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Homology as a relation of correspondence between parts of individuals[☆]

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Abstract

The recognition of correspondences has long been a fundamental activity among systematists. Advocates of *Naturphilosophie*, such as Lorenz Oken, drew far-fetched analogies between taxonomic groups and all sorts of other things, including the Persons of the Trinity. They treated change through time either as analogous to an ontogeny or as the product of divinely instituted laws of nature. Darwin changed things by making the taxonomic units strictly historical, implying that they are not classes but rather individuals in a broad metaphysical sense. That means that taxa are concrete, particular things, or wholes made up of parts which are themselves individuals, and that there are no laws of nature for them. Homology is a relationship of correspondence between parts of organisms that are also parts of populations and lineages. It is not a relationship of similarity, and unlike similarity it is transitive. Analogy is a relationship of correspondence between parts of organisms that are members of classes, and is not necessarily due to function. Taxa, like other individuals, can change indefinitely, and the only thing that they must share is a common ancestor. They do not share an essence, Platonic Idea or *Bauplan*, although “conservative characters” may be widespread in them. Iterative homology likewise is a relationship of correspondence, but the nature of that correspondence remains unclear. The difficulties of the homology concept can

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be overcome by treating phylogenetics and comparative biology in general as historical narrative.

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Among systematists the two most popular topics for often heated, if rarely enlightening, argument are: (1) the species problem, and (2) homology. Although these topics are rarely treated together, there is a close connection between them (Ghiselin, 1981, 1997). So far as philosophy goes, the species problem has largely resulted from the mistake of treating individuals as if they were classes, and much of the confusion about homology has resulted from treating correspondence as if it were similarity. To think clearly about such matters one needs to understand the logic and metaphysics of wholes and parts. Another source of misunderstanding, the habit of confounding the ontological issues with the epistemological ones, is beyond the scope of this paper.

Recognizing corresponding parts in animals has long been one of the most important activities of comparative anatomists. The results of such research are nicely illustrated in a comparison of the skeletons of a bird and a man by the Renaissance naturalist Pierre Belon du Mans (1517–1564). He posed the skeletons so as to make them look as similar to each other as possible, and used the same letter to indicate what he considered to be the corresponding bones in the two skeletons (Belon (du Mans), (1555, p. 440–441). Please note that similarity is the relation between the wholes (the skeletons), whereas correspondence is a relation between the parts of those wholes (the bones). “Correspondence” is often translated into German as *Entsprechung* or *Übereinstimmung*. However, when German philosophers discuss the correspondence theory of truth they use the word *Korrespondenz*.

“Morphological” correspondence is not the only such relation that interested early naturalists. Analogizing, often far-fetched, was a very important activity among early 19th century biologists. The speculative excesses of Lorenz Oken (1779–1851) were largely responsible for giving the movement called *Naturphilosophie* a bad name (Breidbach and Ghiselin, 2002; Ghiselin, 2005). Oken erected systems of classification that included literally everything, and revealed correspondences everywhere. His classification of the colors provides an excellent example of his accomplishment (Oken 1831: p. 69):

Red	Fire	Love	God the Father
Blue	Air	Faith	God the Son
Green	Water	Hope	God the Holy Ghost
Yellow	Earth	Vice	Satan

Oken thus “aligned” the colors and the four traditional elements with religious entities. This arrangement allowed him to rank plants as higher or lower, according

to the color of their flowers: those with red flowers, being most like God the Father, are at the top.

