BIOLOGY AS HISTORY

Papers from International Conferences Sponsored by
the California Academy of Sciences in San Francisco
and the
Museo Civico di Storia Naturale in Milan

No. 2

NEW PERSPECTIVES ON THE HISTORY OF LIFE: ESSAYS ON SYSTEMATIC BIOLOGY AS HISTORICAL NARRATIVE

(San Francisco, 21–23 June 1994)

Edited by Michael T. Ghiselin and Giovanni Pinna

California
Academy
of Sciences

Memoirs of the California Academy of Sciences Number 20

New Perspectives on the History of Life:
Essays on Systematic Biology as Historical Narrative

PARTICIPANTS
(Shown left to right in photograph)

Timothy Rowe
Department of Geological Sciences and
Vertebrate Paleontology Laboratory
University of Texas at Austin

Giovanni Pinna
Museo Civico di Storia Naturale
Milan, Italy

Alessandro Minelli
Department of Biology
University of Padova, Italy

James R. Griesemer
History and Philosophy of Science Program
University of California, Davis

David M. Wake
Museum of Vertebrate Zoology and
Department of Integrative Biology
University of California, Berkeley

Charlotte P. Mangum
College of William and Mary

Mikhail Fedonkin
Paleontological Institute
Russia Academy of Sciences

Michael T. Ghiselin
Center for the History and Philosophy of Science
California Academy of Sciences

Robert J. O'Hara
Cornelia Strong College
University of North Carolina at Greensboro

Nicholas D. Holland
Scripps Institution of Oceanography

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October 4, 1996

Golden Gate Park
San Francisco, California 94118

Library of Congress Catalog Card Number: 96-85441
ISBN 0-940228-43-2

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PREFACE

This volume is based upon a meeting held in San Francisco on June 21 to 23, 1994 in conjunction with the Annual Convention of the Pacific Division of the American Society for the Advancement of Science. It was the second meeting dealing with the general topic of biology as history to be jointly co-sponsored by the Museo Civico di Storia Naturale in Milan, Italy and the California Academy of Sciences in San Francisco. The first meeting was a workshop entitled "Systematic Biology as an Historical Science" held at the Milan museum in June, 1993. The proceedings of the Milan meeting, entitled "Biology as History: Systematic Biology as an Historical Science," edited by Giovanni Pinna and Michael Ghiselin, have been published as Volume 1 of the *Memorié della Società Italiana di Scienze Naturali del Museo Civico di Storia Naturale di Milano*. Copies of the first volume may be purchased from the Società Italiana di Scienze Naturali, corso Venezia 55, 20121 Milan, Italy.

The California Academy of Sciences and the Museo Civico di Storia Naturale are both major natural history museums, and both are located in public parks in major cultural centers. Both museums had to be rebuilt virtually from scratch after having been destroyed, the one in San Francisco by the great earthquake and fire of 1906, the one in Milan as the result of an air raid during the Second World War. Institutions like these benefit greatly from the exchange of ideas, as well as specimens, and from operating on a world-wide, as well as a regional basis. A series of international meetings that explored the prospects for doing new kinds of research in the context of the natural history museum seemed an appropriate way to encourage further cooperation. There has been just enough overlap in theme and participants to allow for some continuity. A third conference, on "The Culture of Natural History," has been scheduled for November, 1996, in Milan.

The Planning Committee for this meeting consisted of Marvalee Wake, Giovanni Pinna, and Michael Ghiselin. Among Academy staff we should like to thank Patricia Dal Porto for her organizational performance, and Katie Martin for her work on getting the proceedings published. Alan Leviton helped in ways too numerous to enumerate, but we should at least mention the enormous amount of work he did in setting up the meeting of the AAAS Pacific Division and especially our part of that meeting. The Division co-sponsored the meeting, made its resources available, provided valuable logistical support, and helped to attract an enthusiastic audience. A benefactor of the Academy, Gordon Getty, provided funds for the conference.

Michael T. Ghiselin

INTRODUCTION

Michael T. Ghiselin

Center for the History and Philosophy of Science
California Academy of Sciences
San Francisco, California 94118

The essays presented here are all concerned with the general topic of how systematic biology may be treated as an historical science — one that aims, at least in the long run, at telling the story of life on earth. Systematics is not the only science that presents its findings in such narrative form. Cosmology, with its tales about the "big bang" and the formation of the stars and planets, aims at tracing the history of the entire universe. Geology does likewise on a much more local scale, and the emergence of plate tectonics in the present century is a superb example of the kind of synthesis that historical sciences can attain. Paleobiology is flourishing these days largely because it has linked up its efforts so effectively to the history of our planet in general.

Paleontology deals with the history of life through time, biogeography with the same basic phenomena as reflected in distribution of organisms in space. The various taxonomic specialties, such as zoology and botany, although they originated without obvious reference to the history of life, were set upon an historical foundation — "descent with modification" — by Charles Darwin (1859). Ernst Haeckel (1866) coined the term "phylogeny" for the history of the lineage, in contradistinction to "ongogeny" for the history of the individual organism. He evidently meant phylogeny to be an historical science, complete with narrative accounts of what had happened and why, and not just a bunch of tree-like genealogical diagrams.

The present century has witnessed an increasing legitimation of at least some aspects of phylogenetics. De Querioz (1988) goes so far as to insist that descent should become part of the "axiomatic" structure of systematic biology in general. Nonetheless many systematists seek to decouple the study of systematics from that of events and processes — something that would seem very odd to a student of plate tectonics but has strong roots in comparative anatomical tradition.

Anthropology may reasonably be considered a minor branch of systematic zoology, one that deals with the history of our own species and that of our close relatives. Disciplines that deal with a wide range of cultural phenomena can reasonably be treated in the same spirit. Comparative linguistics developed a phylogenetic approach before systematic zoology did, and the detailed analogies were worked out in considerable detail by August Schleicher (translation 1869), Haeckel's linguist colleague at the university of Jena (O'Hara, 1992, 1993, and this volume). Lately the similarities between cladistic methodologies and those used in disciplines outside of biology proper have received a great deal of attention (Honigswald and Wiener, 1987). Very little, however, has been said in this literature about the narrative aspect of systematics, and much of that for the sake of derision.

And much that gets written is grossly distorted. Cameron (1987:238) for example, writes: "For the zoologist the reconstructed ancestor is a fiction. It is a convenient way of representing the organized information about the relationships of the real animals in question. Nobody tries to reconstruct a living, breathing thecodont or the protodipteron. But the reconstructed text of the textual critic is the real article, in a literal sense the text that Euripides wrote." Whoever may have provided Cameron with this misinformation, he or she was definitely not speaking for all of us.

Of course it is not just the practitioners of historical sciences who tell stories. So do poets and novelists. With scientists, it really matters whether or not the stories in question are true, and that seems to be about as good a criterion of demarcation between science and non-science as any. To be sure, a good poet doesn't trade the truth for a rhyme, and a good novel is supposed to be "true to life." There is indeed a certain ambiguity, in the case of the historical novel, and in that of science fiction, wherein certain constraints of plausibility are accepted as part of the genre — and if one wants to put down serious history one of course makes the comparison with imaginative literature.

Historians have generated a great deal of literature attempting to show that their own enterprise is somehow different from that of the natural sciences. We needn't go into these efforts in detail (for critique see Danto, 1985; Zanzi, 1991; Laudan, 1992), but it is worth noticing that many supposed peculiarities of history are by no means unfamiliar in what biologists would call straight-forward historical sciences. For example, the intentions of human beings are considered important causal influences. True, but the mating propensities and other behavioral dispositions of animals in general are an important aspect of ethology, which, after all, is largely a comparative anatomy of inherited motor patterns.

A philosophically more pretentious claim depends upon a criterion that purportedly demarcates that which is science from that which is not. According to this view, science deals only with universals, or classes; and since history deals with individuals, or in other words with particular things, it is not science. Such notions have been widely enough expressed that it helps to examine them in a bit more detail. We should mention at the outset that the "new ontology" that has had so much effect on the philosophy of systematics over the last quarter of a century arose partly in response to such allegations. It takes the position that an individual is any concrete, spatio-temporally restricted entity, of which an organism is only one of a vast range of legitimate examples. The parts of organisms — all of them, down to the ultimate particles of matter — are individuals in this ontological sense. So too are the earth, the solar system, the milky way galaxy, and the entire universe. Species are of course individuals, and so too are such lineages as clades. Nor need individuals in this sense be restricted to material objects or groups of them: events such as the Permo-Triassic extinction are perfectly good individuals from an ontological point of view. Indeed, anything that may reasonably be said to have a history is probably an individual.

The laws of nature are spatio-temporally unrestricted generalization about classes of individuals. They make no reference to any particular thing, be it to you or me or to the moon. Rather, laws of nature are "about" classes of individuals. Advocates of the new ontology not only freely admit that there are no laws for *Homo sapiens*, they use this as evidence that species are individuals rather than classes (Hull, 1976). This turned the argument of Smart (1963) that biology is not a science on its head, for Smart had claimed that biology has no laws, and therefore is not a science. In fact, it has plenty of laws, but, like the laws of physics, these are laws about classes of individuals (Hull, 1975; Ghiselin, 1988, 1989; Ereshefsky, 1992), not about any taxon in particular. The obvious next step is to insist that either the criterion in question be accepted consistently and across the board, or else that something better be put in its place. For the criterion excludes not just systematic biology (including anthropology) from the sciences, but also geology and astronomy. Smart was not unaware of this problem and tried to wiggle out by noting that physicists observe celestial bodies in order to test their hypotheses about the laws of physics. It never seems to have occurred to him that biologists observe organisms with the same end in mind.

The criterion in question does not stand up under critical examination. Furthermore, once we have recognized the depth of the metaphysical cleavage between individuals and classes, we are in a much better position to appreciate what it is that the historical sciences are all about. Without them, science is a purely abstract matter that deals with everything in general and nothing in particular. The traditional distinction, which goes back to Wilhelm Windelband, between idiographic (etymologically "person writing") and nomothetic (etymologically "law propounding") sciences has long recognized the distinction. And yet the habit of treating history and law as if they were the domains of strictly separate disciplines is to make an ontological distinction function as a spurious guideline for scientific practice. Studying the laws and the particulars together as part of a single research program has proven such a remarkably successful stratagem in the history of the sciences that one would think it hardly needs justification. And yet there are many who insist that the two ought to be kept more than just conceptually distinct. They present us with the sort of "naive inductionist" model that philosophers of science long ago ceased to take seriously. The idea is that one starts with description of brute facts, puts the facts together into ever broader generalizations, and finally arrives at the laws — or perhaps the narratives. The possibility that one might proceed by reiterated testing of hypotheses is simply left out of consideration. Given such an epistemology, it is easy to see why such narrative is so rarely considered as a constitutive part of the process of discovery and testing. But if possible narratives or scenarios and the laws of nature are introduced from the outset, we get a very different picture of the dynamics of investigation. This is not the appropriate place to do more than suggest the role that laws of nature and other generalizations play in the evaluation of reconstructions in the historical sciences. We should emphasize, nonetheless, that methodologists are well aware of them. In just about any science, as in everyday life, we know that certain classes of events are more probable than others, and that some are downright impossible. Any proposition that is necessarily true irrespective of time and place must be true of any particular event. So if a scenario logically entails the falsehood of such a proposition we consider it good evidence for rejecting that scenario. Organisms simply must have a source of energy and they cannot function as perpetual motion machines, so the larvae that subsist entirely upon stored yolk are not recapitulating a stage in which their ancestors did not feed at all! By the same token, we treat scenarios as more plausible, in proportion as they invoke fewer events that the laws imply are improbable. Of course we might opt to treat such contradiction as a refutation of the law of nature in question, but reasonable scientists generally ask for further evidence before doing anything so rash if the laws are well supported by empirical evidence. Furthermore the research program can be designed to test both the laws and the scenarios. (Yes, there is indeed a danger of circularity here — no, it is not an insuperable difficulty.)

In earlier works I have explained how this is accomplished in geology and in linguistics, as well as comparative anatomy (Ghiselin, 1969, 1972), presenting some straight-forward examples. Stratigraphic geology establishes the sequence in which rocks are deposited largely by means of the principle of superposition: the oldest rocks are on the bottom, the youngest ones on top. This is by no means an *a priori* assumption in any proper, philosophical sense, because it is justified by experience and erroneous applications of it can be corrected by empirical data. There is good reason why the water that deposits sediments floats above the pre-existing strata. Furthermore, if the strata should happen to be overturned, one can generally tell that this has happened because cracks in dried mud, wave patterns, varves, and other features necessarily have a definite orientation with respect to the force of gravity (Shrock, 1948). The laws governing language are a bit less familiar, but to give one example, Wang (1987:248) remarks that "it is more likely for two languages independently to undergo the same natural change than for them independently to undergo the same unnatural change. Consequently, the sharing of unnatural changes is more diagnostic of shared history."

Narratives, unlike mere chronicles, do not simply describe what happened, they attempt to explain it. Scientific explanation is by no means an uncontroversial topic among philosophers, and perhaps the less we say about their difficulties with it the better (see the anthology edited by Ruben, 1993).

But we should at least remark that, according to the "covering law model" which is largely associated with the names of Hempel (1942) and of Popper (1962), historical explanation somehow attempts to link up the particular events with at least one law of nature. This model seems — I repeat seems — unsatisfactory on a number of accounts, not the least of which is that the laws which are invoked as predicting what goes on seem much more convincing when applied retrospectively.

Be this as it may, Darwin, after completing a massive treatise on the systematics of barnacles, went on to present what he considered compelling evidence for evolution in general and for natural selection as its basic mechanism in particular, structuring his argument on the basis of its explanatory power. Among his contemporaries, some, including Herbert Spencer, agreed with Darwin that a theory that explains such a wealth and diversity of facts must contain a large measure of truth; but many others, such as Thomas Henry Huxley, did not like that manner of reasoning. Opinion remains divided. However, it does seem that many, perhaps the vast majority, of evolutionary biologists, and practitioners of other historical sciences as well, would agree with the famous aphorism of Dobzhansky (1973) that "Nothing in biology makes sense except in the light of evolution."

So we have very good reason to take the narrative aspect of evolutionary biology very seriously, to assess its possible strengths and limitations, and to see what might be done with it in future research. But as Landau (1991) points out, in a very interesting study on the history of narratives of human evolution, scientists themselves have said very little about the narrative aspects of their own research.

The present volume, although it is not exactly what Landau had in mind, may help to supply the deficiency. The studies presented here provide some conceptual background at the beginning, then go on to discuss some particular cases, mainly having to do with the fossil record and the embryological aspects of comparative anatomy. The chapters turn out to fit together into a coherent whole to a far greater extent than the organizers or contributors originally intended.

Historical narratives are by no means random collections of events, but focus upon details that are deemed to have particular causal significance. O'Hara makes this abundantly clear in his essay on how the past is represented in the historical sciences. Maps provide a particularly good example of how matters get generalized, simplified, and perhaps distorted. He gives some amusing examples of maps that were intended as jokes, ridiculing the provincial attitudes of those who were supposed to draw them. Perhaps equally ridiculous, but something we ought to take seriously, is the manner in which systematic biology is all too often depicted in text books, as if our own lineage were the only interesting object of study.

Griesemer addresses a somewhat related issue in his discussion on periodization. It seems clear, if not altogether obvious, that a choice will have to be made as to how a temporal sequence is to be subdivided if the past is to be treated as a classification, and not just a list, of events. The obvious place to put the breaks are the events that supposedly have important causal significance. Branching points in genealogies are an obvious example, and those systematists who have wanted to represent more than just branching points in their classifications have traditionally used categorical rank to indicate major changes in structure and function. Griesemer discusses how embryology can be periodized in various ways, some of which are able to link the historical narrative up to morphogenetic causes, a theme that gets taken up again later in the book.

The next two chapters deal with the fossil record. Here, the periodization is largely in terms of external, ecological causes. Fedonkin considers early stages in the history of multicellular animals, and develops an ecological scenario that helps to account for their peculiar properties. We should emphasize that he presents data that seem inconsistent with other possible scenarios, including those which invoke total anoxia. Perhaps the most original aspect of his contribution is the attempt to show how the animals have interacted with one another and with the changing abiotic environment through time; it is hard to imagine how it would be possible to infer such interactions on the basis of cladistic data by themselves. The recent advances in paleontology which he reviews underscore the difficulties that have attended the reconstruction of fossil organisms and their conditions of existence. Doing the job properly requires a great deal of thinking, both critical and imaginative.

Pinna's scenario is largely a biogeographic one, and has a strong ecological component. It provides a most instructive example of what can be done with a good fossil record when it is properly analyzed. A great deal of theory in paleontology has been devised to explain what are really artifacts of preservation and misunderstandings of taxonomy. Pinna presents an account of ammonites diversifying in a stable environment and giving rise to descendant populations in a less stable one, where they fail to diversify and found lineages. This scenario accords nicely with the sort of diversity model that Darwin and others have proposed and also with the centers of origin concept to which vicariance biogeographers are so often hostile. But it does not depend on that kind of evolutionary model for its empirical justification. Having provided grounds for rejecting the reality of the phenomena upon which certain macroevolutionary theories have been based, he goes on to confront some claims about the underlying developmental mechanisms with hard data.

Thus we get a smooth transition to the following chapters, in which embryology becomes the dominant explanatory theme. Minelli considers some correlations among the various parts of the body as arthropods have become more complex, and includes the developmental stages in his analysis. There seems to be a definite limit to the number of kinds of parts that an organism can contain, with arthropods for example never having more than four or five tagmata (body regions). He suggests various reasons for this, including conflicting "design" constraints as with increasing numbers of parts. Since the unity of the historical sciences is a major theme in this work, it seems worth while to draw attention to a similar feature of language. Ethnobotanists and other students of folk taxonomy have found that the classification systems they have studied are remarkably uniform in having a hierarchical arrangement with only about five levels, or as systematists call them, "categories" (Berlin, 1992). It would seem that there is also a definite upper limit to the amount of information that can readily be processed by the unaided human brain. Perhaps some very general laws and principles are applicable.

Holland finds it necessary to discuss the various concepts of homology, in order to disassociate his approach from those of certain other workers. The lack of consensus among comparative biologists these days as to what so basic a term as "homology" is supposed to mean reflects a continued failure of the intellectual community to come to grips with the fundamental distinction between classes and laws on the one hand, and individuals and history on the other. Homology and analogy alike are terms for the correspondence of parts of organisms. In the case of homology, the organisms themselves are by definition parts of lineages, and the criterion of identity is community of descent. In the case of analogy, the organisms are by definition members of classes, and the parts are equivalent because of some nonhistorical cause, such as convergence resulting from similar function. Confusion results when people try to mix the two.

Holland's preference for the historical homology concept makes perfectly good sense in terms of the rationale for his research. A very elegant technique allows him to localize a particular kind of tissue component that for good reasons is believed not likely to change its relative position in the body. There is a good precedent for invoking such a criterion, insofar as comparative anatomists have long recognized that the innervation of organs is much less labile than many other features of the body. The new results are most impressive, and when they disagree with received opinion, they are all the more impressive. The alternatives are very plausible, and indeed represent views that have been held by a minority of workers, but perhaps have not received the amount of attention they deserve.

Impressive new techniques are also applied by Rowe to elucidate the history of the mammalian skull. But once again, we have technology in the service of problems with a long history. Rowe emphasizes the point that modern cladistic techniques have helped to correct some serious misconceptions about the supposed polyphyly of mammals and the parallelism of important mammalian characters. On the other hand his own approach has itself tended to break with cladistic tradition, especially insofar as it has emphasized functional analysis. He and his collaborators (Gauthier, Kluge and Rowe, 1988) were able to show that a large number of features of terrestrial vertebrates are causally interdependent: they make it possible for the animals to run and breathe at the same time. This discovery tended to support the notion that in phylogenetic analysis characters ought to be weighted on the basis of whether or not they are functionally interdependent (Gosliner and Ghiselin, 1984). But how to accomplish such weighting in practice remains a serious bone of contention.

The problem that Rowe addresses, namely, how the mammalian inner ear arose, is a traditional one, and the part of the traditional picture that remains intact is one of change in both structure and function with continuity. Part of the jaw gradually became incorporated into the ear. It is a fine example of the principle of succession of functions (*Funktionswechsel*) first propounded by Dohrn (1875; translation in Ghiselin, 1994). Physiological work done outside of a phylogenetic context helps to elucidate the function of the apparatus in question, but only becomes explanatory when incorporated into an historical narrative. Rowe enriches the scenario by adding a morphogentic analysis to the list of causes of change. He is even able to specify how some of the physical forces operate in developing embryos. All sorts of interesting and quite unexpected causal relationships emerge from this research, including the point that the separation of the auditory apparatus from the jaw is not a post-adaptation, but instead is a byproduct of the enlargement of the brain.

Wake takes on the challenge of prognosticating how we might be able to come up with a unitary approach, or a synthesis, of evolutionary and developmental biology. As he points out, this kind of approach has become relatively fashionable of late, partly because of the influence of a book by Gould (1972). Yet I hasten to point out that it is a traditional theme in evolutionary biology, albeit one that has been neglected in elementary text books. Darwin (1868) devoted an entire book to that very theme — though Gould (1972) does not even cite it. Among later writers we should definitely mention Sewertzoff (1931) and Schmalhausen (1946), who had considerable influence upon Dobzhansky, Mayr, Rensch, and other architects of the Synthetic Theory.

One reason why, except to some extent in Russia, such developmental themes have been treated as marginal has been repeated efforts to develop alternatives to natural selection as the fundamental evolutionary mechanism. Hence we get anti-evolutionists (in a broad sense) trying to treat evolution as if it were ontogeny writ large, often under the rubric of "orthogenesis." The idea was to explain change in terms of "laws" rather than "chance" — laws that might or might not have been supernaturally ordained (Hertwig, 1922). "Chance" in this context is a pejorative synonym for "historical contingency" or what most systematists these days consider the main topic of their research. Nonetheless, as Wake emphasizes, a lot of evolutionary biologists tend to emphasize what he and many others call "pattern" over process. This I would take as symptomatic of a static world view, as is the concern for such idealistic notions as the "*Bauplan*" even when translated into another jargon, as in the "zootype" of Slack et al. (1993) to which Wake and also Holland refer. Wake emphasizes the need to separate process from pattern and to keep the two conceptually distinct; but one wonders if what is being confused is not process and product. Indeed it is far from clear to me what authors mean when they refer to pattern and process. By recapitulation, I do not mean a pattern, but a developmental process that has a pattern similar to that of an evolutionary one. The term "reverse recapitulation" advocated by Wake and his collaborators has received a lot of sales-resistance for that very reason. It suggests that the stages have somehow been turned around backward, like a motion picture being shown as the film is rewound.

Wake discusses what he calls the "persistence" of "characters," providing a new way of talking about what used to be discussed in terms of "conservativeness" or "lability" in evolution. Some things clearly have changed more than others in the course of phylogenetic history. In principle, if we understood the underlying mechanisms of development, we would be in a much better position to estimate the lability in question and consequently to reconstruct the history of life. However, it would seem that more than one phenomenon is involved here. On the one hand we have the intrinsic aspect, in the sense that the developmental processes themselves are not readily changed, as suggested by Minelli in the present volume. On the other hand, we have an extrinsic aspect, in the sense that certain changes have not been selectively advantageous. A feature might persist unchanged over long periods of time simply because, as a matter of contingent fact, the organisms remained under conditions of existence where it was advantageous.

Not only is the conservativeness in question largely an extrinsic and contingent matter, it is obviously a matter of degree, so that even if a kind of inertia results from developmental constraints, there is no reason to presuppose that sufficiently strong selection pressures cannot overcome it. There has been an unfortunate tendency of late to express such considerations in pre-evolutionary, idealistic terms, having recourse to such notions as *Baupläne* where a real evolutionist would speak of common ancestors. It seems to me an unfortunate source of confusion when Gould (1983) tries to justify his version of typology by trying to lodge the equivalent of a Platonic Idea in the germ rather than in the Mind of God.

So, rather than talk about abstract patterns and schematic diagrams, it might be better to focus our attention upon concrete beings that really existed and upon historical events that actually took place. Such a narrative account would begin with common ancestors, and would trace the changes that have gone on in the various descendant lineages. In such narrative embryology could play a crucial role, for as the organisms change so must the developmental mechanisms that give rise to them. And our understanding of those mechanisms could play a crucial role in both discovery and explanation. Indeed it already does, as can be seen in the more particular studies by Minelli, Holland and Rowe, as well as in the more general overview provided by Wake.

Looking to the future, we might consider whether to place an even stronger emphasis upon the scenario. Instead of interpreting the tree-like diagram as a representation of characters, treat it as made up of historical events. In that case the emphasis upon process becomes all the more obtrusive, and our thinking becomes increasingly Darwinian.

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MAPPING THE SPACE OF TIME:
TEMPORAL REPRESENTATION IN THE HISTORICAL SCIENCES

Robert J. O'Hara

Cornelia Strong College
100 Foust Building
University of North Carolina at Greensboro
Greensboro, North Carolina 27412

> As to the propriety and justness of representing sums of money, and time, by parts of space, tho' very readily agreed to by most men, yet a few seem to apprehend that there may possibly be some deception in it, of which they are not aware. . . .
>
> William Playfair, 1786, in Tufte (1983:52)

Introduction: The Palaetiological Sciences

William Whewell (1794–1866), polymathic Victorian scientist, philosopher, historian, and educator, was one of the great neologists of the nineteenth century. Although Whewell's name is little remembered today except by professional historians and philosophers of science, researchers in many scientific fields work each day in a world that Whewell named. "Miocene" and "Pliocene," "uniformitarian" and "catastrophist," "anode" and "cathode," even the word "scientist" itself — all of these were Whewell coinages. Whewell is particularly important to students of the historical sciences for another word he coined, one that was unfortunately not as successful as many of his others because it is difficult to pronounce. This word, "palaetiology," was the name Whewell gave to the class of sciences that are concerned with historical causation: the class we might today refer to as historical sciences. Although the disciplines Whewell included under the heading of palaetiology might seem to cut across the conventional academic boundaries of his day and ours — his exemplars were geology and comparative philology — all these fields may nevertheless be examined together, Whewell argued, because of their common interest in reconstructing the past. Just as we may look back, he said,

> towards the first condition of our planet, we may in like manner turn our thoughts towards the first condition of the solar system, and try whether we can discern any traces of an order of things antecedent to that which is now established; and if we find, as some great mathematicians have conceived, indications of an earlier state in which the planets were not yet gathered into their present forms, we have, in pursuit of this train of research, a palaetiological portion of Astronomy. Again, as we may inquire how languages, and how man, have been diffused over the earth's surface from place to place, we may make the like inquiry with regard to the races of plants and animals, founding our inferences upon the existing geographical distribution of the animal and vegetable kingdoms: and thus the Geography of Plants and of Animals also becomes a portion of Palaetiology. Again, as we can in some measure trace the progress of Arts from nation to nation and from age to age, we can also pursue a similar investigation with respect to the progress of Mythology, of Poetry, of Government, of Law. . . . It is not an arbitrary and useless proceeding to construct such a Class of sciences. For wide and various as their subjects are, it will be found that they have all certain principles, maxims, and rules of procedure in common; and thus may reflect light upon each other by being treated together.
>
> (Whewell, 1847, 1:639-640)

This paper is an essay on the palaetiological sciences, dedicated to Whewell on the bicentennial of his birth, an essay that examines some of the "principles, maxims, and rules of procedure" that these sciences have all in common. Its first purpose is to demonstrate the continuing validity of Whewell's classification of these sciences through a study of historical representation in three different palaetiological fields: systematics, historical linguistics, and textual transmission. Its second purpose is to continue the development of an extended analogy between historical representation and cartographic representation that I began in an earlier paper (O'Hara, 1993), an analogy that makes especially clear the common representational practices that are found throughout palaetiology.

To set the stage for what is to follow, I offer here three diagrams, one each from the different palaetiological fields of systematics, historical linguistics, and textual transmission or stemmatics, three diagrams all drawn independently within 40 years of each other in the mid-nineteenth century. The first of these (Fig. 1), familiar to all evolutionary biologists, is Darwin's tree of descent from the *Origin of Species* (1859). The vertical axis of this diagram represents time, while each horizontal line marks an interval of some number of generations: a thousand, or a million, or a hundred million (1859:116–126). Figure 2 is less familiar, even to specialists in the field from which it comes, historical linguistics. This

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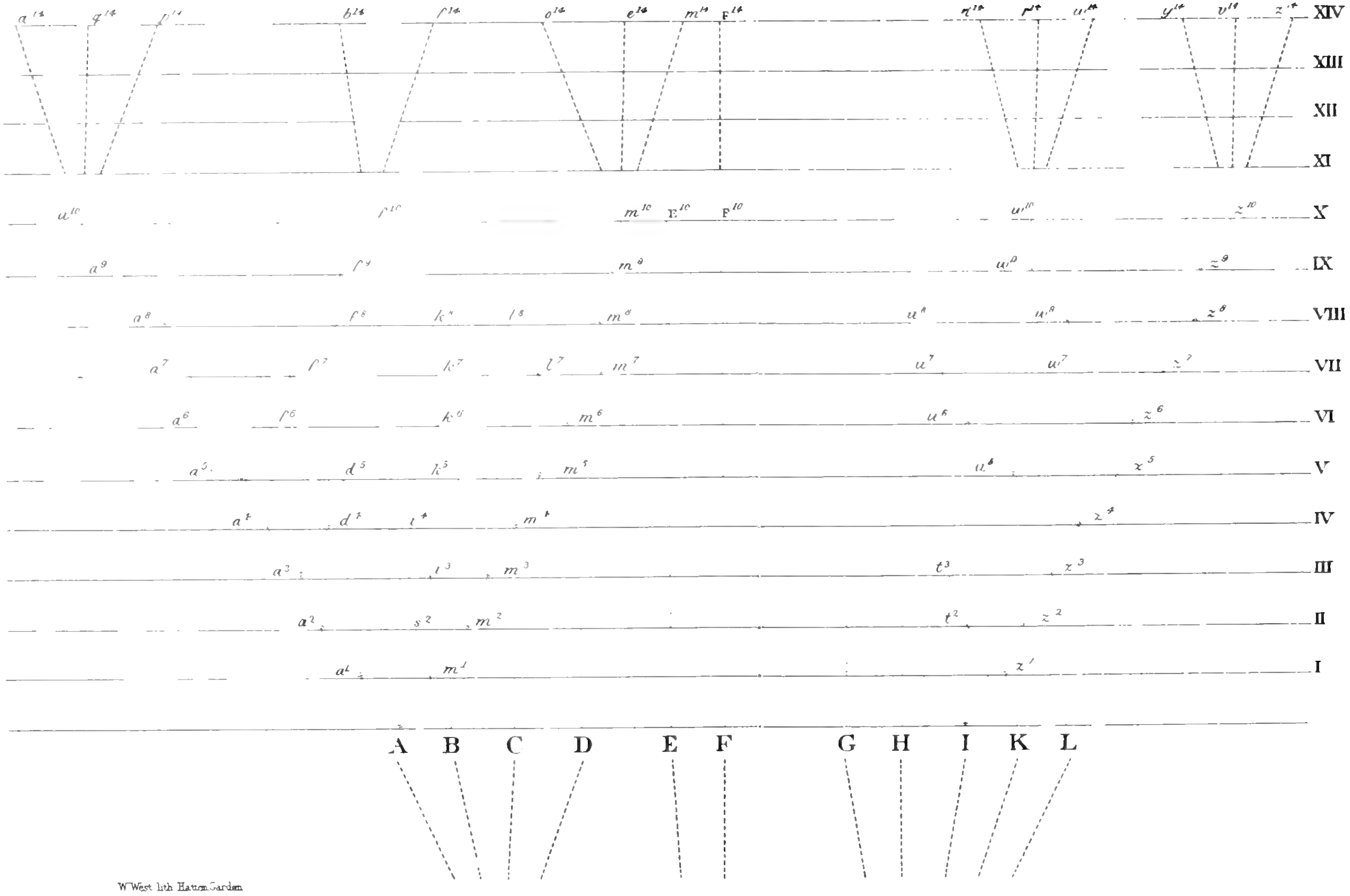

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FIGURE 1. The hypothetical tree of life from Darwin's *Origin of Species* (1859). The vertical axis represents time, with each division standing for some arbitrary number of generations.

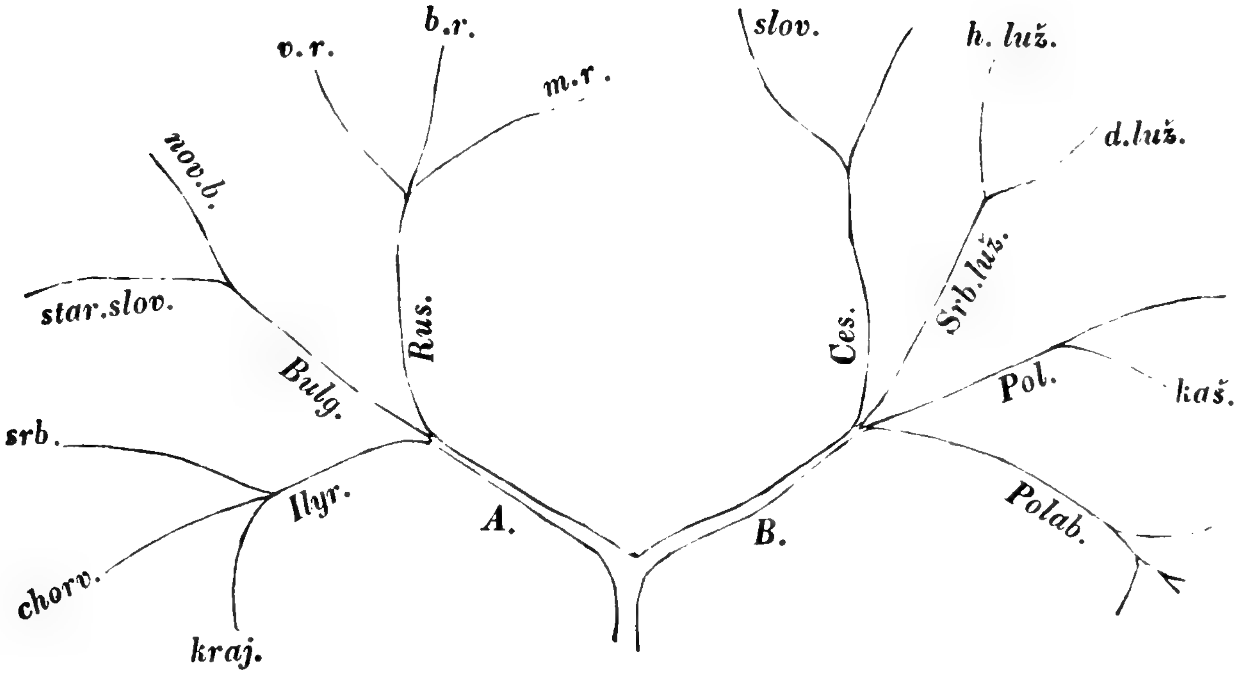

FIGURE 2. A genealogy of the Slavic languages drawn by František Celakovsky at Prague about 1852 and published in 1853 shortly after his death (Celakovsky, 1853; Priestly, 1975). For the only language tree earlier than Celakovsky's (a diagram drawn around 1800 by Félix Gallet) see Auroux (1990).

diagram is one of the first trees of language "phylogeny" and it was drawn, like Darwin's tree in the 1850s, by the Bohemian historical linguist František Celakovsky (Celakovsky, 1853; Priestly, 1975). Figure 3 is a third "tree of history": the first stemma of manuscript transmission, published by Carl Johan Schlyter in 1827 (Collin and Schlyter, 1827; Holm, 1972). As in Darwin's diagram, the vertical axis represents time, and each horizontal line stands for a specific time interval (25 years in this case). What these three diagrams illustrate is that three palaetiological sciences — systematics, historical linguistics, and textual transmission — though they function independently, all produce results of the very same sort using many of the same procedures of inference: they all produce trees of history showing branching sequences of ancestry and descent.

In each of these fields a great deal of attention has been given to the methods of historical reconstruction, particularly so in recent years in systematics, where attention has also been given to the historical character of the discipline as a whole (O'Hara, 1988a; de Queiroz, 1988; Ghiselin, 1991). But in contrast to the amount of attention that has been given to historical *reconstruction* (e.g. Sober, 1988), very little has been written in any of these fields about the problems of historical *representation*. Given that we have knowledge about events that took place in the past — the geological past, or the evolutionary past, or the linguistic or textual past — how do we represent, how do we communicate that knowledge? In particular, how do we use diagrams, which are two-dimensional, *spatial* representations, to depict the *temporal* relationships of events in time?

It might seem that historical representation (as opposed to historical reconstruction) is unproblematic: historical scientists just draw diagrams that illustrate what they know. Historical representation is a more subtle activity than one might suspect, however, and I want to demonstrate this by comparing historical representation — the representation of events in time — with cartographic representation — the representation of objects in space, as we see in ordinary geographical maps. Maps might also seem to be completely unproblematic representations of the world, but in fact they too are rather more subtle than one might expect. In making this comparison I will draw heavily on the work done by cartographic theorists (Toulmin, 1953; Robinson and Petchenik, 1976; Gould and White, 1986; Buttenfield and McMaster, 1991; Monmonier, 1991; McMaster and Shea, 1992), as well as some of my own earlier work on diagrams in systematics (O'Hara, 1988b, 1991, 1992, 1993).

Maps as Spatial Representations

Maps are representations of objects in space, and they succeed as representational devices because they are *selective*: because they omit a great deal of information that map-makers in fact have. Some imaginary Ideal Map that included literally everything in the territory it represented would be useless, because the territory itself could serve just as well (Crampton, 1990; O'Hara, 1993). Cartographers call the process whereby the world is reduced to a map, or a complex map reduced to a simpler map, *cartographic generalization*. The most basic element of the generalization process is the simple deletion of certain objects from the map, objects that exist on the earth but that will not appear on the map. But many other processes are involved in generalization as well, beyond the simple deletion of objects. For example, areal features may have their outlines simplified, and linear features may be smoothed or enhanced (Fig. 4; Monmonier, 1991). A surprising element of generalization is "feature displacement": when two objects are so close together on a map that they are difficult to distinguish, and yet both must be included, the two objects may be nudged apart slightly (Fig. 4). This has the effect of warping the scale of the map in the vicinity of the displaced objects: a unit of distance on the map in that region corresponds to a shorter distance on the ground than does the same unit of distance on another part of the map.

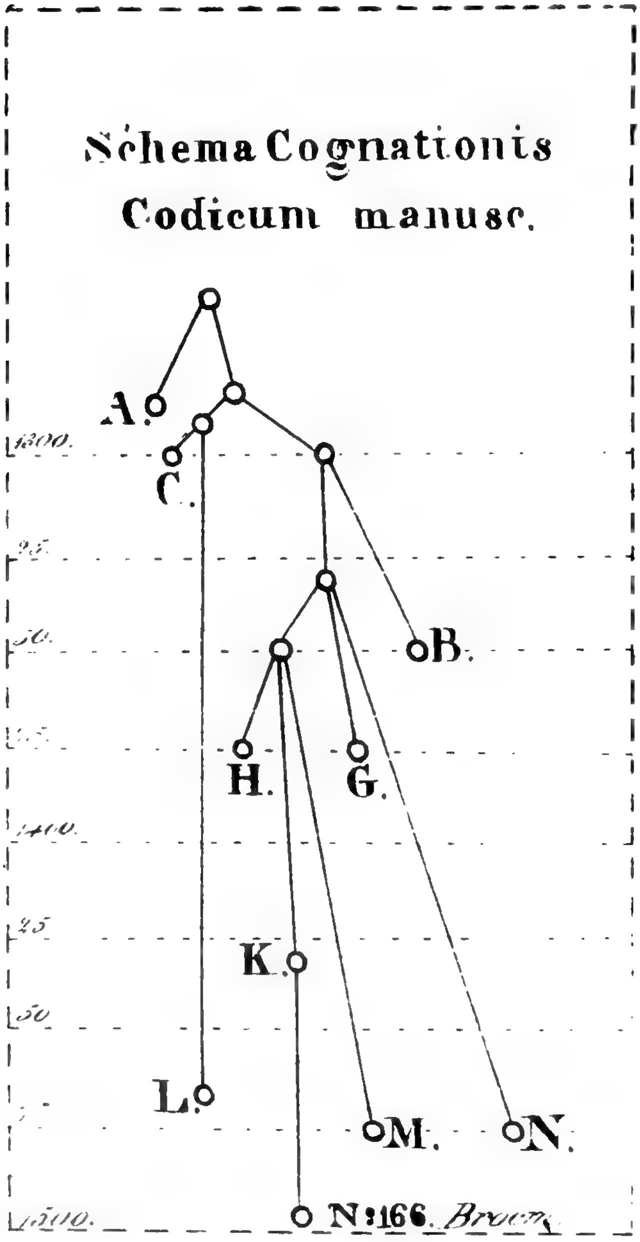

FIGURE 3. Carl Johan Schlyter's stemma of a group of medieval Swedish legal texts, the first diagram of textual transmission ever published (Collin and Schlyter, 1827; Holm, 1972). Notice the remarkable similarity to Darwin's evolutionary diagram, with the vertical axis representing absolute time and horizontal lines indicating time intervals

Cartographic generalization is a concept that has been developed and applied in the context of geographic maps, and one might think at first that such a concept would have little relevance to representations of history — to representations of events in time rather than objects in space. But upon reflection it is evident that we often speak of space and time in the same terms, and so ideas that apply in one domain might well be useful in the other. "Short" and "long" are adjectives that apply to "lengths" of both space and time. We speak of "deep" time and the "distant" past. And in answer to the question "How far is it to the city?" one is as likely to be told "two hours" as "100 miles." In view of the similarity between the language of space and the language of time, then, let us see if the notion of generalization can be applied with as much success to representations of events in time (events as they are reconstructed by palaetiologists) as it has been by cartographers to representations of objects in space.

The Space of Time

Let us begin with the simple case of an historical diagram that is strikingly cartographic in character (Fig. 5). This diagram of phylogeny from Hennig's well-known systematics text (1966) shows a sequence of events at three different temporal scales, two of them by means of insets, just as a city map might have an inset to show the city center and another to show the surrounding region. Apparent in this diagram is a temporal equivalent of what cartographers call aggregation, as when several small lakes are shown on a map as one larger lake. Temporal aggregation is manifest here in the representation of several generations of individual organisms by a single circle in the inset on the right. Similarly, even though each individual organism itself has a temporal dimension (its life span), each is reduced in Figure 5 to a single symbol without temporal extent. This latter phenomenon is called symbolization in cartography, when an object that occupies a definite geographical area (a city, for example) is reduced to a single symbol such as a dot.

In the broad spirit of palaetiology, it is important to realize that these phenomena of temporal generalization are not restricted to evolutionary trees alone, as can be seen in Figures 6 and 7, two recently-published diagrams of the history of the Germanic languages. Figure 6 shows a simplified (highly generalized) version of the entire Germanic tree, ending in the three branches of East Germanic, North Germanic, and West Germanic, the last of these being the branch that includes modern English. Figure 7 shows an enlargement of the West Germanic branch alone: the single lower right branch of Figure 6 corresponds to the entirety of Figure 7, just as an irregular polygon representing the city of San Fran-

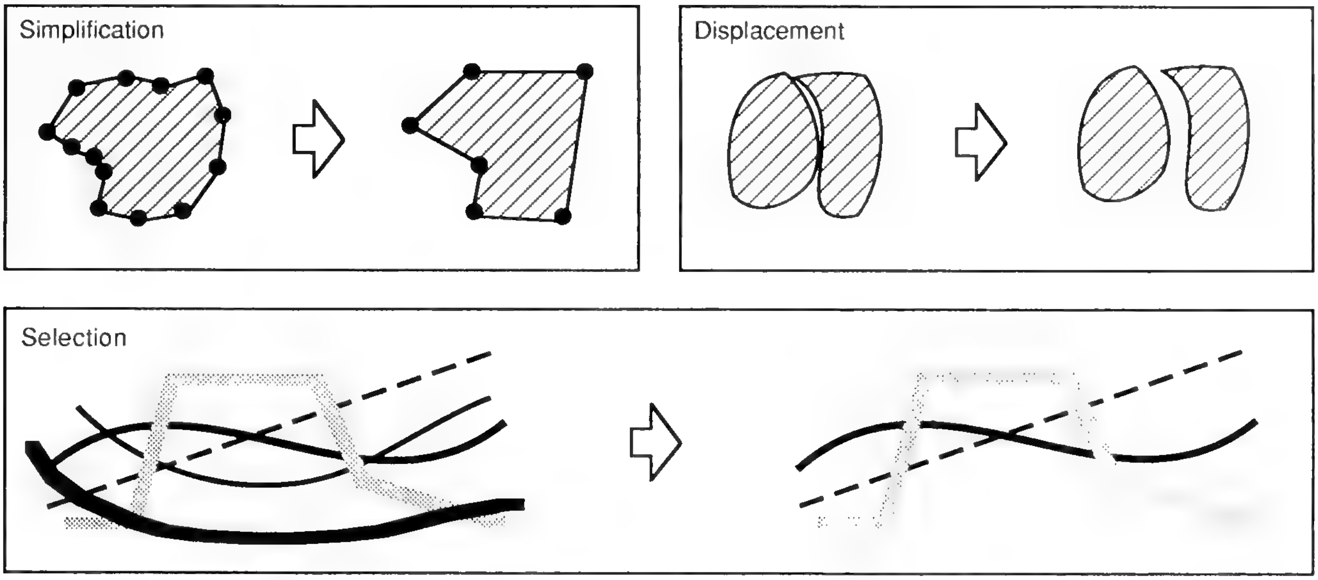

FIGURE 4. Some elements of cartographic generalization, redrawn after Monmonier (1991)

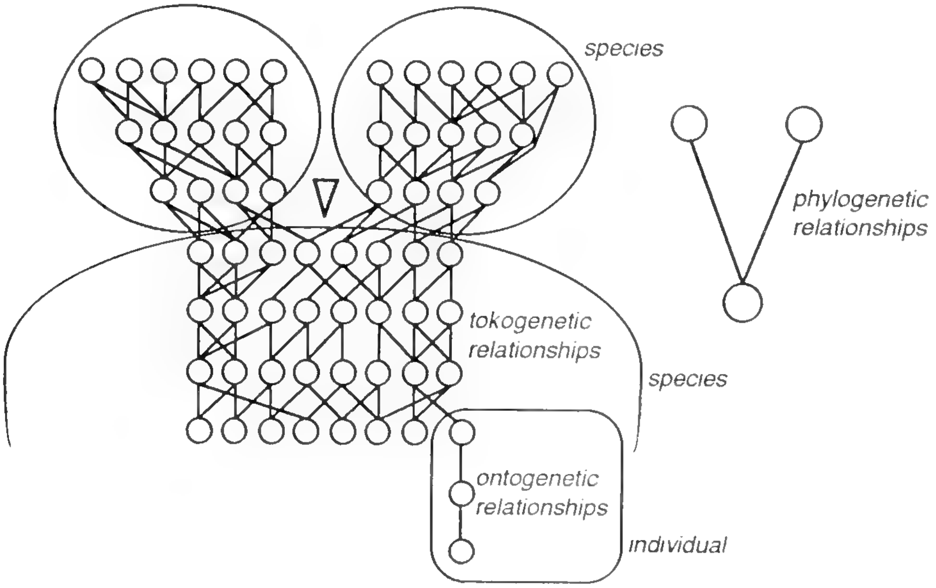

FIGURE 5. A hypothetical phylogeny, after Hennig (1966). Three different degrees of generalization are shown: the central portion of the diagram is resolved to the level of individual organisms, while the inset at the bottom shows the life stages of one individual, and the inset at the right shows a coarser view of the species as a whole. See O'Hara (1993) for further discussion of diagrams of this type, and see Maddison and Maddison (1992:26) for an additional example

cisco on a map of California would correspond to an entire San Francisco street map.

As a representation of objects in space, any geographical map can be generalized in a number of different ways. We could take a detailed map of San Francisco and generalize it into a map showing only the subway lines, or only the railroads, or only the public streets and nothing else. Similarly, any given representation of events in time, such as an evolutionary tree, can also be generalized in a number of different ways (O'Hara, 1993). And just as different generalizations of a map may give the viewer different senses of a particular territory — one that showed all the parks might give a different impression from one that showed only highways and railroad tracks (Monmonier, 1991) — so also different generalizations of a detailed sequence of events in time may give the viewer different senses of what took place within a particular temporal space. Different generalizations of the history of life, for example, may give the impression that evolution is either directed or diversifying (O'Hara, 1992, 1993).

