Homology, convergence and parallelism

Michael T. Ghiselin

California Academy of Sciences, 55 Music Concourse Drive, San Francisco, CA 94118, USA

Homology is a relation of correspondence between parts of parts of larger wholes. It is used when tracking objects of interest through space and time and in the context of explanatory historical narratives. Homologues can be traced through a genealogical nexus back to a common ancestral precursor. Homology being a transitive relation, homologues remain homologous however much they may come to differ. Analogy is a relationship of correspondence between parts of members of classes having no relationship of common ancestry. Although homology is often treated as an alternative to convergence, the latter is not a kind of correspondence: rather, it is one of a class of processes that also includes divergence and parallelism. These often give rise to misleading appearances (homoplasies). Parallelism can be particularly hard to detect, especially when not accompanied by divergences in some parts of the body.

1. Introduction

The Darwinian Revolution was boldly proclaimed in the last chapter of The Origin of Species [1].

There is grandeur in this view of life, with its several powers, having been originally breathed into a few forms or into one; and that, whilst this planet has gone cycling on according to the fixed law of gravity, from so simple a beginning endless forms most beautiful and most wonderful have been, and are being, evolved. (p. 490)

Here Darwin, having provided laws and principles for the understanding of life, compares his accomplishment to that of Newton. That the new biology is an historical science is clear from his pronouncement on the future of taxonomy:

Our classifications will come to be, so far as they can be so made, genealogies; and will then truly give what may be called the plan of creation. (p. 486)

Genealogical classification meant that the diversity of life as expressed by the Linnaean hierarchy with its groups of smaller groups within larger ones corresponds to twigs and branches, and not to more particular and more general ideas, perhaps situated in the mind of God. The concept of homology cried out to be redefined, as correspondence between parts that derive from common ancestral precursors.

But was Darwin’s claim to having been the Newton of biology justified? There has been a long tradition of denying that. Sometimes, it has taken the form of arguing that as the essence of science is laws, biology is not a science. An historically important example is the philosopher JJC Smart [2]. He suggested that there are no laws in biology on the grounds that there would seem to be no laws for Homo sapiens. David Hull, who was beginning to establish the philosophy of biology as a professional academic discipline, realized where Smart had gone wrong. There are no laws of nature for Mars or Saturn either. Saturn and H. sapiens are both individuals, in the sense of concrete, particular things, but the laws of nature, although they apply to individuals refer only to classes (kinds) of individuals. Prior to that time Hull had rejected my suggestion that species are individuals, which was evoked by the ‘nominalist’ notion that species are classes and classes are not real, and therefore species are not real. It seemed to me that if one knows what a species is, and if one knows what an individual is, it should be obvious that species are individuals. But the topic was a major source of confusion, especially as ‘individual’ is ordinarily used as a synonym for ‘organism’. In philosophical curricula, furthermore, species have generally been used as examples of classes. In explaining what is meant by ‘individual’
and ‘class’ to persons unfamiliar with such topics, I have found it expedient to use the example of a chair. The chair upon which one may happen to be sitting is an individual in the sense of a concrete, particular thing. One can sit on it. But one cannot sit upon something that might be called chair in general, or in the abstract—the class of chairs.

Hull immediately recognized some of the broader implications of what came to be called the ‘individuality thesis’. Individuals can change indefinitely and yet remain the same thing. This is of course true of individuals like you and me. We look very different from what we were as infants, let alone zygotes. The same is true of all sorts of other entities, including such cultural individuals as languages and their dialects, and, it was clear to Hull, scientific theories. The Origin of Species remained the same literary work in spite of successive drafts and editions. Likewise, the version of Darwinism that was presented to the world in 1859 has been extensively transformed, and yet remains the same theory. That insight led Hull to launch a sociological research programme, which culminated in a long book [3].

I never claimed that the individuality thesis was original with me, and have been happy to share credit with Hull for working out many of its implications and making it intelligible to biologists as well as philosophers. The breakthrough was my paper entitled ‘A Radical solution to the species problem’, which compared the species of biology with the firms of economics [4]. I have subsequently developed the implications of the thesis both in separate papers and at book-length [5]. For example, Hull suggested that if there are laws of nature for species, they are about classes of species, much as the laws of astrophysics are about classes of celestial bodies, rather than any particular celestial body. I suggested some possible laws, such as that as the effective population size goes up the frequency of fixation of genes by sampling error goes down [6]. Perhaps, the laws of nature in many areas of biology are statistical ones. That may or may not be a good thing. Nonetheless, the comparison between astronomy and evolutionary biology indicates that the practitioners of both sciences are interested in tracking objects of interest through space and time, and in explaining what has happened and why. Discussions of the big bang and the origin of life take the form of explanatory historical narratives. So do the accounts of the origin of the notochord.

