"The contribution of paleontology to teleostean phylogeny," by C. Patterson, is scholarly and strongly historical; it will be of interest primarily to ichthyologists, but contains conclusions which may have significance for systematists working on other groups—neontologists and paleontologists alike. Patterson's most sweeping conclusion is that paleontology must be subservient to neontology in phylogenetic work. The basis for this lies not only in his analysis of the history of phylogenetic work on teleosts and the necessary role that recent groups have played in the understanding of phylogenetic relationships in the teleosts, but also on the fact that recent organisms have more attributes available for study, and thus any given hypothesis of relationships of recent groups can be more severely tested. Patterson points out that the search for more fossils will not necessarily contribute to improved understanding of phylogenetic relationships in a group. In effect, the discovery of previously unknown fossils generally presents new problems, not new solutions.

Finally, Patterson notes that some opponents of cladistics have argued that good taxonomists have long used similar methods. From his review of the history of teleost classification, Patterson deduces, however, that it is not the groups produced by good taxonomists that have remained stable, but rather the groups based on good characters—synapomorphies.—*Randall T. Schuh.*

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COMPARATIVE BIOLOGY AND BRAIN EVOLUTION

Evolution of Brain and Behavior in Vertebrates.—R. B. Masterton, M. E. Bitterman, C. B. G. Campbell, and N. Hotton (eds.). 1976. Halsted Press, John Wiley & Sons, New York. xxii + 482 pp. $29.95.

Evolution, Brain, and Behavior: Persistent Problems.—R. B. Masterton, W. Hodos, and H. Jerison (eds.). 1976. Halsted Press, John Wiley & Sons, New York. viii + 276 pp. $14.95.

These are, respectively, Volumes I and II of the collected papers presented at a conference in Tallahassee, Florida, in 1973. The conference was organized, in effect, to update the 1958 book edited by A. Roe and G. G. Simpson, *Behavior and Evolution*, and was designed to bring together paleontologists, neurologists, and behaviorists in order to discuss problems of mutual interest.

Volume I contains 19 papers covering a broad range of subject matter including the radiation of various vertebrate groups (poikilothermous vertebrates, "later" mammals, and primates), comparative anatomy of vertebrate special senses (olfaction, vision, hearing), comparative anatomy and evolution of the brain, and behavior (learning, tool use, primate social behavior). Volume II encompasses 16 papers that focus on the theory and method of biological comparison. Volume I, then, is more specific and data-oriented, Volume II, more general and theoretical.

There are many papers in both volumes that will appeal to readers of *Systematic Zoology*, and they can be recommended especially to those interested in comparative neurology and comparative methodology. But persons unfamiliar with recent advances in theoretical systematics and vertebrate history should approach many of the papers with caution—some are inexplicably old-fashioned and theoretically naive. This state of affairs arises in part when various workers, not necessarily trained in or frequently involved with comparative problems, are called upon to produce a manuscript for a conference such as this.

This review will concentrate on those papers that should be of general interest to readers of *Systematic Zoology*, primarily in the areas of vertebrate evolution and comparative theory. Unfortunately, space is limited for discussion of a number of fine articles dealing with comparative anatomy and behavior.

The first paper of these volumes, "Origin and radiation of the classes of poikilothermous vertebrates" by N. Hotton III (I, pp. 1–24), provides a curious beginning to the conference proceedings. Apparently designed to review current thinking on early vertebrate evolution, the paper adopts a particularly Romerian approach, an approach that, in this reviewer's opinion, has become antiquated and to a great extent superseded by recent advances in paleontology and systematics. Indeed, the relevant literature of the last 10 years is absent from the bibliography. Part of the problem lies with the traditional paleontological viewpoint and the perception of its role in reconstructing past history:

> "It is also true . . . that . . . the fossil record has yielded a remarkably consistent story over the past 100 years of study and that the increasingly numerous discoveries in this interval have gone far to document biological transitions in a manner consistent with evolutionary theory. Therefore, by the principle of Occam's razor, it must be assumed that the fossil record provides a pragmatically reliable measure of the actual history of the vertebrates—that the earliest record and the first record of abundance of a group indicate, respectively, the times of origin and of primary adaptive radiation of that group, within a practical margin of error."

