Pattern Description, Process Explanation, and the History of the Morphological Sciences

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Abstract

Present morphological thought suffers from an unhealthy eclipse of its own history. The particular forgetfulness that afflicts the field may begin with the claims of Thomas Huxley that morphology had been revolutionized by Darwinian theory. Since morphology is a descriptive effort, and Darwinian theory an explanatory one, Huxley's argument appears to confuse two different things. The argument became so strained, in fact, that he was obliged to distort the history of the science to make it fit his thesis. The same confusion and distortion are apparent today, and become particularly apparent in the resistance to "pattern cladistics." The actual history of morphological description is still the best evidence that Darwin's explanation was not the basis of any major accomplishment, and thus that morphological description must be independent of explanatory theory. The independence that history argues, however, can be maintained in present thought only by getting rid of the confusion. For this reason the conceptual structure — that is, the theory — of morphological description must be distinguished from explanatory theory, and the "Darwinian revolution in morphology" dispelled.

In an 1880 address before the Royal Society titled "The Coming of Age of the Origin of Species," Thomas Hux1ey spoke of the success of Darwinism since the publication of the *Origin* in 1859. He pictured an earlier geology based on catastrophic revolutions and a view of the fossil record that accepted, in conjunction with these revolutions, large gaps between recognized groups. The *Origin*, according to his account, brought about an abrupt revision of these views, banishing catastrophes in favor of gradualism and finding continuity in the fossil record. Indeed, he continued, the thrust of research since 1859, including his own work on the continuity between dinosaurs and birds, was the closure of fossil gaps. The success of this discovery of continuity was so great, he concluded that "if the doctrine of Evolution had not existed Paleontologists must have invented it."

Whig history had been written before, and has been written since, but Huxley's lecture seems an unusually good example of the genre, by which history is made to lead inexorably to the lecturer's position. History had led to Darwinism by the time the lecture was given; Huxley's problem was how to make that result seem inevitable. For this reason Huxley first made an exhaustive dichotomy between catastrophe and gaps on one side and Darwinian gradualism and continuity on the other, and then pictured it as decisively settled by the demand, *made by the facts themselves*, for continuity. It was a good rhetorical strategy, and probably impressed all in Huxley's audience who did not remember a different sequence of events.

In his examination of this lecture Desmond (1982, pp. 58-59) pointed out that catastrophism had waned before the fifties, and that Owen had espoused a gradualist reading of the record in *British Fossil Mammals*, which he published in 1846, and for which Lyell praised him lavishly. Although Huxley referred to his own work on the gap between birds and dinosaurs, it could have been modeled on Owen's work on the gap between fish and reptiles. Both used a transition fossil — *Archaeopteryx* and *Archegosaurus* respectively — and argued that it represented a bridge between the two groups in question because it possessed traits of both. But Owen came to this conclusion by 1858 — too early for Huxley's paradigm shift — and the continuity of the fossil record discovered by Owen did not call, at least to him, for Darwin's theory.

This last point is potentially the most damaging to Huxley's account. He was at pains to make a necessary connection between Darwinian evolution and morphological continuity. In an 1868 lecture he had claimed that only the Darwinian impulse could ever lead a researcher to attempt to bridge the gaps at all. In the 1880 address he turned the argument about and suggested that after the Darwinian program had demonstrated that gaps were only apparent, this evidence of continuity made the truth of Darwinism visible. Thus not only did Darwinism spur discovery of new facts, it was proven by these same facts. It follows from these claims that Owen should neither have been able to demonstrate continuity nor, having done so, to restrain from embracing Darwin. Yet he did both.

Owen was building what Darwinians would call — or interpret as — a tree, and he was doing so without help from a notion of genealogy. According to Huxley's review of his biological work (1894), Owen made solid morphological contributions but his causal speculations were rooted in *Naturphilosphie* and Neo-Platonism. Since he presumed Owen innocent of any leaning towards Darwinian concepts, how might Huxley have explained why Owen mounted the right research program without the concepts that were necessary to it?

Only with embarrassment, it would seem, but he never had to face the question. Owen, on the other hand, seemed destined to be continually disappointed in his attempts to bring up that very problem. He argued on several occasions that he had announced the continuity of groups before publication of the *Origin,* and that he shared with Darwinians their belief in the progressive appearance of new species in the fossil record. Owen thought that this continuity was an empirical discovery that called for explanatory hypotheses, and was bewildered by claims that the evidence was the private possession of Darwinian explanation. He wrote, in 1860 (p. 403),

> As to the successive appearance of new species in the course of geological time, it is first requisite to avoid the common mistake of confounding the propositions, of species being the result of a continuously operating secondary cause, and the mode of operation of that cause.

Desmond (1982, p. 63) found a letter from the Duke of Argyll that reassured Owen on this very point:

> You are quite justified in drawing a broad distinction between "Creation by Law" — (*some* Law) — and the special theory in respect to the precise nature of that Law, which Darwin has put forward.