Oken was a pantheist: he believed that God and the world are one and the same thing. Because God created man in His own image, it made sense to him that everything in the world corresponds to human anatomy. Oken (1807) invented the vertebral theory of the skull. He was able to determine the number of vertebrae that make up the skull by numerological reasoning (Oken, 1840). Such a move makes sense, because God is the perfect being, and therefore expresses Himself in the perfect language, which is mathematics. There are five senses. One (touch) is dispersed throughout the body, the other four are in the head; therefore there are four vertebrae in the head. Furthermore every taxonomic group of animals corresponds to one of the five senses. For human races that worked out:

Caucasian	vision	eye
Mongol	hearing	ear
American	smell	nose
Malay	taste	tongue
Black	touch	skin

In effect, everything in the universe mapped on to everything else. The bottom half of the human body was the mirror image of the top, with the arms corresponding to the legs, the mouth corresponding to the anus, the salivary glands corresponding to the testicles, etc. Each organ corresponded to an entire organism, to a taxonomic group, and also to the world as a whole, which was itself conceived of as an organism, following the creation myth in Plato's dialogue *Timaeus*.

Oken's occult metaphysics, which seems utterly bizarre at first, becomes more readily intelligible when one understands his premises and his style of reasoning. He is a very good example of an idealist, which means, to oversimplify a bit, that he presupposed a very close connection between the natural order and our conceptions of it. Such a close connection makes sense if one believes that an anthropomorphic Deity created the world. Our thoughts would be very much like His; after all, we have been created in His image. God would create the world and everything in it with a Plan in Mind. Given that assumption, a major goal of science was to discover that Plan, which, since it had already existed in the Beginning, was something eternal, unchanging, and beyond space and time. Furthermore, and this is very important, God was not just the designer and the creator of the material universe: he was also the lawgiver. He ordained the laws of nature. Again, those laws of nature were eternal and unchanging uniformities.

Such idealistic notions, whether explicit or implicit, affected scientists' thinking as it became increasingly evident that life has changed over geological time. During that transitional stage of intellectual history there were two basic ways for accommodat- ing change over a series of generations. One was the idea that God had created an ancestral organism that was like an embryo, and a lineage would undergo a gradual

change from potentiality to actuality. The other idea was that God had achieved the same end through unknown, and perhaps unknowable, laws of nature. Oken's English follower Richard Owen (1804–1892) advocated both of these possibilities, albeit at different times in his career. Neither move amounted to becoming an evolutionist in the modern sense of that term. The quasi-evolutionary nature of Owen's thinking is manifest from his treating the entire world ecosystem (as we now call it) as if it were an Okenian *Weltorganismus* with providentially co-adapted species: horses came into being at just the right time to provide human beings with means of transportation. Another form of occult metaphysics that interested systematists in the early 19th century was quinarianism. Advocates of this approach tried to arrange their materials in circles, each made up of five smaller circles.

"Occult" metaphysics suggests the invocation of hidden causes, especially supernatural ones. Unfortunately the kind of metaphysics that interests the patrons of metaphysical bookstores has tended to be confused with the kind of metaphysics that interests academic philosophers. When we begin asking such questions as "Are species real?" we are asking a deeper kind of question than science by itself can answer. We cannot provide an answer unless we ask what we mean by "real" in the first place. Logic helps in addressing such questions, but it does not supply the basic premises. Where to draw the line between natural science (physics) and ontology (metaphysics) is a thorny problem. I like to consider metaphysics as the more fundamental aspect of science, not something different.

Darwin of course revolutionized systematics by making it truly historical. There was a profoundly metaphysical aspect to that revolution, and it was not just a matter of getting rid of the sort of occult metaphysics that we find in the writings of Oken and Owen. Darwin's predecessors had been treating taxonomic groups as if they were classes. In the version of Darwin's evolutionary biology that is generally accepted today, they are individuals. In his original version species and higher taxa functioned as individuals too, but that was not clear either to him or to his contemporaries. Although others have maintained similar positions it was I who first managed to get the point across (Ghiselin, 1974). The Phylocode, which tries to fix the reference of the names of taxa ostensibly (i.e., by "pointing" at the clade), makes no sense unless species and monophyletic taxa in general are individuals. It is the same way that the names of people and other proper nouns are defined. I am happy to take credit for the individuality of species, whether or not I deserve it. I am willing to take the blame for the Phylocode, but not the credit! Here I develop some of my earlier thoughts on how individuality relates to homology and analogy (Ghiselin, 1981, 1997; see also McKittrick, 1994).