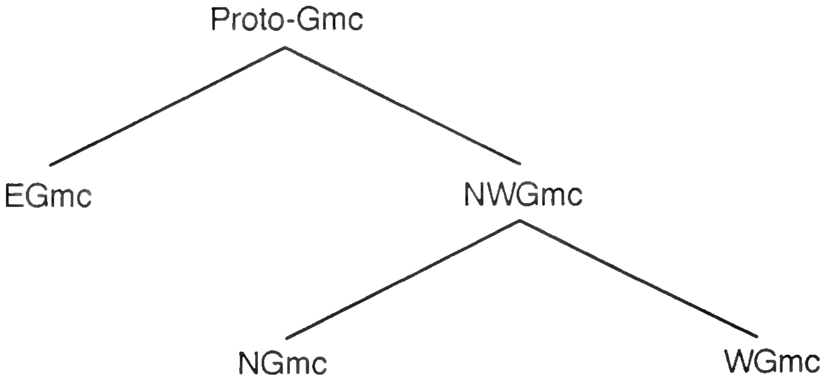

FIGURE 6. A simplified (highly generalized) history of the Germanic languages, after Barber (1993). The ancestral Proto-Germanic language is shown dividing into East and Northwest Germanic branches, the latter dividing again into North and West Germanic. The West Germanic branch, of which modern English is a part, is shown in greater detail in Figure 7.

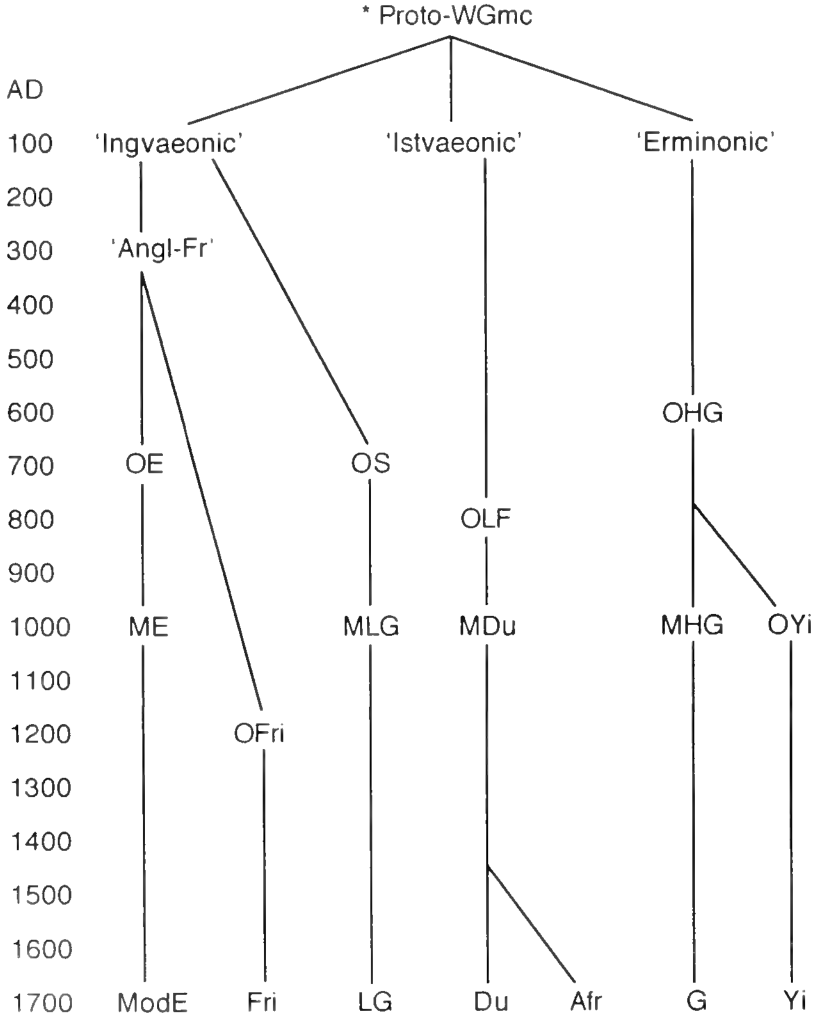

FIGURE 7. A detailed history (relatively un-generalized) of the West Germanic languages, after Barber (1993). The terminal branches shown are Modern English (ModE), Frisian (Fri), Low German (LG), Dutch (Du), Afrikaans (Afr), German (G), and Yiddish (Yi). This diagram is a more highly resolved representation of the lower right branch (WGmc) in Figure 6.

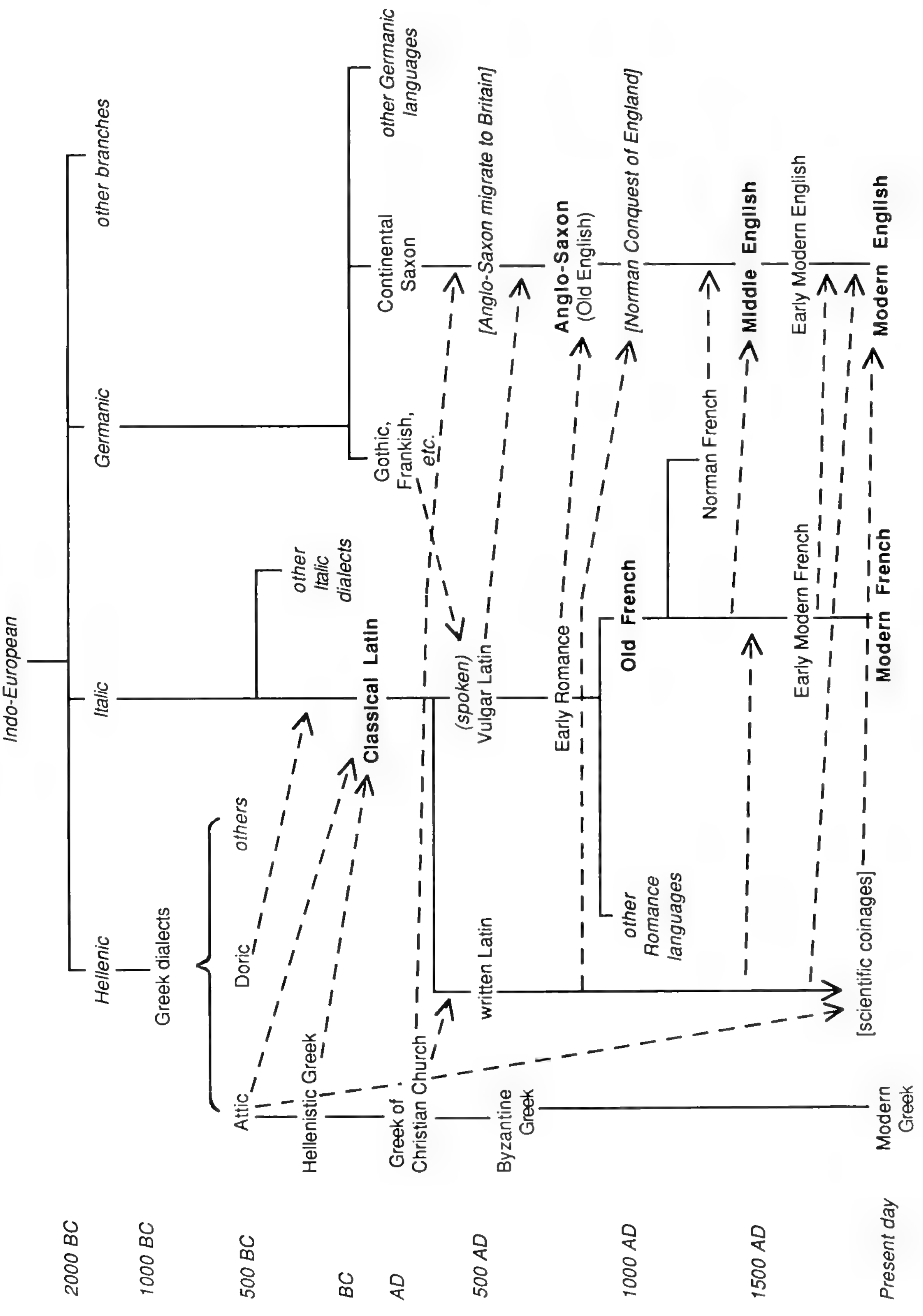

FIGURE 8. A genealogy of selected Indo-European languages, after Powell (1988). In contrast to Figures 6 and 7, which depict only direct transmission, this tree shows not only direct transmission but also borrowing of language elements across the tree.

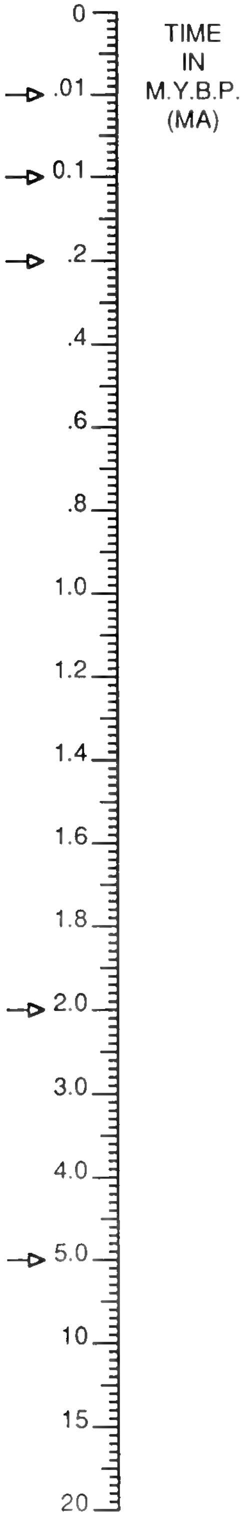

FIGURE 9. A portion of a geological time scale, redrawn after Haq and Van Eysinga (1987). The linear scale stretches out toward the present so that more events can be included. This stretching of the temporal space is equivalent to the practice of feature displacement in cartography, but when it is carried to this extreme in cartography the effect is usually regarded as humorous

Again in the spirit of palaetiology, I offer a linguistic example to show that the same principles apply once again. In the previous diagrams of Germanic language phylogeny (Figs. 6 and 7) the pattern of descent was entirely vertical, and it gave the impression that each language evolved independently and in isolation from its sister languages. From Figure 8, however, a diagram showing the history of selected Indo-European languages (Powell, 1988), we get a very different sense of the growth of Modern English. While there is indeed a line of transmission coming down from the early Germanic languages to Modern English, the ancestors of English are seen here to have received elements from a variety of sources, including Greek, Latin, and French. Does the fact that none of this linguistic borrowing is shown in Figure 7 mean that Figure 7 is false? Not at all: Figure 7 correctly depicts certain classes of events, while Figure 8 depicts many of the same events as well as some additional events. The relations among these diagrams are conceptually identical to relations that can be observed in cartography, for example between a map that shows a number of highways running in parallel, and another map that shows not only those highways but also a network of small roads that connect them.

One of the cartographic phenomena I mentioned above was feature displacement, a local warping of the scale that occurs when two objects are nudged closer together or farther apart in order to accomodate the desire of the map-maker to include a certain collection of map elements. When this is done to a limited extent it isn't noticed, but it can be concentrated for special humorous effect, as in the various entertaining maps that illustrate "A Bostonian's View of the World" or "A New Yorker's View of the World" (Gould and White, 1986). Is there a temporal equivalent of this warping of geographical space? There is, and it can be seen in at least two different palaetiological contexts. The first is in phylogenetic trees that stretch out around particular taxa, most often humans, and which thereby create "A Human's View of Evolutionary History" that is conceptually identical to maps showing "A Bostonian's View of the World" (O'Hara, 1992). A second palaetiological context in which the temporal equivalent of feature displacement can be seen appears in Figure 9, which reproduces a portion of a widely-used chart of geological time (Haq and Van Eysinga, 1987) on which the temporal scale changes repeatedly. The designers of this chart wanted to fit more temporal detail into the time scale in more recent periods, and to do so had to stretch out the temporal space. Once again, this process is conceptually identical to the warping of geographical space that we see in feature displacement, but it is carried here to an extreme that in cartography would be regarded as consciously humorous. It is worthwhile to consider how such warping of temporal space affects our sense, and particularly our students' senses, of evolutionary time and the history of the earth.

Let me close by suggesting a way in which this last question — the effect of conventional patterns of temporal generalization on students' perceptions of evolutionary history might be addressed. Geographers have done quite a bit

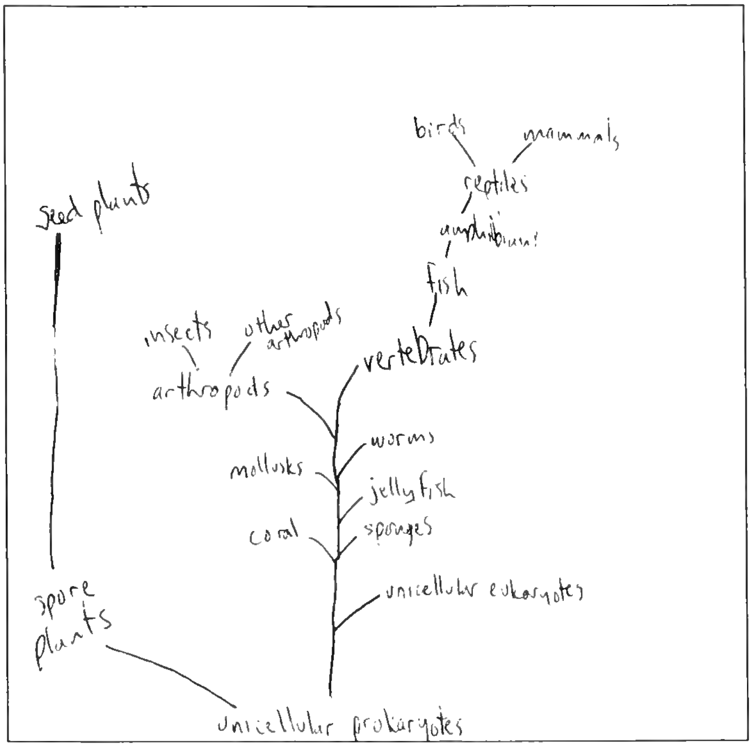

FIGURE 10. An evolutionary tree drawn by an undergraduate biology student at the University of Wisconsin. On the first day of a course on evolution each student was given a sheet of paper and was instructed to "sketch an evolutionary tree of life, and label as many branches as you can. Don't worry if your tree is not perfect, or if you can't remember technical terminology; this is not a graded exercise, and you should not even put your name on the page." Exercises such as this, which are modelled on geographers' studies of "mental maps" (Gould and White, 1986; Saarinen, 1988; Walmsley et al., 1990), may help evolutionary biologists to better understand popular conceptions of the history of life and to develop more effective teaching strategies.

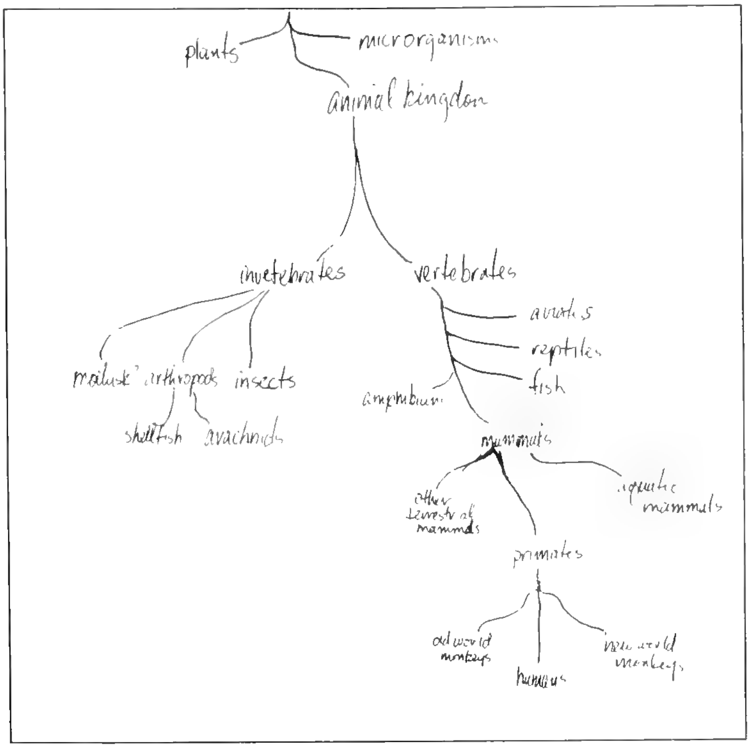

FIGURE 11. A second student-drawn evolutionary tree.

of research on what are called "mental maps" (Downs and Stea, 1973; Stevens and Coupe, 1978; Gould and White, 1986; Saarinen, 1988; Walmsley et al., 1990). If we take any person and ask him to draw from memory a map of his hometown, or of the world, or of any other region, the resulting map will reveal a great deal about that person's knowledge of geography, his perception of the sizes and distances between various geographical objects, and so on. Is it possible to do this same sort of research with historical representations? It is, and I offer here two sample results (Figs. 10 and 11) from a preliminary inquiry of this type, carried out with the assistance of Gregory Mayer at the University of Wisconsin. Students in a large undergraduate course on evolution were asked on the first day of class to draw an evolutionary tree of life as best they could, based on whatever knowledge they may have acquired from general reading or from other courses they may have taken. A great variety of images were produced by the students in this exercise. Many of them have a decided axis that leads to human beings, suggesting that there is still a widespread belief that evolutionary history is progressive or directed (O'Hara, 1992). A number of the diagrams clearly reflect the "five kingdom" arrangement of Margulis and Schwartz (1988), something that many of the students appear to have been taught in secondary school. Very few of the diagrams would be regarded by a contemporary systematist as particularly accurate. I hope to extend this preliminary study to other groups of students at other institutions in the future, and thereby build up a general picture of undergraduate understanding of evolutionary history.

William Whewell, with whom I began this essay, was not only an historian, a philosopher, and a scientist, he was also an educator: he served for many years as Master of Trinity College in Cambridge, and wrote university textbooks as well as essays on the importance of liberal education. Whewell believed that the palaetiological sciences — the historical sciences — were particularly well-suited for inclusion in a general liberal curriculum because they exemplify not only rigorous forms of thought and argument, but also the enormous reach of human reason by taking us farther back in time than previous generations of scholars would have ever thought possible. I think Whewell was right. I also think that by strengthening the ties that bind together all the historical sciences — all the disciplines that try to map the space of time — we will in turn strengthen our own particular special fields, and will be able to do a better job of explaining ourselves to our colleagues and our students in the future.

Acknowledgments

I am very grateful to Michael Ghiselin and Giovanni Pinna for giving me the opportunity to participate in their symposia on historical biology at Milan and San Francisco. Jeffrey Wills and Peter Robinson contributed greatly to my understanding of philology, Gregory Mayer assisted with the "mental tree" project, and Laurie White offered valuable comments on the manuscript. I am also grateful to the many members of my network discussion group Darwin-L, who have done much to enlarge my understanding of the historical sciences.

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PERIODIZATION AND MODELS IN HISTORICAL BIOLOGY

James R. Griesemer

Wissenschaftskolleg zu Berlin
and
Collegium Budapest

Permanent address: History and Philosophy of Science Program
University of California, Davis California 95616-8673

> The nourishing fruit of the historically understood contains time as a precious but tasteless seed.
> Walter Benjamin

1. Introduction

In a previous paper I argued that what makes a science or a scientific theory historical is that its practitioners accept historical narratives as informative (Griesemer, 1996).[1] The informativeness of narratives lies in their contributions of data, explanations, and interpretations to understanding. This view emphasizes a *pragmatic* aspect of historiography in contrast to those that emphasize either alleged intrinsic historical properties of the objects of study or an epistemologically privileged standpoint of historical explanation.[2] One need not take such an ontological or epistemic view to find something importantly distinctive about historical science. Since part of my goal was to explore reasons scientists *call* a theory or science historical and how historical scientists defend themselves against critics, rejection of these commonplace readings of historical science led me to consider pragmatic aspects of historical science.

Given the pragmatic view that a science is historical because its practitioners treat it as such, I here develop the basis for a line of defense of historical sciences against the charge that they are non-scientific or pseudo-scientific. Evolutionary biologists are often lampooned for offering "just so" stories *in place of* empirically grounded, testable, mechanistic explanations. Systematists, paleontologists, and bio-geographers are criticized for offering "pattern" descriptions without "process" explanations, while historical scientists complain that process — in the form of mechanistic models — is routinely injected into historical sciences without benefit of a broad perspective on either the phenomena or the interpretive problems. The message of this paper is that the usual caricature of narrative science that supposedly warrants such derision underestimates or entirely misses the theoretical character and import of narrative science.

The charge against historical science rests on the argument that it *consists in* the "just-so" stories, rather than testable explanations in terms of mechanistic models, but only the latter support properly *theoretical* science. So historical science is really not scientific. Two lines of defense are common (see Griesemer, 1996). One says that historical science is scientific because not all (good) science relies on mechanistic models; some of it is narrative. The other says that the "real" science in historical science isn't really narrative, it is mechanistic just like physics. Neither line of defense gets to the heart of historical science, which is narrative but *not* anti-mechanist. *The historical sciences derive their distinctive characteristic form not from the intrinsic nature of their subject matter, nor from pure narrative, but from theoretical coordination of both mechanism and narrative.* So a better defense is first to identify the respectable theoretical activity associated with narrative construction and then to argue that this activity is not inimical to good mechanistic modeling and explanation, thus showing that historical sciences can be judged favorably on the same grounds as other sciences (e.g., the robustness of their models), even while taking narrative seriously.

The goal of this paper is thus to reveal, illustrate and examine historical scientists' engagement in theoretical model construction and evaluation.[3] The illustrations chosen are not exhaustive, nor do they provide an overview of the historical sciences. Rather, they attempt to demonstrate that certain issues arise in a variety of modeling circumstances as a consequence of the need to choose a temporal framework for a narrative. The examples have been drawn from the emerging intersection of evolution and development.

Scientific modeling depends on establishing a "state space in which state variables, parameters and laws are well defined" (Lloyd, 1988). An important element of the framework for choosing a state space type[4] is what I call a "periodization." Since the formulation of alternative models in historical biology can be linked to distinct modes of adequate mechanical description within the historical periods of a periodization, narratives can be understood as coordinators of mechanical models. Population genetic models, for example, appeal to mechanisms underlying gene transmission, but descriptions of the temporal structure of transmission require choice of a temporal framework. Narratives of genetic events are not mere stories, creations of the narrator without empirical grounding.

Narratives are not usually considered to be founded on robustness analysis of alternative models and modeling frameworks; one simply tells *a* story. But narrative structure depends on the choice of time scale and temporal units such that mechanical descriptions within and among time periods are coherent and robust. So narratives are not singular just-so

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stories indicating how possibly events became ordered in a particular sequence. Rather, they have a more complex theoretical structure. The robustness of the underlying mechanistic models depends, in some measure, on the *periodization* selected as a framework. But then it becomes important in evaluating narratives to assess how well the selected framework supports empirically adequate models of phenomena linked in the narrative. Because evaluation is comparative, it requires consideration of alternative periodizations. These facts entitle one to say that narrative science is deeply theoretical.

While evolutionary narratives have been singled out in criticisms of historical science, I believe that a thorough understanding of historical biology should take account of development as well as of genealogy. Although some historical work has been done on special problems about the relationship between evolution and development, e.g., Gould's study of the recapitulation principle (Gould, 1977), less has been done to explore the ramifications *for historical science* of the general philosophical relationships between evolution and development, save for Ghiselin's penetrating study of Darwin (Ghiselin, 1969). Vermeij (1987) offers a valuable analysis of the hypothesis-forming role of an ecological theory of adaptation for historical inquiry into evolutionary biology. Consideration of relationships between evolution and development can be used to illustrate the coordinating role of periodizations by examining how developmental mechanism plays a role within evolutionary narratives. This is not, of course, the only, or even the most interesting case of coordination, but it is an important one given current moves to integrate evolutionary and developmental theory.

To the standpoint that historical understanding does not lie at the opposing pole of a dichotomy with mechanism, I want to add that mechanical and narrative accounts are *both* facilitated, and indeed linked, by the use of periodizations. This conclusion can be used to defend historical science on the grounds that good history does not in fact do without mechanism; critics and supporters of historical science share a misunderstanding when they suppose it to be purely or solely narrative in form.

In section 2, I discuss the idea of periodization and some reasons for entertaining it in regard to the historical sciences. In section 3, I argue that an important role of periodizations depends on their abstract and hypothetical nature, which makes consideration of *alternative* periodizations a flexible and powerful methodological tool. In section 4, I discuss several examples to show how choice of periodization may facilitate homogeneous, mechanistic explanations within stages and may add to our understanding of the relationship between evolution and development. Section 5 draws some conclusions for the prospects of a defense of historical science from these arguments and illustrations.

2. The Concept of Periodization

My thesis is that there is a central theoretical structure common to all historical work which I call a "periodization." A periodization is a conventional marking of time into parts or stages. In many sciences, periodization is given by "Newtonian time" and very little explicit attention is given to its theoretical role. In other sciences, typically those involving "stage" theories, the duration and structure of the stages or periods is a focus of concern, partly because a poor choice of units leads to difficulty in describing transitions among stages. Periodization plays a more or less prominent role in historical writing: in some cases it amounts to no more than the organization of an annal or chronicle by calendar years or clock minutes, but in others a new periodization may change dramatically what we count as historical events and how we think about their significance. An annal is a simple listing of events in chronological sequence without interpreting their significance. A chronicle is an interpretation of a sequence of events that is simply cut off at some point (often the writer's present) without any assessment of significance or meaning — an unfinished story. A narrative concludes a chronicled story with an interpretation of the significance of the events selected for inclusion in the story.[5]

Periodization challenges how we understand events. In human history, for example, questioning 18th–20th century periodizations of the 16th and 17th centuries that were based on Enlightenment conceptions of intellectual progress, brings into doubt the nature of "The Scientific Revolution" as an historical event (Dobbs, 1994). Similar things have been done to "The French Revolution" and to the concept of revolution in general (Latour, 1993). Of course, the most obvious examples from natural science of how a change of periodization may lead to a changed understanding of events come from geology and paleontology.

Historical studies of how Victorian geologists came to recognize the ancient origins of life through their arguments for the existence of the Cambrian, Silurian and Devonian periods provide particularly good examples: by arguing for distinct, early fossil-bearing strata, geologists pushed back the appearance of life in time and revised their understanding of fossil and stratigrapic sequences.[6] In particular, debate about the use of lithological vs. paleontological criteria for establishing the boundaries of strata and geological periods reflects a changing understanding of the relationship between mechanical description — literally how the rocks are structured and how they got that way — and periodization, how the choice of temporal units in which to describe fossil and rock sequences constrains claims about the existence of geological periods. Although outside the scope of the present paper, application of the ideas developed here to geological examples would be instructive.

Periodization of time is often inextricably tied to regionalization of space, that is, a division of space into regions that identify what counts as a "local" interaction and what would count as "action at a distance." In biology, "individuating" processes such as cell division, organismal reproduction and cladogenetic speciation, which all lead to the creation of new individuals (cells, organisms, species), require that participating entities be in temporal and spatial proximity in very specific senses. A description of the sequence of events of a biological process such as allopatric speciation involves both spatial and temporal sequences. A description of the temporal stages of the cladogenetic process underlying speciation entails a regionalization of populations, for example, into central and peripheral components where founding isolates are formed according to the Mayrian allopatric model. Because of the intimate relationship between temporal and spatial locality with respect to a given mechanical process, temporal descriptions can represent spatial regions and conversely.

A periodization can place constraints on *spatial* relations admissible in a model of an individuating process. Conversely, a choice of spatial relations can constrain the admissible periodization of events described by a model. In embryology for example, spatial relations can reflect temporal sequences: spatially separated sister-cells must, in general, have undergone a certain time-evolution in order to have become spatially separated since the cell-division event that created them. If two cells are next to each other at a given time, but not afterward, then it is likely that they had a common ancestor. This is true to the extent that relative cell movement results from cell division. Patterns of spatial separation of genealogically related elements can thus be used to represent temporal stages. This is common in classical descriptions of developmental stages: e.g., the "late neurula stage of frog development" might indicate a certain *time* in development even though the stage itself is characterized primarily in terms of the *spatial* pattern in which cells on opposite sides of the neural fold are in contact.[7]

Minelli suggests that complexity principles used to interpret arthropod segmentation in terms of tagmata (body regions) may apply to the time dimension as well, ". . . if developmental stages are equated to body segments and major developmental phases (such as insect larva, pupa, and imago) are equated to body regions."[8] He argues that a causal link has already been established by molecular biologists between the temporal dimension of development and the spatial dimension of the longitudinal body axis, citing the pattern of expression of *Hox* genes.[9] Spatiotemporal unity and continuity are properties that "integrate" individuals into historical entities (Hull, 1975). Models that rely on an explicit division of time into units may help identify or define such entities. A periodization provides the framework of temporal units in which that integration (and its mechanisms) can be described — a "state space" in formal modeling terms.

Historical description is facilitated by periodization to the extent that events and objects within periods can be described according to a single perspective on, or "mechanistic" account of, causal processes. The unified perspective that a periodization provides can be characterized as the framework for choosing a state space in which to describe a theoretical model, according to the semantic view of biological theories (Lloyd, 1988). Models are structures that satisfy the law-statements of scientific theories. Theoretical models are abstract structures that make such laws true, and when hypothesized relationships between theoretical models and empirical structures in nature hold, the laws are true of nature as well (Giere, 1988). Theoretical models thus form the middle term of a relation between laws, models and structures identifiable in nature. Tests of hypotheses require comparing structure observed in nature with the structure of models. To the extent that model structure depends on choice of a state space, periodization is implicated in the conditions for testing as well as constructing hypotheses.

Periodizations serve as the framework in which models classify objects and events through *assignment* to a particular unit of time. The assignment reflects laws of coexistence[10] and succession,[11] thus there is an intimate relationship between the form of the (possibly implicit) laws of a theory and a periodization. Natural historians of all sorts make and use such classifications, a fact that extends the reach of the historical to most "mechanistic" fields in biology such as genetics, where time is divided into generations, and biochemistry, where time is divided into reaction cycles. Division of time into stages affords a mode of classification that plays a wide theoretical role in historical science. The ways that temporal classifications articulate with spatial, structural, or genealogical classifications are complex and cannot be pursued further here.

It is advantageous to think of periodizations as frameworks for specifying a state space of models to emphasize that the historian may entertain alternative *periodizations* for a given set of models, objects or events, on the one hand, and to entertain alternative *models* (or state spaces) within a given periodization on the other hand. Models are cheap while data are dear, and it behooves the careful investigator to explore alternative interpretations in order to make the most of data. One way the consideration of alternative models does this is by guiding the search for robust empirical consequences in which the fit between models and data is shown to be independent of the artificial "simplifying" assumptions of any particular model (Levins, 1966; Wimsatt, 1981, 1987). "Robustness analysis" of scientific models *requires* more than one model of a phenomenon for there to be an adequate scientific account of it. By the same token, the robustness of a collection of models to a change of periodization may reveal important generalities about a phenomenon.

Given a conception of narrative pure and simple, the role of alternative models in historical science is easily overlooked. A second *story* does not seem necessary as a "reality check" on a given story. One just tells the story (well or badly) and moves on. But checking the fit of a model to a selected periodization and considering alternative periodizations are common activities in the historical sciences. However these activities are not particularly evident to the casual observer nor are they typically interpreted in the spirit of modeling that is so common in mechanistic sciences. Identifying periodization as an important theoretical activity should help draw attention to this important aspect of historical science.

The most important properties of adequate periodizations are that they support a unified description of events within stages and that they identify breaks or discontinuities between stages. Minelli suggests that the changes occuring within molts of post-embryonic arthropods are ". . . the developmental equivalent of the smooth gradual changes in morphology we can observe with one tagma, along the antero-posterior axis of the body."[12] Other more dramatic changes or discontinuities are the metamorphoses that constitute major developmental events. Both are critical to the mechanistic analysis of the existence and persistence of (theoretical) individuals. In some sense, a gradual tempo and a continuous mode are hallmarks of (simple) biological mechanism. In many historical sciences, all the events within a given stage of a periodization are subject to investigation according to a single developmental-mechanical perspective. That is, the function of periodization is to divide time into stages that are explanatorily homogeneous, and within which a single, ahistorical mode of description can be employed by a single model type. Within-stage events are accounted for as the result of causal processes that can be given non-narrative, mechanical descriptions. For those of a certain bent, stage theories can be considered place-holders until a single, unifying mechanism can be found that makes the whole process explanatorily homogeneous. Transitions between stages are usually poorly explained compared to sequences of events within stages, but narratives string stages together to make some sense out of a whole process and pave the way for more detailed attack on the transitions.[13]

Relative to a given modeling purpose, an adequate periodization will serve to single out, or at least to order, subsets of available mechanical principles with which to interpret within-stage events. In historical biology, embryology is the premier example of the mechanical study of changes in organisms that feeds into the narrative account of evolutionary change in populations, species and higher taxa. Organisms develop so that they reach reproductive condition. The reproductive nexus is what organizes populations genealogically. So the events that take populations from one organism-generation to the next are describable in terms of the mechanisms of development.

Mechanisms at the higher levels are often functions of those at lower levels (as for example organismal development is a function of migration of cells), so the links between embryology and evolution are complex and neither is distinguishable as the purely mechanistic or the narrative partner. An evolution-development narrative would not follow a single "central subject" or individual up the levels of organization, for example, from cell to organism to population to clade. Rather the description of dynamics of individuals at a given level would be linked to individuals at other levels by showing how a choice of time scale appropriate to one level would constrain characteristics of appropriate models at other levels. One example of this is the way geneticists describe life cycles. Because the continuity that population geneticists need is trans-generational, the only cellular events that really matter (in classical models) are the ones leading from zygote to adult to new gametes. The within-generation continuity of the "phenotype" is irrelevant. So a trans-generational periodization for genetical purposes imposes a periodization on embryological events that is coarse-grained from the embryological point of view for the sake of a homogeneous narration of genetical processes.

The mechanical description of embryological events may differ among embryological stages, however, and the coarse-grained periodization of cellular events by the geneticist may not be adequate for other theoretical purposes. The earliest events of metazoan development, for example, are usually described in sub-cellular, biochemical terms relating the positioning and movement of molecules within a single cell. Somewhat later events (at a time when the organism is still a multi-cell) are described in terms of cell-cell interactions. Still later events are described in terms of germ-layer or tissue interactions and movements. Each of these sets of events may occur on a different time-scale. But successful periodization only requires unity of the mechanical form of description within a stage; it does not require that all stages be pursued with the same form or style of description, or that stages be of the same duration. Periodization therefore does not assume any form of reduction to the lowest common physical or chemical denominator in linking together stages in a narrative. Nor does the methodological unity suggested by the practice of periodization suggest any direct linkage among phenomena in different fields such that there can be theoretical unification of the sort promised by the modern evolutionary synthesis (linking genetics, paleontology, development, ecology, and systematics). It is not obvious that narratives constructed from different theoretical perspectives can be unified. We do not need to claim this much, however, to argue the point that a given narrative from a particular theoretical point of view can serve the constructive purposes I have been describing. It would be interesting, but far beyond the scope of this paper, to explore the possibility that apparently incompatible narratives such as the embryologist's and the geneticist's alluded to above could flow together to form new (probably multi-level) theoretical entities.

Causal-explanatory unity within each stage is a necessary but not sufficient condition of adequacy for a theoretical historical model. To be adequate, a model must also support a narrative that links stages. Hull (1975:198) has emphasized that narratives do this primarily by describing a "central subject," a historical entity that functions as the core of a narrative. In addition to dividing time into units within which events can be given unified mechanical explanations, periodizations set the framework for identifying the integration of individuals into historical entities capable of serving as central subjects. In biology, most individuals at a given level of organization are composed of individuals at lower levels. Multicellular organisms are historical individuals that are composed of cells, which are themselves historical individuals at a lower level, composed in turn of organelles and molecules that are historical individuals at still lower levels. By setting the "break points" in a sequence of stages within individuals at a given level and among individuals at lower levels, a periodization constrains the selection of the genealogical links to describe the integration of lower-level individuals into a higher-level individual. Periodization thus plays a role in the identification and individuation of historical individuals.

Historical description involves postulating (or assuming) a rough periodization of the temporal phenomenon of interest based on prior orderings of events into chronological sequence (e.g., a division of time into seconds, minutes, hours, days, years, seasons, generations). Periodization can also be implicit in the formation of a preliminary historical hypothesis to the effect that "events occur in chunks like these." In historical research one roughs out an "annal," which is a list of events ordered in chronological sequence according to the time units of the periodization, and a "chronicle," which is a temporal sequence of events at different times within stages leading to the culminating states at the end of each stage. Events and objects within stages must be consistent with principles of a mechanics adopted for each stage. One attempts to establish narrative connections within and among stages in the model that constitutes the historical explanation. At its crudest, a narrative will relate one event from each of two different stages and be "about," i.e. interpret, the earlier event "in light of" the later one (Danto, 1985).

It is important to see that a periodization model must be constructed prior to the firm establishment even of a chronicle. Without periodization, there is, so to speak, no way to select and describe events *historically*. This will be so regardless of whether history must be narrative or could include pure annal or chronicle forms as genuinely historical (cf. White, 1987). In the context of narrative history, the periodization coordinates mechanical explanation of events with narrative description of a central subject by simultaneously facilitating the identification and selection of events to be included in a narrative and the reification of an individual into a historical entity worthy of being a central subject in a narrative. Without a periodization, not only could there not be a narrative, but there could be no subject of narration. Hull expresses well the dual requirements served by periodization models when he writes that,

> . . . two sorts of linkage are involved in historical narratives: one the cause-effect relation connecting the events associated with the historical entity, and the other the part-whole relation integrating the central subject into a single historical entity (Hull, 1975:187).

These unified, within-stage cause-effect or mechanical descriptions will tend to look rather different than the overall coordinated accounts that describe meaningful sequences among stages because the latter tend to be narrative in form while within-stage descriptions will be causal-mechanical. Although Hull (1975:196) characterizes narrative as ". . . a description of the central subject and the events in which this subject participates," Danto's point, that narrative sentences have a distinctive logical form because they refer to events later than an event of interest but are only "about" the earlier one, must be added to clarify the contrast between mechanical and narrative description (Danto, 1985; see also Griesemer, 1996). This point is critical to understanding historical science, because there is a tendency to *identify* it only with narrative activity and not with the mechanical analysis. But both are critical to historical analysis, and this is more clearly seen through consideration of the central coordinating role of periodization as theoretical model.

3. Periodization and Alternative Models

If the modeling function of periodization is common to all biological sciences, then historical biology will always bear an important relation to ahistorical biology. In Ernst Mayr's (1961) apt terms, ultimate biology (evolution) will always be tethered to some proximate biological theory (e.g., in physiology, genetics, morphology, cell biology, biochemistry) that provides the basis from which to produce the mechanical descriptions of events within periods that are incorporated into evolutionary narrative.

A periodization frames a collection of models in the sense that it defines a space for state descriptions of objects of interest and the events that involve changes in state. The laws of transformation that describe such changes (causes, human actions) are contained in the mechanical theories that apply within stages. As I said above, models are abstract, hypothetical structures. They are applied in the form of hypotheses that the structure of nature conforms to the structure of the model. Most effective science involves formulation of a variety of models that are intended to represent different aspects of the phenomena under study rather than treating the abstract framework of a given model as a true description of nature simpliciter. The art in scientific modeling is choosing a set of models whose artificialities are independent of one another, so that "our truth," as Richard Levins put it, "is the intersection of independent lies" (Levins, 1966:423).

Much as under ordinary circumstances there are no frictionless planes, the beginnings or endings of decades or centuries typically do not mark the most significant historical events just because they are nice round numbers. But the division of time into centuries plays a role in history analogous to that of the frictionless plane in mechanics. It is an idealization that facilitates representation of complex experience, one that helps us identify the mechanisms that explain events and also describe the entities (historical individuals) that participate in those events. Although it may be a false hope that the same set of "forces" that accounts for political events at the beginning of a century will account for events at its end, a one-century periodization is more likely to succeed than a two-century periodization. Here one can envision the trade-off between model "realism" and "precision" that Levins wrote about. An ultimately realistic periodization would have "tick marks" at the same temporal scale as the (lowest-level) individual events, but such a model would be as worthless for purposes of representation and understanding as to treat a cat as if it were a model of a cat. In historical description, even the division of time into segments of arbitrary size allows one to entertain the possibility and feasibility (given current mechanistic understanding) of uniform description of events within segments and to describe the continuity of individuals among segments.

Notice that the concept of periodization introduces a complication into the contrast between annal or chronicle, on the one hand, and narrative on the other hand. A periodization imposes a structure on the ordered, but not necessarily scaled, elements of a chronicle. But it does not fully construct the complex relations between future and past relative to a given event or time that are characteristic of a narrative. A periodization coordinates the relationship between a narrative and the data contained in historical documents by constraining both. The periods structure our views of the data as represented in models and at the same time organize the terms of the narrative. Periodizations, in other words, coordinate the "empirical substructures" specified by chronicles within the framework of a narrative account and stand in analogous relations to chronicle and narrative that models do to phenomena and theory.[14]

The view that historical interpretation involves postulating a framework for theoretical models allows me to express a significant, under-explored problem in the analysis of evolution as a historical science: the relationship between evolution and (embryological) development. I want to consider some examples from evolutionary developmental biology to illustrate the modeling role of periodization. A detailed analysis or case study of the articulation of evolution and development would be premature. Here, the idea is simply that periodization of development establishes the framework for mechanical explanation of *evolutionarily* significant events in which organisms participate. I will assume that organisms constitute historical individuals that are parts of species, which are themselves historical individuals. The main point to be illustrated is that a change in the periodization of development can have substantial consequences for the construction of a historical evolutionary narrative about species or other taxa. This is obviously not a new idea. One could interpret the whole history of the recapitulation concept and biogenetic laws as a matter of the proper periodization and registration of phylogeny and embryology (Gerson MS, ch. 2). What is new is the idea that the periodization of development constrains the structure of theoretical historical models in this field.

Let us consider an illustration of how changing periodization so as to more adequately capture mechanical descriptions of within-stage events may lead to alternative evolutionary narratives. Critiques of historical science that appeal to the story-telling qualities of scientific narratives by analogy with human history neglect the extent to which *human* history depends on central subjects whose robustness to alternative periodization is taken for granted. The scientific revolution may be problematic as a central subject, but Isaac Newton is not. Gibbon, in a famous passage on the difficulties of writing ancient history, shows just how far the human historian may justifiably take the central subjects for granted:

> The confusion of the times, and the scarcity of authentic memorials, oppose equal difficulties to the historian, who attempts to preserve a clear and unbroken thread of narration. Surrounded with imperfect fragments, always concise, often obscure, and sometimes contradictory, he is reduced to collect, to compare, and to conjecture: and though he ought never to place his conjectures in the rank of facts, yet *the knowledge of human nature, and of the sure operation of its fierce and unrestrained passions*, might, on some occasions supply the want of historical materials (quoted in Kiester, 1980:331; emphasis added).

In this passage, knowledge of human nature and the operation of its passions stand as knowledge of mechanisms which drive human history. It is precisely because this knowledge is available for persons that Gibbon has confidence in his central subjects. When human history departs from persons and their biographies as central subjects, however, the theoretical issues are just as profound in human history as in other historical sciences (Hull, 1975). Indeed, it is precisely the departure from familiar and accepted central subjects that leads historical scientists to models which reduce the complexity of mechanisms to a manageable level. The first step in doing this, as I argued above, is to choose periods within which the modes of mechanism are relatively homogeneous.

In one of the most famous attacks on pure story-telling and defenses of the relationship between narrative and developmental mechanics, Gould and Lewontin (1979) argue that alternative "atomizations" of organisms into traits support different adaptive evolutionary scenarios (or even nonadaptive ones). Their favorite example of a non-character, the human chin, tells the story. An idealized and simplified model of development is tacitly assumed in which any adult trait describable by a morphologist is seen as emerging by a simple unfolding. This model takes the periods of trait development to be whole-organism life cycles. The crude mechanics of trait development in this example amounts to little more than the description of chin development as a gradual, continuous unfolding or growth over the whole-animal life cycle (with selection typically acting only on the fully developed adult morphology). From such descriptions, an evolutionary narrative of chin evolution could be constructed. The stages of the narrative are whole-organism life cycles. The genetic mutations that alter the adult chin morphology of offspring are the mechanical events within stages relevant to the evolutionary process. There is no localization of mutation events within a life cycle because life cycles on this model do not have distinguishable periods within them, although the mechanics of mutation suggest that pre- and post-mutation sub-periods could be identified.

Gould and Lewontin observe that "the chin" develops as the interaction product of two growth fields, the alveolar and dentary. These may be under complex genetic control that has a temporal structure within a life cycle. If true, this structure is not well-represented by the idealized model described above. They apply this observation in an argument against Panglossian adaptationism: if development says "no trait there," then it is folly for evolutionists to construct a narrative interpretation (i.e., adaptation explanation) of its evolution. Of course, it also does not follow from developmental mechanics alone that there *is* a trait there. Gould and Lewontin's developmental mechanics does not rule out the chin as an adult trait subject to selection any more than the traditional mechanics rules it in.[15] The critical choice, as John Damuth points out, is in *which* developmental mechanics implies something important about how natural selection actually has acted. "For if one knows," Damuth writes,

> from careful natural history or manipulative or functional studies how and to what degree selection is operating on a character, one knows both the proper scale of periodization and the character's status as a (contemporary, at least) adaptation. How to infer past history of selection is a difficult issue — but no one should be able to get away with either "Just So" narratives *or* "Just So" periodizations. To do so would be to claim a priori truth for one's theoretical models without evidence. (Damuth, pers. comm.)

We can also draw a wider consequence from the chin example for the nature of historical explanation than do Gould and Lewontin. If they are right in their assertion that there has been no selection on the chin as an adult trait, then the whole-organism life cycle is too coarse-grained a periodization to identify some events relevant to the evolutionary narrative of the hominid lineage. The chin is *ex hypothesi* two interacting traits in development, not one which simply emerges as an unfolding. Periodization into whole-organism life cycles (generations) leads to the bad choice of simple unfolding as the developmental "mechanics" of chin formation. A periodization that results in a narrative better suited to the Gould-Lewontin hypothesis is one that takes within-organism developmental stages as the relevant units for the evolutionary narrative. That is, organismal generations are not appropriate temporal units for describing chin evolution because whole life cycles are not temporally homogeneous with respect to kinds of mechanical events (mutations, interactions of cells of the two fields) that cause the adult chin state.

Once organisms are themselves divided up into developmental stages, the effects of mutations on different developmental stages can be included in a mechanically articulated description of the production of an adult chin. But then the evolutionary narrative will change too, because it will have the resources to refer to events within life cycles as *evolutionarily* significant, that is, as bearing significance for changes in the lineage of human organisms leading to the current evolutionary state of the chin. This interaction between developmental model and evolutionary time periodization is one window on understanding the nature of evolution as a historical science.

4. Homogeneous Mechanism in Evolution and Development

The theoretical framework of historical narrative is periodization, the *marking* of time into the units used in the narrative. The logical structure of narrative sentences involves relating events in different time units of a periodization. I suggested that part of the function of periodization is to divide time into stages that are mechanically "homogeneous," that is, stages within which a single "ahistorical" kind of mechanistic description can be produced.[16]

In this section I want to illustrate with examples from developmental biology how the choice of periodization is designed to facilitate mechanical description and explanation within periods. In most cases, the role of periodization is obscured by the fact that temporal stages are initially identified in morphological or spatial terms, and only subsequently measured in clock units. Moreover, there is often a complex interplay between the choice of a periodization and commitment to a particular mode of mechanical description, as is illustrated by the chin example described above. Possession of a convenient tool for mechanical analysis may elicit consideration of alternative periodizations. In the late 19th century, for example, the use of microscopy and camera lucida techniques gave rise to arguments that differentiation occurs earlier in development than does the appearance of germ-layers. And by the same token, a well-entrenched periodization can lead to a search for new tools of mechanical description, for example the use of patterns of homeobox gene expression to establish evolutionary homologies. Let us now consider these two illustrative examples in more detail.