In other words, we may distinguish an empirical regularity, which calls for a cause, from a particular causal theory brought forward to explain the regularity.

We may suppose, therefore, that whatever the opposition between Owen and the Darwinians, their discovery procedures evidently shared important elements. These shared elements, however, were not part of the historical explanation, for on that point there was no sharing, and therefore they must be found in the procedures by which pattern is *detected* and *described.* Huxley collapses the distinction between description and explanation, as much evolutionary rhetoric has done since, for this allows him to make Darwin the revolutionary in morphology. Unfortunately, the result of this collapse is merely confusion, whether it is performed in the 1800s or today. The rest of this paper will examine the role of description in the history of morphology and in current arguments. So little is said about description in taxonomic literature, however, that before I continue it seems prudent to examine this phase of science in greater depth.

The theoretical component of description.

Observation, as N. R. Hanson argued in 1958, is theory-laden, and his statement will need a gloss before we can proceed. Hanson's conclusion does not reduce the usefulness of observation to science, but rather announces the demise of a naiveté that assumed that interpretation begins only *after* we have gained observations to interpret. This was the position of the sense-data theorists, who supposed that perception was a mechanical transmission of the senses, free from conceptual activity. Against this, Hanson argued that we must recognize two forms of interpretation — how we interpret what we see, and how we interpret *in order to see*. Thus observation is already a product of interpretation, for the human perceptual process cannot be innocent of conceptual elaboration.

The fact that concepts must be included in perception was discovered for the modern world by Kant, but it has antecedents that stretch back though medieval thought into antiquity. However one cares to argue the point, all accounts have the dichotomy between the sensible and the conceptual in common. The heart of the argument is that while the operations of our sense organs present us with sensations without conscious effort on our part, all *relations* are conceptual, and must be added by the intentional activity of the observer. Because nothing is intelligible without relations, whether internal or external or both, observation is the result of conceptual elaboration of the sensible report (which report would indeed be useless, because unintelligible, without conceptual elaboration).

Observation is therefore a product of "theory," because it is a product of conceptual elaboration, but this admission does not, in itself, destroy the validity of empirical results. Neither circularity of description nor of explanation is a necessary consequence.

The suspicion of circularity of description rests on the assumption that our thinking *arbitrarily* adds the relations it proposes to the sensible report. It is obvious however that we cannot perceive whatever we like, but only what the sensible report allows us to perceive. The conceptual faculty only *proposes* relations, which proposal must then produce a perception of the same relations (now immanent in sensible structure) if it is to be successful. If conceptual proposals are not successful our thinking moves on to something better, but the replacement often happens too quickly to be noticed. The "double-take" is the rare occurrence that is noticed, for in this case we begin to form a perception which, having resulted in contradiction on some level, is dissolved again and replaced by the second "take." If thinking must propose the relation in the first place, the sensible report determines which proposal is successful, or more successful.

Success consists in seeing intelligible structure. Because we do this whenever we open our eyes we are apt to forget the intellectual activity involved. But the moment our habitual mode of perception is frustrated, by camouflage let us say, the conceptual work of perception becomes conscious. Camouflaged figures often become visible when we are given a sketch of the shapes to look for, where before that revelation their camouflage made them impossible to see by denying some sensible clues that would normally mark a border. Once we look for the right shapes, however, camouflage ceases to mislead. *All* seeing is led by concepts, even as our penetration of camouflage was, but when habitual expectations are met we no longer notice the fact.

Once we *have* seen we may arrange what we have seen in logical schemes — for example, we arrange perceived forms in a hierarchy — but this categorical elaboration merely makes explicit the relations implicit in the perceptual act. The elaboration puts a new face on the same data — like the difference between seeing a group of trees and seeing that there are five of them. We have not added anything to the trees by numeration. Even so, we do not add anything to the topological variants by arranging them hierarchically. If hierarchical relations — various levels of sameness and difference — were not already part of the observed structures they could not be abstracted to form a hierarchy. (I shall take up the problems of completeness and inconsistency, which are other matters, in a later section.)

Circularity of explanation, on the other hand, remains a serious difficulty. If a set of observations were found to be a product of our explanatory theory the same observations could not be used to test the theory. When we consider that the lack of testing power would mean that observation did not constitute evidence for theory, the complaint is deadly. But how could observation be an artifact of theory? By the simple expedient of *describing* phenomena in terms of explanation — i.e., using the language of explanation to describe relations in the data. Results derived from a fixed explanatory framework build explanation into observation, producing that most desired of outcomes — experience that explains itself. As I understand it, the notion that texts read themselves, whether we mean by "text" a set of writings or a set of phenomena, is the strategy of fundamentalism, which does simplify the world, but also makes science unnecessary.