All of this is highly debatable, of course, and the problems attendant with this traditionalist viewpoint are perhaps nowhere better illustrated than in paleoichthyology. Our conceptions of early vertebrate ("fish") interrelationships have advanced considerably during the last decade, not through the discovery of "transitional" fossils but primarily because of the application of a phylogenetic systematic methodology. Anyone familiar with this literature should readily understand that the Romerian view of the fossil record—who said the *Scala Naturae* liveth not?—is not only simplistic but rife with unscientific (untestable) assertions. Thus, statements such as (a) "each class [Agnatha, Placodermi, Osteichthyes, Chondrichthyes, Amphibia, and Reptilia] includes morphological subdivisions that are already distinct . . . and because their distinctness implies independent origin, a case can be made for regarding most such subdivisions as classes unto themselves" (I, pp. 1, 3), or (b) "acanthodians have been regarded as ancestral to all other jawed vertebrates . . . detailed anatomical considerations confirm the idea that they are ancestral to later bony fish without barring them from shark ancestry but tend to confute any such relationship to placoderms" (I, p. 9), simply should not find their way into print. It has become apparent, for example, that most of Romer's and Hotton's "classes" are nonmonophyletic, in which case why do we continue to recognize or name them? If for "heuristic" reasons, then why not "vermes" (for worms, snakes, etc.)? Furthermore, Hotton does not spell out the evidence "confirming" the notion that acanthodians are ancestral to other gnathostomes, a claim that is highly questionable.

Here and elsewhere in these books we read of "adaptive themes," "adaptive processes," "adaptive thresholds," and the like. Why? Perhaps because the authors believe they are studying process, but how we are never told. In fact, is it possible to study process in any historical analysis? Perhaps statements about postulated sequences of change (inferred, not observed, patterns) being *caused* by selection or depicting adaptive modification are really only articles of faith and not subject to scientific analysis (i.e., hypothesis testing). How can we, for example, recover evidence pertaining to selection forces or fitness? It would seem that such evolutionary interpretations of the pattern of the historical record have legitimacy only because evolution by natural selection (adaptation) is ***an axiom of the system***, in which case its application to lower level hypotheses (that is, hypotheses about specific historical events) is trivial. Consequently, what are we to make of such remarks as "When the fossil record and the role of function are properly taken into account, it becomes apparent that vertebrate classes do not merely express distinctive adaptive themes but that they actually come into being as a consequence of adaptive processes" (I, p. 18)? Platitudes, certainly, but this thinking still permeates much of evolutionary biology and paleontology. We have grown very comfortable with what we think we are studying.

If one had to identify the central questions in systematics, certainly it could be said that one of paramount importance is about method: What are the principles of systematic methodology? The question is an old one, and to judge from the continued discussions of recent years (including much of the content of these books), one that has not been answered to the satisfaction of most systematists. Each of us, after all, may have our own opinion as to the preferred method. The second volume of the Florida symposium is directed almost wholly to the question of method and contains much of interest to the theoretically oriented systematist.

In all such discussions it is sometimes useful to attempt to separate what a worker says should be done from what that worker actually does. Very often they do not coincide. The theme of Volume II is comparison, why one does it and how. The feeling one gets from reading these papers is that a gap exists between how these workers believe comparison should proceed and their own practical application. Given the content of their papers I cannot help but feel that all of the authors have practiced comparison in their own way (or the way of their mentor) and now is faced with putting down on paper what their methods are. A clear conception of method seems not to precede their actual work. The conference took place in 1973 with publication in 1976, thus it is surprising that virtually nothing is said about the recent advances in comparative systematics that have taken place since the mid-1960's. Indeed, most of the symposium papers are set firmly within past traditions and thus share a characteristic lack of clarity and understanding about biological comparison.