The idea of a law of nature remains controversial among philosophers of science. At one time, it was popular to conceive of laws of nature as fiats of an Omnipotent Legislator. And the laws of nature were the basis of the ‘argument from law’, according to which there cannot be a law without a legislator, namely God. It seems to me more reasonable to view the laws of nature as manifestations of its uniformity. As a paradigm example, I like to think of the version of the perfect gas laws that I learned as an undergraduate. \( P_1V_1/T_1 = P_2V_2/T_2 \), where \( P \), \( V \) and \( T \) represent pressure, volume and temperature, respectively. Among other things it tells us that when ascending from a SCUBA dive, bad things will happen if one holds one’s breath. The behaviour of gasses is crucial to our understanding of the physiology and evolution of lungs, swim-bladders and floats.

## 2. Hierarchy

I won’t paraphrase Dobzhansky and say that nothing in biology makes sense except in the light of the individuality thesis. But the thesis does make sense out of our hierarchical view of life with its wholes and parts. Consider the sort of hierarchy of classes and individuals that is recognized in the language of biology. Here is an example, with classes on the left and exemplary individuals on the right:

<table>
<thead>
<tr>
<th>classes</th>
<th>individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>genus</td>
<td>Homo</td>
</tr>
<tr>
<td>species</td>
<td>Homo sapiens</td>
</tr>
<tr>
<td>organism</td>
<td>Charles Darwin</td>
</tr>
<tr>
<td>organ</td>
<td>Charles Darwin’s heart</td>
</tr>
<tr>
<td>molecule</td>
<td>a myoglobin molecule therein</td>
</tr>
<tr>
<td>atom</td>
<td>an iron atom therein</td>
</tr>
</tbody>
</table>

The individuals listed on the right are parts, or components, of larger individuals listed above them. To call them instances rather than parts would be to say that Charles Darwin's heart was a Charles Darwin. They are instances of the classes listed on the left. The classes, being abstractions, are not capable of engaging in processes; only individuals can do that. But note that the individuals ranked at different levels engage in different processes, if any. Charles Darwin reproduced, but he did not speciate, and although it would appear that our own species has not speciated of late, it might. The genus Homo is another matter. Being an individual is a necessary condition, but not a sufficient one for an entity to engage in processes. It also has to be cohesive—held together—as species are held together by sex. But genera, families and other higher taxa are not cohesive. All that they share is common ancestry. So although these higher units play an important role in such branches of evolutionary biology as biogeography, it is as strictly historical units. From the point of view of research the message should be clear enough: one should pay close attention to what it is that the individuals ranked at various levels do.

One scientist who got the point was Stephen Jay Gould, whose last book was one long commentary on the individuality thesis [7]. That species are individuals implies the possibility of their being selected. So there may be species-selection, as well as organismal selection, but not genus selection. Gould realized that the individuality thesis accorded with his ideas about macroevolution, including punctuated equilibria. He also concluded that the organism, not the gene, is the basic unit that gets selected. Genes are tracked as a matter of ‘book-keeping’ and not, as construed by Richard Dawkins and other sociobiologists, as that for the sake of which organisms exist. Gould paid a lot of attention to homology, but by ‘homology’ what he often seems to have meant was the genealogical nexus.

## 3. Correspondence

The genealogical nexus is best conceived of as a whole made up of components, which include clades, organisms and organs. The goal of comparative anatomy being to trace the parts of organisms back to common ancestors, it stands to reason that we have technical terms for the relationships of common ancestry and the lack of it among the components of organisms. So homology is a relation of correspondence between parts (organs) that are parts of organisms that are...
parts of lineages [8]. These parts, which are individuals, are called homologues, and homology is the relation of correspondence between them.

As some readers may not find this intuitively obvious, let us consider an imaginary stretch of ribosomal RNA that has been aligned so as to put the homologous nucleotides above one another, and the series of ancestral and descendant sequence data proceeding from top to bottom:

(I) ACGU
(II) AGGU
(III) CGGU
(IV) CGGUU
(V) CG–UU
(VI) GC–UU

In such a lineage, the whole can be modified by changing its parts, for example, by substitution, duplication or deletion. The whole becomes increasingly different from what it was in the ancestral state. But the nucleotides continue to correspond, although it may seem problematic what to do with the ‘indel’ that suggests a deletion.

In the course of evolution, then, lineages composed of organisms become increasingly different, and one might say less similar, with the passage of time. They diverge from the ancestral state, in various and perhaps non-commensurable ways. Their parts, however, remain homologous no matter what happens to the whole. Therefore, the homology relation is transitive, whereas that of similarity is not: if A corresponds to B, and B corresponds to C, then A corresponds to C, but A is similar to B and B to C does not mean that A is similar to C.