The first illustration mentioned comes from the history of embryology at the turn of the century. In the 1880s and '90s, C. O. Whitman, E. B. Wilson, T. Boveri, and others developed an approach to early embryology that Whitman termed "cell lineage studies" (Maienschein, 1978, 1991). Whitman doubted Haeckel's idea that the embryo was homogeneous prior to visible germ-layer differentiation and began to study the earliest cell divisions to get clues about how the germ-layers formed. Each cell division was studied microscopically in a number of invertebrates and the pattern of emergence of germ-layers was correlated with cleavage patterns, movements of cytoplasm, and so forth. But as cell division proceeds, the complexity of the descriptive task overwhelms observation. Cell-lineage work shifts from tracking each cell division to tracking layers at some point in development, perhaps coincident with the visualization of the germ-layers. The net result was that the cell lineage workers extended the time of differentiation in the embryo to much earlier than Haeckel had, and linked it to the cell divisions that could be observed individually rather than to the layers that could be observationally distinguished. In short, the periodization of development had been changed to include a period of differentiation prior to germ-layer differentiation and the mechanics had shifted to a lower level, from the histological level of germ-layers to the cellular level of cleavage divisions. Instead of a relatively few temporal divisions in the germ-layer-based periodization (e.g., appearance of distinct endoderm and ectoderm as one "tick mark" and then emergence of a distinct mesoderm as another), the cell-lineage work identified numerous temporal divisions (in the limit, one for each cell generation). It also pushed and compressed the stages of germ-layer differentiation into a much earlier period of development.

Part of the impact of this work on evolution resulted from the fact that at the cellular level, germ-cells can be considered a germ-layer and the differentiation of germ-cells became a joint problem of evolution and development at that level. Treatment of germ-cells as a "layer" became a prominent part of the theories of Boveri and Weismann in their interpretations of the role of development in the segregation of the germ-line and somatic-lines. But the state space in which these theories are significant depends on the periodization of cell-lineage work. No matter how much a part of "descriptive embryology" it appears to be, this work has a deeply theoretical impact through its substitution of a new periodization.

Consideration of alternative developmental perspectives and mechanics of the sort described by the cell-lineage workers leads to different evolutionary narratives. Leo Buss's (1987) book, *The Evolution of Individuality*, is an example of how a re-periodization of development can lead to a novel evolutionary narrative. By surveying the diversity of times of segregation of germ-line and soma in a variety of taxa, Buss was able to use a "Weismannian" periodization of development to produce an evolutionary narrative that includes a previously unacknowledged level of selection. In Buss's alternative periodization, the units upon which natural selection can operate change between developmental periods and an important effect of the model is to provide the framework for a unified mechanical account of the operation of selection within developmental periods — before vs. after germ-line segregation — that is more fine-grained than the standard selectionist framework.

The tacit periodization of development in the typically idealized, population geneticist's evolutionary theory is that first there is the zygote, then development happens (by cell growth, division and differentiation), and then natural selection operates among variant (adult) phenotypes, to yield a differential propagation of genes into the next generation. (To find examples of this periodization, look at the life cycle diagrams in textbooks of population genetics and evolution.) Selection under this model is inevitably at the organism level because there is no distinction in the tacit model of development that would suggest the existence of entities capable of serving as units of selection (below the level of organisms, but above that of individual cells or genes). However, it is well known that selection can affect any stage of development and that pattern can be laid down even before fertilization. Buss's recognition of developmental diversity in the timing of germ-line separation, of the conservatism of early ontogeny and the diversity of late ontogeny, leads to variability in developmental chronology and to an alternative periodization of the evolutionary process. The timing of germ-line separation relative to other processes of differentiation marks the transition from one developmental stage to another in Buss's periodization of development that supports the new evolutionary narrative.

Between the evolutionary emergence of cells from the primordial soup and the emergence of metazoa from colonies of cells, there must have been a stage in which cell lines competed for germ-line status. If development is divided into early ontogeny (prior to germ-line somatic-line separation) and late ontogeny (after separation), then there is the possibility of a new unit of selection: the cell-lineage within a population of such lineages (colonial proto-organism).The variability in present developmental mechanisms reflects the historically diverse outcomes of the process of natural selection operating within that stage of development. More importantly for understanding narrative, the significance of historical events in which particular cell lines succeeded in capturing germ-line status is established in terms of the current state of multi-cellular organisms at a new, emergent level of evolutionary organization. Level of organization is thus intimately tied to the structure of development, which is revealed by formulating an alternative periodization. The alternative periodization suggests a new mechanical analysis of the behavior of cell lines toward one another and a new interpretation of the multi-level process of selection. Thus our understanding of the evolution of animal individuals must be given an altered historical narrative, one that takes into account the new periodization and includes reference to the new stage in its interpretation of the sequence of evolutionary events.

Turning now to our second illustrative example, one way to link the articulation of development and evolution to systematics, through explicit analysis of periodization, is shown in a commentary by Slack, Holland and Graham (1993). They argue that recent work on the genetics of positional information coded by the *Hox* gene cluster in developing animal embryos reveals a shared derived character common to all animals. They propose that,

> . . . an animal is an organism that displays a particular spatial pattern of gene expression, and we define this pattern as the zootype. The zootype is expressed most clearly at a particular stage of embryonic development: the phylotypic stage (1993:490).

It is a remarkable fact about the *Hox* genes that there is a 1:1:1 relation between their spatial ordering in the genome (from 3′ to 5′ ends of the cluster in the chromosome), the relative timing of their expression, and the anterior limit of their expression domains along the anterior-posterior axis of the embryo. Using these genes, molecular systematists are able to discover and analyze novel homologies among taxa so distantly related that traditional morphological assessment is difficult if not impossible (Holland, 1996:63–70; see also Holland, 1992; Tabin and Laufer, 1993).

I do not wish to evaluate here the evidence for the Slack, Holland and Graham zootype thesis, or review the difficulties with their morphological criteria for the phylotypic stage (a project the authors trace to Etienne Geoffroy St. Hilaire), or evaluate their claimed synapomorphy. Holland (1996:63–70) suggests that the scope of successful taxonomic analyses of homology probably lies somewhere between Geoffroy's wide scope and Cuvier's much narrower scope, but perhaps the truth lies much closer to Geoffroy than systematists once thought. There are two points relevant in the present context. First, Slack et al. are refining the developmental periodization relevant to evolutionary narratives beyond Buss's periodization discussed above. In addition to Buss's pre- vs. post-germ-line separation periods, which we saw are relevant to the construction of narratives describing the evolution of animal individuality, Slack et al. add the phylotypic stage, in which peak expression of the zootypic *Hox* genes occurs, as relevant to the phylogenetic differentiation of animals. This stage will typically occur at a different point in time from the separation of germ and soma, so adding it to Buss's periodization is a refinement. Moreover, in general, the discovery of further genetic events of the same sort that Slack et al. identify pushes developmental periodization to a molecular level which is likely to yield further refinements. In particular, the phylotypic stage is a period defined in terms of the mechanical analysis of the expression of a single class of genes. The Slack et al. periodization is in fact *built* on the foundation of a unitary mechanical analysis of gene expression. One can imagine other stages of development defined by expression of other classes of genes, as indeed recent works on the molecular biology of development acknowledge (Lawrence, 1992).

Second, Slack et al. tie their zootype thesis explicitly to the issue of phylogeny reconstruction by arguing that the zootype is a shared derived character (synapomorphy) for the kingdom Animalia. From the point of view of cladistic systematics, synapomorphies provide the best evidence of phylogenetic relationship. From the point of view of comparative developmental biology, synapomorphies provide the best opportunity for a common mechanical analysis and thus for an integrating narrative. Discovery of synapomorphies in development is facilitated by judicious choice of periodization. It is probably not accidental that the evolutionists most concerned with the relationship between evolution and development at the present time are systematists who make use of cladistic methods. Whether the zootype hypothesis is true or not, the Slack et al. claim illustrates how developmental periodization, the postulation of a new state space in which to frame theoretical models that play a role in historical narratives, is implicated in phylogenetic hypotheses. It is plausible to infer that phylogenetic arguments make some tacit assumption about developmental periodization, just as Sober (1988) argued that all cladistic analyses must assume a model of character evolution.

Several features of the Slack et al. analysis bear on the role of periodization in setting the terms for mechanical explanations within stages and evolutionary narratives among stages. I do not want to claim on their behalf, however, that their intent is to revise the developmental periodization *in order* to discover novel evolutionary mechanisms, although I think it is likely that periodizations may often produce that heuristic effect. Rather, my aim is to illustrate that choice of periodization is tied to the choice of a particular developmental mechanics (*Hox* gene expression) that is used as a tool for phylogeny reconstruction. Slack et al. point out that there are a number of morphological definitions of Sander's concept of the "phylotypic" stage:

> . . . the stage of development at which all major body parts are represented in their final positions as undifferentiated cell condensations, or the stage after the completion of the principal morphogenetic tissue movements, or the stage at which all members of the phylum show the maximum degree of similarity. (Slack et al., 1993:491)

Each of these definitions identifies a form of mechanical description (cell condensation states, morphogenetic tissue movements, degree of similarity) that can be uniformly applied within a stage. By this I mean that each mode of mechanical description requires a small set of procedures and methods that can be applied to embryological materials throughout the stage, e.g., a single set of histological-microscopical techniques for visualizing condensation states. This much is required for any effective mechanical science. But part of the purpose in identifying the phylotypic stage is to facilitate narrative as well as mechanical explanation. The mechanical descriptions are applied to identify the phylotypic stage in different phyla and then used to make comparisons among the phylotypic stages of various phyla to construct a narrative history of the Animalia. The mechanical descriptions lead to identifying the following classically described developmental stages as phylotypic stages:

> . . . the tailbud stage for the vertebrates; the fully segmented germband stage for insects; the fully segmented, ventrally closed stage for leeches; or the nematode after the completion of most embryonic cell divisions. (ibid.)

It is not essential that the same mode of mechanical description be applied to material from different phyla, but only that there is some such mode of description for each. However, the observation critical for the construction of the evolutionary narrative (presented in the form of a hypothetical cladogram) is the *correspondence* between the embryonic stage at which the zootype is most clearly displayed and the phylotypic stage. Slack et al. write:

> The genes of the zootype are not, in general, activated in the earliest stages of development, and although expression may persist for some considerable time, the peak expression, and the simplest pattern of expression, is displayed at the phylotypic stage. This association gives us confidence that the independent proposals of evolutionary conservatism of the zootype and of the phylotypic stages are indeed well founded. (ibid.)

Since the zootype is a pattern of gene expression, the correspondence between zootype and phylotypic stage offers the possibility of a single mode of mechanical description for within-phylotypic stage analysis that can then be used to construct an evolutionary narrative based on analysis of differences in the *Hox* gene clusters of different phyla. The stages of this evolutionary narrative are the durations of taxa exhibiting a particular genetic structure. The mechanical events that are linked in the narrative are changes in genetic structure: from the origin of helix-turn-helix genes predating the prokaryotes, to the origin of homeobox genes predating the fungi and green plants, to the origin of *Hox* cluster genes and the zootype predating the branching of Cnidaria, Platyhelminthes, and higher metazoa (Slack et al., 1993:492, fig. 4).

5. Conclusion

I have argued that joint consideration of evolutionary narratives and developmental mechanics illuminates the nature of historical science. The crux lies in the coordinating role of periodizations in formulating both theoretical models and narratives to describe the integration of historical individuals persisting across periods with mechanical accounts of processes of change occurring within periods. If, as Laudan (1992) has argued, the question at issue in understanding historical science is how knowledge claims in historical sciences are warranted, then I agree that there is no particular significance to the distinction between historical and ahistorical sciences. But the aim of the distinction that motivates my interest is quite different.

My concern has been to introduce the idea that the historical sciences are deeply theoretical, if one interprets periodization as setting the framework of state space type in which theoretical models and narratives can be expressed. The models serve, among other functions, to identify events that can be explained mechanically and also the central subjects of narratives. The models mediate between data and theory and the periodization coordinates the mediating relations. Rather than seek protection from the critics of historical science by emphasizing the distinctiveness of historical phenomena or data, I propose to base a defense of the historical sciences on the distinctive characteristics of their theoretical models. What is distinctive about historical science is that its periodization models *coordinate* narrative and mechanistic accounts and that historical scientists accept the narrative component as a contribution to understanding.

Whether any defense of the historical sciences is effective can only be decided by trying it out. Since what makes a science historical is a pragmatic commitment to narrative understanding, it will always be open to rejection by some scientists and acceptance by others. Historicity entails a commitment to a mode of understanding, not a mode of inference or a theory of reality. It will therefore prove a more attractive strategem, in my view, to defeat the argument that historical science is "bad science" by advertising the virtues of coordination of narration and mechanism by periodization and models than to seek ontological or epistemological priority or distinctiveness for the historical sciences.

Notes

1. My starting points on the notion of narrative are: Danto, 1968–1985 and White, 1987. See White, 1987 for a review of historiographic positions opposed to narrative.

2. On the former see, for example, Hull, 1975, Gould et al., 1987, O'Hara, 1988, Gould, 1989, Ereschefsky, 1992. On the latter see Hempel, 1942, Hull, 1992, Richards, 1992.

3. See Griesemer, 1990 for a similar demonstration of theoretical activity in apparently untheoretical natural history.

4. This term was introduced by Lloyd (1988) in analogy with van Fraassen's concept of model type, and adopted by van Fraassen (1989) to indicate that many clusters of models which specify a theory can have the same state space, e.g., population genetics models expressed in a gene frequency state space. Periodization is an important step in the delimitation of a state space type.

5. See White, 1987, ch. 2 on the distinction between annal, chronicle, and narrative.

6. Rudwick, 1985, Secord, 1986, and Oldroyd, 1900 discuss these episodes, each focusing on a different one.

7. For an example of such a description, see Balinsky, 1975, p. 171.

8. Minelli, 1996:55–61.

9. Ibid.

10. These concern what things can exist at a point in state space, e.g., what combinations of gene frequencies are possible.

11. These concern which sequences of states are possible in a given state space, e.g., if motion is continuous and position is defined along a real-valued axis, then to get from A to B, an object must pass through all the intermediate points between them. In population genetics, gene frequencies range from 0 to 1 continuously, but they can jump from generation to generation, because populations are finite (so a mutation causes a discrete change in the gene frequency).

12. Minelli, 1996:55–61.

13. Historians and philosophers of science may reflect on Kuhn's revolution model of science as a case study of this process. Many of Kuhn's critics rejected his overall account because of objections to his psychological account of the revolutionary transition, while accepting (more or less) his description of "normal science." The Gestalt model was a sort of place-holder for a serious attempt to account for dramatic and creative change in science. Kuhn's achievement was to string together normal science, crisis, and revolution into a coherent narrative structure for many scientific episodes. Many who "reject" the model misunderstand the heuristic value of making such a periodization of scientific change.

14. This pair of relations linking phenomena or data, model, and "high" theory is explored to great depth by Nancy Cartwright (1983). The analogy here rests largely on the fact that periodization sets the state space framework for models. Empirical substructures are the observable elements of theoretical models.

15. I wish to thank John Damuth (pers. comm., 5 Aug. 1994) for helpful discussion on this point.

16. "Ahistorical" is in quote marks because on some (relatively trivial) interpretations of historicality, every mechanistic science is historical. See Griesemer, 1996 for discussion and references.

Acknowledgments

I thank John Damuth, Elihu Gerson, Michael Ghiselin, Nick Holland, Bob O'Hara, Alessandro Minelli, Dave Wake, and especially an anonymous reviewer for helpful discussion and comments on the manuscript and Michael Ghiselin, Giovanni Pinna, and Marvalee Wake for organizing the workshop. The manuscript was written in 1992–93 during a fellowship at the Wissenschaftskolleg zu Berlin and revised, in part, while I was a fellow of Collegium Budapest in 1994–95. I wish to thank the Rektors and fellows of both institutes for providing such splendid working conditions.

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THE OLDEST FOSSIL ANIMALS IN ECOLOGICAL PERSPECTIVE

Mikhail A. Fedonkin

Paleontological Institute
Russia Academy of Sciences
Profsoyuznaya ulitza 123
Moscow 117647 Russia

Introduction

The ecological aspect of the history of life attracts growing attention as a missing piece in a puzzle of pattern and process in evolution (Eldredge, 1989). The whole fossil record demonstrates a fundamentally interactive relationship between the biota and the abiotic environment, and the primary role of organisms in changing the earth from the strange and unfamiliar planet that it was in the Precambrian to what we see today. We are beginning to understand the feedback mechanisms of the global environmental control exerted by the biota.

Paleoecology, defined as the paleontology of the biosphere as a whole, allows us to study global processes that cannot be revealed by such ecological approaches as monitoring that focus upon the present. Long term cycles, resistant trends, and events of global importance in the biosphere are the privilege of paleoecology.

However, traveling backward in time we encounter biotas less and less similar to the Recent one. This is why the role of actualistic interpretation of fossils in paleolecological reconstructions should be decreasingly emphasized as we go backward in time, and increasingly complemented by information from sources other than the fossil record. The multidisciplinary approach that is the core of the Recent paleoecological methodology is especially legitimate with respect to the oldest parts of the history of the biosphere (Schopf and Klein, 1992).

The history of the organic world can be represented by the U-pattern and the N-pattern for the procaryotic and eucaryotic worlds, respectively (Fig. 1).

The U-pattern of the procaryotic world is characterized by rapid (geologically instantaneous) radiation of the procaryotes and their long history of persistence without essential changes throughout most of geological time. This is particularly true of the Cyanobacteria, which seem to have stayed the same both morphologically and ecologically for more than 3.5 billion years.

The N-pattern evolution of the eucaryotes reflects two processes, namely the decline in diversity of the relict groups (the left half of the letter N) and the growing diversity of the new groups (the right half of the N). This pattern means that the general biotic diversity at any time level includes both relict groups and newborn taxa. This seems to be the case even for the earliest faunas, including the oldest known metazoans of the Vendian period (Fedonkin, 1992). Therefore it helps to distinguish those Vendian taxa which gave rise to the Paleozoic groups on the one hand, from those that represent remnants of Pre-Vendian periods of metazoan evolution on the other. The N-pattern approach can be applied to the whole hierarchy of the eucaryotes at every level from the species upward. For instance, Cnidaria and Ctenophora, the two phyla representing the diploblastic grade of organization can be considered relics of the first Eumetazoa (Fedonkin, 1985; Rieger, 1994).

The closer to the present the smaller is the proportion of the relict groups in the animal world. Conversely, when we move back in time we encounter more and more fossil metazoans with unusual body plans. Does this mean that we are encountering forms with unusual physiologies which have no equivalent relationship among Recent animals? In fact, there should be some positive correlation between novelties in body plan and innovations in physiology, so far as these are reflected in the differentiation of the Recent metazoans. Thus we may confidently predict that we will encounter different physiologies among the oldest metazoans. This in turn implies a different relationship of the earlier metazoans to the paleoenvironment. This circumstance necessitates that we reconstruct the abiotic and biotic factors of the global and local paleoenvironments of the Precambrian if we are to understand the nature and early history of the oldest metazoans.

The origin of animals: change in priority of the questiôns "when," "where," and "who?"

The origin of the metazoans is an old but unsolved problem, in spite of substantial progress in modern paleontological and neontological sciences alike. For generations of biologists the major question related to the problem has been: "who" was at the very base of the metazoan tree — what was the grade of organization of the first multicellular animal? In the nineteenth century the priority of this "who" question over alternatives (when and where) was connected with the leading role of comparative anatomy and embryology in the study of the problem of the origin of the Metazoa. Traditionally these sciences were oriented toward the morphology and morphogenesis of Recent animals, rather than toward the biohistorical or ecological aspect of the problem. An additional factor that favored the priority of the "who" question was the dominating paradigm of the monophyletic origin of the Metazoa: the notion of a common ancestor.

Since the end of the nineteenth century numerous phylo-

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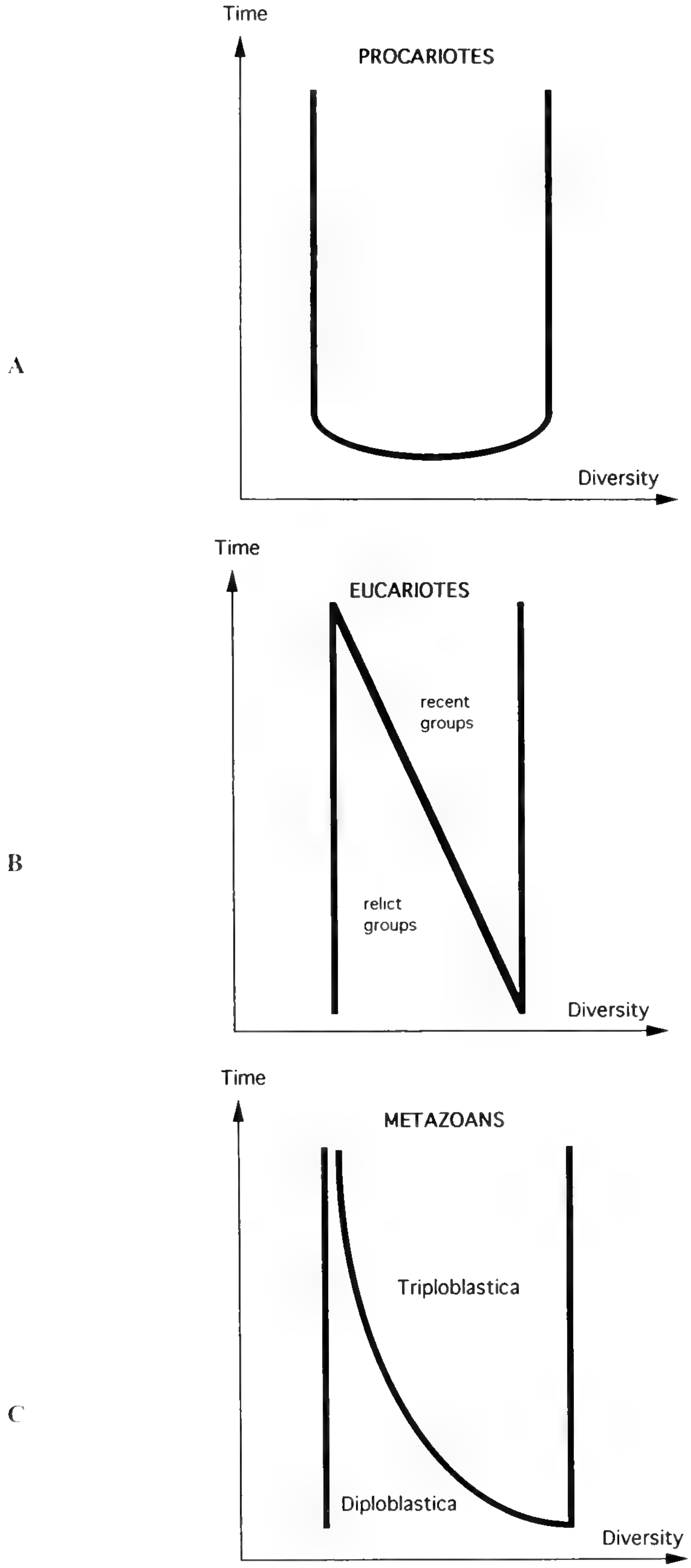

FIGURE 1. U- and N- patterns of the diversity through the history of the organic world. A. U-pattern of the procaryote history. B. N-pattern of eucaryote history. C. N-pattern of the metazoan history.

genetic trees for the animals have been constructed, differing both in their trunks and their crowns. The new science of histology made some contributions to the growing diversity of this orchard, but did not give decisive arguments which would allow us to separate the "good" trees from the "bad" ones. The rise of molecular biology has provided a new instrument for the quantitative measurement of the degree of phylogenetic proximity. The molecular clock approach seemed to promise a way to establish the time of major branchings in the phylogenetic tree. Unfortunately, along with the general methodological difficulties related to problems of homology and analogy that are common for most comparative methods, two fundamental assumptions concerning molecular clocks remain uncertain: the constant rate of the clocks, and their dependence upon generation time. In addition, we have no idea yet of how the whole phylogenetic picture could be influenced by various symbiogeneses which seem to have been widespread in the Precambrian.

This situation suggests that the problem of metazoan origins and the monophyletic paradigm and approaches mentioned above should be set aside. Instead we should be addressing the problems of the time of origin of the newly-appeared metazoans, the primary characteristics of their biotope, their place in the pre-existing ecosystem and their physiologies and modes of life. All these questions, including that of the time of metazoan origin, are connected to the ecological aspect of the problem. The Late Proterozoic was a period of dramatic environmental change, with strong differences between the beginning and the end of the eon. So we have to construct essentially different models for metazoan origins for the moments of 1,000 million years and 700 million years ago, as far as we understand the Precambrian environments. In order to understand how and why it took place we have to know where it took place — in both space and time.

PALEONTOLOGICAL DATA

The first traces of life are as much as 3.5–3.8 billion years old and multicellular fossils first appear in deposits about 2.0 billion years old. However, undoubted trace and body fossils of metazoans appear at the very end of the Precambrian fossil record during the Vendian Period about 620–550 million years ago. The famous Ediacara fauna and its worldwide equivalents in other Vendian deposits manifest an episode in the global expansion of the oldest known invertebrates. These faunas seem to reflect the stage of evolutionary stasis which followed the earlier radiation (or series of radiations and extinctions) of older multicellular animals. To avoid misunderstanding of terms I use the word "Ediacara" to specify the type of fauna and the term "Vendian" for the Terminal Proterozoic Period (Sokolov and Fedonkin, 1984).

The Pre-Vendian history of the metazoans still remains obscure. The search for the oldest animal fossils has mainly revealed a large number of Proterozoic pseudofossils and dubiofossils (see critical analyses of the problem in Cloud, 1968; Hantzschel, 1975; Glaessner, 1979a; Fedonkin and Runnegar, 1992). Nevertheless the morphological characters of some problematic body fossils imply that animal (and even metazoan) life existed long before the beginning of the Vendian Period (Sun, 1986; Sun, Wang, and Zhou, 1986; Fedonkin, Yochelson, and Horodsky, 1994).

The late Proterozoic decline of the stromatolites, which was especially dramatic after 0.85 billion years ago, might be considered indirect evidence of increasing metazoan activity (Awramik, 1971; Monty, 1974; Walter and Heys, 1985). This conclusion is open to question because perhaps some alternative or additional biotic and abiotic environmental factors could have led to the decline of the stromatolite communities as globally dominant in shallow water ecosystems (Semikhatov and Raaben, 1994; Fedonkin, 1994, 1996).

Extrapolation from the evolutionary rates of the major Phanerozoic phyla down to the Precambrian led Durham (1970) to conclude that the common ancestor of the deuterostomes lived between 0.8 and 1.7 billion years ago, which would move the time of metazoan origin to an even earlier time period. However, recent molecular data indicate that plants, diploblastic metazoans, and triploblastic metazoans were produced by three closely-related groups that radiated almost contemporaneously (Christen, 1994). Discoveries of Vendian and Cambrian problematic fossil taxa, which cannot be placed in the existing system of metazoans, suggest that we need a more complex scenario of early metazoan evolution than the one that was invoked twenty to thirty years ago.

NEONTOLOGICAL DATA

Data from the comparative anatomy, embryology and histology of Recent metazoans allow us to work out phylogenies with reasonably good resolution within separate major clades. However, the variety of incompatible models indicates the inadequacy of classical neontological methods for solving the problems of the origin of the major phyla and the early history of the metazoans. Excessive parallelism in somatic evolution and too few homologous characters that can be recognized in different phyla make us look for complementary approaches.

Recently Valentine (1991, 1994) attempted to avoid these methodological difficulties. His approach was based upon the idea of Bonner (1965, 1988) that the best single metric of an organism's complexity is the number of cell types that it possesses. Valentine extrapolated from a modern grade of 210 cell types (observed in recent mammals) through the average of 30 and 50 cell types that should have existed in the producers of the oldest horizontal trails, and the primitive higher invertebrates respectively. He obtained an estimate for the origin of metazoans of 680 million years ago.

MOLECULAR DATA

The last decade has been marked by intensive study of molecular phylogenies based upon moleculecular sequences, especially 18S ribosomal RNA (Field et al., 1988) and 28S rRNA (Christen et al., 1991). These data have been interpreted using distance methods (Field et al., 1988; Raff et al., 1989), cladistic approaches (Ghiselin, 1988, 1989), and parsimony techniques (Patterson, 1989; Smith, 1989; Lake, 1990; Bergström, 1994).

Molecular analysis has all the weaknesses in common with comparative methods in general; that is why the orchard of phylogenetic molecular trees is growing even faster than did that which arose from the classical approaches. Nonetheless there is some consensus that the metazoans emerged during a period of intensive diversification, and from the same branch of the eucaryote stock from which arose vascular plants and fungi. Evidently the appearance of the tissue grade of organization was followed by a rapid diversification of the phyla (Christen, 1994).

Applying molecular clock approaches to cytochrome *c* and globin molecules, various authors have estimated that radiation of the living animal phyla took place at least 900–1,000 million years ago, and that the first metazoans could have appeared even earlier (Dickerson, 1971; McLaughlin and Dayhoff, 1973; Runnegar, 1982a, 1986). Although these estimates have been criticized (Erwin, 1989), the possibility of a relatively long Precambrian history of the metazoans still cannot be ruled out (Runnegar, 1992). According to Chapman (1992), the molecular data suggest an evolution of eucaryotes much further back in time than was previously suspected. Therefore we may speculate about the origin of the eucaryotes around 2.5 billion years ago, and about the massive radiation of the fungi, photosynthetic protists and animals between 1.5 and 1.0 billion years ago. Thus metazoans could have appeared no earlier than during that time interval. Let us now consider the global environmental conditions during the Middle and Late Proterozoic, a period of time known as the Riphean (1.6–0.65 billion years ago).

Sources of paleoecological information

Paleoecological information can be acquired from rather heterogeneous sources. The uncertain nature of many Precambrian fossils compels us to follow non-biological approaches to paleoecological reconstruction, including evidence from sedimentology, paleogeography and paleoclmatology.

One very important fact is that most of the fossil localities of the Vendian fauna occur in silicoclastic facies that accumulated in rather cold climatic zones. The only fossil locality of Vendian metazoans in carbonate rocks is thin-laminated bituminous limestone of the Khorbusuonka Series, Oleniok Uplift, North of the Siberian Platform (Fedonkin 1985, 1990; Vodanjuk, 1989), and this locality is less fossiliferous than those in the silicoclastics. The relatively low diversity of body fossils and extreme rarity of trace fossils in this series may indicate that for most of the known Vendian metazoans, unlike those of the Cambrian, the native biotopes were not basins with carbonate sedimentation. This unique locality requires further detailed study with respect to paleogeography and paleoecology, for the basin was dominated by stromatolite communities during most of the post-glacial (Post-Varangerian) portion of the Vendian. The close proximity of stromatolites, both stratigraphically and paleogeographically, may indicate conditions unfavorable for metazoans (see below).

Recent paleogeographic reconstructions (see, for instance, Torsvik et al., 1992; Torsvik, 1994) demonstrate that during the late Cambrian and Ordovician a paleo-ocean existed between Baltica and Siberia. Both plates were situated in the southern hemisphere and moved northward 5–8 cm per year. The White Sea region, which has yielded the most diverse Vendian fauna, was about 55°S and the rest of the Russian Platform was at even higher latitudes to the south. What is now northern Siberia (Oleniok Uplift) was oriented toward the south 490–500 million years ago, and was situated about 30°S. Most of Avalonia, where Precambrian metazoan fossils are abundant, was more than 60°S. These data mean that both the Russian Platform and Avalonia, and even the Oleniok Uplift of northern Siberia, were situated far to the south, in the colder waters of the Vendian paleo-ocean.

There is strong evidence that the majority of the Vendian silicoclastic basins that were inhabited by an abundant and diverse fauna were paleogeographically situated in relatively high latitudes with a moderately cool climate. The conclusion that the cold water basins were favorable is supported: 1) by the presence of purely silicoclastic sedimentation and absence of carbonates in the various fossiliferous facies; 2) by the stratigraphic proximity of tillite-bearing deposits below the beds containing the soft-bodied fauna (Varanger glacial deposits and their correlatives all over the world) and also, presumably above beds with Vendian metazoans (glaciation at the Vendian-Cambrian boundary); and 3) by paleogeographic reconstructions based on paleomagnetic data.

More detailed study of the sedimentological control over the distribution of the Vendian body fossils and trace fossils indicates that their inhabitants were most abundant in shallow water environments. Sedimentological analysis of the type locality of the Ediacara fauna (Golding and Curnow, 1967; Gehling, 1983, 1988) led to the conclusion that the fossiliferous facies represent offshore, storm-wave base environments and that the organisms were predominantly benthic. This may be true for the Eidacara assemblage, but it is not true for Vendian metazoans as a whole. In sequences elsewhere in the world, fossiliferous facies containing the Vendian-type fauna are far more diverse.

The apparent dominance of benthic forms in the Ediacara assemblage and in its world-wide counterparts may be just the result of how the fossils happened to be formed, in other words, a taphonomic artifact. While they were in their living position, benthic animals deformed the sediment. Next they got buried alive and undistorted by sediment that was transported by storms or other events. And then biological degradation proceeded inside the sediment, so that the products of decay would have been concentrated in the sediment around the corpse. This led to a faster diagenesis of the sediment in this particular space, and thus to the fossilization of the structures imprinted by the animal that lay buried in the sediment.

EVIDENCE FROM THE FOSSILS IN THE VENDIAN TAPHONOMIC WINDOW

The uncertain nature of many Ediacara forms, and the taphonomic peculiarity that affects the taxonomic work of paleontologists makes us use a taxon-free characterization of the Vendian metazoan communities. The usefulness of this approach is demonstrated by the study of both marine and terrestrial ecosystems (Damuth et al., 1992).

Considering the fossil record in its entirety, the mass preservation of soft-bodied metazoans in the Vendian deposits that accumulated in the normal, well-aerated marine basins was a relatively brief episode in geological history. The Phanerozoic record does demonstrate a few exceptional cases of preservation of soft-bodied invertebrates — for instance, the world famous localities of the Middle Cambrian Burgess Shale, Pennsylvanian Mazon Creek, Jurassic Solenhoffen, and some others — but these localities are most unusual, given the general background of the fossiliferous formations dominated by skeletal remains. Classical paleozoology is primarily the paleontology of skeletons. Therefore what is an exception in the Phanerozoic part of the fossil record is the norm for its Precambrian portion, although the taphonomic window to early animal life seems to have opened for a relatively short period of time (approximately from 620 to 570 million years). The preservation of abundant soft-bodied metazoans which is observed in the variety of silicoclastics appears to have ceased well before the end of the Vendian. The biotic and abiotic factors which could promote the preservation of the soft-bodied animals have been discussed in detail elsewhere (Fedonkin, 1985, 1992; Gehling, 1986, 1991). But in a sense the Vendian taphonomic window was opened as a result of increasing body size and growing abundance of metazoans. Vast epiplatform basins appeared as the result of a glacio-eustatic transgression of the sea onto the continents at the beginning of the Vendian period. Therefore, both the body size and the total biomass of Precambrian metazoans could increase very fast during the initial stage of the pioneering colonization of free ecospace that was made available. An old idea (since Darwin's time) that the Precambrian animals were of small size and thus could not be preserved, can now be applied to the apparent absence of Pre-Vendian fossil metazoans — the small size possibly resulting from lower concentration of oxygen in the sea water (Runnegar, 1982b).

The experience of classical paleontology with Phanerozoic materials, largely consisting of skeletal remains, makes it evident that the fossilization of soft-bodied animals is a rare and exceptional taphonomic event. Given the great variety of extant non-skeletal metazoan groups which do not have a fossil record, we would only expect that there would have been an enormous loss of paleobiological information. Trying to determine former biotic diversity on the basis of skeleton-bearing taxa is like trying to estimate the population of ancient Egypt on the basis of the number of pharaohs' sarcophagi.

Mass preservation of soft-bodied metazoans in well-aerated shallow-water sediments distinguishes the Vendian fossil record from that of the Phanerozoic. Skeletal remains are rare in the Vendian. All of these features make it a taphonomically unusual period. The nature of this taphonomic inversion has been discussed by Wade (1968), Glaessner (1984), Seilacher (1984), Fedonkin (1985, 1992), and Gehling (1986, 1991). Major factors responsible for the preservation of soft-bodied organisms in the Vendian are: 1) absence or low activity of predators and scavengers (Glaessner, 1984); 2) low levels of biological processing of the sediment by deposit feeders and other mobile benthos (Fedonkin, 1981); 3) cyanobacterial films which stabilized the sediment after the burial of the animal (Gehling, 1986) and hindered the aeration of the bottom, thereby increasing the rate of hardening of the sediment around the decaying body (Fedonkin, 1987, 1994); and 4) absence of active filterers which could have affected the properties of the water and sedimentological and taphonomic processes similar to those that occurred in the Phanerozoic (Fedonkin, 1985, 1992).

Considering the cold water environment of the Ediacara fauna we could add a low rate of biological degradation to this list of biotic factors that promoted the mass preservation of soft-bodied organisms. Low temperatures are far more effective inhibitors of decay than anoxia (Kidwell and Baumiller, 1990). According to Stanley and Herwig (1994), functional optima of many enzymes participating in bacterial degradation of complex organic compounds are much higher than the temperatures dominating in Antarctic waters.

Change in these biotic factors at the end of the Vendian closed the taphonomic window of Ediacara-type preservation. But what factor or factors opened this window in the first place? The critical points should be body size and tissue resistance of the earlier metazoans, which had to be large and tough enough to leave imprints or to produce preservable and observable bioturbations of the sediment. On the other hand, the great preponderance of sedentary forms relative to pelagic ones in the Vendian faunal assemblages may indicate a connection between the appearance of the metazoans in the fossil record and the colonization of the benthic realm by animals.

Misunderstanding of the taphonomy of the Vendian metazoans has resulted in misinterpretation of the body fossils and in erroneous (indeed extravagant) reconstructions of the anatomy, physiology, and mode of life of these organisms. Thus, all discoidal fossils were at first interpreted as medusae, though most of these extremely numerous fossils were in fact sedentary cup-like polyps or the attachments of colonial, frond-like organisms such as *Charnia*, which could reach 1.3 m in length. Radial cracks in the mesogloea of the medusoids were interpreted as channels of the gastro-vascular system. The flat shape of the body fossils resulted from loss of water from the soft-bodied invertebrates (some of them, for instance medusoids, might have contained about 97% water, like recent coelenterates). Results of decomposition of the soft tissues have been interpreted as primary features of the organisms, leading to speculations about high surface/volume ratio, osmotic modes of feeding, and low oxygen content of the Vendian atmosphere.

BATHYMETRIC ZONATION OF VENDIAN BODY AND TRACE FOSSILS

More than twenty Vendian sequences containing the Ediacara-type faunas are known from all over the globe. Every sequence contains fossiliferous members in a special kind of facies which occupies a small part of the section. As a rule, the taxonomic composition of the fossils does not change much throughout the sequence. A few distinct fossil assemblages can be recognized which have peculiar elements that are rare or unknown in other Vendian metazoan localities, though the distinct character of these fossil biotas could be explained by taphonomic, paleoecological, and/or paeleobiogeographic differences between the compared assemblages. This may be the reason why the oldest metazoans are believed not to manifest any pronounced evolutionary change throughout the Vendian Period.

The only exception discovered so far is the Vendian sequence of the White Sea Region, north of the Russian Platform, where a few distinct faunal assemblages can be observed (Fedonkin, 1981, 1987). Paleogeographically the White Sea region was open to the ocean during most of the Vendian Period (Keller and Rozanov, 1980; Sokolov and Fedonkin, 1990), so that the normal marine shallow-water environments favorable both for animal life and for the preservation of soft-bodied metazoans existed during a period of time long enough to embrace the major events in the history of the biota.

Numerous boreholes drilled in the White Sea region, volcanoclastic members as markers, and abundant acritarchs have made it possible to correlate the separate outcrops (the major source of the metazoan fossils) with the whole section of the Vendian. The correlation has led to the succession of the assemblages, which have some species in common, but also contain some forms known from Vendian localities elsewhere in the world. It turned out that elements of the Nama (Namibia) fossil assemblages appear earlier in the section (e.g., *Pteridinium*), and that elements of the Avalon (Newfoundland) biota appear later (e.g., *Charnia*). Finally, neither of these occur together — nor do they appear at the higher stratigraphic levels where the typical elements of the Ediacara fauna (South Australia) still exist (e.g., *Dickinsonia* and *Tribrachidium*, which seem to have the longest stratigraphic ranges in the White Sea region). This succession was revealed early in the course of discovery of the major fossil localities on the White Sea coast (Fedonkin, 1977, 1981). However, it was clear that some forms existed through a period of time embracing the range of the three faunal assemblages and, what may be more important, the three assemblages are preserved in very different sedimentary facies.

This circumstance led us to consider whether the distribution of the Vendian fauna was under taphonomic or paleoecological control or some combination of both. These are virtually undeveloped aspects of Precambrian paleozoology. If we take into account the body fossils of the benthic organisms and the trace fossils which are preserved in situ, then we are able to see the following bathymetric zonations of the Vendian fossils from the shallow water environments down to the deeper ones:

a) body fossils: *Nemiana - Ediacaria - Charnia*
b) trace fossils: *Skolithos - Palaeopascichnus - Nenoxites*

Though zonations of the body fossils and the trace fossils contain three index names, each name represents an assemblage. An important peculiarity of the bathymetric distribution of the Vendian metazoans was decreasing diversity and decreasing body size of the vagile benthos offshore.

Global ecosystem restructuring in the Neoproterozoic

Taking into consideration the fundamentally aerobic nature of all eucaryotes (Margulis et al., 1976) and the growing body of evidence that at least in animals aerobic metabolism arose only once and has been strongly conserved throughout the history of life (Mangum, 1991), the origin and evolution of the early metazoans could not have been unaffected by the rise of free oxygen levels in the atmosphere and hydrosphere. Oxygen, in turn, being involved in the carbon cycle of the planet may have an indirect relationship to the climatic evolution of the biosphere.

The rise of metazoans during the Late Proterozoic and the incorporation of animals into pre-existing global ecosystems may have been accomplished under extremely severe conditions. Most of the Precambrian fossil record presents evidence of a stable and conservative ecosystem, driven predominantly by procaryotic organisms. Both the procaryotic biota and the environment may have put serious barriers in the evolutionary pathways of the first multicellular animals, and even the unicellular eucaryotes as well. Recent procaryote-dominated ecosystems show no evidence of free ecological space for most eucaryotic organisms. The appearance of metazoans was impossible until the globally-dominating environments changed and the role of the procaryotes as the dominants decreased in favor of the eucaryotes. Radical restructuring of the global ecosystem from the archaic to the new one was accompanied by rise of the eucaryotic trophic pyramid above the network of biogeochemical interactions between microbial communities. In a sense, all the eucaryotic organisms are an epiphenomenon on the procaryotic background.

Over a period of almost three billion years the bacterial communities removed great volumes of various chemical elements from the hydrosphere and buried them in the sediments. On the other hand they injected great volumes of the byproducts of their life activities into the environment. These long-term processes have resulted in irreversible climatic and environmental changes. For instance, the oxygen content of the atmosphere rose due to photosynthesis, at first by cyanobacteria and later by eucaryotic algae. Another example is the withdrawal of carbon dioxide from the atmosphere by the cyanobacteria and the subsequent conservation of carbon buried in biogenic deposits (carbonaceous shales, stromatolites, etc.). As a consequence the greenhouse effect was reduced to produce a very sensitive balance about 850 million years ago. Since that time glacial periods became more or less regular events in Earth history. In such a cold episode we should seek the first appearance of metazoans.

A procaryotic barrier on the metazoan evolutionary pathway

An important biotic factor which might have allowed explosive development of animal life and global expansion of the metazoans in the Vendian basins was the decline of the stromatolite communities during the Neoproterozoic. This decline was especially rapid after 850 million years ago. Vologdin (1962) suggested that the cyanobacteria responsible for stromatolite formation in the Precambrian may, like their Recent counterparts, produced toxins. According to his hypothesis, these toxins inhibited animal evolution in its early stages.

Studies on extant cyanobacteria have revealed a wide variety of toxins (neurotoxins, hepatotoxins, cytotoxins, and others) which may be directly lethal to small metazoans and zooplankton, or may reduce their size and number if the offspring feed on the cyanobacteria (Carmichael, 1994). These toxins, as well as the marginal marine environments with high salinity and fluctuating moisture, seem to be the major factors controlling distribution of metazoan grazers utilizing the cyanobacteria. The Recent bacterial communities of sabkhas, marshes and lagoons of arid climatic zones might be considered analogues for the Precambrian stromatolite communities, which were globally dominant throughout the major portion of Precambrian life history (Awramik, 1984; Knoll, 1985). The faunas that graze in microbial mats are of very low diversity (Farmer, 1992). By comparison to flat bacterial mats, the hemispherical to columnar Proterozoic stromatolites had greater surface area available for contact and interaction between the bacterial communities and their surroundings. This circumstance could have resulted in an even higher concentration of the toxins in the Proterozoic shallow water environments.

The idea that grazing and bioturbation by the early metazoans might have caused the decline in stromatolite diversity and abundance during the Late Proterozoic (Garret, 1970a, 1970b; Awramik, 1971, 1981; Walter and Heys, 1985) seems to be inconsistent with observations on Recent bacterial mats. Dominant grazers on modern microbial mats are insects and crustaceans, but arthropods are unknown from before 550 million years ago (Farmer, 1992). Because most of these grazers are of small body size (less than a few millimeters), they do not prevent the development of the bacterial mats, but rather co-exist with the bacterial communities.

Thus we have to place the first animals into habitats different from those controlled by procaryotic organisms, in particular, by cyanobacterial communities. Primary biotopes of the metazoans should be cold enough to inhibit the stromatolite-forming cyanobacterial communities. Prior to the African Glacial Era, which began about 850 million years ago, cold aquatic environments could exist in a relatively limited area of the polar regions. Begining with the first in the series of four glacial periods during the last 300 million years of the Precambrian, cold water biotopes became more widespread.

The catastrophic decline of the stromatolite communities after having dominated the global benthos for almost two billion years may have been caused by a heterogeneous combination of factors, such as the geochemical, climatic and paleogeographic consequences of long term activity of procaryotic ecosystems and the rise of eucaryotic algae competing with cyanobacteria for nutrients, habitats and light.

The last revenge of the procaryotic communities on the eucaryotic ones may have taken place at the very end of the Vendian. This episode took place after the period of global expansion of the Ediacara fauna. In the northern part of the Siberian Platforms it is marked by thick stromatolite carbonates above the beds with a soft-bodied fauna (Sokolov and Fedonkin, 1984). It is interesting that the black cherts from the uppermost Vendian, which preserved abundant bacterial microfossils, do not contain any objects that could be interpreted as fossil metazoans. This fact may be interpreted in favor of the hypothesis of separate biotopes for the oldest metazoans and the widespread cyanobacterial communities. That could be true for the first eucaryotes as well.

The cold cradle of animal life

Contrary to those hypotheses that postulate a warm aquatic environment for the rise of the oldest organisms, I propose that the first animals, at least, arose in a cold aquatic environment. Cold waters of the Recent ocean, in particular the Antarctic basins, are characterized by some peculiarities that they may share with the Vendian basins inhabited by the Ediacara-type fauna. These characteristics are as follows:

1) silicoclastic sedimentation and no carbonates
2) pronounced vertical circulation of the water
3) high concentration of phosphates, nitrates, and other metabolites
4) better aeration of the water
5) less transparent water
6) contrast between meager life on the continent and abundant life in the water
7) high total biomass of the living organisms, especially plankton
8) higher bioproduction by primary producers
9) short trophic chains
10) low biotic diversity
11) low stability of the biocoenoses
12) dominance of herbivorous planktotrophs among planktonic metazoans
13) low proportion of predators in the plankton — which may, however, have undergone population explosions during some seasons
14) large proportion of coelenterates (medusae and ctenophores) among the predators
15) dominance of attached forms among the benthic invertebrates
16) dominance of soft-bodied forms in the benthic communities

17) larger body size than in the forms of the same species living in warmer waters
18) dominance of forms with direct development (no pelagic larval stage)
19) seasonal variability in light regime and resource limitation
20) low rates of metabolism and growth
21) long duration of individual life
22) long generation time
23) low rate of biological degradation.

(Zernov, 1934; Borogov, 1974; Margalef, 1977; Lipps and Hickman, 1982; White, 1984; Berezina, 1984; Pearse, McClintock and Bosch, 1991; Stanley and Herwig, 1993.) It is remarkable how many of these characters can be seen in the Precambrian metazoans and their environments.

I should reiterate that most of the fossil localities of the Vendian fauna occur in the silicoclastic facies accumulated in moderately cold climatic zones. Thus the Vendian fauna may well have had all the advantages of the cold water habitats plus one more important factor which used to be overlooked: an absence of the stable bacterial ecosystems forming stromatolities.