But of course phenomena do not interpret themselves, and the fundamental concepts necessary to elaborate relations in taxonomic data are logical rather than causal, as any cursory examination of the history of taxonomy will show. The fact that the theoretical component of our observations *may* be drawn from our explanatory theory does not mean that it must be. Our descriptive concepts — those used to formulate perception — need not be the same as our explanatory concepts. In this case the circularity that destroys the notion of evidence would be avoided. This principle seems sound, and that is why it is surprising to find some authors invoking explanatory concepts in the descriptive phase, a practice that gives rise to a debilitating circularity.

Huxley walked over that line when he attempted to make Darwinian explanation necessary to discovery of patterns it was invoked to explain. He says this, of course, in order to claim success and evidence for his program: success, in that it made a unique prediction and then confirmed the same; evidence, in that this confirmation could be explained only by Darwinian theory. The first claim is contradicted by the existence of Owen's work, the second, by reason. When the accomplishments of the period are reviewed, one can agree with both Owen and Huxley that the closure of the fossil gaps is a major project, and with Owen that however the pattern is explained, both sides agree on the progressive appearance of life — read "differentiation of major groups" — and the morphological continuity between groups. The principles held in common, therefore, are the *descriptive* concepts necessary to elaborate differentiation and continuity.

Closing the Gaps in 1859

Let us re-examine the issues set forth by Huxley in the light of the preceding arguments. The "gaps" in question opened between major groups, like fishes and tetrapods, or birds and everything else. If one held that these groups were entirely discrete, the gap — i.e., a discontinuity in morphology — was to be expected. The revolution in morphology that Huxley describes consisted of a proposal of continuity that led to a detection of the same. This sequence seems to be modeled upon actual events, but events that had already taken place by the publication of the *Origin*. As two recent studies (Appel, 1987; Laurent, 1987) have shown, we must look back to the Paris debate between Geoffroy and Baron Cuvier, and its aftermath, to find the transition after which Huxley constructs his fiction.

The battle lines of that famous event are indeed those of discreteness and continuity. Cuvier and Geoffroy had been long-time friends, although their approach to biological form was divergent. By the time of the debate (1830) Cuvier was recognized as the greatest anatomist in France, and his influence was so commanding that to some he was the establishment, rather than its best representative. He had opposed Lamarckian evolution, held for the fixity of species, and demonstrated that the varied forms of animals could be *teleologically* understood — i.e., that structure reflected function. He had looked on with interest as Geoffroy developed his "philosophical anatomy," tracing "affinities" of organisms on the basis of "analogous" organs, an idea generally recognized but not previously given a central position. He gave Geoffroy credit for working through homologies, as they are now termed, of vertebrate structure to a greater degree than had previously been attempted, but he noted that this mode of comparison, while as old as Aristotle, was but a secondary principle. The primary form of comparison was teleological.

If teleology is the basis of comparison of organisms, the regularity discovered by observation should be the covariance of structure and function. Different groups should possess unique structures, commensurate with their lifestyles, and where homologies between these groups exist so does continuity of function. Geoffroy's proposal of complete morphological continuity between major groups represented, to Cuvier, an excess doomed to failure. In 1828 he stated unequivocally that fishes were a discrete group with unique structure.

In order to provide a morphological basis of comparison, Geoffroy made the first attempt at rigorous definition of what now appears to be a familiar standard — the "principle of connections" — postulating that within the common plan of a group a standard part, or "analogue," was identifiable by its *connections* to other parts — i.e., analogues occupy the same position in a topological schema, or can themselves be mapped, according to their internal composition, on the same schema. In his *Philosophie anatomique* (1818) he argued: "we will always find in each family all the organic materials found in another," for "An organ is sooner altered, atrophied, or annihilated, than transposed." The "organic materials" are the units recognized by connections, and the real nature of the "common plan" is a set of connections, a kind of map, within which the elements connected may alter in shape, size, orientation and function, but not in the order of connections — throughout all changes the positional schema is conserved. Terminal organs may even be subtracted (annihilated), if there is no use for them, but subtraction is not transposition or creation of new materials.

Geoffroy did not refrain from speculation on the cause of this constant topology. He hypothesized a mechanism based on blood-flow, and set himself in opposition to notions of divine intervention or *vital force* in favor of naturalistic explanations. He spent most of his effort arguing that animals do indeed share a constant topology, however, and when he did advance causal speculations he justified them by the need to explain his topological results. His explanations do not seem to have had much impact on succeeding generations, but the opposite is true of his descriptive proposals.

Disagreement between Cuvier and Geoffroy broke into open dispute before the French Academy in 1830. While both Cuvier and Geoffroy presented extreme positions in the debate (Geoffroy suggested that even *embranchements* were transforms of one another), the underlying question was clear. Would groups be looked upon as teleologically distinct, or morphologically continuous? After the debate both sides claimed victory, and as the dust settled biologists began the task of integration. The future of the science would consist of some combination of teleological and morphological approaches.