The usual contrast-term for ‘homology’ is ‘analogy’, but analogy is a relationship of correspondence between the parts of individuals that are members of classes. Having such a contrast-term is useful when we want to convey the idea that organs are of separate historical origin. However, when Richard Owen (1804–1892) defined ‘homology’ and ‘analogy’, he said that homologues are the same organs in different animals, irrespective of function, and analogues are organs in different animals having the same function [9]. It has long seemed to me that anatomists rarely if ever use ‘analogy’ in this way, and that separate origins is what really matters. Analogues might have no function at all. However, the word ‘function’ is equivocal. On the one hand it means the role of a part in the economy of an organism (its office). On the other hand, it means how a part such as an organ works (its functioning). Functioning often consists of ‘temporal parts’. For example, the human gut is a kind of disassembly line. The stages of processing include uptake, mechanical breakdown, digestion, absorption and defecation. So we might reasonably ask whether the defecation of vertebrates is homologous to that of molluscs. If we could trace these actions back to a common ancestral precursor, the answer would seem to be yes.

4. Similarity

Much to Owen’s credit, he treated both homology and analogy as relations of correspondence, not of similarity. The concept of similarity is rather problematic in biological classification and in classification generally [10]. I was quite critical of it during the days that numerical taxonomy, with its notion of overall similarity, was in vogue [11]. The trouble is that such similarity involves putting things together on the basis of incommensurable criteria. Overall, similarity seems all too subjective for what purports to be objective natural science. Defining homology as ‘resemblance due to inheritance from a common ancestry’ is even more problematic [12, p. 78]. Of course mimics resemble their models, but the resemblance is in the eyes of the beholding predator.

Classes, of course, do not have common ancestors. The various chemical elements in the periodic table are classes of substances that share common properties of scientific interest due to the laws of nature. The atomic weight has been considered the defining property, or essence of various elements. Gold has the atomic number 79. The halogens have the same valence, but differ in atomic number. Wagner got this point wrong when suggesting that transmutation of atoms changes the essence, or definition, of the class [13, p. 272]. What happens is that the individual atoms cease to be instances of one class and become instances of another. Different laws may now apply to them, but the laws remain the same. Fortey & Jefferies definitely got it wrong when they said ‘Homology, as the word is commonly used in comparative anatomy, can be defined as fundamental structural identity between species, which means a recurrence of the same law content’ [14, p. 213]. No such identity exists, and there are no such laws.

5. Homoplasy

Populations living in similar habitats and making their living in the same way tend to have much in common by way of their functional anatomy: they tend to undergo convergent and parallel evolution. But there is a category mistake if we treat ‘convergence’ as the ‘opposite’ of ‘homology’. Convergence is an evolutionary process, not a relation of correspondence. It is one of the alternatives to divergence. The term ‘homoplasy’ is widely used for causes of similarity that tend to mislead phylogeneticists, including convergence, parallelism and reversion [15]. To this list we might add, among other things, secondary loss.

6. Parallelism

I wrote my doctoral dissertation on the phylogeny of opisthobranch gastropods, a group of molluscs noteworthy for their rampant parallelism [16,17]. Subsequently, my collaborators and I have developed explanatory historical narratives for the evolution of chemical defence, which turns out to be the ‘driving force’ behind their evolution [18]. The ancestral stock took to feeding upon organisms that were protected by toxic or repugnant secondary compounds. The chemicals derived from food were then co-opted by the snails in their own defence, with two major consequences. There was divergent evolution in the form of an adaptive radiation, in which different lineages made use of a wide variety of food items both as nutriment and as a source of defensive chemicals. There was also parallel evolution, because with the shift from mechanical to chemical defence, snails evolved into slugs in separate lineages. Parallelism has been a difficulty for working out the evolutionary history of the group. But this has not been an insuperable one because some of the changes, especially in different parts of the body, are divergences. On the other hand, if the only alternative is a
change from an ancestral to a derived condition (e.g. snail to slug) one is not in so fortunate a position.

A major question addressed in the present issue is how we should interpret the evidence suggestive of homologies between the nervous systems of arthropods and those of vertebrates[19]. These could be a straight-forward matter of ancestral conditions having been retained, albeit perhaps not being expressed as we now find them. Or there may have been some precursor that was modified in the same way, and with the same result—which would give us a kind of parallelism. Thus, pseudomonomorphism may have given rise to what we would consider the real thing upon more than one occasion. Parallelism, rather than divergence, might result because of a kind of ‘gridlock’ due to functional or developmental constraint, such that only one derived condition can evolve. Another possibility that comes to mind is physiological (or functional) necessity.