How representative is the Precambrian fossil record?

The absence of a hard, mineralized skeleton in most of the Vendian metazoans should make them more or less equal with respect to preservation potential. Under conditions favorable for the preservation of soft-bodied animals the number of species collected should reflect the real biotic diversity, and the number of fossils should correspond proportionally to the abundance of each particular species. These expectations, however, are not confirmed by what we see in the field nor in the extensive collections of the Vendian fauna.

Though many species of the Ediacara fauna are globally distributed, their proportion in each particular fossil locality sometimes differs. Some facies of the Vendian sediments are characterized by mass preservation of one or two species. Good examples are the beds with thousands of polyp-like *Nemiana*, which are widespread in the Vendian of the Ukraine, White Sea, Northern Siberia and the Northwest Territories of Canada. Selective preservation in this case has to do with the mode of life of these sedentary forms.

Although the number of specimens of Vendian animals that have been collected throughout the globe is close to 10,000, their taxonomic diversity remains very low. Over 215 fossil species from the entire Vendian fauna have been described, but less than half of these taxa have proven taxonomically valid (Fedonkin, 1987; Runnegar and Fedonkin, 1992). Even adding about 25 forms of trace fossils which have been preserved along with the imprints of the soft-bodied animals leaves the diversity of Vendian metazoans at a very low level. This fact and the diversity at higher taxonomic levels lead us to suspect that the Vendian fossil record reveals only a very small portion of the actual biotic diversity of the fauna.

An obscure radiation

The Varanger glaciation (0.65–0.62 billion years ago) was the most intensive one in the series of glacial episodes that took place in the Late Proterozoic (Chumakov, 1968), as is confirmed by the distribution of tillites of this age all over the globe. Glacial periods have been accompanied by strong environmental shifts, including radical climatic and geographic changes. For instance, marine environments have been affected by the vast shelf glaciers and floating ice, sharp fluctuations in sea level, decreasing area of shallow water habitats of the shelf down to a small strip at the edge of the platforms, growing temperature gradients, climatic and geographic isolation, increasing frequency of storm events, etc. (Fedonkin, 1987). Glacio-eustatic regressions greatly reduced the area of benthic shallow water habitats, and that may have had a negative effect upon the marine biota as a whole. The importance of the shallow water habitats for the Late Proterozoic ecosystem may be underlined by the fact that 83% of the total benthic biomass in the Recent ocean is concentrated on 8% of the substrate, i.e., on the shelf (Leont'ev, 1982). During the Varanger glaciation life was concentrated in the pelagic waters, which were nutrient-poor and ecologically homogeneous. That was a prelude to the Vendian radiation of the metazoans. The Post-Varanger glacio-eustatic transgression over the continents saw a rapid radiation of megascopic soft-bodied invertebrates known as the Ediacaran fauna.

Along with the new born taxa of high taxonomic rank which may have appeared during the early Vendian radiation of the metazoans (some of which persisted into the Phanerozoic) the Ediacaran fauna may well have also included some pre-Vendian relicts. Even though the time span and the stratigraphic range of the Vendian fauna may be pretty long, as of now it does not document any prominent sequence in the appearance of major fossil groups. This fact leaves a few possibilities open: 1) the post-Varanger radiation of metazoans was very rapid, and what we see is a stage of evolutionary stasis accompanied by global expansion of the new born taxa, or 2) the invertebrates had a long cryptic period of earlier (pre-Vendian) history, but remained of small body size and thus cannot be discovered by traditional techniques. Early metazoans may have lived in environments that have not yet been studied.

A scenario for the metazoan radiation can be constructed by the same methods that are used in comparative anatomy of Recent invertebrates for the study of the phylogenetic relationships and origins of the major groups. Taking into account all the limitations of the fossil material and the low diversity of the known Vendian metazoans, we attempt to reconstruct a very general sketch of their history prior to their sudden world-wide expansion. The reconstruction should be based upon an analysis of the diversity at the level both of the entire biota as well as within major taxonomic groups, paying special attention to the body plan, mode of growth, and those structures that can be indentified in later invertebrates.

Colonization of the shallow water epiplatform basins by the metazoans required time for adaptation to new environments, increase in number of individuals, and formation of populations. All these processes may have been accompanied by an adaptive radiation which would seem to have taken place over a geologically brief period of time just before the moment when the Ediacara fauna expanded globally. This world-wide expansion of the metazoans marks a period of their maximum abundance in the Precambrian, and, simultaneously, of evolutionary stasis.

General characteristics of the Vendian fauna

The Vendian taphonomic window allows us to envision the world of the oldest animals represented by their body fossils as follows: 1) large body size or even gigantism (compared to the small, shelly fossils of the Cambrian); 2) weak sclerotization of the integument, absolute dominance of soft-bodied forms, and extreme rarity of organisms with a mineral skeleton; 3) high diversity of life forms; 4) an ecologically diverse community, with sedentary forms, vagile benthos, nekton, plankton and pleuston; 5) relatively few infaunal metazoans, active filterers and scavengers; 6) dominance of seston-feeding sedimentators and detritivores; 7) population density at its maximum in the upper sublittoral zone; 8) short trophic chains; 9) a high proportion of cosmopolitan species; 10) no bite marks or regenerated structures in the body fossils; 11) high diversity in body plans; 12) low diversity at the species level; 13) dominance of diploblastic over the triploblastic organisms both in number of species and in number of individuals; 14) no clear sequence in the appearance of the major fossil groups in most Vendian sections.

Ichnological record of the Vendian metazoans

The possibilities for a taxonomic interpretation of the trace fossils are limited, for with rare exceptions it is difficult to identify the organisms that produced them, not just at the species level, but even to taxa of higher rank. Nonetheless our knowledge of the oldest metazoans is too limited to ignore these fossils. The well-known metaphor of "fossil behavior" applied to the trace fossils does not exhaust the great potential of paleoichnology for the study of early metazoan evolution. Being preserved in situ, most trace fossils contain some information on the environment of metazoan life activity and on the effect of the animals on the sedimentary fabrics. Careful study of the trace fossils yields valuable information about the producer of the trace: mode of locomotion, feeding habits, behavioral patterns, body morphology, taxis sensitivity, some physiological functions, etc.

A general overview of the Vendian ichnological record reveals the following:

1) normally no correlation between the body fossils and the trace fossils; 2) grazing trails, crawling trails, feeding burrows and dwelling burrows (in descending order of abundance and diversity); 3) basically "two-dimensional" behavioral stereotypes (meandering predominates); 4) maximum diversity in shallow water facies; 5) decreasing diversity and size in deeper facies; 6) shallow penetration into the sediment; 7) body size of the producers less than that of Cambrian counterparts; 8) locomotion dominated by peristaltic modes of locomotion (by pedal waves or hydrostatic skeletons); 9) widespread feeding on small food particles or cropping on benthic microorganisms; 10) coexistence of different ethological groups in the shallow water ichnocoenoses; 11) weak bathymetric zonation; 12) low biological processing of sediments; 13) at the very end of the Vendian and into the Early Cambrian, increasing body size and diversity of the behavioral patterns, deeper penetration into the sediment, and more intensive biological processing of the sediment.

History of the Vendian metazoans

Metazoan diversification seems to have been very rapid in the Vendian. A period of relatively slow evolution or even stasis in the middle part of the Vendian (Redkino time) was followed (Kotlin time) by mass extinctions of many metazoans and decrease in body size of others.

The Vendian metazoan communities may have been extremely vulnerable (Fedonkin, 1987). The stability of ecosystems used to be correlated with high biotic diversity and long trophic chains, but this seems not to be the case for the Vendian faunas. The shortest trophic chains in the Recent ocean are found in regions with high phytoplankton productivity. Those biocoenoses with short food chains produce a huge biomass but are of very low stabilty (Berezina, 1984). An additional factor that might have increased the vulnerability of the Vendian fauna could be a low replacement rate of generations in the groups of animals of large body size and consequently longer life span. According to the concept of selective extinction (Lewin, 1982), the species characterized by larger body size and slower generation replacement are affected more intensively by extinction.

The decline in taxonomic diversity of the phytoplankton and the increase in buried vendotaenian algae in the sediments of the Kotlin basins (Sokolov and Iwanowski, 1990) may indicate eutrophication of the shallow marine environments, which, by analogy with present day eutrophic basins, may have acted as a selective factor in favor of forms having small body size.

An hypothesized miniaturization in some metazoan groups close to the end of the Vendian (Fedonkin, 1987) can be indirectly confirmed by the fact that the first metazoans with skeletons to undergo an explosive radiation in the early Cambrian were indeed very small creatures (Rozanov and Zhuravlev, 1992; Bengtson and Conway Morris, 1992).

The second increase in body size of invertebrates took place at the very end of the Vendian (Rovno Stage of Russian nomenclature). This event, observed in the paleoichnological fossil record, coincides with the increasing colonization by invertebrates of the bottom sediments of shallow water environments, and was immediately followed by the rise of small shelly organisms (Fedonkin, 1990). Trace fossils of the Rovno Stage are more diverse, larger, and deeper than those which are known from the earlier Redkino and Kotlin Stages. Active colonization of the sediment by the vagile benthos, as well as new strategies of bioturbation, facilitated the aeration and decomposition of buried organic matter (Fedonkin, 1987; Droser and Bottjer, 1988).

Actually the Vendian-Cambrian transition was the time of a rapid vertical expansion of the habitats of benthic metazoans due to the colonization of the deeper sediment below the surface of the substrate and also to the appearance of skeletons and reef-like structures that supported organisms well above the bottom. Such habitat expansion increased the diversity of the microenvironments both within the sediment and on the greatly-enlarged surface of such biogenic structures as reefs and exoskeletons. Growing environmental diversity in the benthic realm may have given additional opportunities for an adaptive radiation of the new born Early Cambrian groups of invertebrates.

Our ability to reconstruct the early evolution of the metazoans on the basis of what we know from the Vendian fossil record is strongly dependent upon opinions concerning the systematic position of the fossils known as the Ediacara fauna. These opinions, however, are widely divergent due to the variety of approaches to the interpretation of these Precambrian fossils. Consequently there are incompatible models for early metazoan evolution.

Here I will only mention the non-metazoan interpretation of the Vendian body fossils (Seilacher, 1984, 1989, 1994; Norris, 1989; Bergström, 1991). Grouping all of the macroscopic fossils into one constructional model (the Vendozoa, later renamed as Vendobionta) is based on schematic, two-dimensional reconstructions and an inadequate understanding of taphonomic processes. Invention of the Vendobionta as a special kingdom or as syncytial protists does not seem necessary. Critiques of the Vendobionta concept from the position of taphonomy, comparative anatomy, and phylogenetics have been provided in several recent works (Gehling, 1991; Valentine, 1992; Fedonkin, 1992, 1994; Jensen, 1993; Conway Morris, 1993).

According to the classical approach developed mainly by Australian paleontologists, the Precambrian fauna should be placed into the following taxa: phylum Coelenterata (classes Hydrozoa, Anthozoa, Scyphozoa, and Conulata, medusae of uncertain systematic position, and problematic Petalonamae), phylum Annelida (class Polychaeta), phylum Arthropoda (superclass Trilobitomorpha or Chelicerata), phylum Pogonophora, and phylum Echiurida, with some forms treated as of uncertain systematic position even at the level of the phylum (Glaessner, 1984).

More recent classifications of the Vendian fauna (Fedonkin, 1987, 1991, 1992; Jenkins, 1992; Runnegar, 1992; Runnegar and Fedonkin, 1992) include some extinct classes and phyla in addition to extant phyla. This change in the systematics reflects growing realization that the Vendian metazoans represent a very peculiar mixture of organisms. Some of them can be considered relicts of those groups which appeared long before the Vendian, while the other (newborn) taxa may represent the ancestors of groups that evolved successfully throughout the Phanerozoic.

Body plan analysis of the major groups of the Vendian fauna (Fedonkin, 1983, 1985, 1991, 1992) has led to a few important conclusions concerning the systematics and early evolutionary history of the metazoans. Domination of coelenterate-grade organisms in the Vendian may mean that at a very early stage in evolution the whole range of diversity of the metazoans could be realized at the diploblastic level and this diversity in respect of body plans might be greater than it is at present. In this sense the two phyla Cnidaria and Ctenophora look, indeed, like relics of the first Metazoa (Rieger, 1994).

Morphological evolution of the coelenterates seems to have followed a path from forms with a concentric body plan to organisms with a radial organization of the body. Lineages of radially-arranged coelenterates evolved from forms with non-regulated growth of numerous antimeres to forms with regulated growth and stable symmetry (Fedonkin, 1985, 1992). Teratological deviations from characteristic symmetry in some extant groups may be interpreted as illustrating the wider range of morphological potential that could be realized in the geological past.

Early coelenterates seem to have evolved from polypoid life forms with a sedentary mode of life, passive suspension feeding, and predominantly asexual reproduction into medusoid life forms with a free-swimming mode of life, more sophisticated feeding behavior, sexual reproduction, and more complex morphology of the gastrovascular and reproductive systems.

Body plan analysis of the Vendian metazoans which can be interpreted as Bilateria (Triploblastica) seems to indicate that the evolutionary formation of bilateral symmetry and of metamerism are closely related, at least in some metazoan lineages. Hardly expected was some evidence in favor of cyclomeric theories of the origin of metamerism (Fedonkin, 1985).

Metazoan impact upon the global environment

An explosive radiation of invertebrates was accompanied by the appearance of new physiologies that could strongly affect the environments of the Late Protozoic and the Early Cambrian. This influence could be especially strong during the periods of growing metazoan abundance. The most important consequences for the biosphere as a whole may have resulted from the following phenomena connected with the life activities of the metazoans:

1. Bioturbation of the sediment resulted in its better aeration, which, in turn, allowed the progressive colonization of the sediment beneath its surface by a wider variety of aerobic organisms. Both aeration and increasing life activity within the sediment promoted the recycling of metabolites in marine ecosystems. On the other hand, the bioturbation disrupted the substrate stability that is necessary for the formation of such biogenic structures as the stromatolites.

2. Biomineralization has resulted in the formation of bioclastic deposits and in the creation (with other non-metazoan groups of organisms) of the reef as a mechanically stable biotope and a special ecosystem with a great diversity of habitats.

3. Filtration of the ocean water by actively filtering organisms has a great impact on the global ocean ecosystem. The

rise of active suspension feeding or filtering in metazoans at the beginning of the Cambrian has radically changed the properties of the sediment and water habitats (Fedonkin, 1987, 1992).

The study of filtering in marine planktonic crustaceans (Vinberg, 1967) has revealed that during 24 hours 1 milligram of living weight of the organism is able to filter 360 milliliters of water. Calculations made by Bogorov (1974) indicate that a volume of water equal to that of the entire world ocean gets filtered within just half a year! The most densely inhabited portion of the ocean water (0–500 meters in depth) is filtered by the organisms in 20 days. To provide one concrete example, Dankers (1993) estimates that on average the western Dutch Wadden Sea contains 294×10^6 kg of mussels (fresh weight). This population would pump 920×10^6 m^3 of water every day. The western Wadden Sea contains $4{,}500 \times 10^6$ m^3 of water at low tide. This is a volume that would be biologically cleared during about five days by the mussels alone, but there are other filtering groups as well. An important aspect of such biofiltering is that undigested fine particles packed into fecal pellets settle to the bottom far more rapidly than do separate fine particles suspended in the sea water.

The rise of active filter-feeding organisms such as sponges, brachiopods, and many mollusks, arthropods and echinoderms in the Early Cambrian should have made the ocean water clear and the photic zone deeper, thus providing opportunities for photosynthesizing organisms to occupy deeper levels both in the water column and on the bottom. The expansion of the photic zone thus could have resulted in better oxygenation of the pelagic and benthic habitats via the activity of the chlorophyll-bearing organisms.

Removal of fine particles from the sea water and packing them into pellets should have increased the permeability of the sediment, leading to a better aeration and colonization of the subsurface bottom environments and to more rapid oxidation of the buried organic carbon. These factors simultaneously reduced the preservation potential of the soft-bodied metazoans.

4. Increasing length of trophic chains during the Vendian and even more so in the Cambrian decreased the loss of major biophile elements and of energy from the ecosystems because of more efficient biological recycling. That could lead to global oligotrophication of oceanic waters. This hypothesis is consistent with the general decrease in buried organic carbon during Early Cambrian time (Knoll, 1992) as well as by the radiation of Early Cambrian phytoplankton having external processes, spines, ornamentation and very small cell size (Yankauskas, 1989). All these morphological peculiarities of the Early Cambrian phytoplankton can be interpreted as means to develop a very large surface-volume ratio that would give some advantage in an oligotrophic environment (Fedonkin, 1987, 1993). One should note that 70% of the biomass and 80% of the chlorophyll in the oligotrophic waters of the Recent ocean belong to the picoplankton.

Some of the feeding habits that were so common in the Vendian metazoans, such as the passive uptake of food particles by many sedentary suspension feeders, were rendered ineffective by the oligotrophication of the Early Cambrian ocean. This factor may have caused the elimination of some Ediacara species from the shallow marine habitats in the Early Cambrian, or even slightly earlier.

Conclusion

The ecological aspect of early metazoan evolution is of key importance for an understanding of the states of the biosphere during the Late Proterozoic. Very much remains unclear. Due to the uncertain systematic position of the oldest animals and their, evidently, unfamiliar and perhaps extinct physiologies, a taxon-free approach to the paleoecological reconstruction as well as non-biological techniques can be especially effective. Any phylogenetic models based on the classical neontological or recent molecular data must be put into, and thus checked by, the paleoecological context which is a time related aspect of geological history. The problem of the metazoan origin in the procaryote-dominated (and, in some extent, antagonistic) world makes us search for a kind of a contemporary "parallel realm" controlled by the eucaryotes. The idea of the "cold cradle of animal life" is an attempt to solve this problem. However, we have to face a rather hard question concerning the metazoan colonization of the habitats historically belonging to communities dominated by procaryotes for at least 3 billion years. An essential part of this story should be the role of the eucaryotic unicellular organisms (algae, protozoans and fungi), which is still unknown in detail in spite of the great recent progress in the study of the Late Proterozoic microfossils. The impact of the metazoans upon the global environment and ecosystem was in fact stronger and far more diverse than one caused by their direct action, such as bioturbation, filtration, biomineralisation or respiration. After their first appearance, metazoan species reached a very high density of population, which in some Vendian marine biotops was already comparable to the recent one. Thus, even at the level of a relatively low species diversity the oldest metazoans had become an important factor regulating the biomass and consequently the environmental functions of the primary producers and other organisms at the lower levels of the trophic pyramid.

Acknowledgments

The author is grateful to Drs. Michael Ghiselin, Giovanni Pinna and Marvalee Wake for organizing the conference and providing hospitality. This paper is part of project 9305-05-8816 supported by the Russia Foundation for Fundamental Research. My special thanks are due to Dr. Ghiselin and to Dr. Ellis Yochelson for critical discussion and careful editing of the manuscript.

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BIOGEOGRAPHIC CAUSES OF DISCONTINUITY IN THE FOSSIL RECORD OF THE AMMONITES

Giovanni Pinna

Museo Civico di Storia Naturale
Corso Venezia, 55
20121 Milan, Italy

Introduction

The evolutionary models that palaeontologists create on the basis of palaeontological material are often dependent upon theoretical assumptions about the fossil record. These models differ profoundly, depending upon whether the fossil record is thought to be complete enough to supply a picture of the biological past that is very close to how events really took place, or if, on the contrary, the record is considered to be so full of gaps as to invalidate any palaeontological evidence with respect to the mechanisms that operated during evolution.

On the basis of the palaeontolgical data, most phyletic lineages seem to have evolved in a discontinuous way. If we assume that the fossil record is substantially complete, then the evolutionary process will be subject to interpretation as just such a discontinuous process. If, on the contrary, we admit the possibility that the fossil record is incomplete, and therefore unable to supply a real image of the past, we will be able to suppose gradual evolution.

The debate on the completeness of the fossil record has marked the whole history of palaeontological studies on evolution, starting with Lamarck and Cuvier, and has resulted in two different visions of the evolutionary process. These can be exemplified by Simpson's gradualist vision, in which microevolution and macroevolution are but two aspects of the same continuous process, and by Schindewolf's saltationist vision, in which microevolution and macroevolution represent two intrinsically different processes.

The Reasons for Incompleteness of the Fossil Record

It is well known that fossilization is a selective process and that its selective power (the so-called taphonomic filter) depends on several factors, among which the most important are the nature of the organic remains and the conditions of the sedimentary environment. It is also known that geological factors, such as the amount of stratal condensation, affect the continuity and the completeness of the sedimentary series, and thereby the completeness of the fossil record.

Nonetheless, other factors exist that are unrelated to the selective effect of the fossilization process and to the action of geological events and that, even under the most favorable environmental and organic conditions, can affect the completeness of the fossil record, and thus contribute to the appearance of discontinuities in phyletic lineages. These are *biogeographic factors* related to the disjunction of phyletic lineages due to population movements among adjacent biogeographic provinces, and in turn related to the environmental conditions of the provinces.

The aim of this paper is to explain how such biogeographic factors can produce apparent discontinuity in the fossil record, something that is difficult to intepret in the absence of a complete picture of the distribution of the group under consideration in space and time. As an example, I will discuss the evolution of the Toarcian (Lower Jurassic) subfamily Phymatoceratinae, which took place in two adjacent biogeographic provinces, and I will show that the discontinuities in the development of the phyletic lines found in one of the two provinces are essentially due to biogeographic factors.

Biogeographic Provinces During the Toarcian

So far as the ammonite faunas are concerned, different faunistic provinces can be identified during the Toarcian. Among these are a Sub-Mediterranean Province, corresponding to the extension of the epicontinental seas over part of continental Europe (especially France, Germany and England) and a Mediterranean Province, corresponding to the western part of Tethys basin, sedimentary deposits of which outcrop especially in Italy, North Africa, Greece, the Balkans, the Caucasus (Fig. 1).

The ammonite faunas of the two provinces have a basically different structure. On the average, the ammonite fauna in the Sub-Mediterranean Province has a relatively low taxonomic diversity and a high number of individuals, while in the Mediterranean Province it has a relatively high taxonomic diversity and a low number of individuals. Such faunal structure would indicate, at least as far as the ammonites are concerned, a r-selective environment for the Sub-Mediterranean Province and a K-selective environment for the Mediterranean Province. Hallam (1975) ascribed these faunistic differences to environmental instability and stability, respectively, in agreement with the model of Sanders (1968, 1969). The study of Phymatoceratinae has shown that some faunal mixing among the two provinces took place at different times. Individuals belonging to mediterranean endemic groups occasionally dispersed to the Sub-Mediterranean Province, but without giving rise to continuous phyletic lines; however, only on two occasions did mediterranean groups establish permanent populations in the Sub-Mediterranean Province that gave rise to new phyletic lineages.

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Editors, M. T. Ghiselin and G. Pinna

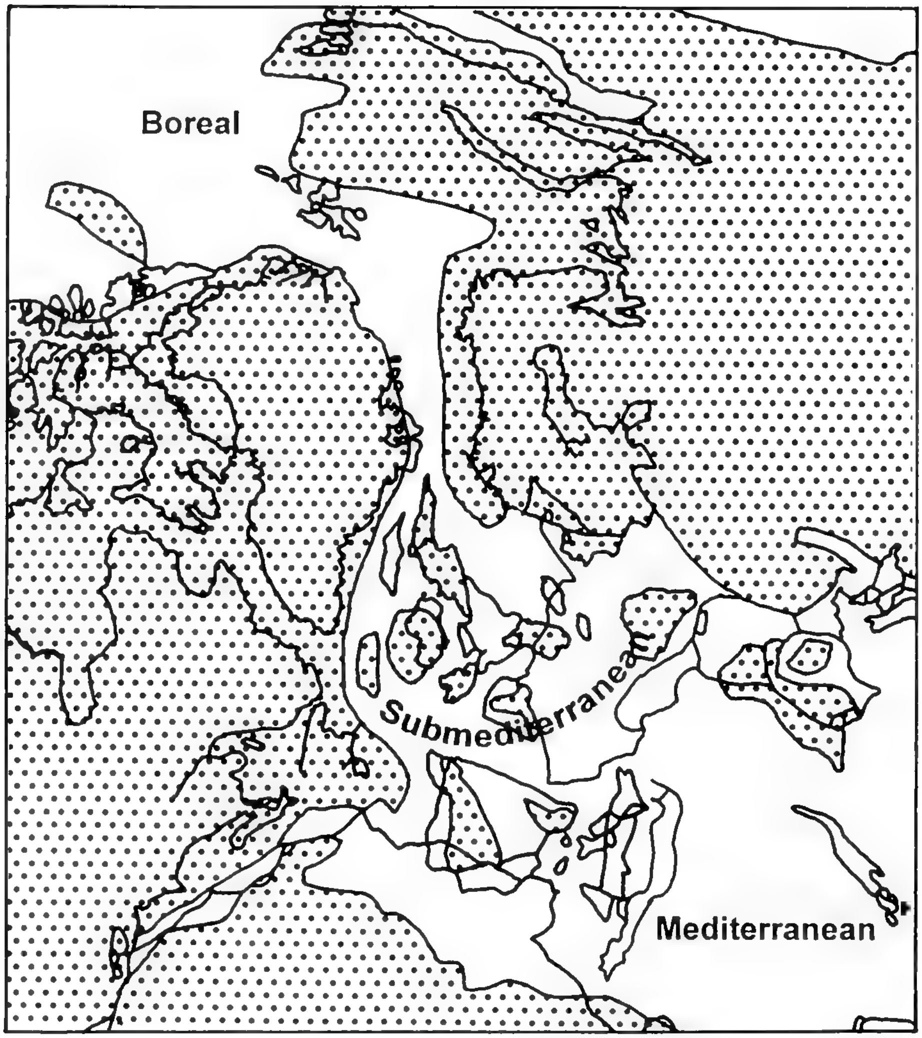

FIGURE 1. Map of Europe and adjacent regions as they appeared in the Toarcian, showing Boreal (upper left), Sub-Mediterranean (center) and Mediterranean (lower right) faunistic provinces for ammonites. Land is stippled. (After Smith, A. G., Smith, D. G., and Funnell, B. M., 1994)

Because of the population movements of ammonites between the two provinces, the different structure of the different environments takes on remarkable importance. In fact, it is highly probable that most of the population movements take place from saturated and highly-competitive K-selective environments to non-saturated, moderately-competitive r-selective environments. In the specific case of the ammonites and the two provinces considered here, there was a general tendency for mediterranean groups to invade the Sub-Mediterranean Province in successive stages during the Toarcian.

Stratigraphy of Toarcian

Because of the differences in ammonite faunas in the Sub-Mediterranean and the Mediterranean Provinces, the bio-stratigraphic zonations in the two provinces do not match, being based on endemic zonal index species in each province. However, correlation between the two biostratigraphic zonations is possible because of repeated entries of mediterranean transient isolated forms into the Sub-Mediterranean Province and because migrations into the same Province that twice established permanent populations. Reference is here made to the following correlational stratigraphic scheme:

Sub-Mediterranean Province	**Mediterranean Province**
levesquei Zone	meneghinii Zone
thouarsense Zone	erbaense Zone
variabilis Zone	
bifrons Zone	bifrons Zone
falciferum Zone	serpentinus Zone

Evolution of the Subfamily Phymatoceratinae

In 1957 Arkell (in Arkell, Kummel and Wright, 1957) considered the subfamily Phymatoceratinae to be a polyphyletic group, derived from several members of the Hildoceratidae, and he ascribed to it eight genera, including *Haugia* and *Phymatoceras*. The genera *Denckmannia*, *Lillia* and *Chartronia*, previously established by different authors as separate taxa, were considered as synonyms of *Phymatoceras*.

The subfamily Phymatoceratinae is not applied here in the wider sense of Arkell, but instead more precisely as a monophyletic group consisting of five phyletic lineages derived from one another during Toarcian (Pinna and Levi-Setti, 1973). The five phyletic lineages lead to the following groups of forms, which are considered, partly arbitrarily, as representing genera:

1) group of *Ammonites erbaensis* Hauer, 1856, corresponding to the genus *Phymatoceras* Hyatt, 1867,
2) group of *Lillia narbonensis* Buckman, 1898, corresponding to the genus *Chartronia* Buckman, 1898,
3) group of *Hildoceras* (*Lillia*) *chelussii* Parish and Viale, 1906, corresponding to the genus *Lillia* Bayle, 1878,
4) group of *Denckmannia tumefacta* Buckman, 1898, corresponding to the genus *Denckmannia* Buckman, 1898,
5) group of *Ammonites variabilis* (d'Orbigny, 1844), corresponding to the genus *Haugia* Buckman, 1888.

Gabilly (1976) revised the Phymatoceratinae of the stratotype of Toarcian (Thouars Region, France), in the Sub-Mediterranean Province. He ascribed to the subfamily the genus *Phymatoceras* and also the genera *Denckmannia* and *Haugia*, which he supposed were derived from it.

The phyletic relationships derived by Gabilly do not correspond to those of the Phymatoceratinae of the Mediterranean Province, for they were carried out on an intermittent fossil record. The fossil record of Phymatoceratinae in the Sub-Mediterranean Province (with the exception of the genera Haugia and Denckmannia) does not reflect the true phylogeny of this group of ammonites. Rather, it corresponds to occasional entries of transient individuals and to migration populations of separate phyletic lineages that evolved continuously in the Mediterranean Province.

Such discontinuity in the fossil record had the following effects:

1 — The lack of transitional forms resulted in an erroneous systematic interpretation. United in the same genus were species that, in the light of the different Mediterranean faunas, would seem to belong to different entities. For instance, in the systematic scheme drawn by Gabilly the genus *Phymatoceras* includes both *Phymatoceras* s.str. and representatives of the genus *Chartronia*, while the genus *Denckmannia* includes both *Denckmannia* s.str. and representatives of the genus *Lillia*.

2 — The incompleteness of the fossil record precluded documentating the cenogenetic and palingenetic mechanisms by which the evolutionary novelities appeared (observable only in relatively continuous series) and in turn it prevented establishing ancestor-descendant links of the different forms.

3 — The incompleteness of the documentation, without any kind of data on the evolution of the group that took place in the Mediterranean area, prevented the systematic identification of many forms, resulting in the establishment of five new systematic entities out of nineteen analyzed species.

Comparative study of the Mediterranean and Sub-Mediterranean faunas (Pinna and Levi-Setti 1971) made it clear that the phyletic lineages corresponding to the genera *Phymatoceras*, *Chartronia*, and *Lillia* are endemic to the Mediterranean Province, while those corresponding to the genera *Haugia* and *Denckmannia* are endemic to the Sub-Mediterranean Province.

Therefore the five phyletic lineages evolved in parallel from the stem group consisting of the genus *Phymatoceras*, which thus became paraphyletic, three in the mediterranean area and two in the sub-mediterranean area (Fig. 2).

In the Mediterranean Province:

— the genus *Phymatoceras* originated from the genus *Hildaites* at the beginning of brifrons Zone and evolved until becoming transformed into *Catulloceras* ssp. at the beginning of meneghinii Zone,

— the genus *Lillia* originated from the genus *Phymatoceras* in the middle of bifrons Zone and then died out in the upper part of erbaense zone,

— the genus *Chartronia* evolved in the middle of bifrons Zone from the genus *Phymatoceras* and then died out in the upper part of erbaense Zone, or little earlier.

In the Sub-Mediterranean Province:

— the genus *Chartronia* populated the Sub-Mediterranean Province in the middle of the bifrons Zone with primitive forms, identical to coeval mediterranean forms; those forms established permanent populations that evolved and gave rise to the sub-mediterranean endemic phyletic lineage of the genus *Haugia*,

— the genus *Phymatoceras* populated the Sub-Mediterranean Province at the beginning of varibilis Zone with forms identical to coeval mediterranean forms, which established permanent populations that evolved and gave rise to the sub-mediterranean endemic phyletic lineage of the genus *Denckmannia*.

As already mentioned, there was a constant trend of the populations of Mediterranean ammonites to invade the Sub-Mediterranean Province during the Toarcian, as a consequence of the environmental structure of the two provinces.

Adaptation to an r-selective environmental regime is possible only for a small part of the populations previously adapted to a K-selective regime, due to several factors limiting the capability to carry out a r-selective strategy. Furthermore, the selective pressure on the populations of a K-selective regime constantly tends to force the populations themselves to migrate into regions that are undersaturated and where competition is low. Both of these contrasting factors probably affected the mediterranean ammonites.

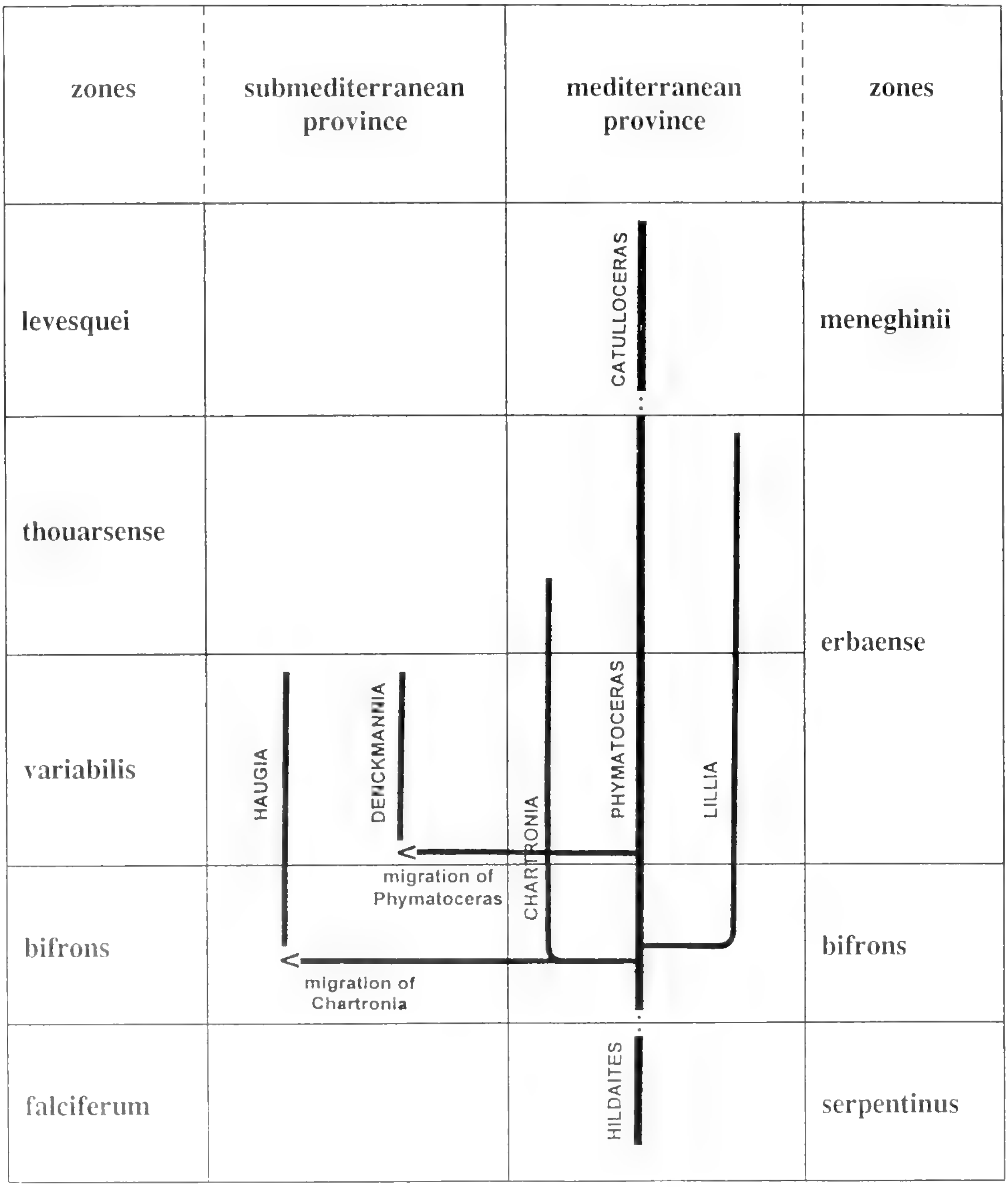

FIGURE 2 Phylogeny, biogeography and stratigraphic distribution of Toarcian ammonites of the subfamily Phymatoceratinae. Note origin in Mediterranean Province and migration to Sub-Mediterranean Province

Consequently several isolated forms or small populations of Mediterranean ammonites, belonging to chronologically different species, ventured in successive stages and in different periods into the Sub-Mediterranean Province, forming a discontinuous fossil record.

Such populations only rarely succeeded in establishing themselves in the new selective regime and originating submediterranean phyletic lineages. We saw that in Phymatoceratinae this happened only twice, with the development of the phyletic lineages of the genera *Haugia* and *Denckmannia*, derived from migrations of mediterranean populations of the genera *Chartronia* and *Phymatoceras*.

This sequence of events produced a discontinuous fossil record of the three mediterranean phyletic lineages in the Sub-Mediterranean Province, a fossil record constituted both by the transient isolated forms that repeatedly entered the province and by the migrations that at two separate times established permanent populations of *Phymatoceras* and of

Chartronia. On the contrary, in the Mediterranean Province the fossil record of the three endemic lineages (the genera *Phymatoceras*, *Chartronia* and *Lillia*) shows a continuous and gradual evolution, and for every phyletic lineage it is possible to identify one single form for each successive time interval.

On the other hand, in the Sub-Mediterranean Province the fossil record of the two endemic phyletic lineages shows a gradual and continuous evolution, completely analogous to the evolution observed in the Mediterranean Province within the three phyletic lineages that are endemic to this province.

Because of the forced direction of the populating movements, the fossil record of the sub-mediterranean endemic groups is almost non-existent in the Mediterranean Province.

In conclusion, it may be inferred that in the subfamily Phymatoceratinae groups endemic to a certain area followed a continuous and gradual evolution, even though evolution seems discontinuous when observed in areas that are different from those where the groups are endemic. Because such a scenario seems to apply to other groups of toarcian ammonites (Pinna and Levi-Setti, 1971), we can generalize by stating that the discontinuity observed in many ammonite phyletic lineages is at least partly due to biogeographic causes, that is by movements into areas of low-selective regime by populations of groups endemic to high-selective regime areas.

Modality of Appearance of the Features in Phymatoceratinae

The great abundance of individuals on the one hand, and the planispiral shape of the shell, allowing us to follow the ontogenetic development of the single individuals, on the other make ammonites excellent material for the study of both mechanisms of appearance of new characters and heterochronies of development. Ammonites have been used to this aim by many palaeontologists (Waagen, Wurtemberger, Neumayr, Hyatt, Pavlov, Schindewolf and more recently Callomon, Dommergues and Landman), who created several evolutionary models about the relationships between ontogeny and phylogeny.

Historically, the relationship between ontogeny and phylogeny in ammonites led to two opposite interpretations of the processes by which features appear and develop.

At first, palaeontologists, including Hyatt, Buckman, Trueman and Spath (in early papers), supported a palingenetic process for evolution in which new stages were added at the end of ontogenesis and adult features of the ancestor were pushed back into the juvenile stages of the descendant. Because such evolutionary process would bring about a direct recapitulation in the history of the individual of the history of the phyletic lineage, it always had to involve an accelerated ontogenesis. Moreover, such process could be easily explained by invoking the inheritability of the acquired features. The main consequences of the recapitulationist vision of evolution were the finalization of the evolutionary process (for instance Hyatt's theory of racial old age), orthogenetic evolution, and the parallel evolution of phyletic lineages, resulting in polyphyletism. From the standpoint of systematics, another consequence, stressed by Donovan (1973) and related to the concept of evolution by parallel lineages, was the huge multiplication of systematic entities, something which has always been sought by stratigraphers.

Then, starting mainly from Pavlov's work (1901), most students of ammonites — among them Spath, Brinkmann and Schindewolf — supported a cenogenetic process for evolution, in which juvenile features of the ancestors would be shifted to the adult stages of the descendant (proterogenesis of Schindewolf, 1936). Such an evolutionary process led to the denial of recapitulation and acceleration, and it made possible a "rejuvenation" of phyletic lineages (the "*escape from specialization*" of Hardy, 1954). By excluding extinction as the inevitable fate of every evolutionary lineage, it justified the elimination of any finalist interpretation and, therefore, of any intrinsic evolutionary force. Moreover, the cenogenetic model allowed palaeontologists to overcome some of palaeontology's typical biases, including the directionality and the linearity of phyletic lineages as the result of an intrinsic evolutionary power, and the idea of the progressive decrease in the evolutionary potential. And, above all, it allowed us to suppose a genetic continuity compared to a morphologial discontinuity.

A new interest in the role played by heterochrony in the evolutionary processes arose in 1977, with the publication of Gould's volume *Ontogeny and Phylogeny* and with the further analysis of different heterochronic processes by Alberch et al. (1979) (see McKinney 1988, McNamara 1990, McKinney and McNamara 1991). It has been demostrated that evolution of ammonites follows heterochronic processes that are both cenogenetic (paedomorphosis) and palingenetic (peramorphosis) (Landman 1988, Dommergues 1990).

In the three mediterranean phyletic lineages of the subfamily Phymatoceratinae, evolution is expressed primarly in the ornamentation, which becomes stronger and more elaborate (in *Phymatoceras*, *Lillia* and *Chartronia*), and to a lesser extent the shape of the shell resulting in increasing of the involution (in *Chartronia*), and an attenuation of the ventral furrows (in *Lillia*). All the modifications take place through peramorphosis: during the evolution of the three phyletic lineages the morphologic changes always take place with gradual progression at the end of the ontogenetic growth, so that the three phyletic lineages can be considered as peramorphoclines according to McNamara (1982). In the shell of the most evolved forms of each phyletic lineage, up to three different morphologic stages in a recapitulative sequence can be observed.

The same heterochronic model is applicable to the evolution of the sub-mediterranean genus *Haugia*.

Peramorphic modifications are not the general rule for the ammonites of the mediterranean Toarcian: in the family Dactylioceratidae (Pinna and Levi-Setti, 1971), for instance, the evolution in most phyletic lineages results from paedomorphosis, while peramorphic processes are highly limited.

Continuity and Discontinuity in Evolution

Whether the morphologic modifications occur through peramorphosis or paedomorphosis, analysis of the ontogenetic changes in ammonites allows one to reconstruct the phyletic lineages. What makes the analysis possible is the fact that the spiral shape of the shell allows observation of successive, different growth stages in the individuals (that is to say the period of persistence of a given morphologic stage) and the development of such stages during evolution (that is to say the change in the extension of a given morphologic stage). We observed that during evolution a new feature may move forward starting from the early stage of ontogenesis, and involving more and more adult stages in the case of the paedomorphic processes; or it may move backward toward more and more juvenile stages in the case of peramorphic processes. When we have a very complete and therefore continuous series of forms, such shifts appear highly gradual.

The greater the completeness of the fossil record, the greater the evidence that change has been gradual. This means that this kind of process can easily seem to be discontinuous, because the improbability of demonstrating absolute continuity where all generations are documented. Even in this theoretical case the process would still seem discontinuous, because the appearance of a new feature or a whole set of features will always represent a discontinuity if compared to the previous situation.

At this point it is necessary to agree on the terms "continuity" and "discontinuity" with respect to the evolutionary process. So far as ammonites are concerned, we can say that the successive evolutionary changes described in different phyletic lineages by different authors consist of changes of a comparable magnitude; the changes in the shape of the shell or of some of its features, the appearance of some features such as as grooves or carinae, or the changes in the ornamentation follow one another from one form to the following form in the same fashion, although not at the same rate. Despite this, such changes have sometimes been considered as discontinuous (for example, this idea was implied by Spath) and sometimes as continuous (see Landman, 1988). I agree with Simpson, who wrote (1944, p. 50)

> In its crudest form, the distinction between continuity and discontinuity in evolution is almost meaningless. The developed organism is absolutely discontinuous from its parent, and any real difference between the two, however small, is discontinuous; there is no morphological continuum.

Continuity is a sequence of discontinuities, the intervals of which can be made shorter and shorter by the progressive improvement of the fossil record, but which can not be eliminated. In fact, even if were we able to find as fossils all organisms of all the generations that made up a given phyletic lineage, there would still be among these organisms the discontinuities that are inherent to the essence of individuality.

Therefore we may paraphrase the statement of Otto Schindewolf, who was one of the biggest supporters of discontinuity, as follows:

> The search for a series of successive transitory stages between two types, proving the gradual creation of a new structural type, will be vain, since the perfect continuity between two successive types does not exist.

Conclusion

As pointed out by Dommergues (1990, p. 162)

> . . . ammonoids constitute a rather homogeneous group organized around a single Bauplan from which only a few groups deviate appreciably. . . . Moreover, it is probable that, throughout the range of the order, most ammonoids inhabited homologous or at least similar marine ecosystems. These morphofunctional and ecological continuities allow extrapolation of general palaeobiological assumption from only a few detailed analyses of trends. . . .

Dommergues statement justifies extrapolating the results of the study of the mediterranean and sub-mediterranean Phymtoceratinae, and concluding that the biggest discontinuities found in the evolution of phyletic lineages among ammonites in general cannot be ascribed to discontinuities in the evolutionary process. Major discontinuities are not of phyletic origin, but are due to biogeographic factors, while lesser ones can be ascribed to the discontinuity that is intrinsic to individuality itself.

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SEGMENTS, BODY REGIONS, AND THE CONTROL OF DEVELOPMENT THROUGH TIME

Alessandro Minelli

Department of Biology
University of Padova
Via Trieste 75
I 35121 Padova, Italy

Four main dimensions of structural and/or developmental complexity are identified in the organization and life history of arthropods. These dimensions correspond to the antero-posterior and dorso-ventral body axis, to the proximo-distal axis of the appendages and to the temporal axis of (post-embryonic) development. Patterns of change are very often concordant along two or more of these dimensions. No structural or developmental axis is partitioned into more than about 5 major units (e.g., tagmata). Speculations are offered as to the possible relationships between these aspects of organizational complexity and Kauffman's (1993) model of genomic organization. The importance of the segmental organization of the body as a basic structural condition is de-emphasized. Tagmata, rather than segments, are regarded as the primary target of natural selection.

Segmented Animals

Early in the nineteenth century, Cuvier (1817) pointed to segmentation as a basic feature of animal morphology. Segmentation was characteristic of the Articulata, one of his four main divisions (*embranchements*) of the animal kingdom. Cuvier's Articulata embraced the segmented groups that we currently identify as the annelids and the arthropods, but not the vertebrates, whose organisation Cuvier regarded as different enough from that of the other segmentally organised animals as to warrant the status of an independent *embranchement*. However, even the seemingly unlikely comparison between vertebrate and arthropod segmentation was proposed by Étienne Geoffroy Saint-Hilaire, Cuvier's friend-rival at the Muséum d'Histoire Naturelle in Paris in one of his most hazardous comparisons. Geoffroy's (1820a, 1820b, 1822) efforts to treat an arthropod as a kind of vertebrate living inside its vertebrae was all too easily ridiculed, whereas the homology between annelid and arthropod segmental organisation has remained unchallenged until very recently.

Today, we approach the study of segmentation from the vantage point of developmental biology and especially of the molecular genetics of development. The new evidence definitively confirms the very perceptive point of view of the Russian comparative morphologist Beklemishev (1969 [1964]), who interpreted segmentation as a kind of symmetry which is not a uniquely derived, hence homologous, feature. Rather, he considered that segmentation easily emerges as a formal concept of rational morphology, on the one hand, and as a concept of functional anatomy, on the other. There is no longer any doubt, that segmentation develops in different animal groups through different morphogenetic pathways.

In insects, segmentation goes on, basically, within the (prospective) ectoderm, whereas in vertebrates and annelids segmentation starts within the mesoderm. Cell proliferation may, or may not, be required for segmentation. In some animals the segments appear synchronously, as in *Drosophila*; in others, and more commonly, in an antero-posterior sequence. In my view, there is now evidence enough to regard annelid and arthropod segmentation, not to say vertebrate segmentation, as independently derived. If this view will prove to be true, then the major support to Cuvier's Articulata will be seriously shaken. In this context it may be useful to point to recent molecular evidence suggesting a not-so-close relationship between arthropods and annelids (Field et al., 1988; Eernisse et al., 1992; Ballard et al., 1992; Whitington, 1993).

In this paper, I will discuss some hitherto overlooked aspects of the body organisation in one of these groups of segmented animals: the arthropods.