Let us remember that Geoffroy's proposal concerned the "ideal" — read "logical" — relations of form. It rested on the postulate of a set of invariant topological relations — termed "connections" — within a variation of potentially everything else. Forms compared by this standard become differing executions of the *same* topology, and since they are isomorphic on this level, each must relate to any other as a *transformation* of that other. I must emphasize, however, that in this context the term "transformation" indicates pattern and not process. Thus Owen defined "homology" (a word with topological significance in geometry) as "the same organ under every form and function," where sameness is recognized by identity of connections. Gaps between major groups are closed by understanding those groups to be continuous through transformation (differing executions of invariant topology), and "bridge" fossils provide a "graded series" to clarify homologies. Again, the transformation postulated here is topological only, and thus is a *logical* rather than *historical* relation. This same relation, however, was to provide the evidence used to support hypotheses of physical transformation when such hypotheses were advanced.

By the time Darwin published, he looked on some aspects of Geoffroy's work as authoritative, and made appeal to them in chapter 13 of the *Origin*: "Morphology" (1859: p. 434)

> What could be more curious than that the hand of a man, formed for grasping, that of a mole for digging, the leg of the horse, the paddle of the porpoise, and the wing of the bat, should all be constructed on the same pattern, and should include the same bones, in the same relative positions? Geoffroy St. Hilaire has insisted strongly on the high importance of relative connection in homologous organs: the parts may change to almost any extent in form and size, and yet they always remain together in the same order. We never find, for instance, the bones of the arm and forearm, or of the thigh and leg, transposed. Hence the same names can be given to the homologous bones in widely different animals...

Darwin's next paragraph invoked the revolution of which I spoke above, for it correctly opposed Cuvier's teleology to Geoffroy's morphology:

> Nothing can be more hopeless than to attempt to explain this similarity of pattern in members of the same class, by utility or by the doctrine of final causes. The hopelessness of the attempt has been expressly admitted by Owen in his most interesting work of the *Nature of Limbs*. On the ordinary view of the independent creation of each being, we can only say that so it is; — that it has so pleased the creator to construct each animal and plant.

Notice that Darwin appealed to the authority of Owen in rejecting teleology. He acknowledged this debt because Owen, in *On the Archetype and Homologies of the Vertebrate Skeleton* (1848) and *On the Nature of Limbs* (1849), had worked through the issues of the Cuvier-Geoffroy debate and placed Geoffroy in a secure position. (In these works Owen substituted "homology" for commonality of structure, and used "analogy" for commonality of function.) In order to secure Geoffroy's morphology, however, Owen had to answer the teleological argument.

Cuvier's teleology postulates that structure is determined by function, leading to a discontinuity of structure whenever there was a discontinuity of function. Owen answered that this view, like that of the protestant theologians in Britain (one should call to mind Paley's argument on the watch), would design animals to fit their mode of life as machines are designed to fit their function. But in machines, he points out, both the materials and the *plan* of construction are determined by the function. Even Cuvier would have to admit, however, that animals often adapt a single underlying plan to several functions. If the same structure supports differing functions, topology is more basic than teleology, and the admission of such topological invariance reveals the failure of the teleological program. "The teleologist," wrote Owen (1849), "would rather expect to find the same direct and purposive adaptation of the limb to its office as in a machine," but morphological investigation shows that limbs built for flying, running, swimming, digging, etc, are all constructed on the same plan.

Darwin's gloss of Owen continued with Owen's modification of Geoffroy's postulate that all vertebrates contain the same bones, or at least, the same centers of ossification. Finding that no juggling of skeletons could produce the same "organic materials," or even the same centers of ossification, Owen tried another strategy. He generalized on all skeletal forms by finding a common denominator: the vertebrate archetype. This structure, essentially repetition of vertebrae, would serve as a basis if one preserved enough teleology to modify the vertebra as the need demanded. Thus the skull area of the archetype consists of four vertebrae, which become the modern skull by an expansion of the spinal cord and a consequent ballooning of the vertebrae. By extension and metamorphosis, vertebral processes become ribs and sternum, and finally, becoming "teleologically compound," such extensions form limbs. The schema is too arbitrary to produce empirical confirmations, but that problem was not immediately apparent to Owen or his followers.

The archetype itself, when cast in diagrammatic form, looks like a fish. To the literal-minded Darwin, that is exactly what it signified. Thus he postulated an "ancient progenitor, the archetype as it may be called," and filled out the rest of the program after Owen's ideal schema, approximating a teleology of design through his own "natural selection" (1859; pp. 437-438) :

> An indefinite repetition of the same part or organ is the common characteristic (as Owen has observed) of all low or little modified forms; therefore we may readily believe that the unknown progenitor of the vertebrata possessed many vertebrae; the unknown progenitor of the articulata, many segments; and the unknown progenitor of the flowering plants, many whorls of leaves. We have formerly seen that parts many times repeated are eminently liable to vary in number and structure; consequently it is quite probable that natural selection, during a long continued course of modification, should have seized on a certain number of primordially similar elements, many times repeated, and have adapted them to diverse purposes.

