where a factorial concept of homology finds its most natural application.

Implications and Prospects for a Factorial Concept of Serial Homology

Far from being a mere semantic issue, the meaning and scope of serial homology can affect the formulation and testing of hypotheses about specific evolutionary events, and the way we pose questions in the exploration of evolutionary mechanisms.

Costs and Benefits of a Factorial Concept of Serial Homology

A relativistic concept of serial homology can respond to the central question of what is the meaning of being historically homologous (i.e., the same by descent) in the context of the same body. A strict interpretation of sameness by descent is not universally applicable to repeated structures. It is not true that repeated structures necessarily evolved by multiplication of a structure ancestrally present in a single copy. Such a multiplicative evolutionary process is certainly not at the origin of the left and right claws of a crab, the petals of a flower, the arms of a sea star, or the whiskers of a lynx. Thus, in general, common historical derivation must be intended in a less strict (i.e., in a partial) sense, as the involvement/deployment of *something* that is the same by descent, like genes, gene networks, cell patterning, or contributing tissues. In serial homologs we can thus recognize a common evolutionary history, although this has not to be intended strictly in a phylogenetic (cladogenetic) sense.

A factorial concept of serial homology also downgrades the relevance of deciding whether two structures in the same organism that share part of the underlying gene network because of independent gene co-option should be considered serially homologous or, instead, homoplastic. Here is a case where the developmental and the historical concepts of serial homology conflict, but the inconsistency only emerges under an all-or-nothing concept of homology. In the face of the same well-supported facts (e.g., a precise reconstruction of the history of the trait and its developmental control)

disagreement may emerge about whether we are looking at a case of “true” serial homology. However, the question of the “true nature” of a homology relationship rests on an idealized view of how evolutionary change occurs, where identity can be preserved irrespective of any change in attributes (Minelli and Fusco 2013).

This view has its costs. The price of a more inclusive concept of sameness, which allows homology to be partial, is that there are no sharply defined boundaries with homoplasy. As noted by Roth (1984, p. 27), “For good biological reasons parallelism may be difficult to distinguish from homology [and] one must in practice be willing to tolerate some ambiguity between [them].” This should not be seen as a defeatist stance, but rather as a necessary step toward a more realistic (as opposed to idealistic) approach to evolutionary mechanisms and patterns.

From Serial Homology On

Assessment of serial homology can be a research target, but also the starting point for investigating other evolutionary questions. For instance, one can be interested in (1) the morphological evolution of the elements of a series, including the tendency toward increasing or decreasing similarity among them (e.g., Siomava et al. 2020), (2) the evolution of individuation of some or all the elements of the series (e.g., Monteiro 2008), (3) the degree of morphological integration between the elements of the series (e.g., Billet and Bardin 2019), (4) the evolutionary trends in the number of elements of the series (e.g., Fusco 2005), or (5) their ontogeny (e.g., Fusco and Minelli 2021).

Addressing origin and evolution of serially homologous structures separately does not imply that the emergence of a series and its transformations are necessarily independent, or sequential evolutionary processes. However, this distinction, associated to a factorial view, can make it easier to avoid some unwarranted assumptions that not infrequently accompany the study of serially homologous traits.

One of these, already mentioned in the Introduction, is the evolutionary assumption (with the associated narrative) that a substantial similarity is the primitive condition for the elements of a series, as predicted by “Williston’s rule” (see Minelli 2003). This partly reflects the prejudice that evolution tends preferentially to move from the simple to the complex, in this case through a mechanism of “multiplication and change” that allows acquisition of new functions (Fusco and Minelli 2013). However, several cases of evolutionary trends towards less heteronomous series have been documented, based on paleontological and phylogenetic comparative data (e.g., Fusco 2005; Siomava et al. 2020). Also, on theoretical grounds, body patterning (e.g., antero-posterior trunk patterning controlled by Hox genes)

can precede the evolutionary emergence of a series of structures, making the series heteronomous since its first appearance (Minelli and Fusco 2005).

A second unwarranted assumption is the link of serial homology with the idea of “body modules,” like the segments in metazoans. This can take the form of a narrative where the repetitive structures differentiate depending on the segment they belong to, as if segments could be defined independently of the periodic structures that contribute to form them. Several authors have argued for dissociating the serial homology of single periodic structures (e.g., leg pairs, or respiratory openings in arthropods) from the concept of modular-body organization (e.g., Budd 2001; Minelli and Fusco 2004; Fusco 2005; Hannibal and Patel 2013). Body modules such as segments can emerge as epiphenomenal units when the series of multiple features happen to be in register. In fact, it is not always the case (e.g., not in arthropods) that segments correspond to developmental modules, so that different series of repetitive structures can have different spatial periodicity (Fusco 2008). As noted by Roth (1984, p. 27), “Because different aspects of structures are controlled by distinct developmental programs [...], it is sometimes necessary to speak of homologies of different attributes of specific structures, rather than to homologize the structures per se.”

Conclusions

In extreme synthesis, in modern literature developmental (proximal-causes) and evolutionary (ultimate-causes) concepts of serial homology coexist, often mixed-up in argumentation, whereas a factorial concept of serial homology is often adopted in an implicit form.

I have argued that a factorial concept of serial homology can smooth several theoretical inconsistencies, while prompting detailed descriptions of the homology relationship in any specific case of study. An obstinate effort to solve the question of whether something is “truly” serially homologous or not is at odds with what we know about evolutionary change and with what investigators actually do.

Serial homology, and homology in general, are not sharp concepts, and handling of objects with no clear-cut definition, or with context-dependent definition, requires special care and specific reasoning tools. But we are used to that in evolutionary biology (think, for instance, of the concepts of species or novelty), and rational reasoning and formal logic are equipped to deal with some vagueness, so that inference can be quite rigorous once this has been acknowledged and accounted for. The prize is a less idealistic approach to evolution and evolvability.

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