Nowhere are past traditions so firmly identified and adopted than in the first paper of Volume II by Douglas B. Webster (II, pp. 1–11). Webster recognizes Georges Cuvier as the originator of the modern comparative method (II, p. 1):

> "His method is still used and is, in fact, so fundamental that it has passed into current thinking without notice. Yet understanding the power of his method can lead to fresh insights; understanding its mechanics can help keep current analyses as clear and orderly as were Cuvier's own."
>
> "His concern was not with a process of change but with a present reality—animal classification and what would now be called functional morphology."

Cuvier's primary interest, it can be argued, was classification. In his day new organisms were being discovered and described at a rapid rate, and many biologists were struggling with the problem of arranging this diversity into some natural order. For nearly all these workers natural order was assumed to be a manifestation of God's handiwork, not the result of some historical process. Cuvier, as well as his predecessors and contemporaries, sought to recognize order in nature by basing classification on those characters that were unique and constant to a group or on those characters that were deemed "more important." Cuvier certainly did not have precise criteria to recognize importance, rather this was based vaguely on "functional" aspects with, not unexpectedly, sensation (nervous system), motion (locomotor system), and reproduction being the "most important" suites of taxonomic characters. His "functional" criteria, therefore, like those of many modern systematists, were more philosophical constructs than precise scientific notions, and Cuvier himself usually fell back on the empirical distribution of characters to form sets of organisms.

There is little evidence that Cuvier's analyses were clear and orderly (but perhaps more so than his predecessors), but there is reason to believe that many of the metaphysical attributes of Cuvier's methodology are alive and well in contemporary systematics. Many modern systematists, most of whom have had little practical experience in deciphering phylogeny or forming classifications, continue to suggest that functional information is important in choosing taxonomic characters. The argument is at least as old as Cuvier but its clarity has not improved substantially and perhaps only has become more confused with the addition of evolutionary jargon.

Cuvier, according to Coleman (1964, *Georges Cuvier Zoologist*, Harvard University Press, pp. 78–79), was much impressed with the botanist Antoine Laurent de Jussieu, who had published a major treatise on plant classification. De Jussieu sought to group plants in terms of sets of constant, cooccurring characters. Such an approach, in the absence of obtuse argumentation over the functional importance of the characters themselves, seemed to reveal a "natural" order, a hierarchy if you will. As Coleman remarks, Cuvier departed from this approach in that the functional attributes of animals were considered philosophically more useful within animals than within "immobile," "insensitive" plants. Such seems to be the origins of much current systematic tradition. If Cuvier's approach to comparative biology offers "insights" and is still "fruitful," systematists need to be informed how, precisely, that method is to be applied.

Functional morphology has undergone a remarkable advance in the last decade, approaching bandwagon proportions, at least with respect to cornering the job-market in comparative anatomy. Much has been claimed for this "renaissance." While there has been a substantial accumulation in our understanding about how animals work, in this writer's opinion this movement has contributed little to systematic-evolutionary biology, the claims of the proponents notwithstanding. This "functional theme" permeates a number of the papers of Volume II, and to a certain degree is even made the center of a debate by Stephen Gould in his two papers, one on grades and clades (II, pp. 115–122) and the other on analogical comparison (II, pp. 175–179). A straw man is erected, that those workers emphasizing phylogenetic analysis of groups have little desire or interest in functional interpretations of evolutionary events:

> "the phyletic dogma reigns to exalt heritage and relegate habitus; this bias is most strongly expressed by modern Hennigians, who treat analogy as Haeckels' *Fälschungsgeschichte*, something to be recognized and removed lest phylogeny be confounded" (II, p. 177).
>
> "the establishment of phylogeny does not, after all, exhaust the content of evolutionary biology" (II, p. 175).