7. Convergence

In a celebrated essay, Andrew Packard treated cephalopods and fish as exemplifying the ‘limits of convergence’[20]. It has been a long time since a derivation of vertebrates from molluscs has been taken seriously, and that hypothesis does not seem due for a revival. Cephalopod and vertebrate eyes have long served as textbook examples of convergence. The structure and functioning of both makes sense in the light of the laws of optics, so that many of the common features are commonly attributed to physiological necessity. It might be a good idea to consider the later stages of cephalopod and vertebrate evolution as parallelism. Once an eye with a retina has evolved, its functioning can be enhanced by adding certain accessories: a lens, an iris, means of focusing, a more elaborate brain to back it up (surrounded by a protective capsule). It might be an amusing exercise to rewrite Simon Conway Morris’s book Life’s Solution from the point of view of Octopus vulgaris rather than Homo sapiens[21].

8. Discreteness

The bones that make up a skull are good examples of what comparative anatomists like to call characters. They are substances, or material bodies, that have a certain amount of discreteness, and occur as definite units, unlike ‘bone’ treated as a mass noun. That kind of unit is obviously what Wagner has been most interested in when seeking to elucidate the nature of homologues[13]. Treating a lineage or a population of bones as a supra-organismal evolutionary unit is to conceive of it as an individual that in some ways is comparable to a species. A biological species, unlike a genus, is cohesive because it is held together by sex. And both homologues and species evolve separately from other homologues and species. If our goal is to synthesize the mechanistic and the historical aspects of biology, it makes sense to emphasize those units that are cohesive enough to participate in evolutionary and developmental processes.

I once proposed the term ‘Mayr’s law’ for the generalization that, under ordinary conditions, there can be no speciation without an initial period of extrinsic isolation[5]. Calling it Mayr’s law was intentionally ironic because Mayr had adamantly maintained that there are no laws in biology. Now, one of the most important functions of laws of nature in the sciences is that they tell us that certain things are impossible—such as a perpetual motion machine. It looks to me as if the constraints on diversification at the anatomical level and that of the species may be conceptualized in terms of laws of nature that are more than just far-fetched analogies.

9. Innovation

At any rate, what many evolutionary biologists have been attempting to accomplish, beyond just a description of what has happened as taxa have become transmuted, is to find, if not laws of nature, then principles and other widely applicable generalizations. A good historical example is the principle of succession of functions (Functionswechsel) that was elaborated by Anton Dohrn (1840–1909)[22]. It was developed partly to address the question of where new parts and other adaptations come from. Problems of the origin of novelty of course are of interest not only to biologists but to all sorts of people, including historians and even literary intellectuals. What are the prospects for developing a very general ‘mechanics of innovation’?

10. Conclusion

As someone educated as a comparative anatomist in the traditional sense I did not find it difficult to shift to molecular data[23]. If we talk about ‘molecules versus morphology’ we may be overlooking the possibility of studying the morphology of molecules. But whether we focus our attention on genitalia or ribosomes, our goal is to trace items of interest through space and time, to describe what has happened and to explain why things happened that way. Organisms and their components are traced through a genealogical nexus to their common ancestral precursors. Homology is the relation of correspondence between the parts of descendants of the common ancestral precursors. The homologues remain homologues, no matter how much they get transformed. If we had a complete, unbroken series of ancestors and descendants, tracing the homologous parts through lineages would be no problem. But of course our sample is far from complete, and a lot of extrapolation and educated guesswork goes into our reconstructed genealogies.

The changes in question may be quite heterogeneous. In molecular evolution, for example, we have substitutions, duplications, inversions, translocations, deletions and changes in function. As we get farther and farther from common ancestry, such changes accumulate, but rates and directions are likewise heterogeneous. ‘Stasis’, whether real or apparent, suggests no change at all. A pair of lineages might diverge from one another, and then perhaps converge; alternatively they might run through the same kind of modification in parallel. Atavism, or reversion to an ancestral condition, might be considered a kind of convergence. Be this as it may, atavism provides a classical example of how evolutionary history can be inferred and explained on the basis of experiments, and not just the sort of formal comparison that was practised by pre-Darwinian morphologists[24]. Quite a number of lineages of salamanders have become progenetic, ceasing to undergo metamorphosis and reproducing as what might be called aquatic larvae. The ancestral phenotype has been re-evoked by administration of thyroid hormones. It is perfectly legitimate to classify on the basis of shared characters, especially as is now well recognized, derived ones. But let us not make
the mistake of using the term ‘character’ as a synonym for ‘evidence’. An experiment is an operation, not an attribute.

Competing interests. I declare I have no competing interests.

Funding. I received no funding for this study.

Acknowledgement. Linda Holland, Alan Leviton and Paul Kats provided useful comments on early drafts.

References