Because some readers may not be familiar with the philosophy, let me briefly review the basics.

Consider

<i>Classes</i>	<i>Individuals</i>
Genus	<i>Homo</i>
Species	<i>H. sapiens</i>
Organism	Charles Darwin
Organ	Charles Darwin's brain

On the left we have classes, or kinds, and on the right we have individuals that are instances of those kinds. We may briefly summarize the differences between classes and individuals that are of interest for this discussion. (1) Classes are abstract, individuals are concrete. That is very important because (2) only individuals can engage in processes: Charles Darwin could think, but it makes no sense to say that organism in the abstract can think (or do anything else). So too with species: if species were not individuals they could not evolve. I mention in passing that being an individual is a necessary, but not a sufficient condition for engaging in processes. Genera are not cohesive so they cannot do anything. (3) Individuals have no defining properties. For this discussion what matters most is that they can undergo any amount of change and still remain the same particular thing. (4) Classes have instances, whereas individuals do not. It makes sense to say that Charles Darwin was an organism but not that, say, Charles Darwin's brain was a Charles Darwin. The absurdity of saying that he was a *Homo sapiens* is a bit less obvious. For our purposes the important thing is that there is a whole-part relationship between Charles Darwin and his brain. (5) Individuals are spatio-temporally restricted: they have a location in space and time, whereas classes are spatio-temporally unrestricted. (6) The uniformities that we call laws of nature are formulated as true of classes, and make no reference to any particular individual. Consequently such generalizations of systematics as "all mammals have hair" are purely historical, or contingent, propositions. Unlike the laws of nature, which are necessarily true of everything to which they apply, the properties of taxa could have been otherwise.

Perhaps I should mention two senses of "individual" that are not meant. First, "individual" is commonly used as a synonym for "organism"—in the ontological sense being used here, all organisms are individuals but only some individuals are organisms. Second, when Wagner (1989a,b) refers to the "individuality" of homologs, he explicitly states that he means their autonomy. Some philosophers, notably Spinoza, have used "individuality" in that sense too (see Ghiselin, 1997, p. 59–60).

Homology statements are strictly historical propositions. They are not laws of nature and they lack the necessity that characterizes laws of nature. Fortey and Jefferies (1982, p. 213) are therefore seriously wrong when they say that homology is the "fundamental structural identity between species, which means a recurrence of the same law content."

Likewise the efforts of "structuralists" such as Webster (1989) to replace the historical content of comparative anatomy with unknown laws of nature are a waste of time. This is not to say, however, that there are no laws of nature in evolution, including the evolution of development. Those laws, whatever they may be, refer to classes, or kinds, of individuals, such as organisms with metamorphosis. When the data of comparative biology are properly conjoined with the appropriate laws of nature the result is an explanatory historical narrative.

In Darwinian systematics, higher (i.e. supraspecific) taxa are nothing more (or less) than lineages with common ancestry. The only thing that the component lineages, organisms and other individuals must necessarily share is community of descent. Anything else that they share is a matter of contingent historical fact, in

other words something that might have been otherwise. The common ancestor at each node provides the initial conditions, not the laws of nature in any historical narrative. Any assertion that there is something over and above the concrete individual population, with its component individual organisms and their parts, has to be more than a metaphysical posit if scientists are to take it seriously. We should be very suspicious whenever we encounter such terms as “Archetype” and “*Bauplan*,” given that these have so often functioned like Platonic Ideas (cf. Scholtz, 2004). The history of the *Urmollusk* provides instructive examples of the kind of thinking that we need to avoid (Lindberg and Ghiselin, 2004).

One important difference between similarity and correspondence is that the correspondence relation is transitive. If we arrange objects in a series, the parts correspond no matter how different the whole may become. Consider an ancestor-descendant lineage of RNA.