Four Dimensions of Arthropod Complexity

McShea (1993) has offered a comparative quantitative analysis of the structural complexity of the vertebral column of mammals. His paper and, in particular, the complexity indices introduced therein, provide a valuable starting point for this kind of study. However, in the present analysis I will follow a less formal approach, simply applying the following intuitive principles:

1. complexity is not dependent on the number of parts: strictly homonomous sequences of 10, 20 and 100 segments are, as such, of equal complexity;
2. complexity is increased, however, when changing from an unsegmented to a segmented condition;
3. complexity is only slightly increased when changing from a strictly homonomous pattern to a progressive, gradient-like pattern;
4. complexity is highly increased, when developing sharp structural boundaries, as between head and trunk in an insect's body;
5. the above principles may also apply to the time dimension, if developmental stages are equated to body segments and major developmental phases (such as the insect larva, pupa, and imago) are equated to body regions.

To approach a complexity analysis of arthropod organisation, it seems advisable to identify four distinct although related dimensions of the "segmented" architecture of these animals. These four dimensions (Fig. 1) are the antero-posterior and the dorso-ventral body axis, the proximo-distal axis of the body appendages (such as legs or antennae) and the temporal axis of the individual developmental time.

Generally speaking, the longitudinal body axis of arthropods is not at all like the uniform sequence of identical segments that we see in many annelids. The body of arthropods is divided into regions (tagmata), such as the head, thorax and abdomen of insects and the prosoma and opisthosoma of spiders. The number of tagmata is always very small and quite independent of the number of body segments. For instance, the longitudinal complexity (tagmosis) of centipedes is more or less the same (possibly, even a bit higher) in lithobiomorphs, with 15 leg-bearing segments in the adults, as in geophilomorphs, with up to 191 leg-bearing segments. The same pattern occurs within millipedes, or branchiopod crustaceans.

More often than not, the actual complexity of the longitudinal axis of an arthropod is sensibly larger than suggested by the conventional, admittedly stronger, partitioning into two to four tagmata. For instance, the second body region of malacostracan crustaceans (pereion), usually consists of an anterior section, whose appendages are developed as maxillipedes, and a posterior section, whose appendages retain the more conventional shape of locomotory limbs. However, within any major region of the body, segments and appendages generally retain a distinctive uniformity or, commonly, change in a continuous, gradient-like manner. These changes could be obtained, in principle at least, with a very modest amount of information, in addition to that required for building one segment, and for uniformly repeating this segmental unit many times. Therefore, these gradual changes do not sensibly increase the complexity of body architecture. Things are different at the transition points between one region and another, where virtually everything changes, in the external aspect as well as in the internal anatomy. We cannot avoid getting the impression that a lot of different genes are selectively expressed in the individual regions. I am reminded of a notion of plant cell biology: an average plant cell might have something like 20,000 distinct mRNA sequences, 1000 of which, perhaps, are different from those found in another cell type within the same plant (Kamalay and Goldberg, 1980; Alberts et al., 1983). Certainly, this is a point badly in need of extensive comparative investigation.

Moving to the second dimension of complexity, i.e., to the dorsoventral body axis, it is easy to provide examples of dorsal and ventral aspects of the same animal behaving quite independently from one another, even in respect to gross segmentation. A strong dorso-ventral partitioning into two distinct domains is evident, for instance, in pauropods and in symphylids. In several instances, however, the dorsoventral axis seems to allow a partition into more than two domains. A good example is the thorax of the insects. Here, the levels where wings and legs respectively articulate with the segment are quite obvious limits between tergal and pleural, and pleural and sternal partitions.

The third axis of complexity is that of the appendages. In this case too, we can have a very diverse, and often quite high, number of segments, but these are never structured into a very high number of "regions." The very high number of flagellomeres forming the terminal section of the legs in the house centipede (*Scutigera*) or in many harvestmen, does not make the legs of these animals more complex relative to the legs of other centipedes and arachnids. Meristic variation does occur at all taxonomic scales, without seemingly altering the overall complexity of the appendage. For instance, the number of tarsal joints is generally stable in Coleoptera; but the rule of having 5 of them has widespread exceptions, sometimes scattered, sometimes clustered within one family. The same holds true for the number of antennomeres. Most beetles have 11 of them, but this number, very seldom exceeded, is quite often reduced to 10, 9 or even less, without sensibly affecting the shape, or the complexity, of the appendage. The above remark about morphological changes in a gradient along the main axis of the body applies to the axis of appendages as well. The apical clubs, so common in the antennae of beetles and other insects, e.g., Heteroptera, Orthoptera and even Lepidoptera, are examples of easy modifications of a basically homonomous appendage.

To these three morphological axes we can now compare a fourth, apparently unrelated, axis: that of developmental time. At first sight, any similarity between the structure, or complexity, of developmental schedules on the one hand, and the structure, or complexity, of the longitudinal, dorsoventral and appendicular axes of the body on the other, could be suspiciously regarded as merely coincidental. However, a causal link between the temporal dimension of development and the spatial dimension of the longitudinal body axis has been definitely demonstrated by the molecular genetics of development. A detailed, causal relationship has been ascertained between the temporal sequence of transcription and expression of individual *Hom*/*Hox* genes, in *Drosophila* as well as in vertebrates, including the specification of the individual spatial domains under the control of these genes, along the antero-posterior axis of the body. In a few words: earlier equals anterior, later equals posterior. This equivalence has nothing to do with segmentation per se. Rather, it is probably a much more general feature of metazoan organisation, the core of Slack's et al. (1993) concept of zootype. Moreover, there is a hard-wired feature, behind this remarkable correspondence between developmental time and positional specifications along the body axis, i.e., the much conserved linear arrangement of these homeotic genes along the chromosomes, a linear arrangement which is sequentially expressed, thus giving rise to a sequence of body structures that is collinear with the gene sequence.

In post-embryonic development there are two kinds of temporal units comparable to the morphological units that we call segments and tagmata. The temporal "segments" of development are the individual ontogenetic stages separated by a moulting event. Most moults are followed by minor changes only, hardly affecting anything besides body size and variations of colour and cuticular patterns, including the number of setae on selected body parts. In addition, there may be an increase in the number of body segments (in anamorphic arthropods, such as millipedes), but this is a sim-

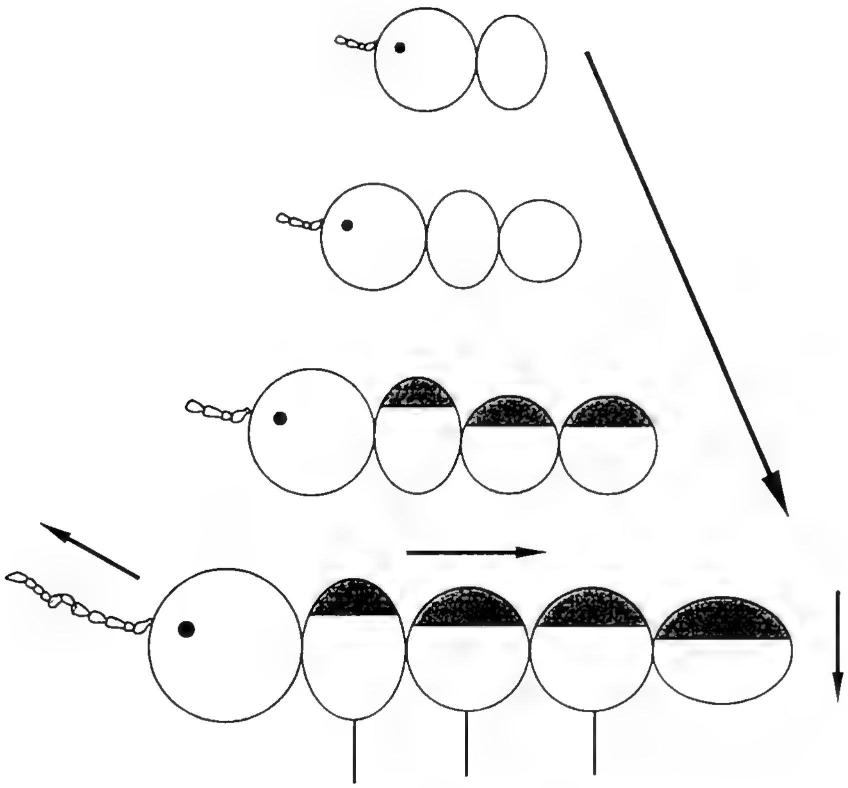

FIGURE 1. The four dimensions of arthropod complexity discussed in the text. Large arrow: temporal axis of developmental time. Small arow, left: proximo-distal axis of the appendage. Small arrow, center: antero-posterior body axis. Small arrow, right: dorso-ventral body axis

ple meristic change not entailing any sensible increase in complexity. The changes accompanying all these moults are the developmental equivalent of the smooth, gradual changes in morphology that we can observe within one tagma along the antero-posterior axis of the body. A few moults, however, are accompanied by major changes deserving the name of metamorphosis. These major developmental events are always few in number, as are those separating larva from pupa and pupa from adult in holometabolous insects.

Correlations

A striking feature of arthropod complexity is that within the same animal degrees of, or variations in, complexity along any one of these four axes are very often coupled, with equivalent degrees of, or variations in, complexity along one, or more, of the other axes.

Examples of a correspondence between the complexity of the antero-posterior axis and the complexity of developmental schedules are found in millipedes and hymenopterans.

All millipedes (Diplopoda) develop by anamorphosis, i.e., they hatch from the egg as larvae with a small number of segments and progressively add more and more segments moult after moult. There are, however, three different kinds of millipede anamorphosis, recently redefined by Enghoff et al. (1994) as euanamorphosis, teloanamorphosis and hemianamorphosis, exemplified, respectively, by julid, chordeumatid and glomerid millipedes. In euanamorphosis, the number of moults is not strictly defined nor is the number of segments, which continuously increases through life. In teloanamorphosis, the number of moults is fixed, as is the number of segments, which are progressively added at each moult. In hemianamorphosis, the number of segments is fixed, but it is reached after a few moults: afterward the animal continues to moult, but without any further increase in the number of segments. The complexity of these developmental schedules increases from euanamorphosis through teloanamorphosis to hemianamorphosis. Correspondingly, the complexity in the regionalisation of the body increases, from the very uniform trunk of the euanamorphic julids to the much more specialised trunk of hemianamorphic glomerids, with gross specialisations affecting the foremost and the hindmost segments of the body.

In Hymenoptera, we can contrast the plesiomorphic development of sawflies (with several, morphologically uniform, caterpillar-like larval stages), with the highly derived development of many Parasitica, whose developmental schedule is more complex. This complexity manifests itself with a first larva, often of bizarre unsegmented shape, that is markedly different from the second, or mature, larva, which is of more conventional shape. Again, as in millipedes, this contrast is mirrored by the contrast between the simple, plesiomorphic abdomen of sawflies and the highly modified, and sometimes very complex, abdomen of many Parasitica. What

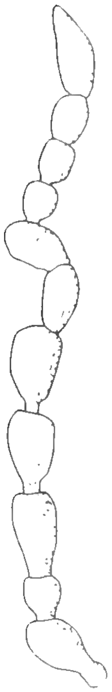

FIGURE 2. Antenna of the male of the blister beetle *Meloe proscarabaeus* (Coleoptera: Meloidae)

is interesting for our argument is that a more complex pattern also evolves here along the dorsoventral axis. Lateral to the main tergal plates, a couple of laterotergites are split off on several abdomen segments of representatives of a number of families of these hymenopterans, e.g., segments 3–7 in Platygasteridae and segments 2–6 in Scelionidae.

In other instances, an unusually complex post-embryonic development is accompanied by unusually complex appendages.

One example involves the blister beetles (Meloidae), a family of beetles with hypermetamorphic post-embryonic development. The standard developmental schedule of blister beetles comprises a primary larva (the very mobile triungulin), followed by a secondary larva of very different shape, which in turn is followed by a resting pupa-like stage and, again, by an additional active larva, more or less similar to the secondary one, and finally by the conventional pupa and the adult! With this unusual developmental complexity we can match the morphological complexity of the antennae of many (not all!) blister beetles. This feature deserves particular attention, because it is not simply an example of that "lesser" structuring we find in the antennae of many beetles, with more or less distinctly gradient-like changes in the shape of the basal or the terminal antennomeres. Of much more interest to us, the modifications we see in the antennae of a few meloid beetles do not affect the proximal or the distal antennomeres, but exclusively a few intermediate ones! (Fig. 2) That means that blister beetles can operate a shape control in a region of the appendage that usually exhibits no plasticity at all. Thus, in blister beetles antennal complexity parallels developmental complexity, by obtaining a control over the mid-point of a previously uniform sequence (of antennomeres, or of developmental stages). I do not think that the unique antenna of *Meloe* occurs in a hypermetamorphic beetle merely by chance.

More examples are to be found among arachnids. Here, the only groups that undergo sensible post-embryonic developmental changes, with clearly distinct larval/nymphal stages (true metamorphosis), are mites and ricinulei. These arachnids go through a six-legged larval stage, before getting the eight-legged nymphal and adult condition. However, this developmental complexity is not without a counterpart in the complexity of the main body axis, as is suggested by the cumbersome and idiosyncratic nomenclature introduced to identify the regions we can often distinguish within the body of a mite: gnathosoma, hysterosoma, idiosoma, meta-podosoma, opisthosoma, propodosoma, podosoma. These terms are more numerous than those used for spiders or scorpions. In mites, this complexity has no clear counterpart in the structure of the legs, but this fact is possibly explained by the very small size of these arthropods, a formidable limit to any further attainment of complexity beyond the standard degree of arachnid legs. At least there is no place, in the legs of mites, for more patterned articulations. On the other hand, very complex apical structures, in the shape of adhesive pads, hooks, etc., are common in mites. This explanation is supported by the slightly complex leg of Ricinulei, which are not so small as mites. More generally, the effect of an extremely small body size (or cell number?) on the development, or the maintenance, of structural complexity is evident in several arthropods, a good example being the fading of segmentation in the gall-building eriophyid mites, whose total length is often less than 100 μm. In these cases of size-induced reduction, the indiscernibility of parts may open formidable problems of homology (Wagner 1989).

In several instances, a striking correspondence is found between the structural complexity of the main body axis and the structural complexity of the appendages. The two groups of arachnids in which the body ends with a multi-segmented, flagellum-like section (Palpigradi and Uropygi) also have strikingly segmented tarsi, especially on the first pair of legs. Again, the more evidently segmented body of Amblypygi, in comparison to their sister group (Araneae, the spiders), is matched by the uniquely high degrees of segmentation of the tarsi of the I leg pair in Amblypygi, without any counterpart in spiders.

Bristletails (Archaeognatha) and silverfishes (Zygaentoma) are the hexapod equivalent of Palpigradi and Uropygi in that their body ends in a multi-segmented filum terminale, whose flagellar organisation is matched by that of the cerci and other appendages.

In other instances, the correspondence between longitudinal body axis and appendicular axis is found in their respective developmental schedules. One example is provided by centipedes. Within this group some forms (Scutigeromorpha and Lithobiomorpha) develop by anamorphosis, i.e., by progressive increase in the number of segments during post-embryonic development. In these centipedes, the number of antennal articles also increases during post-embryonic life. In contrast, those centipedes (Scolopendromorpha and Geophilomorpha) which develop epimorphically already having their total segment complement when hatching. These centipedes also have fully-formed antennae at birth, with 14 articles in all Geophilomorpha and 17 in most Scolopendromorpha.

A more impressive correspondence between antero-posterior axis of the body and proximo-distal axis of the appendages is offered by copepods. As recently pointed out by Izawa (1991), Hulsemann (1991) and Ferrari (1993), during their copepodid stages these tiny crustaceans add new segments to their appendages, according to the same "progression rule" that they follow in adding new segments to the body. Copepods differentiate one more body (or appendage) segment after each moult, always in subdistal position, until the final pattern is achieved. However, that is not yet the whole story. The body is characteristically marked by a mechanically important flexure, which may be placed in front of the fifth pair of legs or just behind them (thus allowing the traditional distinction between podoplean and gymnoplean copepods). This major singularity, which is clearly superimposed to the basic tagmosis (as demonstrated by its ontogenetic shifting from a more anterior position to its final, podoplean or gymnoplean position) is mirrored in the appendages by the geniculation of the antennules of most male copepods, a segmental singularity of the same kind as that of the antenna of *Meloe* just referred to.

Other examples clearly show a threefold/fourfold correspondence in structural complexity between body, appendage and development.

A first example concerns branchiopod crustaceans. In this group, there is a large range of structural models and developmental schedules, whose complexity changes in a concerted way. In the Cambrian *Rehbachiella* (Walossek, 1993), the number of segments is fairly high, as is the number of podomeres forming each of the body appendages, as is the number of moults undergone by the animal during its post-embryonic life. In addition, the body segments are very uniform, except for the transition between leg-bearing and legless segments; the appendicular joints are also very uniform; and the sequence of stages during ontogeny is very regular, indeed, at the highest degree we currently know for any arthropod. Specialisation, i.e., the attainment of complexity, increases in anostracans, conchostracans and ostracods, in the order, but always bringing together corresponding changes along all three main dimensions (body, appendage, developmental time).

Additional lines of evidence support the hypothesis that all of the main dimensions of arthropod organisation evolve in a concerted way. One of these is the occurrence of "progradous" development. By this I mean a kind of exception to the rule that morphogenesis proceeds in antero-posterior and proximo-distal sequence. Formally equivalent, in a sense, to these progradous disto-proximal and postero-anterior sequences of morphogenesis are such events as programmed cell death by apoptosis, segment fusion and the like. All of these events are indeed rare and all of them surely require additional genetic information and strong developmental control to overcome the nearly universal retrogradous trend. It is worth noting here that true segment fusion is all but common. What is generally referred to under this name is non-disjunction, i.e., the lack, rather than the reversal, of a basic developmental process. A few examples of progradous development are given in the following three paragraphs.

As to the direction of the differentiation wave along the body axis, two good examples are found in the stomatopods and in the copepods. Amongst stomatopods, there are species in which the trunk appendages regularly differentiate in antero-posterior sequence, while in others the appendages of the hindmost region of the body (pleopods), develop before the appendages of the mid-body region (pereiopods). In copepods, similar instances of the anticipated maturation of some pair of appendages before those in front of them have been recently illustrated by Ferrari (1993).

Something like progradous development in the morphogenesis of appendages has been described for the antennae of a large moth, *Antheraea polyphemus*, by Steiner and Keil (1993). During the pupal stage, the antennae are initially developed as leaf-like blades. These then become progressively segmented through the effect of incisures developing from the edge of the blade towards the prospective rhachis of the antenna.

Much more intriguing is the case of the so-called gonopods of male helminthomorph millipedes. In these animals, with the moult leading to the first (or only) mature stadium, one or two pairs of legs, normally developed as walking legs in the previous stages, are abruptly changed into sexual appendages of unusual, unsegmented, and often extremely complex shape. Interestingly, this specialisation is sometimes reversible. In a few julid species, sexually mature males may moult into so-called intercalary males, which are not sexually mature and bear "sexual" appendages of a shape somewhat midway between typical walking legs and full formed gonopods. A further moult, again leading to a mature condition with typical gonopods, is occasionally observed. Somewhat parallel events are known in peracarid crustaceans, especially tanaidaceans.

Arthropod complexity: some speculations

It is tempting to speculate about the common background to all these dimensions and variations of complexity. Articulating the body into regions means to fix a small number of strong markings along the main axis of the body. These markings act as "hot spots" (Minelli and Schram, 1994) for the subsequent expression of whole alternative networks of structural genes. The same seems to go on with partitioning the appendages into a few major segments. The same also seems to go on, although perhaps to a lesser degree, with the distinction of two or three domains along the dorsoventral axis of the body. The same, finally, goes on with partitioning the developmental sequence into a few major temporal segments, at least in the case of strongly patterned metamorphoses, as in holometabolous insects and many crustacean groups.

This multidimensional correspondence between structuring processes is, perhaps, the expression of related underlying mechanisms.

Recent experimental work on *Drosophila* (reviewed in Anderson, 1995) demonstrates that one and the same molecular signal, the product of the gene *Gurken*, instructs the follicular cells in the ovary to impose both the antero-posterior *and* the dorso-ventral polarity upon the developing oocyte.

On the other hand, there are many indications, in insects, of extensive similarities and even overlappings in the mechanisms of genetic control of segmentation and specification of regions along the longitudinal body axis *and* the appendicular one (e.g., Carroll, 1994).

Along each one of the time/space dimensions we are discussing here, arthropods become partitioned into a small number of units, the transitions (e.g., from thorax to abdomen, or from pupa to adult) being marked by a more or less dramatic choice between alternative developmental subroutines, possibly involving a number of genes which are switched off in the neighbouring domains.

As already remarked, there seems to be a *low* upper limit to the number of body regions. I wonder whether regions could be regarded as a kind of units in competition for the access to some resources, much in the sense of the competition between alternatively specialised cell-lineages within one individual animal, according to the model developed by Leo Buss (1987) in his book *The Evolution of Individuality*. More recently, Buss (1990) has suggested that body segments might be regarded as competitive units, but I think that such competition, if it exists at all, must be very slight. Indeed, segments are in principle equivalent units, like the cells of the same clone. They obviously are in competition for materials, but not for genetic resources, i.e., for activation (or de-repression) of alternative genetic networks. Tagmata, instead, are basically heterogeneous units, possibly relying on alternative genetic networks, whose number (to follow Kauffman, 1993) could be small and thus potentially limiting.

However, there seems to be no need to embrace wild speculations about the functional organization of the genome. To quote Kauffman (1993:53–54), "as systems with many parts increase both the number of those parts and the richness of interactions among the parts, it is typical that the number of conflicting design constraints among the parts increases rapidly. Those conflicting constraints imply that optimisation can attain only ever poorer compromises. No matter how strong selection may be, adaptive processes cannot climb higher peaks than afforded by the fitness landscape. That is, this limitation cannot be overcome by stronger selection." This means that the upper limit to the number of interacting parts (here, tagmata) must always be small, even in what we like to call higher organisms. Maybe this limit is more stringent here, due to the synorganisation of integrated, co-adapted body regions.

Problems and prospects

The concerted variation in complexity of the morphological and developmental body axes of the arthropods is not so general as the previous pages may suggest. Some contradictory evidence and problematic areas shall be cited here.

A first difficulty is that many arthropods can regenerate appendages, or parts thereof, whereas no arthropod is able to regenerate body segments. In this respect, there seems to be no equivalence between the longitudinal and the appendicular axes.

Another problem is that, while dealing with the temporal dimension of development and its complexity, I have deliberately dealt with post-embryonic development only. As for the embryonic portion of development there are several obscure areas. One of these is that the first developmental stages are not yet under zygotic control; we could perhaps describe them as a kind of extended, or prolonged, phenotype of the mother.

Another difficult question is, whether it is meaningful to interpret the temporal partitioning of the embryonic development along the same lines that we use to distinguish a larva from a pupa from an adult beetle or fly.

I have deliberately de-emphasized segments in deference to the importance of structural and developmental complexity. In a developing arthropod, segments behave as building blocks, not necessarily more complex than are other building blocks of developing organisms (cells, for instance, or embryonic sheets). Segmented organization at some stage is probably important to ensure regularity of patterns, including the equal spacing of transient or definitive structures. Think of the problems in establishing a correctly wired nerve cord or providing for the mechanically important regularity in the distribution of coelomic pouches and body wall muscles in a typical annelid. No wonder, that a segmental arrangement of equipotent cells is also transiently expressed by animals which, later on, do not exhibit the slightest trace of segmentation, such as nematodes (Salser and Kenyon, 1994).

Segmentation, however, can also have a functional value in the fully-developed animal, especially in locomotion. This circumstance has obviously been central in establishing the body plan of arthropods. However, as soon as such a functional constraint is no longer at work, segmentation is reduced or disappears altogether. However, in this case too the complexity of the body plan and that of its development (a complexity originally built on the foundation of a segmented germ) is not lost together with segmentation. This complexity is a much more reliable expression of the genetic architecture of the animal, than segmentation per se. Of course, this is not a privilege of arthropods, but arthropods, just because of their segmented, articulated organization, are perhaps more suitable to rational dissection of the issues than are other animals. In this way, the manifold morphological and developmental complexity of arthropods may become a paradigm for metazoans generally.

Acknowledgements

I am very grateful to Michael T. Ghiselin and Giovanni Pinna for inviting me to the very stimulating San Francisco workshop. In particular, I most sincerely acknowledge

Mike's very kind hospitality, as well as the generous support provided by the California Academy of Sciences.

An earlier draft of this paper was carefully read by Michael T. Ghiselin, James R. Griesemer, Nicholas D. Holland and Frederick R. Schram: they provided me with detailed and useful comments, for which I am very grateful.

The work has been supported, in part, by grants from the Italian C. N. R. and M. U. R. S. T.

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HOMOLOGY, HOMEOBOX GENES, AND THE EARLY EVOLUTION OF THE VERTEBRATES

Nicholas D. Holland

Marine Biology Research Division, Scripps Institution of Oceanography
La Jolla, California 92093-0202

During the last decade, developmental genes have been found to be remarkably conserved from one metazoan phylum to the next. This conservation has implications for animal evolution. Among other things, developmental genetic data are now helping to indicate homologies between body regions of distantly related animals. After briefly introducing developmental evolution and homology, the present paper illustrates how this approach can help establish homologies between animals with *moderately divergent* body plans. The focus is on work relating to the origin and early evolution of the vertebrates. A first example uses the protein products of *engrailed* genes to compare mandibular arch muscles of jawless versus jawed vertebrates. The results are relevant to the question of the origin of vertebrate jaws. A second example uses *Hox* genes to compare central nervous system regions of cephalochordates versus vertebrates. The results raise the possibility that the proximate invertebrate ancestor of the vertebrates had a relatively large brain. The success of these rather conservative applications of the method forcefully raises the following question: Over how wide a spectrum of the animal kingdom can one make convincing homologies based on expression domains of developmental genes? There are, at present, several attempts to use developmental genetic data to establish homologies between body regions of animals with *highly divergent* body plans. Most notably, there has been a revival of the once scorned proposal that some ancestral arthropod or annelid underwent an inversion of the dorsoventral body axis and gave rise to the vertebrates. It will be interesting to see whether this relatively radical approach can be substantiated by the rapidly advancing knowledge of developmental genes in a diversity of animal phyla.

The celebrated 1830 debate between Cuvier and Geoffroy Saint-Hilaire, although it covered a variety of issues, was triggered by their deep differences over how broadly the notion of unity of composition (also termed unity of plan) should be applied. In other words, the question was: Over how wide a spectrum of the animal kingdom should one try to establish homologies? Cuvier, for all his insistence on the primacy of function over form, still recognized homologies based on form — but only between animals with quite similar overall body plans (e.g., between mammals and birds). In contrast, Geoffroy had absolutely no reservations about comparing structures between animals with radically different body plans (e.g., between vertebrates and molluscs). In the opinions of Appel (1987) and Corsi (1988), the debate did not resolve this issue clearly.

For a century and a half following the debate, biologists continued to be divided into those taking comfort in the narrower vision of Cuvier and those daring to consider the broader, more exciting, but seemingly less reliable vistas of Geoffroy. Most recently, striking advances in developmental genetics have revived interest in this old controversy and have suggested to some (like Gould, 1991 and Slack et al., 1993) that Geoffroy was, after all, closer to the truth than Cuvier.

In recent years, the evolutionary implications of data from developmental genetics have been discussed under the rubric of "developmental evolution" ("devo-evo" for short) or, more soberly, "comparative molecular genetics" (Lawrence and Morata, 1994). Such data can enrich evolutionary discussions in several ways. For instance, one can construct family trees of developmental genes (Schugart et al., 1989; Schubert et al., 1993) or one can study developmental gene duplication events in evolutionary lineages (Garcia-Fernàndez and Holland, 1994). The present paper, however, is concerned with only one way of utilizing developmental genetic data: namely, the use of expression domains of developmental genes as phenotypic characters for helping to establish homologies between body parts of distantly related animals. This approach, although often employed during the last few years, has not yet been thoroughly discussed in relation to homology — not even in the most recent book on the latter subject (Hall, 1994). Thus my present purposes are: (1) to review the barest essentials of developmental genetics and homology and (2) to illustrate our method by discussing two examples from our recent work, which is relevant to the origin and early evolution of the vertebrates. Coverage of developmental genetics is strictly limited here to facts essential for what follows. Readers wishing a fuller introduction to the field are referred to the references cited in this section, which have been selected for readability and breadth of view.

The last decade has witnessed the unexpected discovery that the molecular machinery of development is remarkably similar from one animal phylum to the next (De Robertis et al., 1990; Holland, 1990, 1992; Lawrence, 1992; McGinnis and Krumlauf, 1992; Jacobs, 1994). Several kinds of developmental genes and their protein products include structural motifs that are highly conserved across a wide range of animal phyla — a concrete example would be the correspondence of a particular homeotic gene in a fruitfly with a particular *Hox* gene of a vertebrate. Conservation is evident not only at the level of base and amino acid sequences, but also in the spatiotemporal patterns of gene expression in the embryo. All this conservation of sequence and expression has frequently been assumed to reflect a conservation of function. This assumption very recently has begun to find experimental support (McGinnis and Kuziora, 1994).

The best known example of a conserved motif in devel-

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opmental genes is the homeobox (McGinnis, 1994), a sequence of 180 base pairs encoding a 60-amino acid homeodomain which is part of a protein that can bind to DNA and act as a transcription regulator. The most conspicuous (although not the only) function of homeobox genes is to specify positional identities to body regions along the anterior-posterior axis of developing embryos. Two such homeobox genes will be used as examples later in the present paper, after a review of homology.

The most recent and synoptic review of homology (Hall, 1994) reveals that today's biologists are more divided than ever on most aspects of the subject, including its uses, concepts, definitions, and recognition criteria. Therefore, a brief review of homology will be useful here for clarifying what my co-workers and I are doing and, just as importantly, what we are *not* doing. I will sidestep some aspects of homology such as its utility at the level of populations, communities and zoogeographic zones. These topics are thoroughly explored in the chapters in Hall (1994).

Before discussing concepts and criteria of homology, it is only fair to recognize a couple of general difficulties with the subject. The most fundamental is the lack of consensus about how the human mind functions in identity recognition. Biologists are usually content to leave this issue to philosophers and psychologists while getting on with the business of comparing features of different organisms.

The second pervasive problem with homology concerns biological identity. Unlike deductively proven mathematical identities, inferences about biological identities do not have probabilities of one. For example, when we homologize two structures, the probability that we are correct ranges from close to one (say for a mammalian femur versus a bird femur) to considerably less than one (say for annelid setae versus brachiopod setae). The lower the probability, the less comfortable we feel, and there is as yet no agreement on how to quantify our discomfort. Simply passing the buck to a computer rarely makes this problem disappear. Thus, like much else in the historical sciences, homologies and the phylogenies built upon them may not be falsifiable in the strict sense of Popper. Again, most biologists, in order to transact any business at all, tend to leave this problem to the philosophers.

The concepts and criteria of homology are easiest to review in approximate chronological order. Up to the late 1700s, the homology concept was *intuitive* (which is to say there was no concept at all). Even so, some good homologies were made: a well-known example was Belon's comparison of bird and human skeletons in 1555. No explanations were offered, and no recognition criteria were stated.

From the late 1700s through the mid 1800s, the homology concept was *idealistic*. The explanation was that structures in different organisms are homologous because they correspond to the same archetype = to the same Law of Nature = to the same Idea in the mind of God. During this era, the structures in question were usually those of adult, extant organisms, although features of embryos and extinct species were sometimes included in the analysis. In comparing a given structure in two different organisms, the chief criteria for recognizing homology were usually considered to be the following: (1) positional equivalence within the overall body plan, e.g., in different groups of higher vertebrates, the temporal bones have similar positions within comparable systems of other skull bones; (2) special quality, e.g., the testes of all vertebrates agree in special features (like seminiferous cysts and tubules) without necessarily having equivalent positions; (3) transition, such that, in a comparison between two species, apparently dissimilar structures are recognized having positional equivalence or special quality if united in a series by transitional structures in additional species. It should be understood that transition in this context does not refer to the substitution of one base for another in a nucleic acid. It should also be understood that each criterion is known by a variety of names; however, this changes nothing, beyond making some authors a little harder to read.

Since the mid 1800s, the dominant homology concept has been *historical*. The basic explanation is that structures are homologous because they correspond to an equivalent structure in a common ancestor. The chief recognition criteria are the same three used during the era of idealistic homology. To these three criteria, a fourth is sometimes added: this is the congruency criterion, which means that each suspected homology should be examined in the context of other lines of relevant evidence (clearly, if one line of evidence contradicts another, something has to be wrong).

Over the years, several amendments have been made to the historical homology concept. As a result, the categories of compared features have increased well beyond structural parts of adult organisms. First came the addition of embryonic primordia, with the connotation that, in different animals, structures derived from an equivalent embryological primordium are especially likely to be homologous. Later additions included physiological and behavioral characters. Most recently, there has been wide acceptance of molecular traits as indicators of homology — originally at the level of metabolic pathways and later at the level of base and amino acid sequences in genes and their protein products, respectively. At this point, it became important to distinguish between orthology (correspondence between molecules in two different organisms) and paralogy (correspondence between molecules within the same organism). Increasing the number of categories of evidence for homology has raised the unresolved problem of what to do when different categories do not support one another. For example, molecular biology suggests lampreys and hagfishes should be grouped together, but morphology indicates that lampreys are more closely related to gnathostomes than either is to hagfishes (Forey and Janvier, 1994).

An additional development within the historical concept of homology has been the augmentation of the criterion of transition. First there has been the use of stratigraphic data to give a time dimension and directionality for changes in homologous structures, and second there has been an increased insistence that transitional character states must be functionally credible.

In recent years, even as the historical concept was being refined, another concept, that of *biological* homology, was introduced. This concept is built upon the notion of the epigenetic landscape that Waddington (1940) originally proposed in a purely developmental context. Waddington's ideas, as transplanted to the realms of homology and evolution, yield the following explanation: developmental constraints conserve homologous traits by channeling development to permissible end-points separated by virtually impossible end-points. Thus homologies should be underlain by (and, in the thinking of some, should be equivalent to) networks of inductive interactions that become very hard to alter even in part. It is commonly, but by no means universally, proposed that the chief criterion for recognizing biological homology is the discovery of conserved networks of epigenetic interactions during development (for a critical review of this notion, see Hall, 1995). In all, the biological homology concept has defied crisp definition so far, primarily because the underlying notion of constraint is still so contentious.

At this point, it is useful to interpolate a paragraph to record the current attitudes of cladists toward homology problems. A few cladists think that they can somehow build a cladogram without prior consideration of homologies. The remaining cladists — for whom a data matrix of good homologies is the prerequisite for good tree building — hold various combinations of beliefs, and I will mention only a few recurring themes. In dealing with homology *concepts*, some cladists prefer to avoid reference to ancestors (1) either by adhering to the historical concept but reformulating it in terms of synapomorphy (2) or by embracing the biological concept, which they sometimes redefine in terms of continuity of information instead of gene networks. In dealing with homology *criteria*, some cladists reject transition, evidently because this criterion is partly grounded on paleontological information that can sometimes indicate a series of transitions along an unbranched segment of a lineage (i.e., anagenesis); such data may be considered inappropriate for a strictly cladistic analysis based only on branching.

To return to the main stream of the present paper, I agree with Minelli (1993) that more than one concept of homology is probably defensible; indeed, the most appropriate concept to use could be determined by the level of biological organization under consideration (Hall, 1994). I was brought up in the tradition of the historical concept, but think the biological concept is strengthened by recent advances in developmental genetics and is probably superior for accommodating phenomena of serial homology. Even so, for what follows, I will use the historical and not the biological concept. My reasons are strictly practical and not doctrinal. The problem with the biological homology concept is that little if anything has yet been discovered about regulatory gene networks in animals of the greatest phylogenetic interest (e.g., monoplacophoran molluscs, peripatus, pterobranchs, appendicularian tunicates, amphioxus, hagfishes, etc.). Thus, for my purposes, I will fall back on the historical concept.

Here, then, is the crux of our approach. Within the framework of the historical homology concept, we are using the criterion of special quality sequentially at two different levels of organization. The first level is molecular: at this point, homologies between genes are identified from the overall agreement of aligned sequences of bases or of the amino acids encoded by them. The second level at which we use the criterion of special quality is phenotypic: at this point, spatiotemporal expression patterns of homologous genes, as detected by the presence of their mRNA or protein products, are used as phenotypic characters to indicate homologous structures between species. It should be understood that such gene expression data help establish homologies, not in isolation, but in conjunction with other relevant characters.

Implicit in our approach is the assumption that there is a one-to-one mapping among the genetic, epigenetic (gene network), and phenotypic levels of organization for the particular genes we are studying. For instance, in the words of Akam (1995), "*Hox* genes are not just markers for homology, they are part of the mechanism that defines it." This seems to be so, but little can yet be said about such a mechanism except that it probably involves at least the following two features: first, *Hox* genes and their contiguous gene networks appear to remain relatively stable over evolutionary time, and, second, the modest changes that have occurred in *Hox* expression domains and in *Hox* interactions with other genes can alter phenotypes dramatically (Day, 1995). Obviously, the assumption of one-to-one mapping may not hold for developmental genes when multiple hierarchical processes interact strongly to produce a phenotype (Hinchliffe, 1994), and in some other instances (Hall 1995).

My first example compares a jawless vertebrate (a lamprey) with gnathostome vertebrates; details of this work are in Holland et al. (1993). The parts compared are specific jaw muscles, and the genetic marker is the *engrailed* gene (*en*). The most comprehensive comparison of *en* genes with one another and with other homeobox genes is in Bürglin (1994). Only one *en* gene is known in lampreys (Holland and Williams, 1990), while two or three paralogs of *en* have been found in each major gnathostome group.

The first step in our homology recognition is a comparison of amino acid sequences in the lamprey and mouse *en* proteins. Most of the amino acid sequence for the homeodomain of lamprey *en* was determined by Holland and Williams (1990). When this sequence is compared to the amino acid sequences in engrailed homeodomains of other vertebrates (sequence data from Scott et al., 1989), the amino acid identities range from 75%–80%; in contrast, only 45%–50% amino acid identities are found when homeodomains are compared between lamprey *en* and any of the vertebrate *Hox* genes. Thus, homology between the *engrailed* genes of lamprey and gnathostomes is established by the high proportion of shared, identical amino acids.

The second step in our homology recognition begins with the detection of the expression domain for lamprey *en*. For a series of lamprey embryos and larvae, *en* expression is detected by exposing them to an antibody raised against mouse *en* protein. Cells expressing the gene can be demonstrated by immunohistochemistry, which produces a dark reaction product in whole mounts and histological sections. The first detectable *en* expression is seen at the stage of early head development; at this time, the gene product appears in neural tube cells at the midbrain/hindbrain boundary

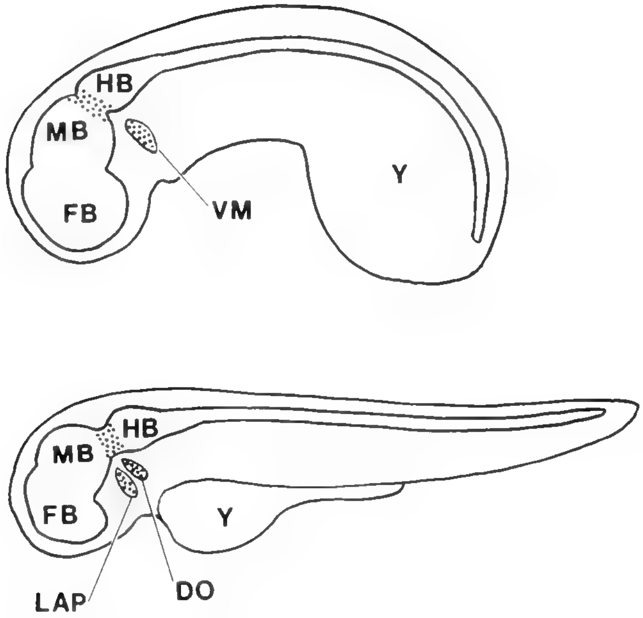

FIGURE 1. Early expression domains (stippled) of *engrailed* in developing lamprey (above) and zebrafish (below). Abbreviations are: **FB** forebrain; **MB** midbrain; **HB** hindbrain; **Y** yolk; **VT** future velothyroideus muscle; **LAP** levator arcus palatini; **DO** dilator operculi. Based on data from Hatta et al. (1990) and Holland et al. (1993).

and in some paraxial mesoderm cells at either side of the mandibular arch. During the following week, the mesoderm cells continue to express *en* while differentiating into the velothyroideus muscles, which provide much of the power stroke for the velum.

Figure 1 compares our data from lamprey embryos with the expression domains of *en* that Hatta et al. (1990) demonstrated in the head of zebrafish embryos. In both embryos, there is a zone of *en*-expressing cells in the neural tube at the midbrain/hindbrain boundary; this is not a very exciting discovery, since both gross and fine neuroanatomy long ago revealed that this region of the neural tube is homologous between lampreys and gnathostomes. Far more intriguing is the similarity between part of the myogenic mesoderm of the embryonic mandibular arch of lampreys and zebrafish (Fig. 1). Zebrafish *en* is expressed in mesenchyme cells of an initially single premyogenic condensation, and expression continues as they differentiate into two of the jaw muscles (the levator arcus palatini and the dilator operculi). We propose that these *en* expression domains (in conjunction with patterns of peripheral innervation) can be used as phenotypic characters to help establish homologies between (1) the velothyroideus of lampreys and (2) the levator arcus palatini and dilator operculi of teleosts.

Our proposed homology between velar muscles of lampreys and some of the jaw muscles of gnathostomes is relevant for the long-standing question of the phylogenetic origin of the jaws of vertebrates. The traditional, textbook scenario, formulated over a century ago by Balfour, derives the jaws from elements of a relatively undifferentiated cranial arch in the proximate common ancestor of the vertebrates. Recently, the broad outline of this scenario has been retained by Mallatt (1996), who has fleshed it out with a wealth of new detail. He has interpreted our data on lamprey *en* to be consistent with his scenario, which starts with a common ancestor that lacks a muscularized velum: in the line leading to the living, jawless vertebrates, there was a centripetal migration of the most anterior circlet of superficial branchial constrictor muscles to form the velum of jawless vertebrates; on the other hand, in the line leading to the jawed vertebrates, these same muscles stayed in place and took on additional functions in suction feeding while retaining the primitive ventilatory function. Alternatively, our lamprey *en* data might also be used to support a converse scenario for the origin of the vertebrate jaws (Jollie, 1977; Forey and Janvier, 1993, 1994). For these authors, the proximate, common ancestor of the vertebrates had a muscularized velum that was retained during the evolution of the jawless vertebrates, but gave rise to the jaws of gnathostomes. It will be interesting to see whether any further evidence will be obtained to support this challenge to the traditional scenario for the origin of vertebrate jaws.

My second example compares two different subphyla of the phylum Chordata: namely a cephalochordate, amphioxus (*Branchiostoma floridae*), versus the vertebrates. The parts compared are regions of the dorsal nerve cord, and the genetic markers are *Hox* genes — specifically, *AmphiHox3* in amphioxus versus *Hox* genes of vertebrates. Details of cloning, sequencing and in situ hybridization of the amphioxus gene are in Holland et al. (1992a).

As the first step in our homology recognition, the amino acid sequences of the homeodomains are compared between *AmphiHox3* of amphioxus and *Hox* genes of vertebrates (sequence data from Lonai et al., 1987; Scott et al., 1989; Holland et al., 1992a). This comparison of homeodomain amino acids between amphioxus and vertebrates gives the following percentages of identities when *AmphiHox3* is compared to the following *Hox* genes: 92% for vertebrate *HoxB3*; 87% for vertebrate *HoxA3*; 87% for vertebrate *HoxD3*; and 60-80% for all the *Hox* genes of vertebrates. In this example, homology is established between *AmphiHox3* and vertebrate *HoxB3* by the high percentage of identical amino acids in the respective homeodomains. This homology is further supported by the corresponding position of the introns in both genes and by the exceptionally long amino acid sequence downstream from the homeodomain in both gene products.

The second step in our homology recognition begins with the detection of the expression domain for amphioxus *AmphiHox3*. For a series of amphioxus embryos and larvae, expression of this gene is found by in situ hybridization with a riboprobe recognizing the mRNA message for *AmphiHox3* in whole mounts of embryos and larvae. The first detectable expression of *AmphiHox3* is seen in posterior, undifferentiated mesoderm and in the dorsal nerve cord of neurula embryos a few hours after hatching. The anterior limit of neural expression is at the boundary between the fourth and fifth somites, where it remains for approximately the next week of development. The somites are convenient fiducial marks for judging the anterior boundary of expression of *AmphiHox3*.

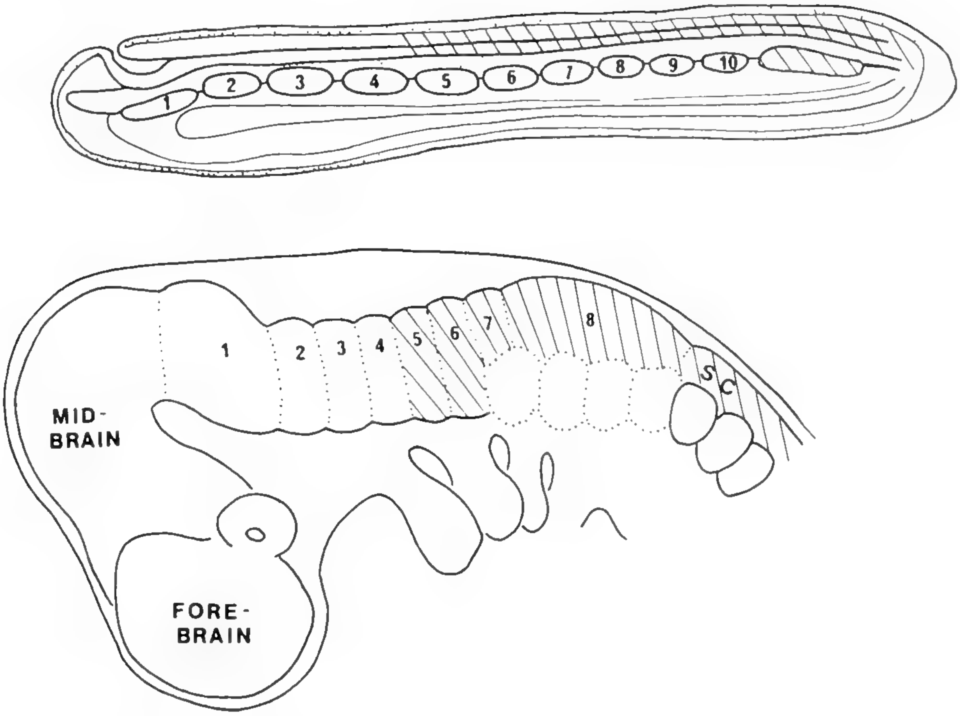

FIGURE 2. Expression domains (diagonally hatched) of *AmphiHox3* in an amphioxus embryo (above) and of *HoxB3* in a generalized vertebrate embryo (below). The mesodermal somites of the amphioxus embryo are numbered, as are the hindbrain rhombomeres of the vertebrate embryo. Based on data from Holland et al. (1992a).

Figure 2 compares the expression domain of *AmphiHox3* with the expression domain of its homologue (the equivalent of mouse *HoxB3*) in a generalized vertebrate embryo. In the vertebrate, the anterior limit of *HoxB3* expression is halfway between the rostral and caudal limits of the hindbrain (at the boundary between rhombomeres four and five). We thus propose that the anterior limit of *AmphiHox3* expression in amphioxus marks a location homologous to the middle of the vertebrate hindbrain.

Our work on *AmphiHox3* immediately raises the question of the extent of the amphioxus hindbrain. Our recent, unpublished work on expression of the amphioxus *engrailed* gene (*AmphiEn*) places the anterior limit of the hindbrain far anteriorly in the central nervous system (a conclusion already tentatively reached from a neurochemical study by Holland and Holland, 1993). It thus seems likely that amphioxus embryos have a very large hindbrain; indeed, one of my colleagues refers to them as "swimming hindbrains." The small percentage of the central nervous system rostral to the proposed anterior limit of the hindbrain might be largely or entirely a homologue of the vertebrate diencephalon (according to neuroanatomical data in Lacalli et al., 1994).

If one accepts that the expression domains of developmental genes can help establish homologies, it should be possible to correlate many parts of the central nervous system between amphioxus and vertebrates. This can be done by demonstrating expression domains of other developmental genes (additional *Hox* genes, *Krox*, *Pax*, *Emx*, *Otx*, *Dlx*, and the like) already known to mark specific regions of the vertebrate brain (Holland et al., 1992b). For amphioxus, this approach could reveal the posterior limit of the hindbrain and help establish the identity of the small region of the central nervous system lying anterior to the hindbrain.