As we have seen above, Darwin moved away from transcendental entities. Geoffroy's school of "philosophic anatomy" dealt with the "ideal" or "philosophic" relations of the forms, but Darwin wanted to arrive at something more concrete. In his chapter on "Doubtful Species" he had mentioned that some forms are so closely linked by intermediate gradations that naturalists are unsure of how to rank them. He then points out that when viewing such a series of graded forms one seems to be seeing a *process* of change (1859; p. 51) :

> These differences blend into each other in an insensible series; and a series impresses the mind with the idea of an actual passage.

The notion that historical process is immediately seen in morphological evidence runs through the language of Darwin's text, culminating in his advice, in chapter thirteen, that a "philosophic" approach to the evidence is unnecessary (1859; pp. 438-439) :

> Naturalists frequently speak of the skull as formed from metamorphosed vertebrae; the jaws of crabs as metamorphosed legs, the stamens and pistils of flowers as metamorphosed leaves…. Naturalists, however, use such language only in a metaphorical sense; they are far from

> meaning that during a long course of descent, primordial organs of any kind — vertebrae in the one case and legs in the other — have actually been converted into skulls or jaws. Yet so strong is the appearance of a modification of this nature having occurred, that naturalists can hardly avoid employing language having this plain signification. On my view these terms may be used literally...

The metaphoric quality of previous language was produced by the mental reserve that described the forms of a graded series “as if” they pictured an actual passage, or the topological identity of two forms “as if” one was produced by a physical distortion of the other. We might use the same terminology in describing the relation of geometric forms when those forms are produced by a systematic change in the execution of a constant topology. A series of parallelograms, for instance, which begins with a right-angled form and departs successively from that, might be described in terms of physical transformation by suggesting that “We take the right-angled box and gradually squeeze it flat.” Such descriptions are obviously metaphorical, aimed at the set of relations by which the forms are related rather than a process by which they are formed. After all, the “passage” or movement from one form to the other, whether in the geometric or biological example, is contained in the human imagination rather than the static shapes. This is why Geoffroy termed it “philosophical” rather than actual.

For Darwin these distinctions must have seemed merely faint-hearted. In the quote above Geoffroy’s “philosophical” relations become *merely* figurative ones, the “plain signification” of which, if we will but recognize it, is “an actual passage” — i.e., a process. It would seem that the collapse of the distinction between description and explanation was central to Darwin’s argument before Huxley adopted it.

If we take Darwin at his word, this literalism with its attendant genealogical explanation, is his real contribution to the science of morphology. Beyond this he merely adopted earlier integrations of teleology and morphology, and according to Laurent (1987) he was not even the first to explain logical transformation by descent. But I do not care to address claims of priority here — it is enough that Darwin himself limited his contribution to a literal interpretation, arguing that he could “see” the events of his explanation in the morphology.

The project of “closing the gaps” was neither invented by Darwin nor claimed by him, because he admitted that it had been adopted from Owen, and thus ultimately from Geoffroy. He does take credit for changing the proposal from a “philosophic” to a “literal” one, but the enabling insight was still drawn from Geoffroy’s technical advances, and the search for continuity is always performed as a search for topological similarity. Although the evolutionary meaning of “homology” now obscures the original topological concept, it is still recognizable. As Goodwin wrote in 1984, using Owen’s term: “Homology is an equivalence relation of a set of terms which share a common structural plan and are thus transformable into one another. This is therefore a logical relation independent of any historical or genealogical relationships which the actual structures may have.”

Topology and Hierarchy

The advance in description that I have been tracing was the attempt, however incomplete in results, to compare on the basis of invariant topology. In order to examine the implications of this principle more closely, however, I turn briefly to the second descriptive proposal that grounds taxonomy.

If animals can be compared on the basis of a common-plan standard-part order, or what Owen termed “special homology,” the results of that comparison should provide a measure of resemblance, which measure has been found in a hierarchy of topological variation. (In order to avoid confusion at this point I should perhaps mention that a proposal of hierarchical ordering of special homologies differentiates this research program from that of numerical taxonomy, which compares organisms on the basis of "overall resemblance." Whatever other differences accrue at later points, the main difference between cladistics and numerical taxonomy rests not on the hierarchical proposal but on the means of comparison. The former is topological in the sense defined above, the latter is not.)

A hierarchy of less general variants subordinated to more general ones is a logical possibility that the standard of comparison admits. That variations should have a regular distribution, however, or that this regularity should be hierarchical, does not follow from the standard of comparison, and must be determined empirically.

In order to make this determination we must again propose the relations we seek before we can expect to find them, since relations must be thought before they can be perceived. The hierarchical proposal is older than Aristotle, but while not unchallenged, the proposal has lasted through many periods of biology, presumably because it enjoys reasonable empirical success — i.e., congruence between observed data and conceptual relation — whatever our explanatory reasons for liking it. After all, differing proposals of order may be compared on their measure of descriptive success, without reference to explanatory justification. It follows that the proposal could be replaced by any order that could show greater success — greater congruence between data and conceptual pattern.