1. ACGU,
2. UCGU,
3. UCGA,
4. UGGA,
5. UGCA,
6. UGCAA,
7. UACGA,
8. ACGA.

We begin with the initial molecule 1, which undergoes a series of substitutions, such that the wholes become increasingly less similar. However, each nucleotide in 1–5 corresponds to the nucleotides above it, irrespective of whether it is identical. The relationship of identity is a difficult one, but in this case it means sharing all of the properties of interest. In this case, it means being one of the nucleotides rather than any of the three alternatives. It would be a mistake to say that there is 75% homology between 1 and 2, 50% homology between 1 and 3, etc. These percentages are not of homology, but of homologue identity. Molecule 6 shows a duplication. A in 5 is homologous to AA in 6, and the whole differs even more from 1. Molecule 7 shows an inversion: now two of the corresponding nucleotides are not homologous to those above them, but GCA in 6 and ACG in 7 correspond to each other. These are homologous parts: there is no relation of “partial homology” between them (another mistake). And finally, a deletion (of a U) is shown in nucleotide 8. A locus, or place, has ceased to be occupied. Note that 8 has become superficially similar to 3. CGA in both would line up were it not for the “alignment gap” that has been provided. The gap indicates an empty place, something that bothers persons who conceptualize such places as if they were nonexistent things. They may also find it difficult to imagine empty niches even though a job opening may seem less problematic. It seems to me that the notion of “positional homology” as suggested by Minelli and Schram (1994) is superfluous once we recognize that positions, as well as parts, can correspond. Such notions of partial and incomplete homology (Gegenbaur, 1870) are quite unnecessary in the context of real historical narratives.

Consider the eyes of bilaterians for example. If the eyes of protostomes and deuterostomes can be traced back to a common ancestral precursor, these organs may reasonably be said to be homologous in vertebrates and cephalopods. But obviously quite a number of new parts, such as lenses, corneas, and irises have been added, independently since common ancestry, to what was originally a very simple structure. The additional corresponding parts are of course analogous rather than homologous.

Please note that in the above example the truth of the narrative is not a problem for the simple reason that it is an assumption, or posit, that is presupposed for the sake of explication. It might indeed be problematic to somebody observing the sequence to decide whether the change from 5 to 6 had been a duplication or an addition, or that from 6 to 7 an inversion or a pair of substitutions. But such epistemological issues are irrelevant to the definition of the terms, which are strictly theoretical ones and are defined that way.

Homology is a relationship of correspondence between parts (individual homologues) of individual organisms, which are in turn parts of individual genealogical wholes. Again, unlike similarity, it is a transitive relation. Analogy is also a relationship of correspondence, again between parts of individual organisms, maybe in different species. However, the analogues are not parts of organisms that are in turn parts of larger wholes: instead they are parts of organisms that are members of classes. The relation of analogy is *not* transitive, because the classes have to be similar, if perhaps in a far-fetched way. The reason for the similarity and the correspondences may be mere coincidence, or it could be due to laws of nature. Organisms have to be organized, and they are often organized in more or less the same way. Usually the term “analogy” refers to correspondences between parts of wholes that are similar because of convergent evolution. Unfortunately, Richard Owen defined analogy as correspondence between organs having the same function. As I have pointed out before (Ghiselin, 1976), this is not a proper definition of the term as it has generally been used by anatomists, including Owen himself. There are usually functional reasons for convergence, but analogs may or may not have the same function, and not all organs with the same function are analogs.

For an example of analogs that do not have the same function, consider how we might compare a protostome, such as a nudibranch, with a deuterostome such as myself. The notion that the dorsal surface of the one corresponds to the ventral surface of the other goes back to Étienne Geoffroy Saint-Hilaire. Lately it has been taken very seriously by students of evolutionary developmental biology (see Nübler-Jung and Arendt, 1994). Suppose, for the sake of argument, that Geoffroy was right. Then my body can be aligned with that of the nudibranch so that we face each other and the right side of my body is homologous to his and her left side. But viewing both of us from above, we can see that the left sides are analogous. Most of us would not say that the left sides have the same function in the two organisms. “Side” is a morphological concept rather than a physiological one. When one organism resembles another because of mimicry, the corresponding parts do not necessarily have the same functions. Snails that mimic tunicates sometimes have acid glands that correspond to zooids.