The presence of a large hindbrain in amphioxus runs counter to the usual view that the cephalochordate central nervous system comprises an extremely long spinal cord and a minute, anterior brain (the cerebral vesicle). Even from the few results we have in hand, it seems likely that the vertebrate brain did not evolve solely from the paltry cerebral vesicle of an amphioxus-like ancestor. Instead, vertebrates may have evolved from a proximate ancestor with a surprisingly large brain.

The animals compared in each of the examples above are much more distantly related than Cuvier would have liked, although they are all members of the phylum Chordata. In principle, however, our approach could be extended to compare body regions between even more distantly related animals — if their overall body plans are relatively similar. For a concrete example, the discovery of *Brachyury* expression in the stomochord of the phylum Hemichordata would strongly indicate that this anterior gut diverticulum is the homolog of the notochord of the phylum Chordata. Akam (1995) has criticized the use of single developmental genes as indicators of homology; however, there is little doubt that demonstration of *Brachyury* in the stomochord would be the decisive piece of information for settling the century-old controversy over whether hemichordates have notochords.

We now come to the unresolved question of what happens as we compare animals with increasingly diverse body plans. Slack et al. (1993) were the first to push the envelope. They compared the later (phylotypic stage) embryos of widely divergent phyla of metazoans and extracted a lowest common denominator "zootype." This is a simple, worm-like form with its anterior-posterior axis divided into regions distinguished by the expression of different *Hox* genes during development. Slack et al. (1993) suggested that the order of the expression domains of these genes is a very ancient arrangement, probably already in place in the common ancestor of all bilateral animals. This conclusion appears valid, probably because the authors avoid precise anatomical identifications of the body parts being compared.

Another comparison of animals with very diverse body plans concerns the eye. Unlike a vague body region of a zootype, the eye is a very well-defined organ. *Pax-6* genes (which include not only a homeobox, but also another conserved motif, the paired box) have turned out to be the master control genes specifying eyes in a wide variety of invertebrates and vertebrates (Quiring et al., 1994; Halder et al., 1995). *Pax-6* itself is not a major repository for the developmental blueprint of eyes (although Gould 1994 seems to imply that it is): instead, this gene is the upstream trigger for developmental gene cascades that result in eye development. Thus, as clearly expressed by Patel (in Barinaga, 1995), the *Pax-6* results could well mean that all animal photoreceptors are homologous as cells, but not that all animal eyes are homologous as organs. It is too early to be certain, but, when the overall gene cascades downstream from *Pax-6* are elucidated for eye development, there could be substantial differences from one phylum to the next.

To date, the most interesting and important attempt to homologize body regions in widely diverse animal phyla is focused on the possible reversal of the dorsal and ventral axes during the origin of the chordates. Geoffroy Saint-Hilaire was the first to propose such a notion — a decade before his debate with Cuvier (details in Cahn, 1962). This idea, which has been in great disrepute for most of the twentieth century, has now been revived by several developmental geneticists (Gehring in Wright, 1994; Arendt and Nübler-Jung, 1994; Nübler-Jung and Arendt, 1994; Holley et al., 1995; Travis, 1995). Although data on the expression domains of a few isolated genes would not be good grounds for stampeding us all the way to Geoffroy's extreme position, there is more going on here: interactions within networks of dorsal-ventral patterning genes are beginning to be discovered. It seems likely that the body region homologies being proposed will become more convincing in proportion to the number of interacting genes elucidated. Just how large a constellation of gene interactions would have to be elucidated in order to demonstrate a convincing homology remains an unanswered question. This is a question that bids fair to preoccupy biologists for years to come.

The recent developmental genetic comparisons of animals with highly divergent body plans forcefully raise the issue of what to do if structures traditionally considered to result from convergent evolution should be shown to develop under the control of homologous genes and gene networks. As if this problem weren't knotty enough, an even more radical step has recently been taken by Minelli and Schram (1994). They have proposed that: (1) Especially important combinations of organ-specifying developmental genes occur at a relatively few, fixed locations ("hot spots") along body axes. (2) The hot spots are the same within major groupings of animals (roughly encompassing a few phyla each). (3) A given hot spot might become coupled to different cascades of down-stream genes in different animals (Krumlauf [1994] admits the possibility of such differential coupling, but stresses that it lacks experimental support at present). (4) Phenotypically dissimilar structures (say an appendage versus a gonoduct) resulting from a similar hot spot should be considered "positional homologies." As a result, structures never before mentioned in the same breath — not even as convergences — could be related as positional homologies. These ideas are not supported by the recent work of Burke et al. (1995), who found instances where *Hox* expression marks phenotypic characters and not fixed axial positions. However, much more needs to be discovered about developmental genetics before the validity of positional homology can be adequately tested.

In conclusion, even the relatively scanty developmental genetic data now in hand can indicate body part homologies when the animals being compared have body plans that are *only moderately divergent*. Within these limits, there is much useful work to be done, as exemplified here by our results from lampreys and amphioxus.

However, there are more radical ways to proceed in developmental evolution. The risks are greater, but so are the potential rewards. As more is learned about developmental gene cascades in more kinds of animals, we may be able to compare organisms with *markedly different body plans* and make convincing homologies between organs or body regions. Clearly, homologies of just this sort would be the most useful ones for working out the broad outlines of the evolutionary relations among the animal phyla.

It is an intriguing possibility that a more perfect knowledge of comparative molecular genetics — not just for a few "model system" animals, but for a healthy variety of metazoan phyla — will give us a much clearer picture of the true topography of the tree of animal life, so long sought. The new genetic data have started being used to push the principle of unity of composition to the sort of extremes that once delighted Geoffroy Saint-Hilaire. The ultimate success of this radical approach cannot yet be foreseen clearly (it is even possible that Cuvier might someday have the last laugh). Even so, the mood of developmental evolutionists is currently one of anticipation and excitement.

Acknowledgments

This manuscript was improved by the critical comments of Linda Z. Holland, Jon Mallatt, Margaret McFall-Ngai, an anonymous (and very astute) reviewer, and my fellow participants in the *Symposium on New Perspectives on the History of Life* at the California Academy of Sciences. This work was supported in part by NSF Research Grant IBN 92-21622.

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BRAIN HETEROCHRONY AND ORIGIN OF THE MAMMALIAN MIDDLE EAR

Timothy Rowe

Department of Geological Sciences and
Vertebrate Paleontology Laboratory
University of Texas at Austin
Austin, Texas 78712

The mammalian middle ear forms a distinctive chain of tiny ossicles whose parallel histories in ontogeny and phylogeny are among the most famous in comparative biology. During pre-mammalian history the auditory chain was attached to the mandible, where it functioned in sound transmission to the inner ear. In mammals ancestrally the chain was torn free from the mandible and displaced to a new position behind the jaw. In early mammalian ontogeny the auditory chain begins development as a part of the mandible that is later torn free and displaced backward, recapitulating the evolutionary transformation. Participation by mandibular elements in auditory transmission predates the origin of mammals by more than 100 million years; what is distinctly mammalian is that the mandibular elements become detached from the jaw and repositioned behind it. Two competing theories have attempted to account for this transformation. An evolutionary hypothesis argues that natural selection for improved high frequency audition is the mechanism, while a developmental hypothesis contends that ontogenetic onset of functionality in jaw muscles is the driving mechanism. Neither hypothesis accounts for both the evolutionary and developmental transformations, or for the repositioning of the ossicles behind the jaw.

Phylogenetic analysis indicates that the distinctive inflated mammalian neocortex arose at the same time that the middle ear became detached from the jaw, in the last common ancestor of extant mammals. A study of cranial development in didelphid marsupials using high resolution X-ray CT, histological, and cleared and stained specimens implicates differential growth of the brain in detachment and repositioning of the ossicles. In early ontogeny the brain is a hydrostat that mechanically loads and displaces surrounding tissues, and in mammals it grows to unprecedented size. The ear ossicles approach their mature size during the third week of postnatal development while still attached to the jaw and participating in a continuous arcade of elements extending from the fenestra vestibuli to the mandibular symphysis. The brain continues to grow for nine additional weeks and in the process it bursts the arcade. As the circumference of the growing brain expands, the ossicular chain is torn away from the mandible and carried backwards to its adult position behind the jaw. Unlike the competing hypotheses, the geometry of the growing brain accounts for detachment of the auditory chain from the mandible in both ontogeny and phylogeny, for the precise path of subsequent posterior displacement of the auditory chain during development, and for the timing and extent of this movement. A heterochronic increase in the rate and duration of brain development, which arose in Mammalia ancestrally, may have been the driving force behind the origin of the distinctive middle ear.

Introduction

The study of evolutionary morphology is more than a century old, yet one might argue that we remain largely ignorant of the mechanisms of morphological change that have operated historically. While many potential mechanisms have been identified and some studied experimentally, very few are yet mapped onto phylogenies and hence few historic instances of transformation are fully explained. This situation promises to improve with the emergence of the new discipline of evolutionary developmental biology (Hall, 1992; Hanken, 1993; Hanken and Hall, 1993; Wake et al., 1993, 1996), and as it becomes more fully integrated with phylogenetic systematics. The recognition of heterochrony requires an explicit, corroborated phylogenetic framework and it is this point that makes phylogenetic systematics fundamental to understanding the evolution of development (Fink, 1982; Kluge, 1988). Together, phylogenetic systematics and evolutionary developmental biology afford means to recognize episodes of heterochrony and heterochronic cascades, to discriminate between genetic and epigenetic factors controlling development, and to map onto cladograms these hierarchical agents of change as they have operated historically.

An illustration of how these disciplines might be integrated can be found in a problem involving the origin of the mammalian middle ear (Rowe, 1996), in what is among the most famous transformations in comparative anatomy. The middle ear in extant mammals forms a chain of ossicles that hangs suspended from beneath the adult cranium and comprises one of the most distinctive osteological characters of mammals. The parallel ontogeny and phylogeny of these bones is one of the most celebrated recapitulations known (Goodrich, 1930; de Beer, 1958). The middle ear bones began their phylogenetic histories as hearing ossicles while located in an ancient position extending between the fenestra vestibuli, their point of connection to the inner ear, and the dentary bone of the lower jaw. The ear ossicles thus participated in a continuous arcade of elements extending from the mandibular symphysis to the cochlear housing of the skull. The craniomandibular joint was formed between two bones in the chain, the quadrate and articular, which served the dual functions of hearing and feeding (Allin, 1975, 1986; Bramble, 1978; Crompton and Parker, 1978; Kemp, 1982; Kermack and Kermack, 1984). Over a 100 million year span of pre-mammalian history the middle ear ossicles were gradually reduced in size while the dentary was enlarged until it came to participate in the craniomandibular joint. In the next step of this history, coinciding with the origin of the "crown group" Mammalia, hearing and feeding were decoupled as the chain of ossicles became detached from the mandible. The dentary bone was the only element remaining in the lower jaw, and the craniomandibular joint was established

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Editors, M. T. Ghiselin and G. Pinna

solely between the dentary and squamosal bones. During this transformation, the morphology of the ear ossicles and their anatomical relationships to one another were largely conserved, but as a group they migrated to a new location entirely behind the condyle of the dentary. Detachment of the ossicles from the mandible produced the condition that occurs universally among adult mammals and that, under the typological practices of Linnean taxonomy, was widely regarded as the definitive mammalian character (Olson, 1959; Simpson, 1959). Despite its importance, the mechanism causing this evolutionary detachment of the auditory ossicles from the jaw and their backward displacement has remained poorly understood.

In the early ontogeny of extant mammals several of the middle ear bones differentiate and begin to grow in their primitive positions along the mandible and, for a time in early development, there is a continuous chain of cartilages extending from the oval window to the mandibular symphysis. Later, the ossicular chain separates from the mandibular arch and moves backwards from the jaw to assume its derived position suspended solely by the cranium in a new location entirely behind the mandible. Ontogeny thus recapitulates phylogeny in what would seem to be a highly unlikely transformation, the detachment of the ossicular chain from the mandible and its repositioning in a new location behind the jaw (Toeplitz, 1920; de Beer, 1937, 1958; Rowe, 1988; Filan, 1991).

The evolutionary transformation from a "mandibular ear" (suspended between cranium and dentary) to a "cranial ear" (suspended only from the cranium) involved significant redesign of the most intricate regions of the skull. If the ear functioned for 100 million years while attached to the mandible, why did it detach and shift to a new location? Why is this transformation recapitulated in the ontogeny of extant mammals? My goal in this study is to describe the morphogenesis of detachment and repositioning of the chain of middle ear ossicles in ontogeny and phylogeny. Although generally viewed as the culmination of a long, gradual evolutionary history, I argue later that the episode of detachment occurring in the last common ancestor of extant mammals was qualitatively different from the preceding 100 million year history of ossicular reduction.

Two hypotheses, one evolutionary and one developmental, have attempted to account for the detachment of the ossicles. The evolutionary hypothesis (Allin, 1975) views pre-mammalian history as being shaped by selection for high frequency hearing. It views the detachment of the ossicular chain from the mandible as merely an extension of this trend, but it says nothing of the developmental mechanism that might have engineered this transformation. The developmental hypothesis (Herring, 1993a; Maier, 1987), on the other hand, argues that the onset of functionality of the jaw muscles tears the chain away from the mandibular arch but it does not attempt to describe this transformation in an evolutionary framework. Neither hypothesis addresses both the developmental and phylogenetic transformations, however, nor do they explain the repositioning of the auditory chain to its new location behind the craniomandibular joint. Are the evolutionary and developmental hypotheses complementary, or are they mutually exclusive? Does some other single mechanism address both the ontogenetic and phylogenetic transformations?

Answers to these questions may lie not so much in the ear and craniomandibular joint, where they are usually sought, as in the developmental and phylogenetic history of adjacent parts, particularly the brain. The histories of the mammalian middle ear and brain were believed to be largely independent of each other and to be the evolutionary products of separate morphogenetic mechanisms, an image compounded in the paleontological literature by assertions of convergent evolution in both regions. But unrecognized associations between the brain and middle ear emerge by mapping the variable features of both regions onto a corroborated phylogeny of mammals and their closest extinct relatives (Figs. 1, 2). These associations manifest the hierarchy of heterochrony and implicate a single cascading mechanism in both the ontogenetic and phylogenetic transformations of the mammalian middle ear.

Materials

This study of ontogeny and phylogeny was based upon osteological preparations of adult and developmental specimens of a diversity of mammalian species, and examination of the major collections of synapsid fossils in North America, Europe, Russia, and South Africa. The principal source of developmental information was a densely sampled growth series for the extant didelphid marsupial *Monodelphis domestica*. Didelphids are among the least-encephalized of living mammals and most closely resemble the ancestral mammalian condition in many features pertinent to the present study (Jerison, 1973; Reig et al., 1987). A growth series of more than 200 individuals was obtained from the Southwest Research Foundation (San Antonio, Texas). In *Mono-delphis domestica*, the gestation period is 14–15 days (Fadem et al., 1982; Kraus and Fadem, 1987). The life span of *Monodelphis domestica* is approximately 3 to 4 years. The term "adult" in this case refers to "retired breeders" that were shipped without precise age data by Southwest Research Foundation but with the general description that retired breeders range in age from 9 to 36 months. Specimens dating from postnatal days 0, 1, 10, 15, 27, and 36 were serially sectioned using conventional histological techniques and stained with azocarmine. Approximately 100 specimens dating from day 0 through adults were cleared and double stained for cartilage and bone, and dried skeletons dating from postnatal day 27 through adults were also prepared.

Serially sectioned embryos of *Didelphis* documenting the earliest stages of skeletal condensation (stages 32–35 of McCrady, 1938) were generously provided by the Wistar Institute. These specimens comprise a small fraction of the extensive collection described in McCrady's (1938) classic monograph on embryology of the opossum. Most of this once preeminent collection was tragically lost in the 1950s, but a few sets of serial sections survived and were sent to me by Wistar. I located some additional fragments of the collection in the National Museum of Medicine. The stains are now badly faded on nearly all surviving slides, but the preparations are still useful for studying the early phases of skeletogenesis; catalog numbers indicate that they include several of the sets of sections used by McCrady to define the developmental stages of *Didelphis*.

To augment conventional developmental preparations, complete three-dimensional data sets of dried *Monodelphis* skulls dating from day 27 through old age were generated using an ultra high resolution industrial X-ray CT scanner (Rowe et al., 1993; 1995). This tool can exceed the resolution of medical CT scanners by two orders of magnitude and it produced exceptional imagery of complete *Monodelphis* crania in 100 μ thick consecutive serial sections. A complete 3-D data set of imagery was generated for each of 5 skulls along sagittal, coronal, and transverse axes. A comparative framework for studying the CT imagery of *Monodelphis* was provided by an earlier study (Rowe, et al., 1993, 1995) in which a 3-D data set of CT imagery for the extinct synapsid *Thrinaxodon liorhinus* was generated in 200 μ consecutive serial sections along the three orthogonal axes. *Thrinaxodon* (Figs. 1, 2) has long been of central interest in early mammalian history because it preserves much of the primitive morphology that we might expect to have been present in a distant ancestor of mammals. The opportunity to compare serial sections of individual specimens simultaneously along different axes while handling the intact specimens themselves offered an exceptionally rich opportunity to visualize all details of complex three-dimensional morphology in comparing the derived *Monodelphis* with its more primitive relative *Thrinaxodon*. The *Thrinaxodon* specimen was generously made available by the Museum of Paleontology, University of California, Berkeley (sp. no. UCMP 40466).

Systematic Framework

The systematic framework of this analysis was critical to its outcome. The following discussion is based on the understanding that mammals are the sister group of other extant amniotes (Fig. 1), a conclusion that rests upon analysis of developmental and adult morphology of both hard and soft tissues in a series of phylogenetic tests that included both extinct and extant taxa (Gauthier et al., 1988, 1989; Gauthier, 1994). The term Mammalia is a node-based name (de Queiroz and Gauthier, 1990, 1992, 1994) for a clade whose membership derives from ancestry rather than "defining" characters. The name is used in reference to the taxon stemming from the last common ancestor of extant mammalian species (Rowe, 1988, 1993; Rowe and Gauthier, 1992), what is sometimes referred to as the "crown group" Mammalia.

Two additional taxa are referred to below that include mammals and some of their extinct relatives (Figs. 1, 2). The term Cynodontia is another node-based name referring to the taxon stemming from the last common ancestor shared by Mammalia and the extinct Late Permian taxon *Procynosuchus* (Kemp, 1979, 1980; Rowe, 1993). Cynodonts thus include mammals and their closest extinct outgroups. The extinct taxon *Thrinaxodon* is a basal member of Cynodontia whose anatomy is almost uniformly plesiomorphic. *Thrinaxodon* has been of interest to paleontologists for more than a century in understanding the 100 million years of history immediately prior to the origin of mammals (Rowe, 1993; Rowe, et. al., 1993, 1995). The term Synapsida refers to a still more inclusive taxon (Fig. 1). Synapsida is a stem-based name (de Queiroz and Gauthier, 1990, 1992, 1994) for the taxon that includes mammals and all extinct taxa closer to mammals than to other extant tetrapods (Gauthier et al., 1988; Rowe, 1988).

The phylogeny of mammals and their extinct relatives has received a great deal of attention over the last century and it was one of the first segments of Vertebrata to be studied phylogenetically (McKenna, 1975). During the last decade, a number of independent analyses of early mammalian phylogeny were conducted (Gauthier et al., 1988; Rowe, 1988, 1993; Wible, 1991; Wible and Hopson, 1993) using taxon morphological-character matrices designed for analysis with maximum parsimony software such as PAUP (Swofford, 1986–1994), MacClade (Maddison and Maddison, 1992), and HENNIG 86 (Farris, 1986). Although these studies reached different conclusions on certain points of relationship among extinct taxa, the results for all extant and most extinct taxa were identical. The studies also disagreed in certain judgments on character independence that caused different authors to split or lump suites of cranial features along different lines. This disagreement is significant from systematic and morphological standpoints, but the conflicting decisions on how to score characters did not affect the topology of the most parsimonious trees generated in the separate studies. In fact, in two batteries of tests (Rowe, 1988, 1993), characters of the skull could be entirely removed from the data matrix and the postcranial data alone recovered the same tree as did the complete skeletal data set for the taxa of interest to the present study. The trees in Figures 1 and 2 show only points of relationship that are consistent with all analyses, and they provide the systematic context in which the histories of the middle ear and brain are discussed below. Readers are referred to the original analyses for details of phylogenetic methodology.

Paleontologists have long maintained that both the mammalian middle ear (Olson, 1959; Simpson, 1959; Kermack and Kermack, 1984; Allin, 1986; Miao, 1991) and inflated brain (Kielan-Jaworowska, 1986; Miao, 1991) evolved convergently among synapsids. The genealogy supporting this view was developed with phenetic methods which treated Mammalia as an evolutionary grade and held that participation by the dentary and squamosal bones in the craniomandibular joint constituted achievement of that grade (Rowe, 1993). Under the phenetic paradigm, the Late Triassic-Early Jurassic fossils *Morganucodon* and *Sinoconodon* were viewed as the oldest mammals because they are the oldest fossils that have a load-bearing dentary-squamosal joint, and their anatomy was taken to reflect the ancestral states of mammalian characters. Because they retain a mandibular ear and an uninflated brain, it followed that the ancestral mammal did as well (Patterson and Olson, 1961; Edinger, 1964; Hopson, 1979; Crompton and Jenkins, 1973; Jerison,

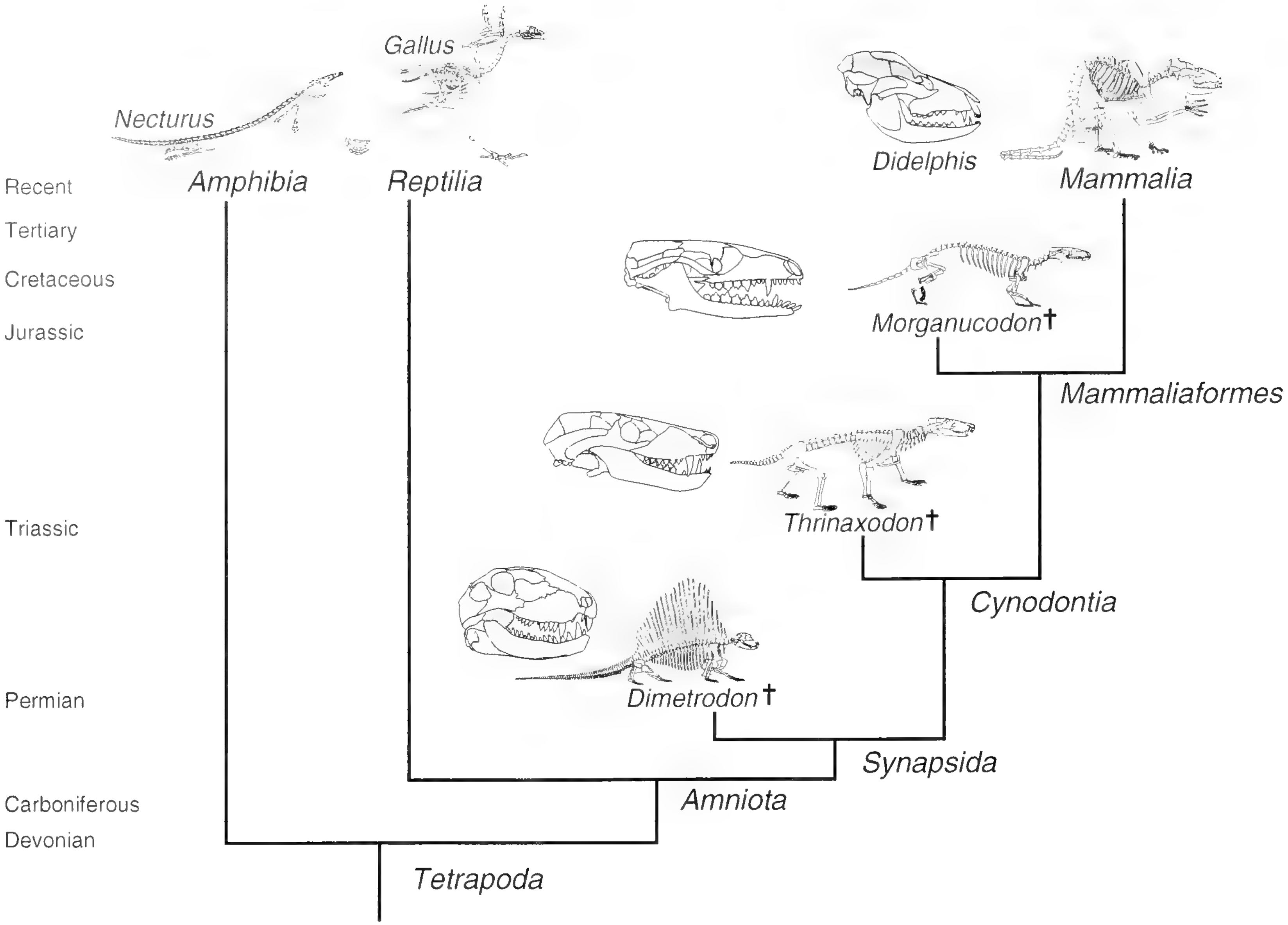

FIGURE 1. Phylogeny of the major groups of extant tetrapods and selected extinct relatives of mammals, based on phylogenetic analyses by Gauthier et al. (1988) and Rowe (1988, 1993).

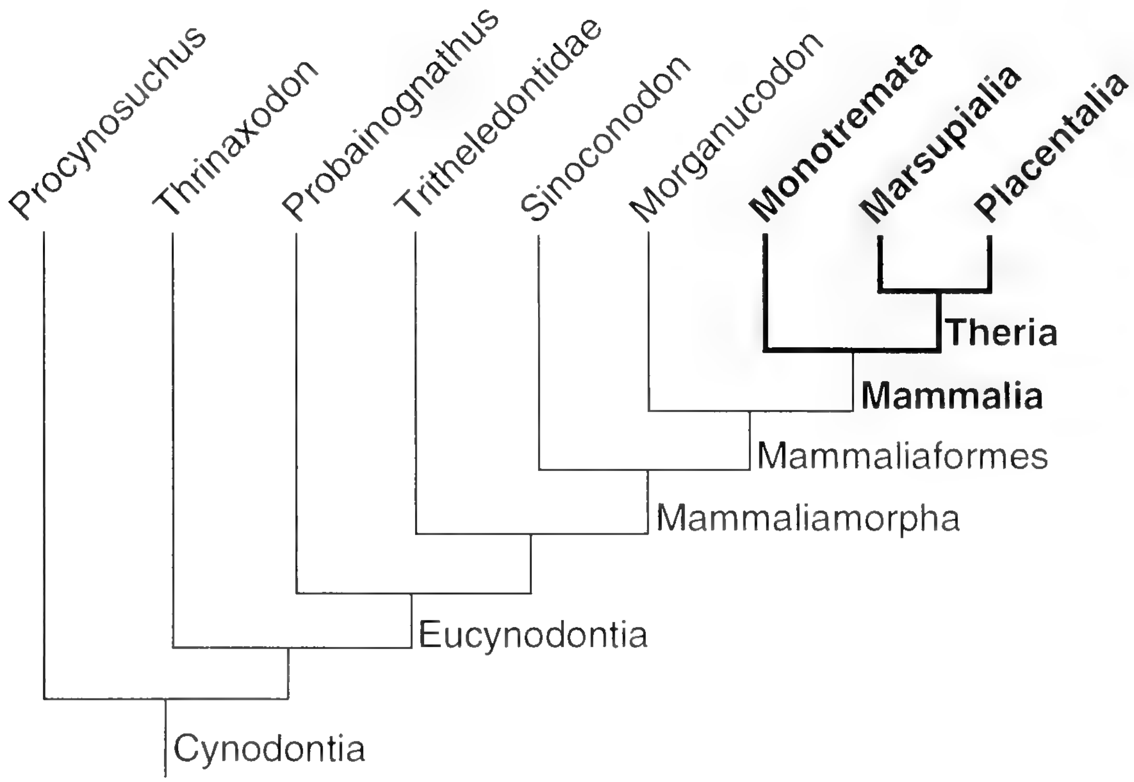

FIGURE 2. Phylogeny of the major groups of living mammals and some of their closest extinct relatives among Cynodontia. The topology among these taxa is consistent with the results of separate analyses by Kemp (1983), Gauthier et al. (1988), Rowe (1988, 1993), Wible (1991), and Wible and Hopson (1993).

1973, 1990). Consequently, the inflated brain and "cranial" ear must have evolved convergently in the lineages containing modern monotremes and therians after the two groups diverged from their last common ancestor.

In contrast, the more recent phylogenetic outlook views Mammalia as a clade, a position corroborated by the many features from all systems that distinguish mammals from other extant taxa (e.g., appendix B in Gauthier, et al., 1988). Additionally, there are extensive lists of synapomorphies from all parts of the skeleton based on analyses of extant species and fossils (Gauthier et al., 1988, 1989; Rowe, 1988, 1993; Wible, 1991; Wible and Hopson, 1993; see also Kemp, 1983, Zeller, 1993). The analyses concur that monotremes and therians are more closely related to each other than to *Morganucodon* or *Sinoconodon*, and that the latter two taxa are consecutive plesiomorphic outgroups to Mammalia (Figs. 1, 2).

Phylogeny of the Middle Ear Ossicles

Early in synapsid history, the bones adjacent to the craniomandibular joint (CMJ) undertook the new function of transmitting airborne sound vibrations to the inner ear while maintaining their primitive structural role in the masticatory system (Allin, 1975, 1986; Crompton and Parker, 1978; Gauthier et al., 1988, 1989; Kemp, 1982; Kermack and Kermack, 1984). An unbroken chain of bones extended from the fenestra vestibuli to the symphysis of the mandibles and at first "mandibular" hearing was probably restricted to low frequencies owing to the massiveness of all bones in the transmission pathway. Vibrations received by the mandible reached the inner ear via the articular and quadrate, which formed the CMJ, and from the quadrate via a massive stapes to the fenestra vestibuli (Fig. 3). A rich fossil record documents the gradual increase in relative size of the main tooth-bearing element, the dentary bone, while the "post-dentary" elements, the articular, prearticular, surangular and angular, were reduced to tiny, delicate ossicles. The quadrate, quadratojugal and stapes, which were suspended from the cranium throughout this history, were also reduced. Over roughly 100 million years of pre-mammalian history, the bones of the auditory chain were gradually reduced while the dentary took on a correspondingly increased structural role in the mandible.

Biomechanical analyses describe the reduction of the bones in the auditory chain as a sound transduction mechanism increasingly sensitive to high frequencies (Allin, 1975, 1986; Bramble, 1978; Crompton and Parker, 1978; Kemp, 1982; Kermack and Kermack, 1984). A host of intricate oropharyngeal functions unique to mammals probably arose concurrently (Smith, 1992; Crompton and Hylander, 1986). *Morganucodon* is a transitional form in that its middle ear ossicles morphologically resemble and probably functioned much like

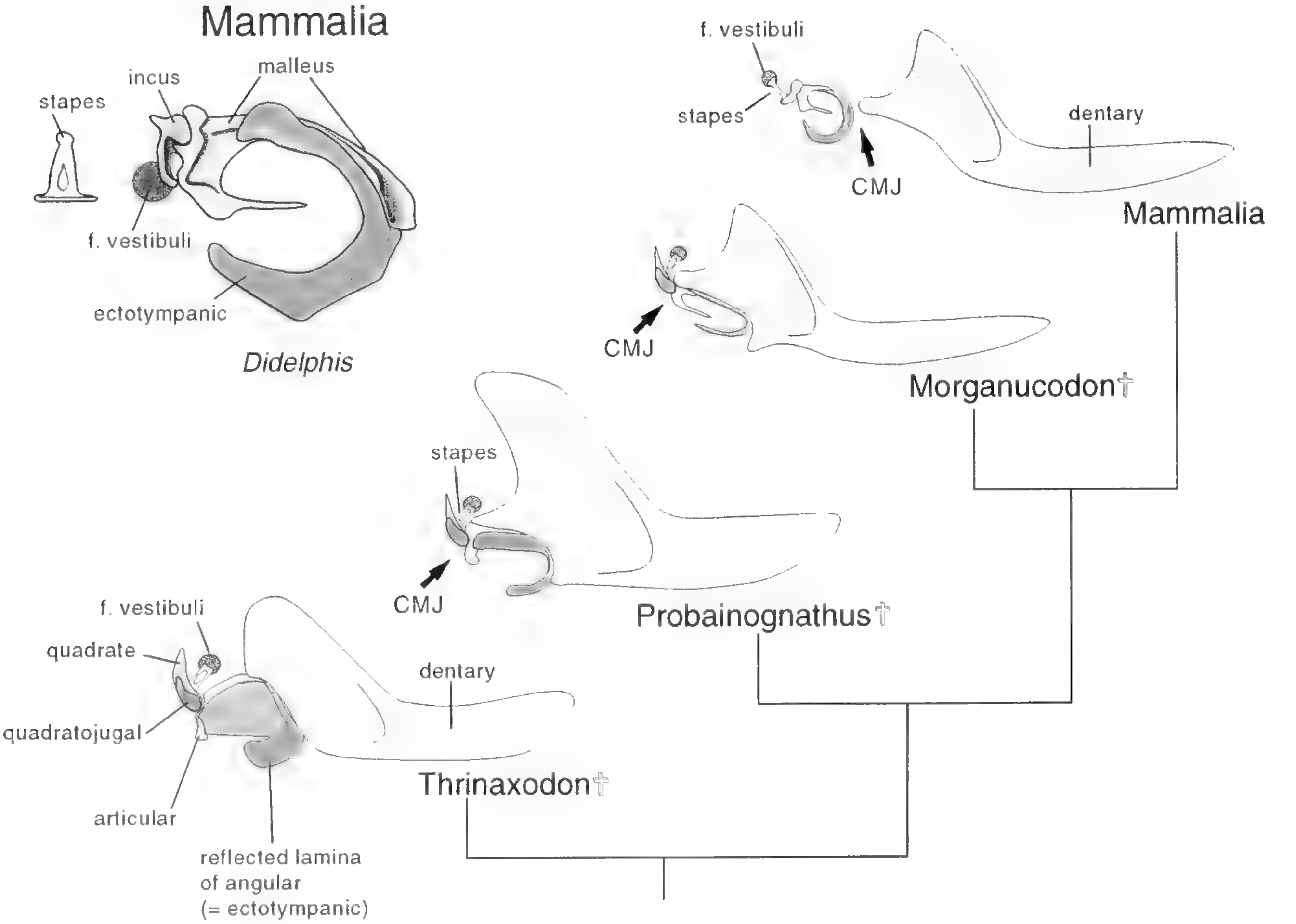

FIGURE 3. Major stages in the evolution of the mammalian mandibular arch. The angular (= ectotympanic) is shaded red, the articular (= malleus) is in green, the quadrate (= incus) is in light blue and the quadratojugal is in dark blue (after Rowe, 1996).

the mammalian ossicles (Allin, 1975), but they remained attached to the mandible where they articulated into a narrow groove along the medial edge of the condylar process of the dentary and hung suspended beneath the dentary. The quadrate and articular also persisted as structural elements in the CMJ (Crompton and Hylander, 1986). In pre-mammalian synapsids, mastication and hearing were never fully decoupled.

This situation is transformed in mammals, in which the postdentary bones are separated from the mandible in adults. In addition, the entire auditory chain is displaced to a new position entirely behind the mandibular condyle where it is suspended solely by the adult cranium (Fig. 3). The dentary alone forms the adult mandible, and together the dentary and squamosal form the entire CMJ (Kemp, 1983; Gauthier et al., 1988, 1989; Rowe, 1988, 1993; Wible, 1991). The origin of mammals coincided with the shift from a mandibular ear to a cranial ear as the auditory and masticatory systems became decoupled. In many mammals the ear ossicles are widely separated from the new CMJ and lie behind intervening secondary auditory structures such as a tympanic process or bulla, which are derived features within Mammalia (Rowe, 1988, 1993). In their new position, the quadrate (= incus) remains attached proximally to the stapes and distally to the articular (= malleus), while the prearticular (= os goniale) and surangular (= ossiculum accessorium mallei) are tightly bound or fused to the articular, and the articular is ligamentously attached to the angular (= ectotympanic or tympanic) which supports the tympanum. The pre-mammalian linkages between the postdentary elements of the auditory chain are thus largely conserved. The major difference is that the quadratojugal fails to ossify and is represented, if present at all, by a thin ligament. Apart from becoming separated from the dentary and repositioned behind it, the mammalian cranial ear probably functions much as did the mandibular ear of *Morganucodon* (Allin, 1975, 1986).

Biomechanical models elegantly explain the pre-mammalian evolutionary reduction of the ear ossicles as a function of hearing and integrated compensatory change in the mandible (Allin, 1975, 1986; Bramble, 1978; Crompton and Parker, 1978). But these models fail to predict or even explain detachment and repositioning of the auditory chain, admitting that the function of the auditory chain was probably not significantly altered by its detachment from the mandible. Some other mechanism must be involved.

Associated Characters

The phylogenetic analysis of mammals and their extinct relatives provided a suite of additional synapomorphies that diagnose Mammalia and that arose at the same time the auditory chain was displaced from the dentary. The association is complex, involving the reduction and loss of bones that were present in *Morganucodon* and more distant out-groups, as well as fusions between elements that primitively remained separate throughout life. Hypertrophy and heterotopy occurred in other elements, and structures that presumably were primitively cartilaginous later became ossified. Nevertheless, their phylogenetic association raises the possibility that some or all of the transformations occurring in Mammalia ancestrally shared a common morphogenetic origin.

In the skull, the pterygoid transverse process and paroccipital process were both reduced in size. The quadratojugal and tabular were lost, as were the proatlas, atlantal rib, and axial prezygapophysis in the neck. The squamosal became hypertrophied to form the entire roof of the glenoid fossa. Also hypertrophied are the occipital condyles, which became extended upwards to enclose roughly two-thirds of the foramen magnum. The distal end of Reichert's cartilage became fused to the otic capsule where it ossifies to form the adult mammalian styloid process. Other fusions occurred between the atlantal intercentrum and neural arches to form the distinctive ring-like mammalian atlas. Between these modifications of the atlas and those of the occipital condyles, the mammalian craniovertebral joint was substantially redesigned. The cribriform plate was ossified, and the maxillary turbinates became ossified as well. In addition, secondary ossifications appeared on the limbs and girdles. More detailed discussions of these and other characters are presented elsewhere (Rowe, 1988, 1993; Gauthier et al., 1988; Wible, 1991).

While there is no obvious pattern linking all of these structures, a large number of them cluster around the brain and lie in the same degree of proximity to the brain as the middle ear ossicles. The influence of an inflated brain was suggested earlier as a dominant morphogenetic influence in shaping the unique features of the mammalian skull (Rowe, 1988, 1993). The nature of this influence can be seen more clearly by comparing the pattern of skeletal change with a common pattern found in the development and phylogeny of the brain.

Ontogeny and Phylogeny of the Mammalian Brain

A large brain of unique design is one of the most characteristic features of extant mammals (Fig. 4). The central region of the forebrain, the telencephalic pallium, differentiates in a singular pattern to form the isocortex (neocortex) and pyriform cortex (Northcutt, 1984; Ulinski, 1986; Reiner, 1991; Butler, 1994). The mature isocortex forms two inflated hemispherical lobes linked by a well-developed dorsal commisure. Each hemisphere has a columnar organization of six radial layers that are generated in ontogeny by waves of migrating cells which originate from the ventricular zone and move radially outwards (Rakic, 1974, 1988; Walsh and Cepko, 1992) and tangentially (Tan and Breen, 1993) to achieve their adult positions. This inside-out pattern of neural development is unique to mammals (Butler, 1994) and is responsible for much of their comparatively huge cortical volume. The mammalian cerebellum is also large in comparison to that of other vertebrates, with an extensively infolded surface and a distinct central lobe or vermis (Edinger, 1964; Jerison, 1973; Gauthier et al., 1988). For convenience, I refer to these features collectively as an "inflated" brain. The cerebellum follows a different developmental pattern than does the cortex, but the cortex and cerebellum share a common history in that an episode of expansion in both regions occurred simultaneously with the detachment of the ossicular chain.

The fossil record of extinct synapsids reveals several successive episodes of cerebral inflation (Fig. 5). During early synapsid history, the primitive tetrapod condition obtained in which the brain failed to fill the adult endocranial cavity. There is evidence in the orbitosphenoid bone of basal synapsids and basal therapsids that the olfactory bulb was suspended at the rostral end of a long thin peduncle which transmitted the olfactory tract (Romer, 1940; Cluver, 1971). Apart from this, few details of brain structure are preserved (Jerison, 1973; Hopson, 1979; Ulinski, 1986).

The basal cynodonts *Procynosuchus* (Kemp, 1979, 1980) and *Thrinaxodon* (Hopson, 1979; Rowe et al., 1993), from the Late Permian and Early Triassic, respectively, are the first synapsids in which the brain filled the adult endocranial cavity. Information about the external morphology of the brain is preserved in these taxa in the form of natural endocasts and in the impressions left by the brain on the inner surfaces of the bones that enclose it. The data sets generated using X-ray tomography (Rowe et al., 1993, 1995) were especially informative in interpreting bone morphology with respect to the structure of the brain (Figs. 6–8). The olfactory bulbs appear as a slight swelling at the rostral end of the forebrain. This reflects a second step toward the mammalian condition in that the olfactory tracts have evidently become engulfed from behind by the cortex, so that the olfactory peduncle and external expression of the olfactory tract are absent, as in mammals. At this stage, however, the circular sulcus, which topographically demarcates the olfactory bulb and cortex in mammalian brains (Figs. 4, 5), is not yet reflected in either endocasts or the bones that lie adjacent to these structures. The forebrain was narrow, undivided, and tubular with broad dorsal midbrain exposure between the cerebrum and cerebellum. A long, narrow pineal foramen (Fig. 6D) indicates the persistence of a pineal eye. Comparison of the cross-sectional anatomy of *Thrinaxodon* and *Monodelphis* in coronal (Fig. 6) and transverse (horizontal) CT imagery (Fig. 7) provides a graphic view of the extent to which the brain expanded during the subsequent descent of mammals.

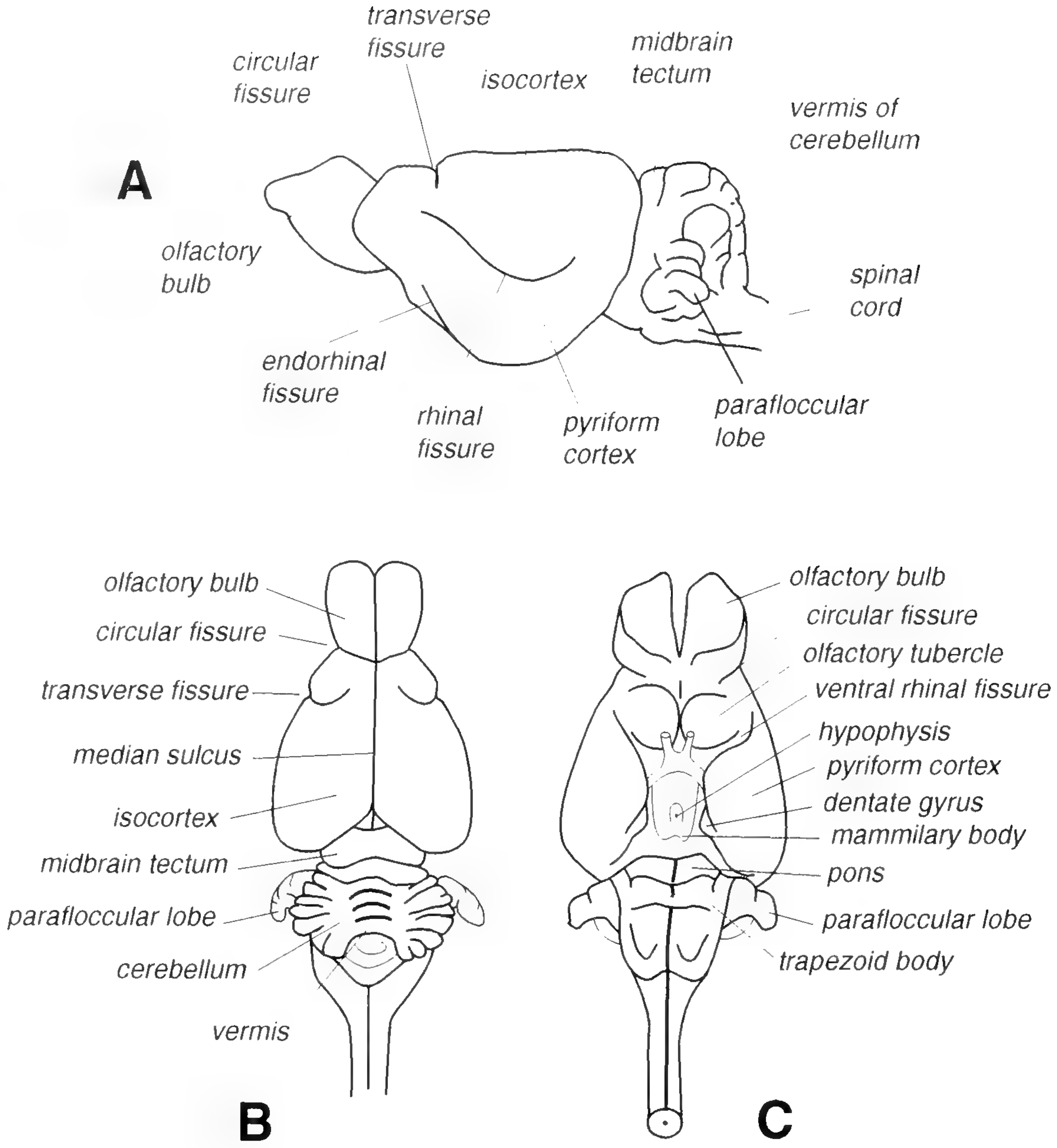

FIGURE 4. Diagram of the brain of *Didelphis virginiana* in left lateral (A), dorsal (B), and ventral (C) views. Based on Ulinski (1971) and Wyman (in Coues, 1872).

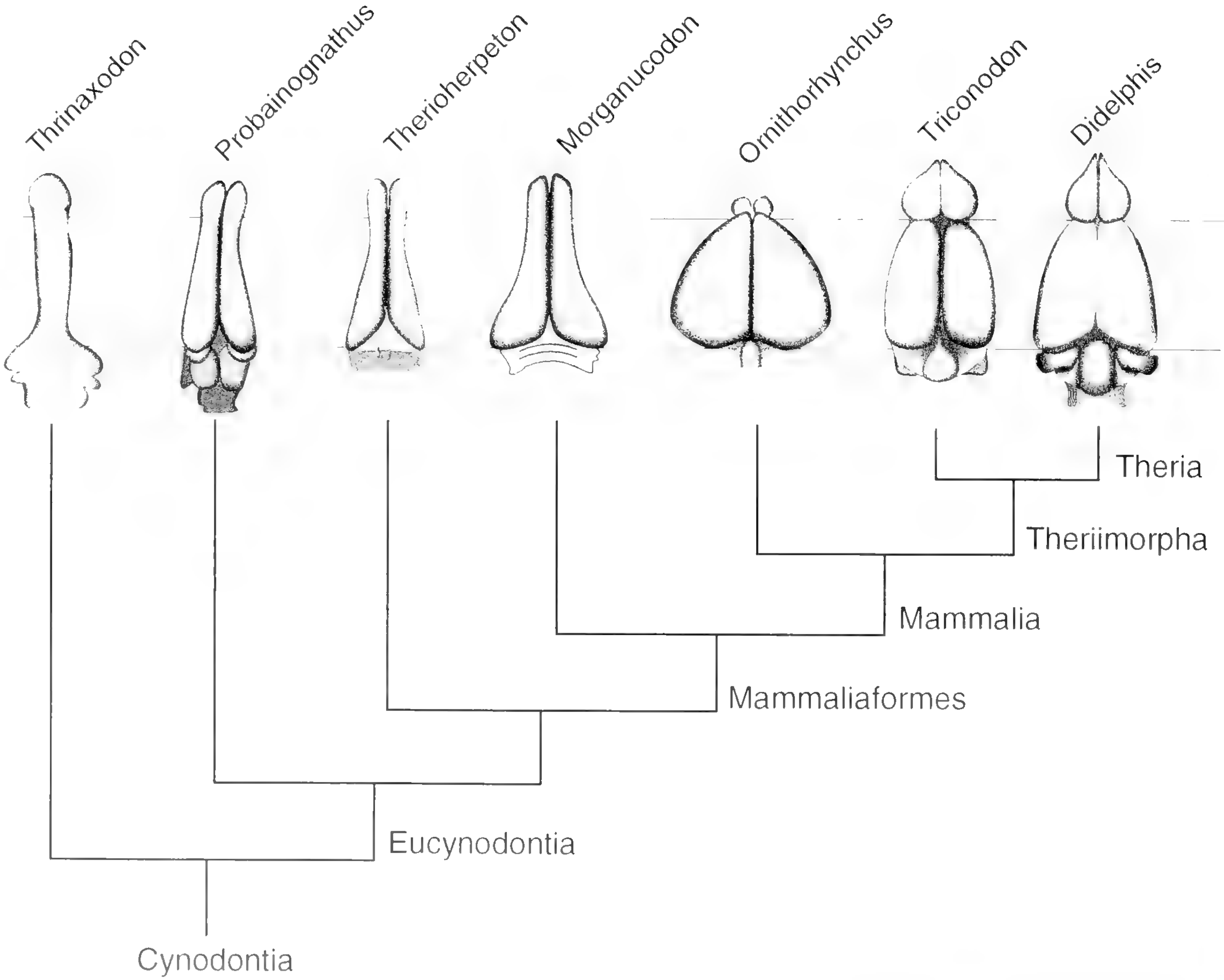

FIGURE 5. Cynodont endocasts in dorsal view, mapped onto a phylogeny of cynodonts (from Rowe, in review). *Thrinaxodon* is based on endocasts illustrated by Hopson (1979) and high resolution X-ray CT imagery of *Thrinaxodon* (Rowe et al., 1993). *Probainognathus* endocast is after Quiroga (1980). *Therioherpeton* endocast is after Quiroga (1984); *Morganucodon* endocast illustrated from impressions on fronto-parietal bones (Kermack et. al, 1981); *Triconodon* endocast is after Simpson (1927); *Ornithorhynchus* and *Didelphis* were illustrated directly from latex endocasts made from Recent specimens.