That descriptive proposals can only be justified by descriptive success is not well understood. Panchen (1992; p. 239), wonders why I decline, in a 1985 paper, "to postulate that the natural order is a comprehensive hierarchy." He clarifies his concern a few pages later (p. 243) when he remarks that "the existence of a hierarchy embracing all living things is in doubt," and adds that unfortunately "the only valid method of revealing it [the hierarchy] is that of cladistics, which depends absolutely on its *a priori* existence. This dilemma is insoluble." I agree that *this* problem is insoluble, which is why I am relieved that cladistics need not make hierarchy into an *a priori* truth. I cannot see why any science worthy of the name should dictate the results of observation before observing. Obviously we "reveal" nothing about nature through *a priori* decisions.

The circularity that Panchen raises is created by describing the data in terms of the explanation — i.e., by postulating that "the natural order is a comprehensive hierarchy," or supposing such a postulation necessary. But as I have been arguing, hierarchical order is not part of the explanation, but part of the description, and is produced by logical elaboration of topological data. Since it is an empirical postulate, it is always provisional, and should not be legislated. The empirical success of hierarchical ordering has established this order as the most successful so far, and that is justification enough for a provisional postulate. There will be reason to shift our procedures when and if more successful proposals of relation show up — and as long as we have not succumbed to *a priori* demands, we shall be able to do so.

Although parsimony is a side issue, it should be briefly examined. Having proposed a hierarchical order we will need, as in the case of topological comparison, methodological principles by which to select, from a plethora of possible hierarchies, the one that serves our purpose. Upon reflection, our choice of order has already determined that method. The attempt to elaborate hierarchical relations in data proposes that the data are part of a specific hierarchy that we desire to recover. If all character information were congruent with a single hierarchy then selection would be automatic. If some characters contradict the report of others, however, we select the most complete hierarchy that can be constructed from the data, which is the hierarchy with fewest contradictions (incongruence) between data and hierarchical order. The hierarchy selected in this manner will be best supported by evidence, for it maximizes congruence between data and hierarchical pattern.

The procedure for this selection is currently termed a parsimony program. If included in the explanatory concepts parsimony would carry ontological implications, but at the descriptive level it does not do so. Of course, its use implies the methodological assumption that the best supported hierarchy is the best candidate for the original order. This does not seem an unlikely procedure, considering that it is also the only candidate. Any alternative hypothesis throws doubt on the framework proposal that the data record a hierarchy. Due to its methodological status, such a method of minimizing incongruence could be used on any data set, taxonomic, linguistic, or other, in order to find the most complete hierarchy that the set admitted.

With this much understood, we see also that a further principle is entailed in the decision to use a data set that is not completely congruent. Data are elaborated according to the proposal of hierarchical relations, but this proposal necessitates the assumption that the hierarchy is the real order of correspondences. By this logic, if the hierarchical order is real, incongruence is not. Or rather, *random* incongruence is not real — i.e., it is a product of human error rather than an aspect of nature. (Let me caution here that I do not mean to legislate an *a priori* rule. I am only working through the logic of the postulate, always provisional, by which we propose to order topological data.)

Non-random incongruence — incongruence that shows a repeated pattern — represents an order that lies outside the hierarchy of congruent characters. Hybridism, for example, can produce two equally parsimonious hierarchies for the same organism, differing only through the placement of one terminal branch. But random incongruence, because it can only be included by a random set of hierarchies, is not evidence for hierarchical order at all. Recognition of such incongruence as real would seem to reject the postulation on which the whole program is based, since it assumes that nature contradicts the proposal of hierarchy. (Obviously, if incongruence were the *general* result of our attempt to order data, we would have little reason to suppose the hierarchical proposal successful.)

Because random incongruence is explained as error, it provides an added test of "homology." The parsimony program distinguishes those apparent correspondences (homologies) that are distributed hierarchically from those which are not. If *real*, topological correspondence is hierarchically distributed; the postulations of correspondence that produce random incongruence are erroneous. This test of correspondence — by taxic congruence — may appear to take precedence over direct topological comparison because it is able to correct the former, but the impression is illusory. The hierarchy is one of topological variations. Congruence is able to test *individual* postulations of correspondence because it shows them to be irregularities in a larger order. Since that order is detected by combining the results of many direct comparisons, it is ultimately topological evidence that is brought to bear on the suspect homologies, and the generality of that evidence is decisive.

Present taxonomy is therefore grounded on two empirical proposals — that organisms may be compared topologically and that the variants revealed by such comparison are ordered hierarchically. Implicit in these proposals is that no other form of description reveals such a strong regularity. Darwin accepted the same procedures in chapter thirteen of the *Origin*, and his explanation was matched to this description. Because their content is descriptive, the same proposals are found in Owen and his French forerunners. Huxley's notion of a Darwinian revolution in morphology is just as untrue when applied to present morphology as it was when applied to the morphology of 1880.