The imaginary series of nucleotides given above has been oversimplified for didactic reasons. Obviously, it treats only ancestor-descendant relationships and not those between collateral relatives. Less obvious is its treating different nucleotides at the same site as if a nucleotide had been transformed rather than replaced. Of course when such a replacement occurs, the whole molecule is transformed but remains the same individual molecule lineage. Some morphologists want to restrict “homology” to relations of correspondence between organs or other parts, and not to properties of those parts. Although that may be going too far, it makes a great deal of sense. Organs and their properties are members of two different ontological categories. Organs are substances of which attributes can be predicated. Much confusion has resulted because the term “character” is equivocal: it conflates the parts with their properties (Ghiselin, 1984). The distinction between character and character state suggests the difference but does not fully clarify matters. Sometimes the problem is solved by such locutions as “The wing of a bird is homologous to the wing of a bat, but only as an anterior appendage, and not as a wing, to which it is analogous.”

Failure to make the part–attribute distinction has led to the mistaken notion that homology and synapomorphy are the same thing (Patterson, 1982; De Pinna, 1991). An apomorphy is an attribute that is shared by the component organisms of a lineage, such as a clade: it is not the relation of correspondence between the parts of those organisms. Synapomorphies are generally characterized as shared innovations, and such innovations can be members of various ontological categories. These ontological categories include process (such as innovation), substance (such as molecule), attribute (such as inverted), place (such as the site of a nucleotide) and relation (such as homology). When chromosomes and molecules evolve there are changes in place: inversions and translocations for example. If we say that the change from 5 to 6 above was a duplication of A, then the apomorphy would be the attribute “A duplicated” and the homology would be the relation of correspondence between A in 5 and AA in 6.

The transitivity of the homology relation implies that it is logically possible to trace parts through intermediates in a series that has become transformed to such an extent that the initial wholes would seem to have nothing in common with the ones at the end of the series. Some authors have expressed mild dissatisfaction with that circumstance (Stevens, 1984). So far as I can tell, however, that dissatisfaction merely represents a propensity to conceptualize taxa as classes. Much stronger claims are made by those who insist that there must be something invariant among the items being compared. Sometimes we are told that the entities being compared must share a *Bauplan*, as when Wagner (1989a, p. 51) says “Two structures are called homologous if they represent corresponding parts of organisms which are built according to the same body plan.” I am not sure exactly what a body plan is supposed to mean here, surely not an idea in the mind of God of which all the organisms are imperfect copies. But if the anatomical structure of the body is meant, it seems perfectly reasonable that the derived organisms might be extensively remodeled and nonetheless one still might find some homologs. Parasites often lose important parts that were present in their free-living precursors. In the animals that I study, opisthobranch gastropods, we can of course trace parts back to those in

animals that have undergone only a moderate amount of restructuring since the common ancestors of interest. However, when the constraining influence of the shell has been removed, we get “slugs” that are highly modified anatomically. Traditional classifications expressed the morphological divergence by means of a large number of orders.

Homology is a relation of correspondence between parts in the context of the wholes in which they occur. These wholes include lineages at all levels, even within single organisms. It is therefore not correct to say that homology relations are necessarily between the parts of different species. When Fitch (1970) introduced the distinction between paralogy and orthology he did *not* say that paralogs originate within species, whereas orthologs originate at the time of speciation. But this interpretation has sometimes been made. It is not exactly what happens, and it illustrates some of the problems and paradoxes that we experience when trying to individuate parts of evolving lineages. For methodological purposes Hennig (1950) treated ancestral species as ceasing to exist, or becoming extinct, at the time of speciation. However, they do not unequivocally cease to exist, but rather get transformed into clades, which are noncohesive individuals and may be ranked as genera. If orthologs arise at speciation, then all of the ancestral proteins likewise cease to exist when the populations diverge.