I would recast the debate: is the analysis of grades and analogs really useful and does it lead to scientific (testable) generalizations? The generalizations that Gould would have us derive from grades and analogs (his "functional theme") are cloaked with the concepts of natural selection and adaptation, concepts I would claim are *axiomatic* within the system of evolutionary biology and therefore not themselves subject to testing at the level of historical reconstruction. If so, the concept of grades reduces down to a trivial case of observation (and functional inference): there are a number of taxa that locomote alike, feed alike, breathe alike, or what have you. To state that they entered similar adaptive zones, were subject to similar selection forces, or exhibited similar adaptive design criteria is superfluous, because such statements appear to be untestable. They are untestable because we have no way of recovering information about selection or individual fitness, information that would seem to be absolutely necessary to test such generalizations. It is one thing to *believe* that specific functional characteristics of taxa are adaptations that evolved by natural selection and quite another to consider such statements within the realm of empirical science. It is time the grade concept was placed on the shelf and forgotten.

The above remarks should *not* be taken to mean that functional interpretations within an evolutionary context are not possible. Methods are available to erect phylogenetic hypotheses (see below), and functional data can be interpreted within the framework of those hypotheses. With recent organisms functional interpretations may be sought through direct observation or comparison with other structurally similar organisms whose functional attributes can be studied empirically. Functional interpretations of fossil taxa must eventually be reducible to comparisons with Recent taxa. The task of making these functional interpretations, of either Recent or fossil taxa, reduces Gould's "defense of the analog" to a trivial statement at best or another straw man at worst: in comparing functional properties, one must always compare structurally similar organisms about which we "know" something of their functional properties. For purely functional, as opposed to phylogenetic, statements it may not matter whether those taxa are close or distantly related; obviously, in the majority of cases the closest living relatives will be compared. Gould suggests that in functional comparisons, homologous structures not be the basis of comparison:

> "The analog is the paleontologist's only source of experimental material; for it is a replicate (however imperfect) in testing of any functional hypothesis. Homologous organs cannot be used in experiment, for similarity of function only reflects the unenlightening fact that the same organ is present in two or more creatures. However, the convergent evolution of similar structures fulfills, at least imperfectly, the criterion of independent replication that any experiment requires. Any adequate theory of functional morphology must ex-

> plain the constraints on adaptive design by studying how different organisms react to the same selective regime" (II, p. 177).

But does it not make more sense when inferring the functional properties of fossil organisms to study the homologues of closely related, living organisms in which functions are better understood? That is why vertebrate paleontologists studying jaw mechanics of fossils investigate jaw function in the closest living relatives rather than the "jaws" of insects. And how can we ever study the "same selective regime"? What most workers—and presumably also Gould—mean is "living under similar environmental conditions." If these workers would admit that these discussions about "selection" and "adaptation" are axiomatic verbiage, I would have few complaints; my contention, however, is that language captures peoples' thought processes and can impose a "world view" that precludes them from considering alternative viewpoints regarding the scientific analysis of nature. If natural selection is to be invoked, it seems essentially axiomatic; if it is to be defended, it is only because there is not yet a better alternative.

All of the above leads to the relevant question: what is the goal and method of comparative biology? It probably would be fair to say that the majority of the participants in this symposium view the primary goal of comparative biology to be the reconstruction of life's history. Unfortunately, none of the participants comes to grips with a method to obtain that goal. There is much discussion—most of it merely repeating decades of previous debate—on the definition and recognition of homologous attributes but little understanding of how this fits in with constructing phylogenetic hypotheses. There is no mention of the reformulation of the homology problem over the last 10 years by phylogenetic systematists. That reformulation eliminates the conceptual and methodological problems created by the influence of the evolutionary definition of homology (i.e., tracing features back to the common ancestor) and focuses the argument on the meaningful issue: similarity. Bobb Schaeffer (II, pp. 169–173) seems to be one of the few to grasp this problem: "most investigators (whether they admit it or not) assume that two or more structures are homologous unless there is reason to believe otherwise. This operational approach *promotes comparison and generates hypotheses* . . ." (my italics). In Hennigian terminology similarities can be postulated to be synapomorphies (=derived homologies) at some level of the hierarchy and symplesiomorphies (=primitive homologies) at all lower levels. These synapomorphies define nested sets of taxa, and the object is to choose the hypothesis of relationships that maximizes the congruence of the various synapomorphies (see E. O. Wiley, 1975, SZ 24:233–243). Phylogeneticists, it seems to me, have solved the "homology problem" by showing its connection to the concept of different kinds of similarity (primitive, derived) and uniting the definitional and operational aspects of the word in a hypothetico-deductive framework. All of this has been actively discussed in the literature since Hennig's 1966 book (*Phylogenetic Systematics*, University of Illinois Press), hence it is perplexing that no one in the symposium chose to consider the issue.