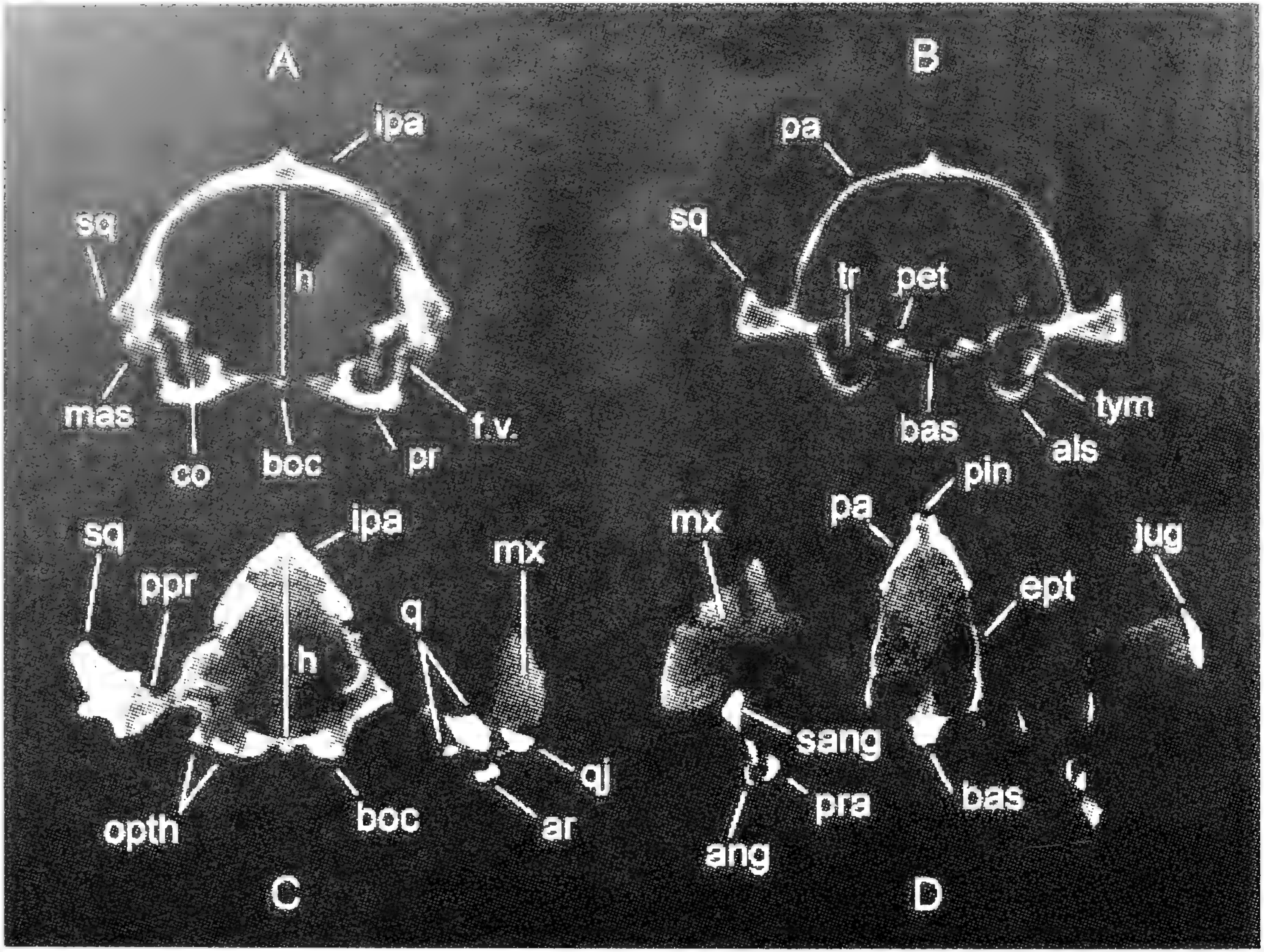

FIGURE 6. Coronal X-ray CT sections through comparable regions in *Monodelphis domestica* (A, B) and *Thrinaxodon liorhinus* (C, D), scaled to the same endocranial height (h). Sections A and C transect the cochlear region. Sections B and D transect the skull further forward, near the level of the hypophysis. A and B are from Rowe (in press), C and D are from Rowe et al. (1993). See List of Abbreviations for key.

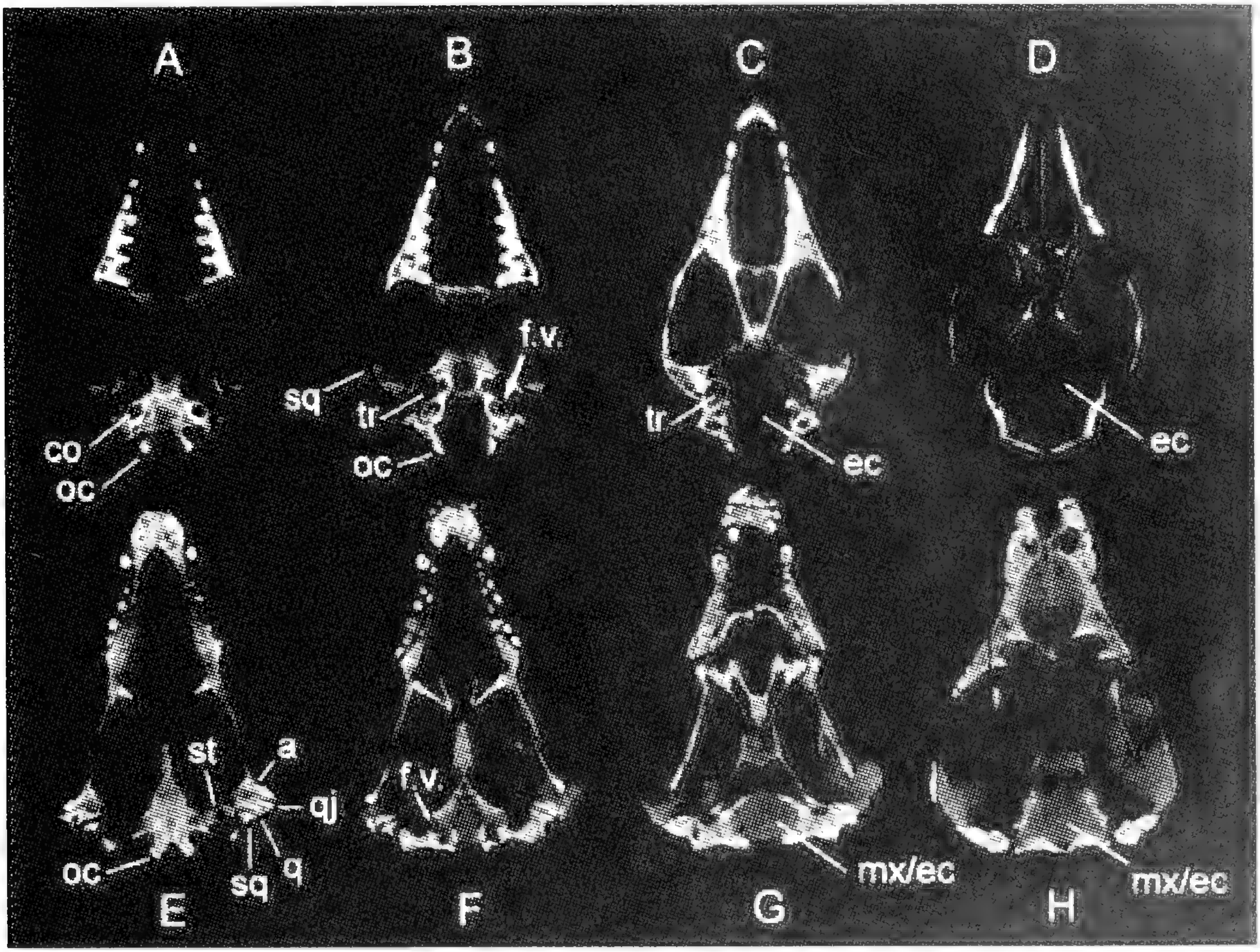

FIGURE 7 Transverse X-ray CT sections through *Monodelphis domestica* (A-D) and *Thrinaxodon liorhinus* (E-H). Sections A and E transect the floor of the braincase; sections B and F transect the fenestra vestibuli; sections C and G transect the middle of the foramen magnum, and sections D and H transect the roof of the foramen magnum. From Rowe (1996). See List of Abbreviations for key

A second episode of cerebral inflation is recorded in an endocast of the Middle Triassic cynodont *Probainognathus* (Quiroga, 1980). The endocast of *Probainognathus* is for the first time "brain-like" (Jerison, 1973) and has begun to leave deep impressions of its outer surface in the walls of the osteocranium. There is now a median sulcus marking the division between right and left olfactory bulbs and dividing the forebrain into two incipient cerebral hemispheres (Fig. 5). At this stage the "hemispheres" remain more tubular than hemispheric, but cortical volume is relatively larger than in *Thrinaxodon*. The pineal foramen is closed and the pineal eye lost. The midbrain remains exposed dorsally, but it is sunken between the enlarged forebrain and cerebellum

A somewhat more inflated brain is reported in the taxon stemming from the last common ancestor of mammals and tritheledontids, on the basis of fossils from Early Jurassic sediments (Rowe, 1993). *Therioherpeton* (Quiroga, 1984), a poorly known basal member of this group (Fig. 5), has a brain-like endocast reportedly larger than *Probainognathus* (Quiroga, 1980) but no newly differentiated features are discernible. Scaling may introduce an element of artifact into the perception of a larger brain, for the basal members of this clade are much smaller than *Probainognathus* and more distant cynodonts. Other early Jurassic fossils indicate that further inflation occurred in the taxon stemming from the last common ancestor of *Sinoconodon* and mammals. This is suggested by such features as bulging of the parietals outward into the temporal fenestra and bony flooring beneath the cavum epipterycum (Crompton and Luo, 1993; Rowe 1993). The inner surfaces of the parietal-interparietal of *Sinoconodon* (Patterson and Olson, 1961, Edinger, 1964; Jerison, 1973) and *Morganucodon* (Kermack et al., 1981) preserve impressions left by the divergent caudal poles of the forebrain, which span a wider curvature than in *Therioherpeton*. Like those of more plesiomorphic cynodonts, however, the olfactory bulbs remained almost cylindrical and lacked any topographic demarcation from the cerebrum Additional plesiomorphic features include confinement of the

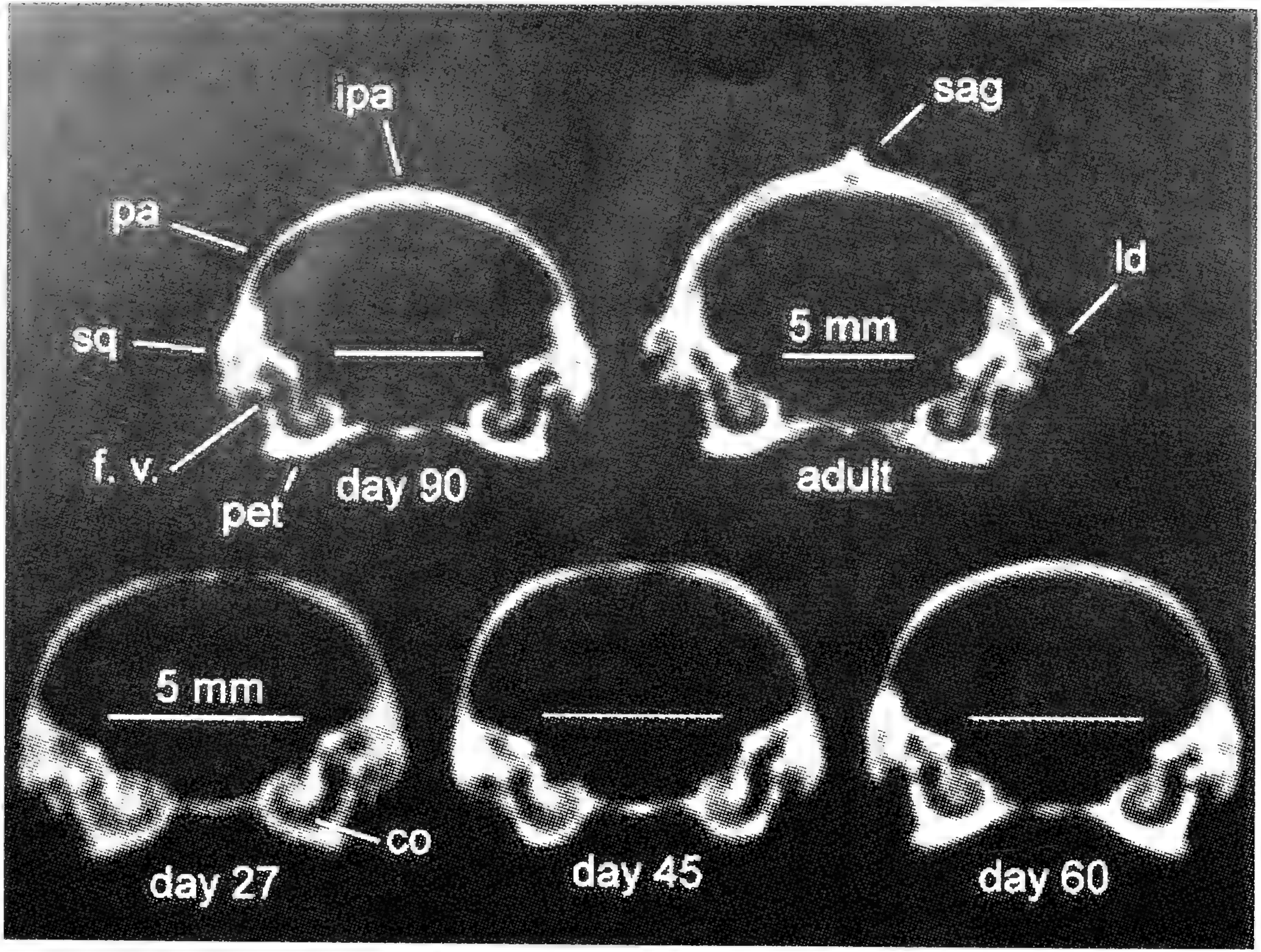

FIGURE 8. Coronal X-ray CT sections through a growth series of skulls of *Monodelphis domestica*, scaled to the same size (from Rowe, in press). All sections represent 100 μ thicknesses and transect the fenestra vestibuli (f.v.), where the stapes passes sound vibrations to the middle ear. The scale bar is 5mm in all sections. Note the progressive thickening of the parietal (pa) and interparietal (ipa) bones and the formation in the adult of the sagittal (sag) and lambdoidal (ld) crests. See List of Abbreviations for key.

cerebral hemispheres to a narrow space between the ascending processes of the epipterygoids (alisphenoids), persistent exposure of the midbrain dorsally, and the front of the braincase remaining unenclosed.

The next major episode of cerebral expansion is recorded in features shared by all extant mammals and which are most parsimoniously interpreted as having arisen in their last common ancestor. The olfactory bulbs are inflated, hemispherical, and sharply differentiated in their external morphology from the cortex by the circular fissure, which now is visible on endocasts for the first time (Fig. 5). The forebrain is greatly inflated into two hemispherical lobes that expand backwards to cover the midbrain. It appears that this is the point in history at which the cortex differentiated into a separate isocortex and pyriform cortex. The isocortex, present in all mammals, is recognizable in endocasts of relatively primitive mammals by its degree of inflation, convex hemispherical form, and backward expansion over the midbrain. In external morphology of the brain itself, the isocortex is also distinguished by both the circular fissure and rhinal fissure. The rhinal fissure classically has been used to identify the isocortex boundaries in endocasts of placentals (Jerison, 1973, 1990). However, it is rarely discernible in endocasts of the small, primitive taxa of relevance here. For example, the rhinal fissure is visible on the surface of didelphid brains (Ulinski, 1971) but it does not appear in their endocasts. The circular fissure is generally discernible in small endocasts and is the more diagnostic of the two fissures among the taxa of interest. An additional innovation of the mammalian brain is that the cerebellum is inflated and deeply folded, with a distinct vermis projecting rostrally along the midline between the caudal ends of the cerebral hemispheres. These cerebellar features are not discernible in the bones of the braincase of *Morganucodon* and more distant relatives.

The oldest fossils preserving skeletal apomorphies derived within Mammalia are from Middle Jurassic sediments (Rowe, 1988, 1993), and an endocast displaying the mammalian features described above is preserved in the Late Jurassic *Triconodon mordax* (Simpson, 1927). In *Triconodon* the mandible is comprised solely of the dentary, and its enclosed Meckelian sulcus indicates that the ossicular chain had become detached from the jaw. The preserved features in this endocast are similar to didelphid endocasts in shape and relative size (Fig. 5). In later mammalian history the rate of brain evolution varied remarkably among the lineages that have survived until today, with didelphids reflecting the least subsequent evolution and cetaceans and primates showing the greatest. Cerebral inflation in mammals is widely held to have evolved in relation to the invasion of a nocturnal and perhaps arboreal niche. Cortical expansion and differentiation into isocortex and pyriform cortex support heightened olfactory and auditory senses (Jerison, 1973), and coincident, overlapping sensory and motor maps of the entire body surface (Lende, 1963a, b, c). Cortical expansion has also been implicated in the evolution of endothermy (Jerison, 1973; Allman, 1990). The enlarged cerebellum is related to the adaptive coordination of movement through a complex three-dimensional environment (Thach et al., 1992).

The origin of the inflated brain in mammals reflects an episode of heterochrony in which the brain began to grow both faster and longer into ontogeny than it did in non-mammalian cynodonts. This is clearly an instance of peramorphosis, where the descendant ontogeny transcends the terminal state achieved during development by its ancestors (Gould, 1977; Alberch et al., 1979; Fink, 1982; Kluge, 1988). Without more knowledge about the relative timings and growth rates of developmental trajectories in the extinct outgroups, it is not possible to discern what type of peramorphosis (hypermorphosis, acceleration, predisplacement) has occurred. In the absence of direct experimental evidence, the most likely genetic moderation of this event now appears to lie in the homeobox genes and homeodomain proteins which direct early patterning in vertebrates generally (Rakic, 1988; Wilkinson et al., 1989; Keynes and Lumsden, 1990; Gilbert, 1991; Langille and Hall, 1993; Rubenstein et al., 1994; Holland, 1996:63–70). In the developing hindbrain, homeobox genes control the identity of rhombomeres, which are segmental bulges that confine clones of cells and domains of differential gene expression (Walsh and Cepko, 1992). Forebrain segmental patterning is now known to be under a similar control (Rubenstein et al., 1994). Simply specifying more segments during early pattern formation may produce an enlarged adult brain, although there is as yet no experimental verification (Marx, 1992). Whatever the genetic control, it is evident that a heterochronic perturbation of the central nervous system occurred in mammals ancestrally, producing differential growth of the brain that launched a cascade of secondary, epigenetic effects.

Epigenetic Influences on Cranial Development

It is well established that familiar physical forces and dynamic processes are significant mechanisms in pattern formation and morphogenesis throughout ontogeny (Oster et al., 1985, 1988; Newman and Comper, 1990). These forces and processes include, among others, gravity (Malacinski, 1984), adhesion (McClay and Ettensohn, 1987; Armstrong, 1989), diffusion (Crick, 1970), interfacial tension (Steinberg, 1978; Heintzelman et al., 1978), mechanical loading (Hoyte, 1966, 1975; Moss, 1968; Hall, 1984a,b,c, 1992; Wong and Carter, 1990; Herring, 1993a,b), electrical potentials (Bassett, 1972; Metcalf and Borgens, 1994; Metcalf et al., 1994), maternal biological rhythms (Lloyd and Rossi, 1993), viscous flow, phase separation, Marangoni effects, convective fingering, chemical concentrations, and density (Newman and Comper, 1990). Newman and Comper (1990) argued that morphogenic and patterning effects are the inevitable outcome of these recognized physical properties of cells and tissues. Many of these forces and processes can affect skeletogenesis, and there is ample observation and experimentation to indicate that the skeleton is responsive to a hierarchy of such influences from the time of earliest condensation of proskeletal tissues through old age (Wong and Carter, 1990).

Newman and Comper (1990) refer to these mechanisms as "generic" physical processes, while others (e.g., Hall, 1990, 1992; Herring, 1993a,b) refer to them under the more inclusive term "epigenesis." These forces may complement and act in concert with biomolecular (genetic) processes, or they may operate by themselves, or not at all in any particular developmental episode. When invoked, they may have broad spatial effects that touch different populations of cells and different tissue types. Many of these processes are known to have nonlinear responses to relevant control variables, such that small changes in rate or magnitude of a process, or through limited interaction between parts can lead to profound effects in the resulting morphology (Mittenthal, 1989). Hall (1990, 1992) refers to this as the spatial and temporal cascading effect of ontogeny, which can produce new and unexpected consequences for adult structure. Major morphological reorganizations in phylogenetic lineages may arise by the action of these mechanisms at different times in ontogeny. The effects potentially are more profound as the forces act during earlier stages in development.

A vast medical, anatomical, experimental, and theoretical literature describes the response of postnatal craniofacial growth in humans and other placental mammals to mechanical loading (e.g., D'Arcy Thompson, 1942; Huber, 1957; Moss, 1958, 1968; Hoyte, 1966 1971, 1975; Bassett, 1972; Pritchard, 1972; van Limborgh, 1972; Buckland-Wright, 1978; Spyropoulos, 1978: Babler and Persing, 1982; Hurov, 1986; Storey and Feik, 1986; Carter, 1987; Carter and Wong, 1988; Wong and Carter, 1990; Herring, 1993a,b). In the earliest stages of skeletal development, mechanical loading is probably far less important to basic patterning than cell-to-cell adhesion, surface tensions, chemical gradients, and other epigenetic forces that act primarily at molecular and cellular levels. But from the time that tissues are differentiated and individual organs begin to grow, a new level in the epigenetic hierarchy may be expressed as loads are generated by differential growth.

Growth and form of the skull reflect the dynamic interaction of structural elements and epigenetic forces throughout ontogeny. Through much of organogenesis and early growth, the most significant forces are generated by expansion of the brain and its special sense organs, especially the eye. That the embryonic brain actually loads surrounding tissues is evident in the nature of its growth. Brain enlargement in early ontogeny is driven by a combination of tissue growth and hydrostatic volume increase in the medullary cavity. Following neurulation, the tubular brain becomes a hydrostatic reservoir as the rostral neuropore closes and the spinal neurocoel becomes occluded and the medullary cavity between them fills with an increasing volume fluid. Proper intraventricular pressure is required to drive brain expansion (Jelinek and Pexieder, 1968; 1970a, b; Desmond and Jacobson, 1977; Goodrum and Jacobson, 1981; Pacheco et al., 1986). The law of LaPlace describes the distending tension in the wall of a cylindrical vessel at any given pressure as directly proportional to the vessel's radius (Gardner, 1973; Pacheco et al., 1986). The volume of the medullary cavity increases at a linear rate while brain tissue growth increases exponentially, in part as a mechanical requirement to prevent the brain from bursting as its outer tension rises. Cerebral loading onto surrounding tissues is thus proportionate to the sum of hydrostatic load plus the load from the growing cerebral tissue. Severe deformities of the skull accompany pathologies such as microcephaly and anacephaly, which result from disruptions in ventricular pressure during early development (D'Abundo, 1905; Weed, 1920; Nañagas, 1925; Young, 1959; Hoyte, 1966; Moss, 1968; Gardner, 1973; Herring, 1993a).

By the time the first skeletal condensations appear in mammals, the tissues in which they differentiate are already stretched around a cylinder that is relatively larger than that occurring even in the terminal stages of ontogeny of the closest extinct relatives of mammals. As can be seen in the comparative CT sections of *Monodelphis* and *Thrinaxodon* (Figs. 6, 7), the mammalian bones span cerebral surfaces of greater curvature and are correspondingly thinned, suggesting that the materials to construct the skull did not increase at the same accelerated rate of growth as the brain. In *Monodelphis* the cranium is largely enclosed by bone in the fourth week but the brain continues to grow through the twelfth week and the skeleton is continually remodeled throughout the intervening period (Fig. 8). Both experimental and teratological evidence indicate that cerebral loading affects skeletal growth from the very beginnings of mesenchymal condensation, through chondrogenesis, and for a considerable portion of skeletal growth.

In addition to influencing connective tissue growth, mechanical loads can direct cell differentiation. An outstanding example is the adaptive and compensatory responsiveness of mammalian secondary cartilage and intramembranous bone to loading in the mechanical environment created during the repair of bone fractures, an ability that is expressed early in ontogeny and which persists into adult life. For example, along angulated fractures in broken limb bones, first chondrogenesis and then endochondral ossification are induced by compressive loads on the concave side, while intramembranous ossification commences on the convex side of a repairing shaft (Pritchard, 1972; Hall, 1975, 1984a, b, c, 1992; Herring, 1993b; Wong and Carter, 1990). Another such modulation is the condylar secondary cartilage of the mammalian dentary. Loading initiates the differentiation of secondary cartilage in cells that can differentiate either as chondroblasts or osteoblasts. Reduction of condylar loading suppresses secondary chondrogenesis and initiates intramembranous ossification (Hall, 1984a, 1992; Herring, 1993b).

The developing cranial muscles may generate loads of comparable magnitude to those of the developing brain as they grow and begin to twitch and contract, and they have been implicated in the detachment of the auditory chain (Herring, 1993a; Maier, 1987). Experimental data indicate that embryonic muscular movement not only loads the skeleton, but that these loads are critical to the proper differentiation of joints and joint capsules (Drachman and Sokoloff, 1966; Murray and Drachman, 1969; Laing, 1982). As muscles approach maturity they become capable of exerting far greater levels of load than the growing brain or developing myoblastemata. Muscular loading induces the mature form of such features as the coronoid and angular processes of the mandible, it contributes significantly to shaping the mature craniomandibular and craniovertebral joints, and to growth of the lambdoidal and sagittal crests (e.g., Hoyte, 1966, 1971, 1975; Spyropolous, 1978; Hurov, 1986; Carter, 1987; Carter and Wong, 1988). In generating these extreme levels of force, muscular loading can induce a new level in the hierarchy of epigenesis which may be expressed long into ontogeny after the effects of differential growth are spent (Fig. 8).

When Maier (1987) and Herring (1993a) implicated muscle loading in the detachment of the auditory chain, they followed earlier authors (e.g., Allin, 1975; Crompton and Parker, 1978) in supposing that mammalian ontogeny recapitulates the transformation between two functional joints, that is from a functional primary CMJ between the palatoquadrate and articular cartilages to the mature CMJ between the dentary and squamosal bones. More recent research suggests that this is not the case. In a histological study of the developing CMJ in *Monodelphis*, Filan (1991) found no evidence to suggest a functional joint ever forms between the quadrate and articular cartilages before they become detached and the dentary-squamosal joint becomes functional. In captivity, the young do not begin eating solid food until they are 4 to 5 weeks old (Fadem et al., 1982; Kraus and Fadem, 1987), following detachment. Secondary condylar cartilage and the beginnings of a synovial capsule also appear during the fourth week at the joint between the dentary and squamosal and signal the onset of CMJ loading by the masticatory muscles that insert on the dentary. It is difficult to precisely define a time at which the dentary-squamosal joint becomes functional, because for a time the contacts between condylar cartilage and the squamosal and the auditory ossicles and the otic capsule are equally large (Clark and Smith, 1993). As ontogeny progresses, the masticatory muscles transmit increasing loads to the CMJ and correspondingly its surface increases, mostly through a process of lateral accretion as the width between the right and left CMJs increases (Fig. 12).

Muscular loading fails to completely explain the developmental transformation of the ear ossicles in mammals. While muscular loading might contribute to early differentiation of the mandibular and auditory elements and to the initial tearing of the connective tissues that bind the ossicular chain to the mandible, this interpretation is complicated by the timing of the event in different mammals. In marsupials it takes place after birth and the young have begun to suckle, while in placentals it occurs before birth, making it difficult to identify a common mechanical setting. More importantly, the force trajectories of the masticatory muscles are oriented in such a way that the mandibular condyle is pulled upwards and backwards into the roof of the glenoid, compressively loading the craniomandibular joint (Crompton and Hylander, 1986). It is difficult to see how this action could lead to the posterior repositioning of the auditory chain behind the dentary condyle; masticatory loading would be more likely to press the dentary backwards against the postdentary bones than to separate the two. If the masticatory musculature is involved at all, its role is only part of the story and some other mechanism must be responsible for widely separating the auditory chain from the mandible.

Development of the Middle Ear Ossicles

The developing auditory chain has both endochondral and intramembranous components, and both types have attachments to the mandible that are broken as ontogeny progresses. Three cartilages are present at birth in *Monodelphis*. The stapes has already budded from Reichert's cartilage and forms a tiny rod with a small footplate that lies in the center of the opening of the fenestra vestibuli. Both the stapes and the petrosal eventually contribute to the formation of the mature footplate in later in ontogeny as a complex stapedial articulation develops at the fenestra vestibuli. Articulating with the distal end of the stapes is the caudal moiety of the palatoquadrate cartilage, which is braced against the ventrolateral edge of the otic capsule and which will ossify to form the incus (= quadrate). Meckel's cartilage forms a continuous elongate rod that bends downward at its rear end at nearly a right angle (Fig. 9). During the second week, the rear extremity is cleaved from the mandibular ramus of Meckel's cartilage, forming the cartilage in which the malleus (= articular) ossifies. The two pieces become separated when Meckel's cartilage degenerates and is resorbed during ossification of the dentary.

The intramembranous ossifications have a contrasting developmental history. At birth, both the dentary and ectotympanic (= angular) have begun to ossify in a common membranous sheet external to Meckel's cartilage, but at this stage their growth centers are widely separated and an expanse of connective tissue intervenes (Fig. 9). During the first three postnatal weeks, the ectotympanic grows in positive allometry relative to the dentary. As the ectotympanic grows, it expands against the developing angular and condylar processes of the dentary, and the two bones are held together by fibrous connective tissue that arises in the osteogenic membrane. During early ontogeny the ectotympanic lies in its ancestral position hanging beneath the condylar process of the dentary. By the end of the third week the ectotympanic is approaching its adult size. At this time its growth rate slows and shifts into a negative allometry that persists for the remainder of ontogeny. At roughly this same time, the ectotympanic is torn free from the dentary (McClain, 1939; Clark and Smith, 1993). During the next 9 weeks the auditory chain migrates backwards from beneath the condylar process and eventually comes to rest entirely behind and medial to craniomandibular joint (Figs. 3, 9).

The key to understanding both the detachment and subsequent relocation of the auditory chain may lie in an interplay between the differential growth among elements of the mandibular arcade and the brain. The brain balloons upwards and backwards from the developing facial skeleton and grows steadily for the first 12 weeks (Fig. 10) of postnatal ontogeny (Ulinski, 1971). The relative positions of the CMJ and fenestra vestibuli are convenient markers to follow in tracing cranial remodeling in the wake of cerebral growth (Figs. 11,

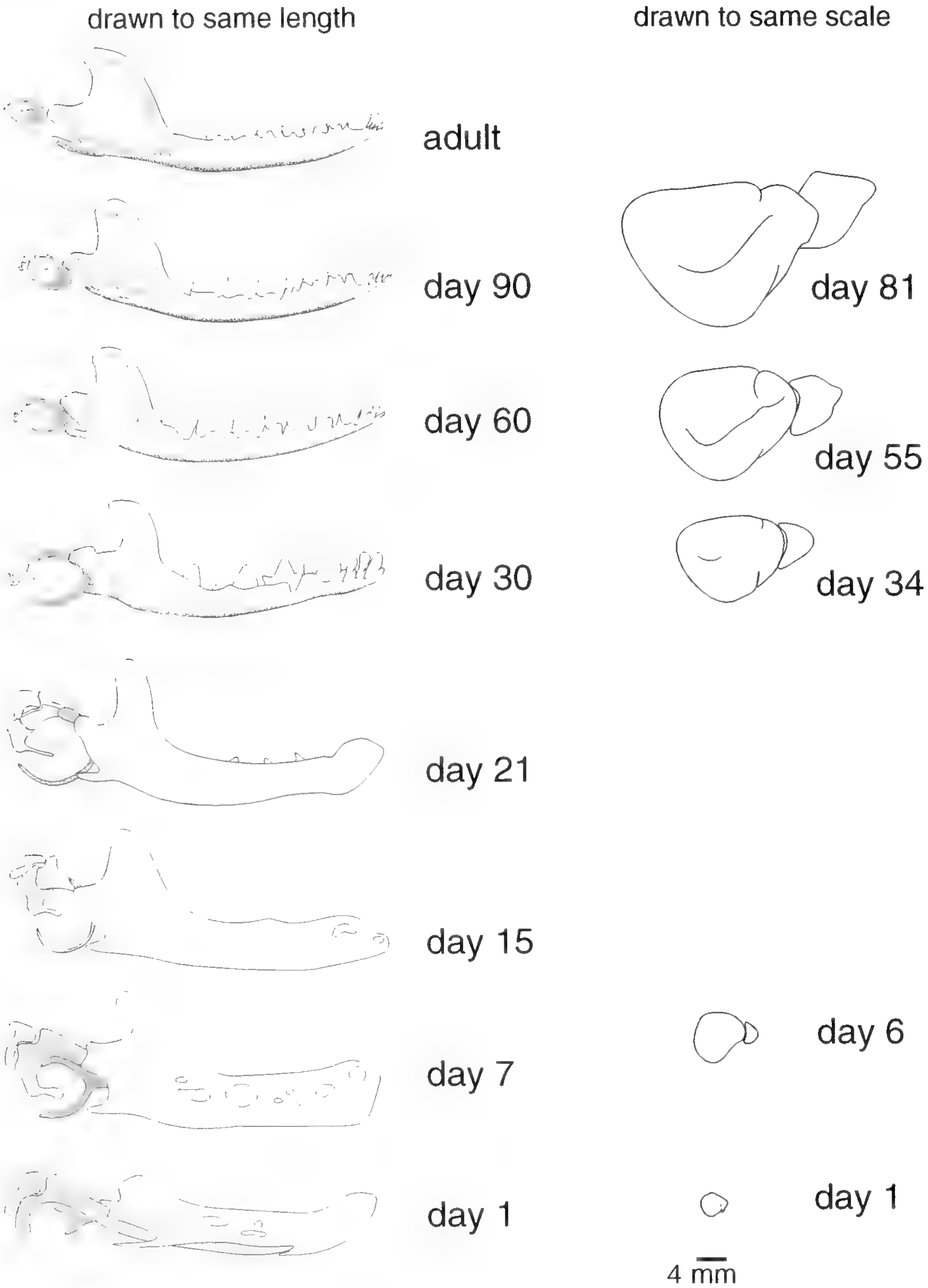

FIGURE 9. Left: Development of the mandibular arch in *Monodelphis domestica*, based on video imagery of a cleared and double-stained growth series, drawn to same length. Cartilage is shaded blue and the membranous ectotympanic is in red. Right: Growth of the forebrain in *Didelphis*, from birth to adult (modified after Ulinski, 1971), drawn to same scale. Based on Rowe (1996).

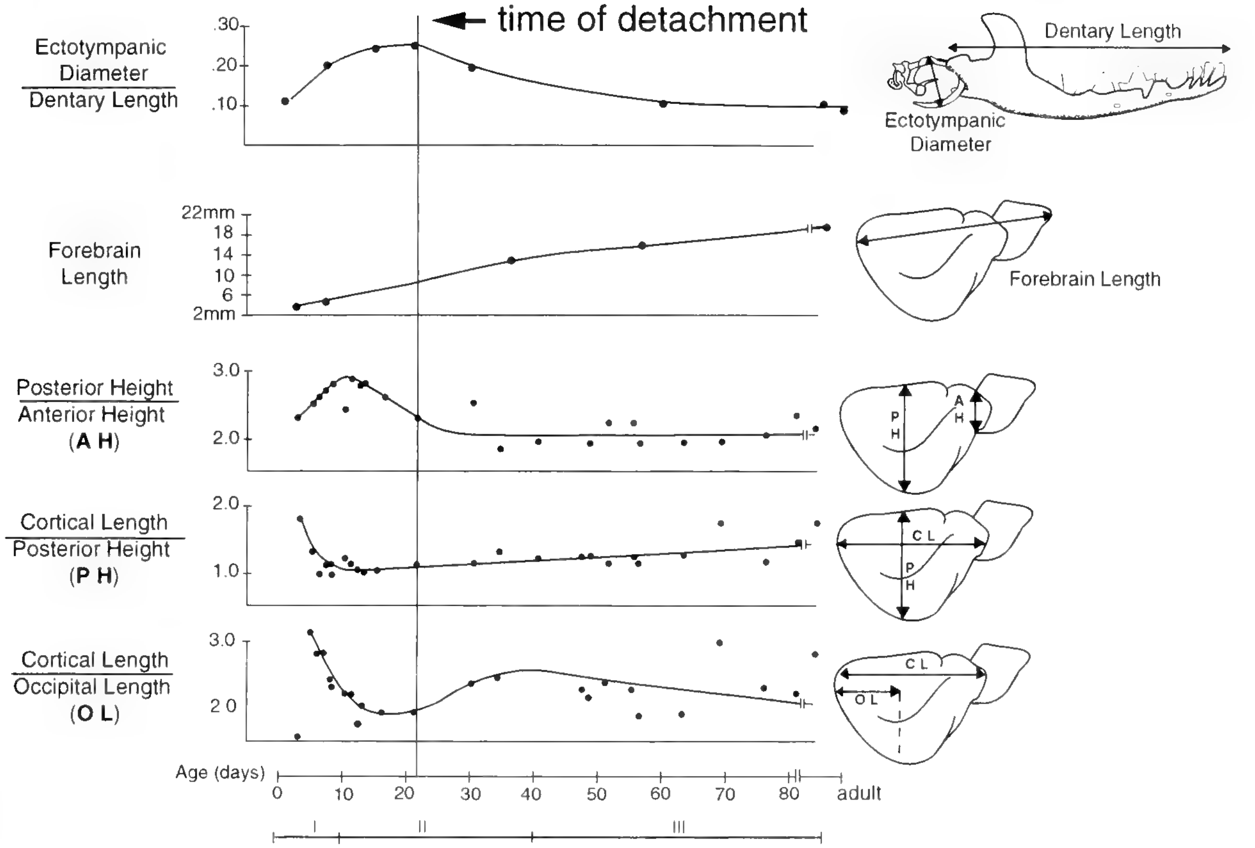

FIGURE 10. Differential growth of the forebrain (based on *Didelphis*, after Ulinski, 1971) and ectotympanic (based on *Monodelphis*). In the top graph, growth of the diameter of the ectotympanic is plotted as a function of the length of the mandible. In the second graph, growth of the total combined length of the olfactory bulb plus cortex is plotted as a function of age. In the lower three graphs, relative growth of the different parts of the cortex is plotted as a series of ratios defined by the dimensions depicted on the mature brain. The ratios show a phase of ventrocaudal growth (days 0–10), a phase of anterior growth (days 11–40), and a phase of occipital growth (days 41–81). From Rowe (1996)

12). At birth, the fenestra vestibuli lies immediately behind and medial to the CMJ, in a relationship similar to that found in adult *Morganucodon* and *Thrinaxodon*. The fenestra vestibuli and CMJ both lie external to the developing cerebral vesicle, along roughly the same "latitude" of cerebral circumference, which I refer to informally as the cortical "equator" (Fig. 11). As the brain grows, the magnitude of curvature of equator grows as well. The distance between the fenestra vestibuli and the CMJ, which both lie on the equator, also increases. The entire rear part of the skull appears to be pushed backwards from the facial skeleton and mandible by the growing brain.

The equatorial segment between the fenestra vestibuli and the CMJ defines an *arc of detachment* (Fig. 12) whose magnitude of curvature expands as the brain grows. As curvature of the *arc* expands, the fenestra is displaced progressively backwards. For about the first three weeks, the ear ossicles grow at a sufficient pace to keep up with the growing *arc*, thus maintaining their primitive linkage between the fenestra vestibuli and the mandible. As the ossicular growth rate slows and shifts into negative allometry, the brain continues its pace of growth for nine additional weeks and undergoes a ten-fold increase in volume during that time (Ulinski, 1971). During this time the *arc* nearly doubles in curvature, bursting the primitive arcade of skeletal elements that had spanned from the mandibular symphysis to the fenestra vestibuli. The middle ear bones maintain their attachment to the fenestra vestibuli and follow its trajectory backwards from the time of their detachment at the end of the third week until the brain stops growing in the twelfth week.

The timing of detachment prevents the disruption of function in the middle ear bones because it occurs before the onset of auditory functionality. The ear is unresponsive to sound until the 6th week and only thereafter does the auditory tract become myelinated (Langworthy, 1928; Larsell et al., 1935; McCrady et al., 1937; McCrady, 1938; McClain, 1939). The geometry of the widening *arc of detachment* accounts for the detachment of the auditory chain, for the precise path of its subsequent posterior displacement, and for the timing and extent of this movement in both ontogeny and phylogeny.

Discussion

The phylogenetic concordance of the inflated brain and the cranial ear implied the unexpected possibility of a causal

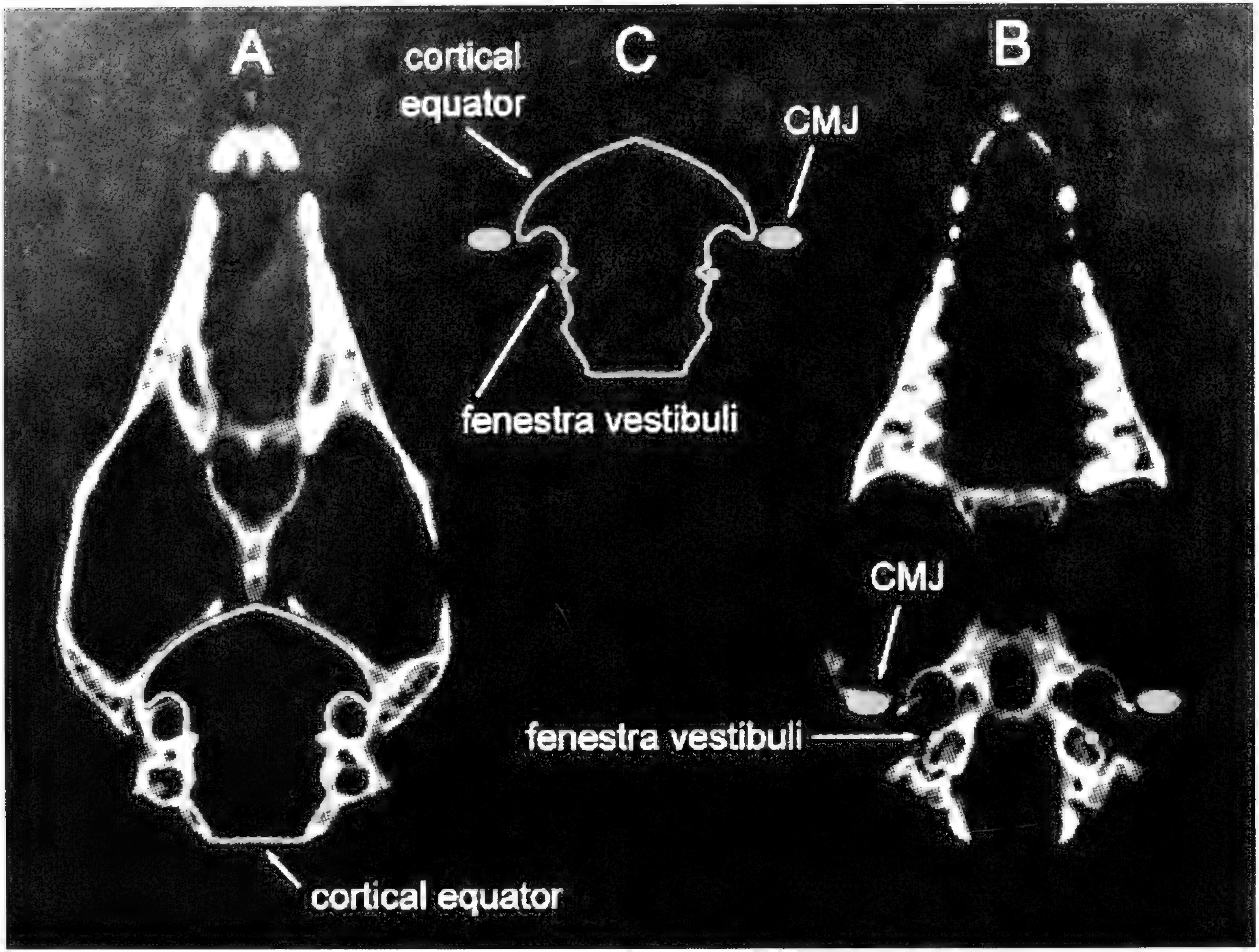

FIGURE 11. Landmarks for measuring brain growth. A) Transverse CT sections through the braincase at the greatest lateral width of the cortex, showing the slice plane used to illustrate the *cerebral equator* in Figure 12. B) section through the glenoid fossa and fenestra vestibuli (left). C) In the center, the positions of the CMJ and fenestra vestibuli are positioned relative to the cerebral equator. Individual slice thickness is 100 µ; slices A and B are 500 µ apart. (CT imagery from Rowe (in press).)