Genes, chromosomes and even entire genomes are replicated in such a manner that, given enough data, it is a straightforward task to trace the changes in their component parts through successive generations. Homology statements therefore can function as parts of an historical narrative in which mutations, recombinations, inversions, translocations and other events are traced through a genealogical nexus. Matters become more complicated however, when we have to deal with organs and organ systems, which are produced by developmental processes more remote from the genes themselves. Germ, soma and developmental processes all evolve. Arthur (2003) refers to “developmental reprogramming” but the basic idea that evolution occurs by changes in ontogeny was an integral part of Darwin’s theory. Contrary to what De Beer (1971) expected, there is no reason to expect that homologous organs will necessarily remain under the control of homologous genes. For the same reason a “shared set of developmental constraints” as suggested by Wagner may or may not characterize a pair of homologues. (Wagner, 1989a, p. 62; Wagner and Misof, 1993.) Both chromosomes and developmental systems are individuals: they can change indefinitely and they sometimes change a great deal.

Of course, some parts of the genome, some developmental processes, and some organs and organ systems are evolutionarily less labile than others, and change very slowly, if at all, over vast periods of time. That is why those of us who study phylogenetics find certain parts of the organism such as ribosomal RNA more useful than others in our efforts to work out distant relationships (e.g., Field et al., 1988; Giribet, 2002; Halanych, 2004). Traditionally such parts have been called “conservative characters” (cf. Wagner and Misof, 1993). Such conservativeness however, does not mean that those parts are like the laws of nature and therefore altogether immutable under every imaginable circumstance. Unlike the elements in the periodic table, they are *not* natural kinds. Nor does that conservativeness give us

an excuse for treating them as if they were ideas in the mind of God. It is curious that Gould (2002), whose macroevolutionary theory was based on the idea that species are individuals, and who wrote a whole book about the contingent nature of evolutionary history (Gould, 1989), nonetheless tried to find archetypes in the genome (see Ghiselin, 2002). Gould could not accept the fact that the hierarchy of life is contingent all the way down.

There are also relationships of correspondence between the parts within individual organisms, for which, many years ago, I introduced the term “iterative homology” (Ghiselin, 1976; see Roth, 1994). These include the relationships between the parts of metameres, cyclomeres and antimeres. There are also similar correspondences between the parts of different “morphs” of an individual species, such as the two sexes of gonochoristic animals (sexual homology). For these relationships it does seem likely that common developmental mechanisms control the structure of the diverse components of the wholes of interest. Whether we are dealing with correspondences between the parts of a single organism, or with correspondence between the parts of separate organisms within the same species, the wholes are cohesive, integrated and organized as single units with co-adapted parts. That very integration sets a limit to the degree to which the various parts can diverge from one another. Above the species level, that constraint no longer exists, and that is one reason why the species is a unit of such fundamental importance in evolutionary biology. Supraspecific taxa are purely historical entities, sharing a common ancestry. Because they lack cohesion, their component species can diverge indefinitely.

Iterative homology and iterative analogy are not restricted to bodily parts. Like evolutionary homology they can be found in languages, artifacts, socioeconomic systems and countless other behavioral and cultural entities. Consider, for example, the ontology of national states, first by distinguishing between classes and individuals:

<i>Classes</i>	<i>Individuals</i>
Country	Canada, USA
Province (or State)	Ontario, California
County	York County, Orange County

The main point of interest here is that both Canada and the US are organized in much the same way, and there are correspondences between, say, their capitals (Ottawa and Washington). Both show a kind of modular organization, such that the provinces and states might be compared to metameres or chromosomes. Each of the US has a centralized government in what we call a “state capital,” and in turn it consists of counties, each with its “county seat.” The components in each subunit correspond to one another. We might ask whether, or to what extent, we are dealing with analogy or homology. The economic advantages to centralization and standardized parts are nothing mysterious. (For a discussion of such topics as modular professors, in modular departments, teaching modular courses to modular students, see Ghiselin, 1989). As one might expect, both centralization and standardization have originated independently in various civilizations. So one might

treat some correspondences between parts of similarly organized states as manifestations of laws of nature: relations between parts of members of classes. On the other hand, legal systems are products of both legislation and historical contingency. Institutions and customs are often modeled on other institutions and customs, creating lineages.