Closing the Gaps Today

As the last section has argued, continuity in morphological evidence is found descriptively, if it is found at all. Huxley's version of events did not recognize this demand, and I have been at pains to correct his history. The central problem, however, is Darwin's literalism, which Huxley was applying. It is still a problem, although it is rarely noticed. Since the victory of Darwinian ideas in the realm of opinion the popular view holds, with Darwin (1859; pp. 438-439), that "during a long course of descent, primordial organs… have actually been converted...." to very different structures. Of course, we do not observe the actual process: "Yet so strong is the appearance of a modification of this nature having occurred, that naturalists can hardly avoid employing language having this plain signification." It is obvious that the verbal habit is widely shared today. Darwinian literalism, in fact, controls the *imagination* of the modern to such a degree that the term "transformation" has only the "plain signification" mentioned above — i.e., a temporal process in which the earlier form changes into the later. Very little attention is paid to the circularity that results from describing the morphology with terms drawn from explanatory theory.

Given the prevailing mood of literalism one of the most interesting comments on morphology in recent years was Patterson's 1982 argument that one finds two distinct meanings of homology in present systematics. The one that he prefers he terms "taxic homology" and gives as an example the more or less inclusive homologies (synapomorphies) that allow our arrangement of the groups within the Gnathostomata. Each of these homologies implies a hypothesis of grouping, and thus can be tested both by topological similarity and by congruence.

On the other hand, the attempt to work through what he calls "transformational homologies" — like the hyomandibula of fishes with the stapes of mammals — advances no new hypothesis of grouping (the postulation depends upon the inclusion of both fishes and mammals in the Gnathostomata) but makes a hypothesis of literal transformation. Patterson argued that such hypotheses produce no empirical confirmations since the topology is unclear and the test of congruence cannot be applied (no new hypothesis of grouping is implied). Patterson labeled this form of homology "vacuous" of empirical content, arguing that only taxic homologies could be submitted to any meaningful test.

As Patterson has demonstrated, transformational homologies do not carry any new hypothesis of grouping, so the generality of evidence cannot be used to test them. That leaves topology, and if this is also indeterminate, transformational homologies will be untestable. The taxic approach applies the descriptive concepts of topological constancy and hierarchical congruence to elaborate the raw data, and its empirical content consists in the same data with its relations made conceptually explicit. Lacking these descriptive tools transformational approaches reduce to applications of explanatory hypotheses to descriptive projects — i.e., the discovery of homologies. Unfortunately, an explanation of observed facts does not add to the facts, however likely the scenario may seem. The approach is empirically empty because it is an exercise in circularity. The relations made explicit are not those of the data but those of the explanation.

How could we deceive ourselves in this manner? In a discussion of the distinction between taxic and transformational homologies Rieppel (1998, pp. 111-112) presents the transformational approach as an artifact of Darwinian literalization:

> The taxic approach results in a hierarchy of fixed types representing logical relations of form, and in that sense it is ideal as well as static. The transformational approach, however, puts the hierarchy of homologies into a temporal sequence of form in order to ask the question of evolutionary transformation. The static hierarchy of types is reduced to a temporal sequence of forms, homology comes to denote *relations of succession*.

The complaint is not that we account for the phenomena by a hypothesized historical sequence, but that we actually describe them in this manner, seeing "an actual passage" rather than a hierarchy of types in the evidence. Once we have accepted the literal notion of transformation that is what we look to see in morphology. Thus we try to identify ancestry — i.e., what changed into what — based on morphological evidence, as if a series of triangles contained evidence of parentage. Animals do possess ancestry while triangles do not, *but what we can determine about either subject must depend upon the nature of the evidence examined*. Since in either case that evidence consists of the comparison of forms by topological standards, a set of topological relations will be the result. In the case of morphology, the set that Rieppel terms the "hierarchy of types."

Darwin's mode of thought shifted the context of morphological arguments to the degree that Huxley could make his remarks with little fear of challenge, then or now. I think that the real effect of Patterson's argument must be to shift the context of discussion once again. His critique of transformational homology makes the logical priority of the taxic homology quite clear, and his finding that transformational homologies are usually empty of empirical content is in keeping with the circularity of describing data with the terms of explanation. Due to the ubiquitous literalism that he addresses, however, he uses the term "transformation" to refer only to literal change, and does not challenge the literalism of language that maintains the literalism of thought he has faulted.

Transformation Revisited

Rieppel (1998) argued that the hierarchy of types was "static." He meant by this that it was innocent of temporal process, or what most writers seem to mean by "transformation." But certainly when a topologist speaks of one form being a transformation of another no temporality is implied. A transformation in the most general sense is a particular kind of change, one that both preserves and alters — i.e., the underlying identity must remain constant while the appearance or execution of that identity changes. By this standard any homology is a transformation, for it is clear that the idea demands both underlying identity and external difference. Homologous organs are not "the same" physically or sensibly, but can be equated by possession of the same relations. Thus a particular tetrapod limb can be considered a topological transform of another, in that it can be geometrically produced from that other by a set of distortions of the parts.