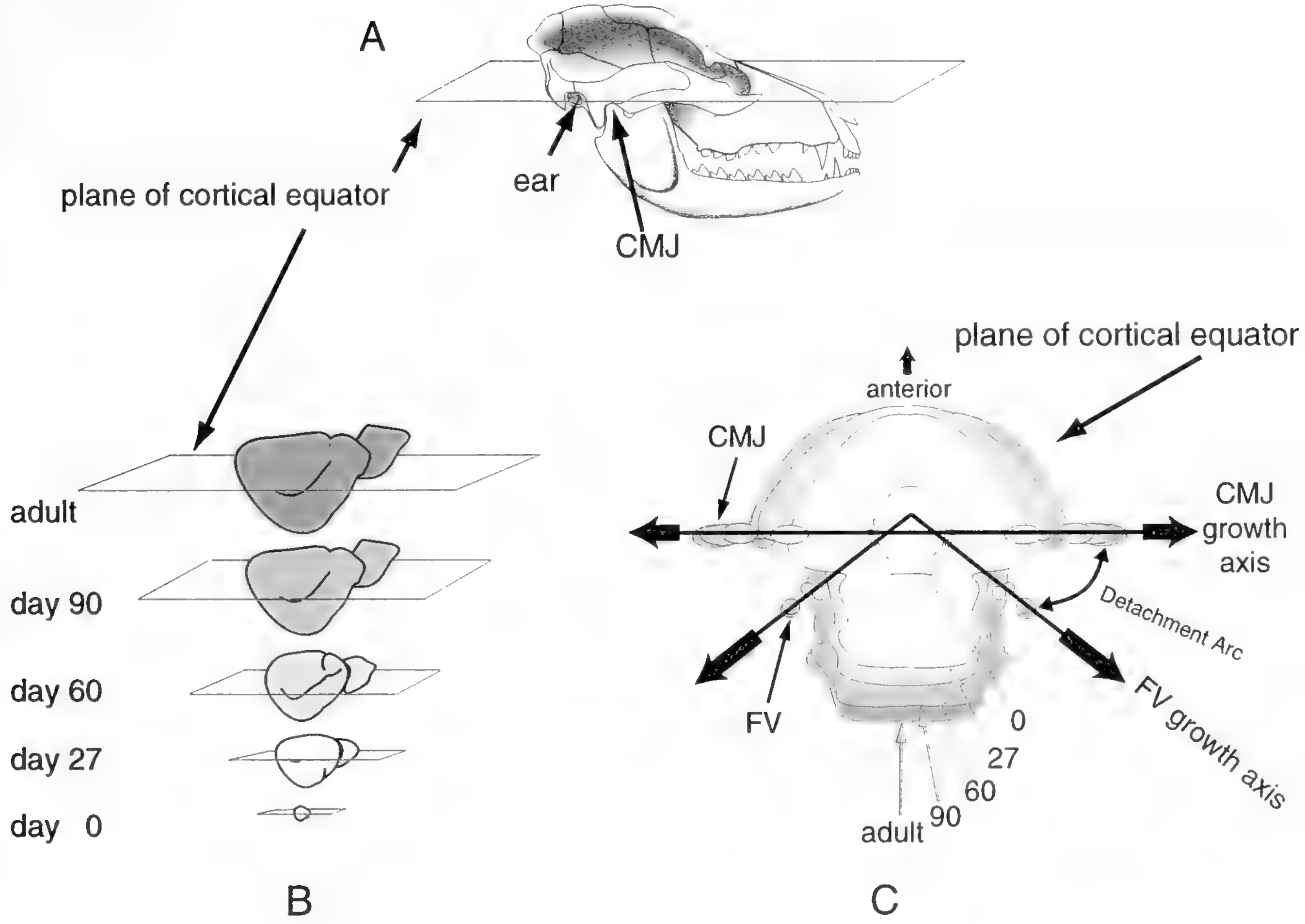

FIGURE 12. A) Location of a 1 mm-thick slice crossing the cerebral equator, fenestra vestibuli, and glenoid across the skull of a didelphid. B) Growth of the forebrain showing location of cortical equator. C) Superimposed cerebral equators of *Monodelphis* from day 0, day 27, day 60, day 90 and adult, relating the growth trajectories of the cerebral equator, fenestra vestibuli, and CMJ. Equatorial profiles taken from high resolution X-ray CT imagery of *Monodelphis*. From Rowe (1996).

relationship between the two structures, and this relationship appears to be corroborated by their ontogeny. The negative allometry of the auditory chain in the wake of continued rapid growth of the brain combine to cause the auditory chain to be detached from the mandible and carried backwards to its mature position behind the mandible. This new relationship originated in mammals ancestrally in an episode of heterochronic increase in rate and duration of brain growth. This one mechanism appears primarily responsible for both the evolutionary origin of the mammalian middle ear and its recapitulation in ontogeny. If this interpretation is correct, an event of fundamental importance in the origin of mammals was a heterochronic perturbation of brain development. As the pace and duration of brain development reached the ancestral mammalian level, a cascade of secondary, epigenetic effects was unleashed that affected virtually all aspects of mammalian life history.

One class of cascading effects involves intrinsic features of the brain and the many functions it controls. The specification of mammalian cortical regions is largely epigenetic as it occurs following neurogenesis, while clones of cortical neurons mingle during subsequent development. Neurogenesis appears to produce a cortex that is initially uniform and that later differentiates into specific functional areas by intercellular interactions (Walsh and Cepko, 1992), a process occurring over a protracted period of postnatal ontogeny. In the newborn opossum, for example, the cortex is unlayered, and subsequent development of its external appearance over the next 10 weeks mirrors many aspects of histogenesis and architectonic differentiation occurring at the same time (Riese, 1945; Ulinski, 1971). The extended duration of cerebral ontogeny that arose ancestrally in mammals afforded the specification of many new structures and an increased capacity for learning, both neuromuscular and associative, which continues long after cerebral differentiation and growth have ceased. Specific changes in cortical circuitry arising with expansion of the mammalian brain are related predominantly to elaboration of sensory components and enhancement of motor control. Modality-specific sensory channels through the thalamus to the telencephalon, which were probably present in amniotes ancestrally, became expanded in association with an extended range of auditory frequencies, enhanced olfaction, and with the sensory function of hair (Ulinski, 1986; Butler, 1994). Also distinctively mammalian are the development of corticospinal (palliospinal) pathways (Northcutt, 1984), and well-developed specific motor nuclei which receive afferents from the cerebellum or basal ganglia, project to specific restricted regions of the cortex, and are situated rostrally in the ventral half of the thalamus (Ulinski, 1986). Mammals are further characterized by divided optic lobes, development of the pons varolii, and elaboration of the inferior olive and pontine nuclei (Ulinski, 1986; Gauthier et al., 1988). These features collectively resulted in elaboration of the sensorimotor system to a degree surpassing all other vertebrates (Ulinski, 1986; Butler, 1994). The effects of this cortical elaboration are manifested during life history in functions ranging from the complex repertoire of mammalian oropharyngeal functions (Smith, 1992) to the maintenance of rhythmic respiratory movements associated with mammalian metabolism (Carpenter, 1976) to the diverse patterns of mammalian locomotion (Bramble, 1989; Bramble and Jenkins, 1993). Some of these functions surely extend into pre-mammalian history, but the marked increase in cerebral differentiation and volume that occurred in Mammalia ancestrally suggests a marked increase in functionality compared with the conditions in *Morganucodon* and more distant synapsids.

Another class of epigenetic cascade induced alterations in structures extrinsic to the brain, especially the adjacent connective tissues. The shift to a cranial middle ear is the most notable example, but virtually all parts of the skull and neck near the brain were also modified. The pattern of skeletal modification is complex, involving an interplay of reduction, loss, fusion, hypertrophy, and heterotopy of the components. Comparable patterns of complex change are manifested by a variety of developmental pathologies of the skeleton which are traceable to early perturbations of the mesenchymal tissues in which the skeleton differentiates and which can be traced to mutations of single genes (Grüneberg, 1963).

Because heterochrony and its secondary effects are impossible to identify without a phylogeny, it is not surprising that the effects of brain heterochrony on the mammalian skeleton were unrecognized under the phenetic Linnean view of early mammalian history. The assertions of convergent evolution and the lack of obvious adult biomechanical or physiological correlation between the middle ear and brain further obscured the relationship of ear morphology to cerebral growth. The discovery of this unsuspected relationship between the brain and ear illustrates the potential value of phylogenetic systematics to the many developmental and experimental disciplines within biology which now operate largely in the absence of a well-corroborated phylogenetic framework. Within such a framework, experimental manipulations of developing mammals can be designed to further test the relationship between genetic and epigenetic factors in ontogeny, and to elucidate the mechanisms of evolutionary change in the historical context in which they evolved.

Acknowledgments

I am grateful to Drs. Michael Ghiselin and Giovanni Pinna for inviting me to participate in this symposium, and for providing such a productive and invigorating forum in which to present this work. I thank Mr. Reuben Reyes for invaluable assistance in generating and processing the exquisite digital datasets of high resolution X-ray CT imagery used in this study. Dr. Rafael de Sa and Ms. Hillary Tulley prepared histological materials and cleared and stained the extensive growth series of *Monodelphis domestica* used here. Mr. Chris Brochu, Dr. David Cannatella, Mr. Matthew Colbert, Dr. Ernest Lundelius, Jr., Dr. Zhexi Luo, and Mr. John Merck, Jr. read earlier drafts of this manuscript, and their stimulating and insightful discussions contributed significantly to all phases of this research. My thanks to John Merck, Egan Jones, and Jeffrey Horowitz, who provided some of the illustrations and assisted with various aspects of generating the imagery used herein. This research was sponsored by National Science Foundation grants BSR-89-58092 and USE-91-56073, University of Texas Geology Foundation, and the Vertebrate Paleontology and Radiocarbon Laboratory.

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List of Abbreviations

als - alisphenoid
ang - angular
ar - articular
bas - basisphenoid
boc - basioccipital
co - cochlea
ec - endocranial cavity
f.v. - fenestra vestibuli
h - standardized height of endocranial cavity
ipa - interparietal
j - jugal
ld - lambdoidal crest
mas - mastoid region of petrosal
mx - rock matrix surrounding parts of *Thrinaxodon* skull
mx/ec - rock matrix in endocranial cavity
c - occipital condyle
opth - opisthotic
pa - parietal
pet - petrosal
pin - pineal foramen
ppr - paroccipital process
pr - promontorium of petrosal
pra - prearticular
q - quadrate
qj - quadratojugal
sag - sagittal crest
sang - surangular
sq - squamosal
st - stapes
tr - tympanic recess
tym - ectotympanic

EVOLUTIONARY DEVELOPMENTAL BIOLOGY — PROSPECTS FOR AN EVOLUTIONARY SYNTHESIS AT THE DEVELOPMENTAL LEVEL

David B. Wake

Museum of Vertebrate Zoology and
Department of Integrative Biology
University of California
Berkeley, California 94720

The relationship of development to evolution has engaged the interest of biologists for well over a century, but the subject has been something of a "fringe" issue for both fields. The famous "three-fold parallelism" between comparative anatomy, embryology, and paleontology predates darwinism, and the issue seems to re-emerge with each scientific generation. Although de Beer (1930) produced a thoughtful book on evolution and development at the beginning of the period of the evolutionary synthesis, it was not seen as being progressive by later workers. Rather, he is credited with having led the rejection of a causal relation between ontogeny and phylogeny, and the neoLamarckian ideas prevalent in the 1930s, evident in the work of MacBride and his students (Churchill, 1980). Embryology has been dismissed as being of only passing interest in the development of the evolutionary synthesis (Mayr and Provine, 1980); Hamburger (1980) refers to the absence of embryology in the synthesis as "the missing chapter," and suggests that only Schmalhausen, whose work did not become available to western scientists until 1949, could have provided it. Dobzhansky, too, felt that Schmalhausen's work had the potential of completing the evolutionary synthesis (Gilbert, 1994), but such was not to be the case, for Schmalhausen was silenced by the era of Lysenkoism in the Soviet Union and his work has not received the recognition it deserves until recently (Wake, 1986). While Huxley and de Beer, and later, Waddington, were concerned with the development-evolution relationship and made important contributions, the promise of a synthesis has yet to be attained. My thesis in this essay is that technical and conceptual advances have at last made such a synthesis an achievable goal.

Despite much excellent work by earlier workers, I believe that it was the publication of Gould's (1977) *Ontogeny and Phylogeny*, which appeared during a period of renewed interest in macroevolutionary phenomena, that stimulated development of an on-going research program into the relationship of development to evolution. His was an historical summary of the idea of recapitulation and of attempts to use heterochrony as a general explanation for departures from recapitulation. In it Gould presented his own effort to model heterochrony (the "clock-face model") and analyze it in evolutionary, ecological and paleontological perspective. In short order, his model was reformulated in a manner that made heterochrony accessible as an area of research (Alberch et al., 1979), and Alberch (1980) threw down the gauntlet in challenging evolutionary biologists to be more conscious of new findings in developmental biology. A Dahlem Conference soon followed (Bonner 1982), and a textbook was published (Raff and Kaufman 1983); the next decade witnessed the publication of many research papers, at levels of organization ranging from molecules to whole organisms. At the end of the decade a period of consolidation occurred, with several more conferences taking place (Müller et al., 1989; Geobios Mem. Spec., 1989; Wake et al., 1991) and three major textbooks appearing (John and Miklos, 1988; McKinney and McNamara, 1991; Hall, 1992). The topic of development and evolution had become a standard expectation of conferences, and summaries of research activity dealing with specific groups are appearing (e.g., Raff, 1992a).

There was a solid intellectual foundation, reviewed by Gould (1977), on which to develop the new research initiatives. Following de Beer's (1930) reanalysis of the biogenetic law of Haeckel, there were several attempts to bring the ontogeny/phylogeny relationship into evolutionary biology. While conducting my doctoral studies on salamander osteology (Wake, 1966) I became intrigued by the possibility that some morphological features of systematic significance might have a relatively simple developmental basis (a fine example is the demonstration by Alberch and Gale [1985] that whether frogs or salamanders have four or five toes can be determined mainly by the number of cells and rate of cell proliferation). Students of salamanders always have before them the specter of the axolotl, and so learn early that to ignore the possibility of paedomorphosis is to imperil one's interpretations. Accordingly, many of us focused attention on heterochrony, which had in the past played such an important role in evolutionary narratives (e.g., origins of vertebrates). Comparative analysis of ontogenies of particular features within the context of the whole organism and its ecology and biogeography (as in my studies of the premaxillary bone, Wake, 1966, 1991) gave promise for understanding how morphology evolves.

The demonstration of the importance of hierarchical interactions in ecology, development and evolution (e.g., community dynamics giving rise to selection on growth rate or adult body size; genome size at the cell level impacting on growth and differentiation rates; Wake, 1991) has many implications. These have been studied from such diverse per-

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Editors, M. T. Ghiselin and G. Pinna

spectives as quantitative genetics (Atchley and Hall, 1991), genome size-cell size-histogenesis (Roth et al., 1990; Roth et al., 1994), genes in relation to morphology (Nijhout, 1990), and molecular and developmental genetics in relation to ground plans (Slack, et al., 1993; García-Fernández and Holland, 1994). Hierarchical analysis has been important in my own work (Wake, 1991; Roth et al., 1994), and I believe the approach is fruitful when exploring the interaction of developmental and evolutionary processes that lead to phylogenetic patterns.

Rather than attempting to summarize an active and dynamic area of research that is changing quickly, I will discuss prospects by focusing on some recent research trends. I first identify some central themes and then present a selection of topics that appear to have promise.

Central Themes

Researchers in the fields of evolutionary and developmental biology both deal with pattern and process, but terms have been made to serve too many masters; pattern and process become conflated, and muddle follows. Process as perceived by evolutionary biologists starts with natural selection, but increasingly is seen as extending to the formation of new evolutionary units (lineage origination, establishment of species), whereas pattern emerges from cladogenesis, extinction, and events related to earth history (mass extinctions, plate tectonics, etc.). In development, process includes a wide spectrum of phenomena, from genetic signaling and autonomous cell activities (e.g., assembly of cytoskeleton, mitosis) to integration (e.g., contact inhibition, adhesion) (Wessells, 1982). As far as developmental pattern is concerned, pattern formation, morphogenesis, and even ground plans are much discussed in developmental biology. There is, however, something of a cultural and sociological gap between primary researchers in evolutionary, as contrasted with developmental, biology (Raff, 1992b). Evolutionists interested in development, especially systematists and phylogeneticists, focus on evolutionary patterns, while developmentalists are more concerned with processes and mechanisms. The mechanisms in evolutionary biology relate to changes in gene frequency (population genetics) and to the effects of many genes on overall morphology (quantitative genetics), while those in developmental biology relate to the genetic basis of patterning in early development, to genetic signaling and cell-cell interactions, etc. Accordingly, there is neither a common theme nor a common vocabulary. Furthermore, while terms are important to evolutionary biologists, developmental biologists are more pragmatic and are unlikely to debate what is meant by the term "gastrulation," for example; they look instead for common themes in gastrulation. Evolutionary biologists, in contrast, disagree on even the most fundamental concepts (e.g., homology, species), which dooms the search for simple mechanisms and makes it difficult to find common themes.

On the other hand, developmental biologists interested in evolution often accept a rather simplistic notion of what an evolutionary term (e.g., *Bauplan*) is, and as a result the application of their sophisticated laboratory work to questions in evolution or phylogenetics appears to fall into the realm of essentialism (e.g., Slack et al., 1993; Patel et al., 1994). Developmental biologists seek commonality — the basis of ground plans, for example; evolutionists celebrate variation and diversity and are wary of generalizations beyond those of formal mathematically based models (e.g., as in population and quantitative genetics). For example, an area of continuing controversy in evolutionary biology has to do with whether there are macroevolutionary rules and principles, or if patterns at high taxonomic levels are just the result of microevolutionary processes being played out over time in an ever-changing world.

Development meets evolution most directly in discussions of transformation of body form. At one time, developmental biologists believed strongly in genetic invention, and some still do (Løvtrup, 1987). Currently there is an increased awareness of hierarchical interactions and of generic, often physically based, factors that regulate developmental processes (Newman and Comper, 1990; Newman, 1993, 1994), and regulation is becoming a theme in the work of some molecular geneticists as well (Carroll, 1994). Evolutionists have been wary of evolutionary interpretations that relied on genes of major effect (e.g., macromutations) since the early 1930s, but they also have been slow to adopt hierarchical thinking, which is essential if modern developmental genetics is to be understood in evolutionary and phylogenetic perspective. Times are changing, and the stage is being set for mutual understanding. It may seem, with the ever-growing literature and enthusiasm generated by those studying *Hox* genes and related signaling systems, that we have entered a new era of focus on genetic invention, but careful attention to this large body of work reveals hierarchical perspectives dealing with levels of organization, interaction, and regulation that offer a means of connecting developmental and evolutionary approaches (see, for example, Carroll, 1994).

There is a renewed interest in ground plans, bauplans, and similar concepts, generated by new knowledge of the stability of developmental systems and the generality of underlying genetic mechanisms and signaling systems (Slack et al., 1993, Patel, 1994). Such interpretations are only possible within a phylogenetic perspective. Similarly, there is renewed interest in what might be termed the limits and conceptualization of "sameness," and this has revived interest in the ancient debate over homology (Hall, 1994). This debate involves central issues in modern developmental genetics (Wake, 1994), for which phylogenetic perspectives are crucial.

The relation of ontogeny and phylogeny — sorting pattern from process

Recapitulation will not die as an evolutionary concept, and as a grand generalization it has its ardent supporters (e.g., Nelson 1978). *Recapitulation* occurs when two taxa being compared share all of their ontogeny (i.e., embryos proceed through time along a definite and knowable pathway, characteristic of the lineage, termed an ontogenetic trajectory), except for the terminal stages. In a recent re-evaluation of the idea, Mayr (1994:231) states clearly, "The observation that the embryo in the development of its organs goes, seemingly unnecessarily, through certain embryonic stages found also in its remote ancestors is an undeniable fact, and must be explained in terms that are neither metaphysical nor purely proximate, but through a conceivable evolutionary scenario." The explanation, Mayr argues, lies in the facts of development — the inducing capacities of surrounding embryonic tissues for a *somatic program*. The somatic program, in combination with additional nuclear genes, directs the development of organisms. The example given is the gill arch system of amniotes, which is functionless as a respiratory system but of critical importance in the development of the head and neck. In his view, recapitulation is irregular, and the explanation is that parts not being used in some manner are quickly lost. This is a strict functionalist, adaptationist explanation fully within the neodarwinian tradition.

However, other workers, while accepting the idea of complicated interactions between parts during ontogeny, focus more on phylogenetic issues. Ontogenies are perceived as being predictable and constrained within lineages, suggesting that they are not mosaic but highly integrated. Evolution occurs mainly by the addition of novel traits to the terminal stages of ontogenetic trajectories (which are repeated, or recapitulated, from ancestor to descendant, differing only with respect to the novel added feature), was formalized by Alberch el al. (1979) as a phylogenetic manifestation of *peramorphosis,* defined as the morphological expression of a particular cell-level process. There is a rich terminology. Gould (1977) and subsequently Alberch et al. (1979) and others redefined old terms as names for "pure" processes, such as *hypermorphosis* — a temporal extension of a developmental process, and *acceleration* — an increase in the rate at which a developmental process proceeds). Thus, process (such as cell division rate) was linked to, but discrete from pattern (the appearance of novel morphology in a descendant, relative to an ancestor). The extreme alternative is *reverse recapitulation*, a phylogenetic manifestation of *paedomorphosis,* the morphological expression of a particular process (among which are *progenesis* — a temporal truncation of development, and *neoteny* — a decrease in the rate at which a development proceeds). In these cases descendants do not show novelty, but rather re-express as adult states conditions found in the ontogeny of ancestors (in practice, phylogeneticists assess conditions in sister taxa and appropriate outgroup taxa, for ancestors can only be inferred, not known).

"Reverse recapitulation" is a rather cumbersome term, but it conveys the impression of derivative taxa "backing down," phylogenetically, an ontogenetic trajectory that is characteristic of related taxa by failing to complete it developmentally. Mayr (*in litt.*) objects strongly to the concept of reverse recapitulation. It was introduced in a strictly formal sense by Alberch et al. (1979), in order to idealize a symmetry between evolution by terminal addition versus elimination of terminal stages. Perhaps "incomplete recapitulation" would be a more neutral term.

Patterns of both recapitulation and reverse recapitulation are kinds of *heterochrony*, phylogenetic differences among taxa with respect to the timing of developmental processes. Heterochrony itself is often treated as a very general term (e.g., Raff and Wray, 1989; McKinney and McNamara, 1991). To treat heterochrony in such a manner has confused evolutionary terminology by conflating developmental process with phylogenetic pattern. For example, Raff and Wray (1989) argue that heterochrony at the level of whole organisms ("global heterochrony") is uncommon and probably not very significant, whereas heterochrony at the level of particular developmental and genic processes is common and important. I would argue that it is global heterochrony that is most likely to have phylogenetic implications, and that to describe subtle shifts in timing of gene action as heterochrony is to reduce the value and utility of the term. Heterochrony with respect to whole organisms and ontogenies has its greatest value in phylogenetics as a relatively uncommon phenomenon. I have in mind such phenomena as the overall body form of larvae versus adults, and ontogenetic trajectories of organ systems (for example, limbs), and parts (for example, presence or absence, and shape, of skull bones) in relation to the whole organism (e.g., Alberch and Alberch, 1981). McKinney and McNamara (1991) argued that recapitulation and reverse recapitulation are unnecessary, and that heterochrony is a sufficient inclusive term for peramorphosis and paedomorphosis, but I disagree. Much of their book is an attempt to make virtually everything in evolutionary biology some kind of heterochrony, thus rendering the concept nearly empty of intellectual content. Confusion is particularly bad with respect to heterochronic processes versus heterochronic patterns. This is where terms like recapitulation and reverse recapitulation are useful, for they are terms relating to phylogenetic patterns.

The word "heterochrony" serves too many masters. The term needs modification and restriction relative to its overuse by McKinney and McNamara. A start would be to expand our process terminology, first by distinguishing process heterochrony from heterotopy (differences among taxa in relative position within the embryo where developmental processes proceed, e.g., the differing results of ectodermal-mesenchymal interactions involving neural crest cells in vertebrates, see Zelditch and Fink, 1995). There is value in developing evolutionary perspectives on heteroplasy (e.g., differing rates of cell proliferation leading to patterns of intertaxon allometry) as well. Workers should be careful to differentiate between developmental mechanics and processes, and phylogenetic pattern.

Reverse recapitulation is manifest in a number of taxa of perennibranchiate but sexually mature salamanders (*Siren Ambystoma mexicanum*, *Necturus*, *Typhlomolge* give examples of independent derivation of the phenomenon in four distantly related families). These are dramatically clear cases, in which derived taxa resemble in their overall morphology the non-terminal ontogenetic states of ancestral or out-group taxa. The term "perennibranchiates" refers to the fact that these taxa retain larval-like gills and remain aquatic throughout life. The processes responsible for the pattern have produced ecomorphologies (phenotypes tightly connected to particular ecologies — in the present case, aquatic versus terrestrial habitats) that are profoundly distinct from those of immediate ancestors (Reilly, 1994). The genetic and developmental mechanisms underlying this evolutionary transition from terrestrial to aquatic adults are relatively simple, for they are readily attained. Within *Ambystoma* (tiger salamanders, axolotl and mole salamanders) close genealogical relatives may remain in the larval state or metamorphose into terrestrial adults, and may even show polymorphism within a species or population (Shaffer, 1993; Collins et al., 1993). In the case of perennibranchiation, the global effects of the phenomenon are superficially evident in morphology and profoundly evident in ecology, but metamorphosis in salamanders is not a dramatic event, and perennibranchiate and fully metamorphosed animals differ little with respect to most organ systems. Reilly (1994) argued that we should examine the genetic, developmental, morphological, ecological and phylogenetic aspects of heterochronic phenomena separately so that we can differentiate between phenotypic plasticity (phenotypic differences caused by environmental rather than genetic differences) and genetic fixation (at the level of species).

Perennibranchiation is dramatic in its ecological implications, but its more long-term, evolutionary and phylogenetic implications are less evident. In salamanders it leads not to radiative evolution, but seems to be a dead end. There are only two genera and a handful of species in each of the exclusively perennibranchiate families Proteidae and Sirenidae. In contrast, organismal-wide paedomorphosis in direct developing salamanders of the family Plethodontidae has had far more profound implications, judging from the combination of morphological and taxonomic diversification. Although the morphological expression of the underlying developmental processes is superficially less evident than in the perennibranchiate taxa, the morphological diversity encompasses a far greater array of morphological combinations and associations, including substantial novelty (Wake 1966, 1991). Furthermore, although direct development is found only in the Plethodontidae, itself only one of the ten families of salamanders, the direct-developing taxa constitute about two-thirds of the living species of salamanders (Wake 1966, 1987).

I first encountered paedomorphosis in direct-developing taxa when I found taxonomic characters (mainly bones and their parts) that varied among taxa with respect to the time of their appearance (Wake 1966). Those characters that appear very late in ontogeny, or that are found only in the oldest and largest members of a population or species (see also Smirnov 1994), suggest that the taxon displays organismal-wide paedomorphosis, and so the entire morphology and morphological ontogeny must be evaluated within this mental framework.

Elsewhere (Wake 1989) I presented an example from salamanders of the genus *Batrachoseps* (Slender Salamanders, family Plethodontidae) of a pattern of intertaxon heterochrony. The species of this western North American lineage all develop directly from eggs laid on land, and there is no larval stage. One infers that the morphology is paedomorphic, in relation to out-group taxa within the plethodontid tribe Bolitoglossini, because all species (currently there are 8 species recognized, but several new species are currently being described) display adult morphologies (such as a very large cranial fontanelle, and only four toes) that represent embryonic or juvenile stages of out-groups and inferred ancestors. This is not very controversial, for the logic and data are relatively straight-forward. However, species vary with respect to other traits (all late-appearing features, such as processes of bones, secondary separation of bones, and presence or absence of bones). It is unclear whether there is a paedomorphocline, a sequence of derived taxa each more paedomorphic than the last (McNamara, 1986), with slender species being more derived and paedomorphic, or a peramorphocline, a sequence of taxa showing progressively more peramorphic characters. If the latter situation holds, relatively robust, more fully developed (with respect to the traits listed above) species are more derived. Having been derived from a paedomorphic lineage (that is, one that has shown reversed evolution), they now would be showing a second reversal in having morphologies that resemble the situation before the paedomorphic phase associated with the establishment of the lineage. Other more complex hypotheses are only slightly less parsimonious. Recent work in my lab shows that different stages of paedomorphosis are displayed within each of two major clades of *Batrachoseps*, so at least the notion of a simple paedomorphocline can be rejected. It is much more difficult to reject the hypothesis that there has been a phylogenetic reversal within the clade that includes the robust species. The very existence of heterochrony implies character instability and suggests that characters are more labile than we generally assume that they are in phylogenetic analyses. While robust phylogenetic hypotheses are essential for correct interpretation, in cases such as I have described, with organismal-wide paedomorphosis, nearly every character becomes suspect, and there is general insecurity in relation to "which end is up" (i.e., character polarity). To give one example from *Batrachoseps*, it is equally parsimonious from out-group analysis as to whether presence or absence of a prefrontal bone is ancestral. All but one of the described species lacks the bone, but a second species gains a tiny speck of bone in the correct position very late in life, following achievement of sexual maturity. Are these two species displaying an ancestral trait, or have they undergone peramorphic evolution within the framework of general paedomorphosis and restored a trait absent from their common ancestor? I know of no way to solve this problem by ontogenetic and phylogenetic analysis of living taxa; this is an instance in which a better fossil record could be decisive.

The reason that Hennig's (1966) cladistic phylogenetic procedures have been so successful among morphologists is that morphological characters often persist for long periods of time, through numerous branching events. Differential *character persistence* is universal. Some systematic characters are labile phylogenetically; others, usually termed conservative, show greater persistence. It is easy to find examples of high character persistence: spiral cleavage in several major and minor taxa, the notochord and brain stem of craniates, and the tripartite body plan of insects. I believe the terminology is appropriate at all levels of the organismal hierarchy. Thus, the *Hox* gene cluster is highly persistent. I distinguish character persistence from *stasis*, persistence of the full morphology through numerous branching events (Wake et al., 1983).

Ontogenetic trajectories display high persistence. This phenomenon has been indirectly recognized by some previous workers in a curious way — they have proposed that paedomorphosis is a kind of escape from specialization for lineages (e.g., de Beer, 1930). Extreme paedomorphosis in miniaturized members of various phyla has led to the loss of traits that are considered parts of bauplans and thus deeply embedded in ontogenetic trajectories (e.g., coeloms; reviewed by Hanken and Wake, 1993).

Character persistence occurs to varying degrees across taxa of any rank. Among salamanders, all plethodontids are lungless, but only some salamandrids are. Most salamanders are five-toed, but three genera of plethodontids have independently become four-toed, and all species of *Batrachoseps* are four-toed. There is a well-justified, general assumption that five is the number of toes that became fixed early in tetrapod phylogeny, and this character has had great persistence, but with noteworthy exceptions that themselves have shown persistence at another level (e.g., the two toes of artiodactyls, limblessness in various saurian clades and in caecilians). But cladistic approaches are invalid when character persistence is low (the "flip side" of character persistence is homoplasy). For example, when dealing with mitochondrial DNA sequences it is risky to attempt to identify synapomorphic and symplesiomorphic substitutions in third positions. It is easier if one is working with a coding sequence, such as cytochrome b, which can be analyzed cladistically at the level of its encoding for amino acids, because amino acids show much greater persistence than bases. Much of the on-going argument over how to analyze adaptation is instead an argument over character persistence. Some workers (e.g., Baum and Larson, 1991) adopt an implicit premise that adaptive traits have high character persistence, while others (Reeve and Sherman, 1993; Frumhoff and Reeve, 1994) believe that such traits have low persistence. Organismal-wide (global) paedomorphosis is, in a cladistic sense, a reduction in persistence in many (terminal) characters at once, and when it is later followed by peramorphosis, confusing degrees of homoplasy are encountered. In such a situation cladistic analysis can be difficult because many equally parsimonious arrangements of taxa are possible, and the most parsimonious may be incorrect because of false information from many traits. This is a pattern encountered within the large bolitoglossine clade of plethodontid salamanders, where early in the history of the clade there apparently was general (high persistence) paedomorphosis and this was followed by peramorphic changes of low persistence (Wake, 1966, 1991; Wake and Elias, 1983). A way out of this dilemma for cladistic analysis is to be able to recognize organismal-wide paedomorphosis at a high taxonomic level, and then code individual traits accordingly.

Failure to recognize organismal-wide paedomorphosis can have profound consequences. For generations the brains of salamanders have been accepted as simple, generalized and primitive with respect to their organization and degree of histogenesis. A recent phylogenetic analysis (as recommended above) has shown that, with a high degree of probability, the brains not only of salamanders but also of caecilians and frogs are secondarily simplified, and the nervous system is only a part of an organismal-wide paedomorphic syndrome (Roth et al. 1993). In the most extreme cases, which are highly derived phylogenetically, the brains take on an appearance similar to those of early embryos of outgroups. This is a deceptively simple interpretation, however, because the secondary simplification is founded on derived patterns of connectivity and organization, and represents a mix of embryonic (i.e., paedomorphic) and derived traits, and in some cases novel characters, not represented in outgroup taxa. Somewhat surprisingly, the most simplified brains are not those of perennibranchiates such as *Ambystoma mexicanum*, but those of direct-developing species with complex behaviors such as members of the genera *Batrachoseps* and *Hydromantes*, and cladistically basal perennibranchiates such as *Necturus* (Roth et al., 1994). The mixing of cladistically derived, reversed (from paedomorphosis) traits with persistent traits can produce substantial morphological novelty. This outcome, termed *ontogenetic repatterning* (Wake and Roth, 1989), can affect many seemingly unconnected traits at once, with profound implications (as in the organization of the neural control of feeding and brainstem organization in salamanders, Wake, 1993).

The relation of ontogeny to phylogeny is no longer studied with the goal of finding phylogenetically ancestral conditions of whole organisms or even of traits, but with the awareness that it is the entire ontogeny of organisms that is subject to evolutionary change. A character cannot be separated from its ontogeny (de Queiroz, 1985), nor can a character be fully separated or isolated from its organismal milieu. Nonetheless, it is the general stability and conservatism of characters and organisms during their ontogeny and phylogeny that encourages us to believe that there are lessons to be learned for phylogeny from ontogeny.

Does ontogeny recapitulate phylogeny? Sometimes, in a limited way, more in some taxa, less in others, and probably never in the extreme form envisaged by Haeckel. The degree to which it does hold is determined only with difficulty, and so the value of recapitulation as a general guide is very low, as has long been recognized (e.g., de Beer, 1930). Nonetheless, it is surprising to find how readily biologists in many fields leap to the conclusion that a trait that appears early in ontogeny and then transforms is likely to display the ancestral condition at its first appearance. Traditions die slowly. Those who would choose to use recapitulation as a premise in their work would be well advised to study such detailed analyses as that of Mabee (1993; see also Mabee, 1989), who showed that for centrarchid fishes only 52% of a large set of characters evolved by terminal addition. Hence use of an ontogenetic criterion for determining character state polarity has low value. The problem of "which way is up" in evolution and phylogeny will not soon disappear!

Hierarchical perspectives on development and evolution.

Development is a hierarchical phenomenon in which a complex of genetic signals, physiological signals, cell-cell interactions, generic physical factors, and self-organizational properties interact to produce an ontogeny. During the past decade there has been enormous progress in our understanding of the nature of hierarchical interactions during the development of the vertebrate head, as exemplified by the paper in this volume by Holland (p. 63). I will briefly consider this issue not from the perspective of the genetic signalling that appears to be so important in head development, but from the perspective of an evolutionist and phylogeneticist, trying to understand how heads have evolved.

That there is a relation of *Hox* genes to neuromeres seems indisputable, and many labs are actively engaged in research to pinpoint the specific mechanisms and interactions that relate genes to morphology. The most impressive evidence that the genes are specifically related to neuromere formation comes from the concordance of neuromere order, the arrangement of genes within gene families on chromosomes, and the general (there are some specific exceptions) sequence of gene expression. At points as yet undetermined, but apparently within the craniate lineage (a critical need is for more work on basal fish lineages), there has been extensive paralogous duplication, resulting in four gene families all showing the same general ordering, but having different specific patterns of expression (Garcia-Fernández and Holland, 1994). This area of research is one in which the zeal to find a common developmental genetic ground plan for the vertebrate head has proceeded with only the most general kind of comparative structure, and with little attention to variation. That is beginning to change, as can be seen from the recent paper by Gilland and Baker (1993), who show that within the general pattern of conservation there is also variation in neuromere-gene relationship. The species differences found indicate the likelihood of shifting relations between genetically determined rhombomere identity and cranial nerves. Although the generality is impressive at this early stage of comparative developmental genetics, the issues of homology and conservatism versus change are likely to loom large in the future. The need for a detailed phylogenetic analysis of the impressive new ontogenetic data, from a broader comparative base than now exists, is critical (Meyer, 1996, presents a detailed exposition of this point).

There long has been controversy concerning the pattern of segmentation of the vertebrate head, and whereas once the issue was one of how many segments were incorporated into the head (e.g., de Beer, 1937), and later the role of novel vertebrate developmental interactions (e.g., those involving the neural crest; Gans and Northcutt, 1982; Northcutt and Gans, 1982), now the issues being raised relate to differences in numbers and identity of rhombomeres and somitomeres, to the nature of differences in head versus body development and organization, and to differences in genome and cell size.

Whereas Gans and Northcutt argued for a new perspective on the organization of the head and focused on novel features associated with interactions of neural crest cells, recent work has gone even further and has focused on major differences in head-body origination. Holland (1996:63–70) and Fernández-Garcia and Holland (1994) have shown that it may be more appropriate to view amphioxus as being mainly head rather than mainly body, in terms of the pattern of gene product distribution during development. Fritzsch and Northcutt (1993) proposed that cranial and spinal nerves of vertebrates may not be homologues, and argued that the old view that ocular motor nerves were homologues of spinal motor nerves and of the so-called somatic motor component of ventral roots of brainstem mixed nerves can no longer be strongly defended. Northcutt (1993) refutes the influential model of Goodrich (1930), based on modification of trunk-like segments in head origins, and argues against a close relationship between nerves and mesodermal derivatives. He envisions as many as four separate cranial-caudal series of special nerves having arisen in the heads of basal vertebrates. These were derived independently with relationship to each of the iterative developmental tissues of the head (neural crest, neuromeres, placodes, somitomeres), each in a different manner. Gilland and Baker (1993) have gone further, making comparisons between the cranial region of vertebrate embryos and the primary gastrula of amphioxus. In their view the vertebrate head is primary, the homologue of nearly the entire gastrula of ancestral chordates, and craniogenesis during gastrulation is the proper structural starting point for examining the critical roles of brain segmentation and of the evolution of functional roles for the neural crest in craniates. These new perspectives have turned old ideas around, and now we have the image of an ancestral vertebrate head that had to invent a body!

One would think, given these new perspectives, that there would be more attention to the region of the craniovertebral joint, but that is generally not the case. As I have pointed out elsewhere (Wake, 1993), the vagus nerve (X) is of special significance because most of the function of this nerve is associated with the body, although it is derived from one to several rhombomeres (the number is unclear and probably varies among taxa) and gives every indication of being a serial homologue of nerves V, VII and IX. Conversely, the motor nucleus of the hypoglossal nerve (XII) lies in the spinal cord of frogs and salamanders, and exits through vertebrae, although it serves head muscles (the origin of these muscles from dorsal somitic muscle that migrates ventrally was of key importance in Goodrich's model). The motor nucleus of the spinal accessory nerve (XI), only recently mapped in amphibians (Roth et al., 1984; Wake et al., 1988; Ota et al., 1987), lies in the vertebral column, outside the brainstem, yet the nerve migrates anteriorly to exit through the head together with the completely separate vagus. De Beer (1937) and other workers thought amphibians had incorporated fewer segments from the body into the head. This issue needs to be thoroughly reevaluated given new findings relating to head organization.

It may be that part of the problem with relation to amphibian head organization arises from the fact that there are fewer somitomeres in amphibian heads (as in elasmobranchs) as compared with teleosts and amniotes (Jacobson, 1993). It is equally parsimonious, with the data at hand, to argue either: 1) that low numbers were ancestral and high numbers have been gained independently in teleosts and amniotes, or 2) that high numbers were ancestral and that low numbers have been evolved independently in elasmobranchs and amphibians, or 3) that low numbers were ancestral and have been retained in elasmobranchs, but were evolved independently again in amphibians. I favor the latter hypothesis, on the grounds that various kinds of somitic tissue are present in very low quantities in amphibians (e.g., sclerotome; Wake, 1970; Wake and Lawson, 1973), that amphibians show secondary simplification of the entire nervous system (Roth et al., 1993), and that modern amphibians have larger than average to enormous genome and cell sizes and they probably arose from ancestors which had large genomes and cells. The connection of this last point is not immediately obvious. However, somitomeres are expansion figures in early embryogenesis that accumulate cells as they expand (Jacobson, 1993), and rhombomeres, like segments, are condensations of cells that require certain numbers of cells before they self-organize. Furthermore, rhombomeres first are laid out segmentally and then they subdivide. I suggest that a major factor in amphibian development (and especially salamanders) has been large cell size, which has led to the reduction and probable loss of resegmentation (often considered to be a universal feature of vertebral formation in tetrapods), in the trunk, reduction through failure of units to subdivide in the posterior head, and possibly with new combinations of the remaining iterative cell masses in the head. Thus the number of segments in the head of salamanders and frogs as compared with amniotes and some fishes could be the absence not of primary segmentation but of secondary segmentation, plus some amalgamation.

There is a strong positive correlation between genome size and cell size in vertebrates, and in large-genomed taxa there are important implications for rate of cell division, morphogenesis and adult morphology (Sessions and Larson, 1987; Roth et al. 1994). This is especially true for relatively small organisms. Miniaturization often leads to disruption of ground plans, and in such taxa as those constituting the marine interstitial fauna, secondary (in a phylogenetic sense) simplification of adult morphology is nearly an expectation (reviewed by Hanken and Wake, 1993). However, it has not been generally appreciated that there is a difference between physical size, in which organisms are compared by mass or linear dimensions, and biological size, in which genome and cell size in relation to physical size, within a phylogenetic framework (in order to determine the direction of character state change), are the important parameters. Using such criteria, the physically large lungfishes (which have the largest genomes, and cells, among vertebrates) are biologically small, but the physically small salamanders (and some frogs) are in effect biological miniatures. In such organisms we should expect, and we do find, paedomorphic morphologies that are secondarily simplified, but are in fact only partially recapitulatory. Thus, the optic tectum and the tegmentum of relatively large genomed salamanders, frogs, and lungfishes are apparently embryonic in histological and some aspects of neuronal structure and organization, but they have fully adult physiological organization and neurological connectivity, comparable to less simplified out groups. Physically small mammals such as shrews are biologically large, in comparison to other small but metabolically less active mammals, but all small mammals are biologically large in comparison with the large-genomed, metabolically slow, developmentally retarded salamanders and lungfishes, some of which are much larger than shrews in physical dimensions. Genome size variation is not great in amniote vertebrates, but in most organisms it is a factor that should not be overlooked.

Increasingly in developmental biology there is an appreciation of the importance of cell number at critical stages of morphogenesis, such as in the organization of early condensations. Busturia and Lawrence (1994) used genetic manipulations to produce *Drosophila* embryos with reduced numbers of abdominal primordial cells; such embryos were unable to produce morphological patterns normally seen in development, but denticle bands were fused to those in adjacent segments and some rows were missing, bristles normally present were absent, and a pigment band was reduced. In another example, molecular-level factors involved in skeletal morphogenesis in mice were examined with respect to the role of the gene superfamily known as transforming growth factor beta (Storm et al., 1994). Mutations known as *brachypodism* result in marked shortening of the limb skeleton. Tickle (1994) observed that the number of founder cells for each limb element might be reduced in mutants, which translates into insufficient growth that leads to digital defects. Alberch and Gale (1985) showed that reductions in cell division rate alone can lead to the reduction in the numbers of digits in both frogs and salamanders.

Prospects for a merger of development and evolution

At present the fields of development and evolution are mainly separate, but there are prospects for an integration. I have given some examples of areas of opportunity. Two book-length treatments have appeared (Raff and Kaufman, 1983; Hall, 1992), but the first predated much of the recent excitement in molecular genetics and the second was written by a scientist whose work has dealt mainly with morphogenesis and not with the molecular biology of development. Those who focus on molecular developmental genetics are mainly focused on genetic invention and novelty (genes of large effect) (e.g., Tabin, 1993; Tabin and Laufer, 1993), whereas developmentalists such as Hall recognize the complexities and hierarchical nature of development, and have established working relationships with quantitative geneticists (Atchley and Hall, 1992), who characteristically focus on many genes, each of minor effect. I believe that the resolution of arguments concerning the merits of these contrasting approaches will come from comparisons of relatively closely related taxa, for most of the research (with a few notable exceptions, e.g., Raff et al., 1991 on sea urchin morphogenesis, and Nijhout, 1990, on butterfly wing patterns), has dealt with too few and too distantly related taxa. There has been a great deal of highly sophisticated developmental genetic work in the past several years, but mainly the focus has been on conserved systems (highly persistent ones, using my suggested terminology). For example the discovery of an apparent common dorsal-ventral patterning signal in insects and vertebrates has renewed speculation that there was a reversal (note the recurrent theme of genetic invention) of the dorsal-ventral axis in some common ancestor (Holley, et al., 1995). However, other workers are focused more acutely on evolutionary issues. The recent work of Carroll (summarized in Carroll, 1994) on the developmental-genetic basis for differences in arthropod body plans stimulated interest in the possibility of analyzing the influence of developmental regulatory mechanisms underlying morphological transitions. Such work may point the way for new investigations into the genetic and developmental foundations of morphological diversity within an appropriate evolutionary and phylogenetic framework.

Evolutionary developmental biology is a field of great promise. Barriers that formerly separated the disciplines of development and evolution are being broken down, and new research questions and programs are being formulated. As the new field develops it will be increasingly necessary to maintain communication with the core disciplines, and this will require that practitioners understand and appreciate the philosophical and conceptual issues in evolution (such as arguments over homology, and methods of phylogenetic analysis) and the methodological and strategic issues in development (such as the hierarchical nature of the interaction of molecular and cytological factors in morphogenesis), so that the empirical core of the fields can be made relevant to both. The success of the new field will depend critically on bringing developmental approaches to the appropriate taxonomic level, such as the populational and interpopulational levels for evolutionary analysis, and the interspecific (i.e., intrageneric or intrafamilial) levels for phylogenetic analysis. There are hurdles, even barriers, to be crossed if a development-evolution synthesis is to be attained. Evolutionists must be convinced that development has something to offer them, and vice-versa. Amundson (1994:576) has offered a penetrating analysis of this issue, and has made clear what the task of students of comparative ontogenies will be "to demonstrate that a knowledge of the processes of ontogenetic development is essential for the explanation of evolutionary phenomena." It will not be easy, as witness the recent attack of Reeve and Sherman (1993) on the concept of developmental constraint. In questioning whether my structuralist (Wake 1991) explanation for why small frogs and salamanders often lose one toe, but a different one in the two taxa (five in salamanders; one in frogs, following Alberch and Gale, 1985), Reeve and Sherman argue that the functionalist (adaptationist) approach must always be conducted first in order to determine if any other kind of explanation is necessary. Amundson (1994) has made a useful comparison between constraint on form and constraint on adaptation that has relevance here. In essence, Reeve and Sherman have made a category mistake. The argument is not about constraint on adaptation but about constraint on form generation; knowledge of the developmental pathways in frogs and salamanders enables predictions (e.g., concerning unknown or unstudied taxa of frogs or salamanders) to be made. This framework leads to the recognition of constraints, not on adaptation but on form. We who are interested in a synthesis of development and evolution must make clear that our goals are not to replace neodarwinism, but to expand it by focusing on form and its causes, the central problem in development. Similarly, we must make clear to developmentalists that study of variation and its genetic basis, and careful phylogenetic analysis, central issues in evolution, have relevance in developmental biology as well.

I have argued elsewhere (Wake, 1991; Wake and Larson, 1987; Wake and Roth, 1989) that a synthesis and integration of three perspectives on the evolution of form are required for a full picture of the question: how do organisms evolve? One of these perspectives is neodarwinian functionalism — the heart of evolutionary biology. A second is biological structuralism — the rules of form generation and transformation, deeply embedded but not totally subservient to developmental biology. The third is history — both the contingencies of history and knowledge of the genealogical relationships of lineages. I believe that we are not far from a time when these three approaches, appropriately integrated, will form the heart of a modern science of evolutionary developmental biology.

Conclusion

We are on the threshold of a new venture in evolutionary biology, the long-awaited merger of studies on the ontogenetic production and phylogenetic transformation of organismal form. This new field is demanding, for it requires understanding of mechanisms of development and of evolutionary change, and perspectives on current dynamics and on history, both the history of ideas and concepts, and the one true but only partially known history of life on this planet. I predict that the years ahead will at last witness a fruitful synthesis that will bring new excitement to developmental evolutionary biology.

Acknowledgments

I thank the organizers of this conference for the invitation to participate in the stimulating discussions, and R. Amundson, F. Bashey, M. Ghiselin, J. Hanken, N. Holland, E. Jockusch, E. Mayr, A. Meyer, S. Minsuk, W. Olson, M. H. Wake, and an anonymous reviewer for discussion and comments on the manuscript. My research has been sponsored by the National Science Foundation and the Gompertz Professorship in Integrative Biology at the University of California at Berkeley.

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ISBN 0-940228-43-2