Our predecessors sometimes conflated iterative and sexual homology with evolutionary homology and provided erroneous historical interpretations. The notion that cyclomeric and metamerous animals were formed by the union of entire organisms into colonies is a good example. Haeckel thought that an echinoderm's body is equivalent to five annelids joined at the head (Haeckel 1866 Vol. II, p. LXIII). Perrier (1881) and others attempted to interpret metamerous animals as linear colonies, with each metamere equivalent to an entire organism. There were similar misinterpretations of sexual homology. Gegenbaur (1870, p. 876) forced an historical explanation onto the similarities between male and female reproductive systems in vertebrates. He maintained that we are descended from hermaphrodites. Darwin (1871: Vol. I, p. 207) went along with that interpretation, which we now know is not correct. Nonetheless, the duplication of parts is an important evolutionary mechanism. Hypotheses that invoke the multiplication of genes, developmental systems, and entire organs are quite legitimate, and some of them are well supported by empirical evidence.

When gene duplications have occurred, the result is a lineage of genes sharing a common ancestor. The multiple descendants can diverge indefinitely, both from the initial condition and from one another, whether they are incorporated in organisms of the same species or in organisms of different species. That makes it in principle a fairly straightforward exercise to trace the correspondences on a phylogenetic basis, provided of course that we have the data. Interpretation is much more difficult however, when we attempt to deal with series of parts within the same body (or within the same species) that somehow co-evolve evidently as a result of being affected by common developmental influences. One is tempted, following Minelli (1992), to view changes that affect both front and hind limbs as something like evolutionary parallelism. In such cases, common ancestry *simpliciter* is not adequate. The rudiments of mammalian reproductive organs that are functional only in the other sex have always been rudimentary in one sex or the other. Certain genes are obviously being expressed to a greater degree in some morphs than in others.

Various authors have attempted to find some more general concept that will include both evolutionary and iterative homology. Much as one can trace the evolutionary homologues back to a common ancestral precursor, one ought to be able to trace the serial, sexual, and other homologues back to some common source. Van Valen (1982) proposed a continuity of information. At least "continuity" suggests that there is some kind of interaction between concrete particulars, i.e., individuals. As Wagner (1989a) points out, "information" seems a bit vague. To me it suggests that something rather like a telephone call is involved. Be this as it may, many of the conceptual difficulties with the term "homology" turn out to be due to misunderstandings of the relationships and the ontological categories that are involved. When we know more about the phylogenetics and the embryology it may

still be difficult, but it should not be impossible, to determine what the relationships of correspondence are, and what their causal basis may be. That should bring to an end the conceptual confusion, the obfuscation, and the habit of treating homology as an occult property.

Evolutionary developmental biology has the potential to become an historical science, the goal of which is to provide an explanatory narrative account of how populations of organisms and their ontogenies have evolved. That is the agenda that Darwin put in place in his extensive writings on the relationship between embryology and evolution, contributions that have been studiously ignored by embryologists working in the “experimentalist” tradition (see Darwin, 1868). Perhaps the best model for what is going on, and should be going on, is the emergence of plate tectonics in the second half of the 20th century. With new instruments, new techniques and new theories, it was possible to understand the forces that shape the evolving earth, to reconstruct the movements of plates, continents, *and other individuals* over vast periods of geological time, and to tell the story of the earth as it really happened. As we develop better theories of what shapes embryos and brings about the restructuring of genomes, developmental processes, organs *and other individuals*, we ought to be able to tell the story of life on earth in a way that is every bit as satisfying to the mind.

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