This symposium and the earlier one on neurology and evolution held by the New York Academy of Sciences (Proc. N.Y. Acad. Sci., 1969, Vol. 167) are similar in that the neurologists and behaviorists invited certain paleontologists and evolutionists to present "the latest view" on vertebrate phylogeny and comparative methodology. This seems a necessary tactic if one believed the statements of some of the participants regarding the "hopeless" task of reconstructing an historical pattern of brain evolution or behavior. These statements may be taken as evidence of their misunderstanding of what comparison is all about. L. Radinsky, a paleontologist, promulgates the traditional paleontological viewpoint (I, p. 228): "There are two kinds of data from which phylogenetic relationships are reconstructed: direct evidence from the fossil record and indirect evidence from comparisons among surviving species." But paleontologists are simply wrong on this point, because the reconstruction of phylogenetic relationships must *always* be based on comparison: We discover a fossil. What is it? Ergo, comparison. The "direct" and "indirect" dichotomy is false because data from fossil or Recent organisms—it does not matter which—must be handled conceptually in the same manner.

Unfortunately, this paleontological perspective influences the thinking of neurologists and behaviorists, creating an aura of despair over the possibility of achieving results in historical reconstruction:

> "(1) behavior cannot be observed in extinct forms; (2) the soft tissue of the CNS (central nervous system) does not usually fossilize . . . and (3) the extinction of many intermediate forms rules out strict historical analysis of behavioral evolution based on observation . . . .There seems to be at present, therefore, little hope for a historical analysis of behavior" (K. H. Brookshire, I, p. 195).
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> ". . . study of convolutional and sulcal impressions of endocranial casts of extinct mammals provides the only source of data regarding brain phylogeny. . . . Paleoneurological studies of endocasts and cranial foramina are therefore the only direct means of evaluating the course and characteristics of brain evolution . . ." (W. Welker, I, p. 277).

As long as neurologists and behaviorists maintain allegiances to fossils as providers of phylogenetic truth, one cannot hope for much advance in our understanding of historical patterns. But fossils are false messiahs. This is not to deny their importance, of course, for they provide additional data. However, it is the comparative method that can provide a key to the past, and it may be suggested that once these methods are applied to more and more organisms, a clearer picture of that pattern indeed will emerge. The problem, as demonstrated repeatedly in these two volumes, is that neurologists and behaviorists, like many of their paleontological and anatomical colleagues, remain uncertain as to just what constitutes a productive comparative method.—*Joel Cracraft, Department of Anatomy, University of Illinois at the Medical Center, P. O. Box 6998, Chicago, IL 60680.*

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Ever Since Darwin: Reflections on Natural History.—Stephen Jay Gould. 1977. W. W. Norton, New York. 285 pp. $9.95.