Of course, "transformation" in this sense has no historical, or even directional, meaning. *One limb does not turn into another*, but both are isomorphic products of the same topology. Direction, or polarity between the more general and the less general variants within the group of compared forms, is also a logical relation, but one that enters only with hierarchical ordering. No such ordering is possible, however, until we have a basis for comparison — i.e., until we have established that the forms compared are transformations (of a constant topology) .Thus transformation is established before direction, and is independent of any temporal reference. (This independence cannot be reversed. Theories of temporal transformation need evidence, and only forms exhibiting topological transformation can provide it.)

The basis of all taxonomic projects is the description of topological relation, and this description is itself a major scientific problem. The invariant element underlying transformation is clearly the point at issue, for a successful formulation of that element would put morphology on a rational footing. Geoffroy tried to make such a formulation with his *unity of organic composition* — the notion that each organism could be compared as transformations of the same "materials" or topological elements. If he had been able to demonstrate a total invariance for all vertebrates, the phylum would consist of varied appearances of the same (the same *law* or relation, not the same *thing),* and while the major groups would show discontinuities of execution, they would demonstrate a continuity of plan. But Geoffroy's research program fell short of its goal. The principle seems very clear when we are dealing with tetrapod limbs, but if we try to extend the analysis to sarcopterygian fins ambiguities arise. Geoffroy's own identification of the bones of the gill cover of fishes with those of the inner ear of fishes succeeded only in showing that these might be homologous, but it produced no test for this conclusion.

Of course diagnostic homologies for the Gnathostomata exist. But what remains unclear is the implication for the whole group of this partial identity. Given that a set of homologies identifies both fishes and tetrapods as gnathostomes, does the *unity of organic materials*, or invariant topology, imply other parts must be homologous as well? Do sarcopterygian fins therefore represent a topological transformation of tetrapod limbs? (I deliberately reverse the probable temporal sequence to emphasize the nature of the question — we are inquiring about topology, not sequence.) We may assert this unity, as the literature of transformational homology can attest, but we may also suppose that both be considered unique and unrelated structures. Either choice makes an interpretation of the principle of invariant topology.

Empirical tests cannot at present choose between these alternatives for it is at this point that the research program — comparison by recognizable invariance — fails. I mean that it tells us neither whether the fin is or is not homologous with the limb. Rieppel (1988; pp. 44-49) has reviewed the limitations of the topological judgment, implying the same conclusion. At present, a decision that fin and limb, or gill and middle ear bones, must be homologous, or need not be, is not determined by evidence, but by our interpretation of the postulate by which we compare organisms — invariant topology. And differing interpretations are still possible, for almost two centuries after Geoffroy made topological comparison the basis of morphology we still cannot determine empirically the degree of invariance that organisms possess.

Our comparisons begin from some form of Geoffroy's postulate, which we assume *in order to see resemblance*, not to interpret the resemblance we have seen. The fact that the degree of invariance cannot be determined empirically in some cases indicates either (1) that the postulate is false, or (2) that our criteria are inadequate to our intention. If the postulate is false our method of comparison may be secondary, as Cuvier claimed, for it would seem that whatever determines when topological invariance will be conserved and when it will not is more important, in just the sense that teleology once seemed more basic. If the postulate is true, our approach is correct (and our groups largely valid). But the research program that could formulate the underlying constant, rendering it recognizable to human perception in all cases, does not yet exist.

How do organisms vary? Our present methods of tracing topology are quite crude, to say the least. We are often guided by intuition, but we do not possess the means to make intuition explicit. Mathematical topology can demonstrate transformations that look quite discrete to the uninitiated — we do not know whether organisms are giving us the same problem. And research into the nature of biological transformation has barely begun. Upon reflection, it is somewhat odd that morphology should have advanced so little toward the solution of a problem that Geoffroy formulated so well. One might even speculate that the Darwinian explanation of taxonomic relations was, in a sense, premature, since the logical nature of those relations is still unclear.

To some degree the success of the hierarchical postulate must have distracted attention from the incomplete formulation of topological invariance. After all, when a hypothesis of topological invariance implies a grouping it can be tested by congruence, and if the generality of evidence (congruence) confirms the hypothesis our problem seems at an end. But this success does not seem adequate to explain the apparent eclipse of the descriptive problem for generations of taxonomists. Yet judging from the literature something like this has happened. Morphology is rendered possible by the theoretical postulates that elaborate the phenomena and provide a standard of comparison. Those postulates are the "theory" of morphological description, and they are just as capable of investigation as explanatory theories. Unlike the latter, however, they have suffered a period of neglect, probably beginning about 1859.

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