Stephen Jay Gould is a very impressive figure. Though only 36, he has produced numerous books and papers. Though formally a professor of geology, he is well versed in biology and in the history of science. He has a knowledge of literature that enables him in this one book to draw on the following authors: Thomas Hardy, Dr. Seuss, Freud, Rossini, Dorothy Sayers, Milton, Karl Marx, Arthur Koestler, Groucho .Marx, Herbert Spencer, Dickens, Mark Twain, Dryden, the Psalmist, Wordsworth, Aldous Huxley, John Locke, Alexander Pope, Voltaire, Bruno Bettelheim, Adam Smith, John Ciardi, Richard Wagner, Pascal, Friedrich Engels, Kipling, Havelock Ellis, Goethe, W. S. Gilbert, J. S. Mill, Benjamin Franklin, and Simone de Beauvoir. His diligence is equally admirable: he measured all the Irish elk fossils with his own yardstick; he visited Darwin's house at Down and examined Darwin's uncut copy of *Das Kapital*; he dug out Agassiz's annotations of Lyell's treatise; he found an obscure essay by Engels and checked it for borrowings from Haeckel; he made a very careful study of Lombroso's work; and he tabulated thousands of species for the spindle graphs in Chapter 15. There can be no doubt of his right to be called an expert.

The 33 essays collected in this book were all printed first in *Natural History*. Being thus addressed to the public, they bring us face to face with what Gould (p. 158) calls "perhaps the most disturbing question about the public impact of science. How is a layman to judge rival claims of supposed experts?" The present reviewer is a layman much concerned with this question. My answer is that the layman must scrutinize the claims carefully, check other works by the various parties, gather the opinions of other experts, and use his own head, eyes, and ears. This is laborious, hence few will try it. Whether it yields any useful results is a question that the readers can judge from the following remarks.

In this book Gould wrestles with many difficult problems: whether natural selection is a tautology; the degree of difference between man and ape; the lack of straight phyletic lines among hominids; foetalization; why human gestation is not longer; the Irish elk; long breeding cycles in bamboos and locusts; the early stages in the development of complex structures; the Cambrian explosion; the Permian extinction; uniformitarianism; differences between the earth and other planets; racism; inborn criminality; biological determinism; race and IQ; sociobiology; and several more. He has a lively style, great learning, and deep concern. Readers of *Systematic Zoology* may scorn *Natural History* as a general rule, but these essays are so diversified and so up-to-date that they should not be read only by laymen.

The great question for this reviewer is whether Gould gives sound solutions for all these problems, but before taking up the substance let me register mild discontent with three small points.——Gould tells us (p. 14) that his essays have a common theme, to wit Darwin's evolutionary perspective "as an antidote to our cosmic arrogance." This concern with arrogance recurs six or seven times and gives the book a faintly moralistic tone.——Gould calls Darwin (p. 32) "one of the most brilliant men in recorded history." Anyone who has studied Darwin will agree that he was not a fool, but is it reasonable to use such superlatives? In the ordinary understanding of the word, Gould himself is far more brilliant than Darwin ever was.——Gould frequently insists that he is a Darwinist despite the fact that he has departed widely from the founder's position by discarding (in recent papers not included in this book) Darwin's basic idea of small changes cumulating gradually over immense periods of time. He has also, by indorsing Goldschmidt's arguments and stressing the evolutionists' failure to solve the problem of macroevolution, taken himself beyond neo-Darwinism (the synthetic theory). He is in new territory and needs a new label.

Now let me discuss three chapters where I venture to think that Gould has gone astray.

The Irish Elk. Chapter 9 deals with hypertely, the idea that natural selection sometimes goes too far and creates a deleterious structure. The classic case is the Irish elk, which developed antlers so enormous that the viewer at once thinks they must have hindered the animal more than they could have helped it.

This situation reveals the power that a theory can exert on the human mind. The Darwinian view is that natural selection can favor only features that are beneficial; in Gould's dogmatic formulation (p. 90) "Darwinian evolution decrees that no animal shall actively develop a harmful structure." Therefore, if a structure looks harmful, there is something wrong with the theory or with our naive interpretation. Gould cannot believe that there is anything wrong with the theory, so he goes to work on the interpretation. He candidly admits that the antlers were useless for fighting, that their annual replacement put a great burden on the metabolism, and that they must have been a heavy load to carry. But then he "explains" them by postulating that they were used for display rather than for combat, i.e., they conferred high status and access to females. Although this facile speculation is insulting to the intelligence of the females, is without proof, and is