



The Concept of Monophyly: A Speculative Essay

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Abstract. The concept of monophyly is central to much of modern biology. Despite many efforts over many years, important questions remain unanswered that relate both to the concept itself and to its various applications. This essay focuses primarily on four of these: i) Is it possible to define monophyly operationally, specifically with respect to both the structures of genomes and at the levels of the highest phylogenetic categories (kingdoms, phyla, classes)? ii) May the mosaic and chimeric structures of genomes be sufficiently important factors in phylogeny that situations exist in which the concept may not be applicable? iii) In the history of life on earth were there important groups of organisms that probably had polyphyletic, rather than monophyletic, origins? iv) Does the near universal search for monophyletic origins of clades lead, on occasion, to both undesirable narrowing of acceptable options for development of evolutionary scenarios and sometimes actual omission from consideration of less conventional types of both data and modes of thought, possibly at the expense of biological understanding? Three sections in the essay consider possible answers to these questions: i) A reassessment is made of major features of both the concept and some of its applications. Recent research results make it seem improbable that there could have been single basal forms for many of the highest categories of evolutionary differentiation (kingdoms, phyla, classes). The universal tree of life probably had many roots. Facts contributing to this perception include the phylogenetically widespread occurrences of: horizontal transfers of plasmids, viral genomes, and transposons; multiple genomic duplications; the existence and properties of large numbers of gene families and protein families; multiple symbioses; broad-scale hybridizations; and multiple homoplasys. Next, justifications are reassessed for the application of monophyletic frameworks to two major evolutionary developments usually interpreted as having been monophyletic: ii) the origins of life; and iii) the origins of the vertebrate tetrapods. For both cases polyphyletic hypotheses are suggested as more probable than monophyletic hypotheses. Major conclusions are, as answers to the four questions posed above: probably not, yes, yes, and yes.

Key words: cladistics, evolutionary genomics, monophyly, origins of life, origins of tetrapods, phylogeny, systematics

Introduction

The theory of common descent (the concept of monophyletic origins of groups of organisms or of major components of the genomes of organisms)

is a fundamental, almost universally accepted part of modern biology. The current, relatively early stage of the conceptual development of the new field of evolutionary genomics includes monophyletic frameworks as the default mode (Henikoff et al. 1997; Tatusov et al. 1997). The identification and characterization of monophyletic groups of organisms are major preoccupations of those researchers who work in the fields of evolutionary and phylogenetic systematics. Cladistic approaches to classification in general and the rooting of phylogenetic trees in particular are enterprises built upon the idea of monophyletic origins of groups of organisms – up to and including the “Universal Tree of Life” for all organisms (Forey et al. 1992; Runnegar 1992; Panchen 1992; Benton 1995; Nielsen 1995; Baldauf et al. 1996; Doolittle et al. 1996; Huelsenbeck et al. 1996; Wray et al. 1996; Hillis 1997; Huelsenbeck and Rannala 1997; Kenrick and Crane 1997; Maley and Marshall 1998).

Recent work on the invasions of the land by organisms (Gordon and Olson 1995) raised the question of the extent to which this near ideological commitment to the concept of monophyly is both theoretically and practically desirable. Serious trade-offs and compromises can be involved which are usually not explicit, often are hardly visible, and have the potential to both adversely impact the processes of evolutionary research and to produce erroneous conclusions. There are substantial unresolved issues relating to operational definitions of the term. These are most apparent with respect to both the structures of organismic genomes and at the levels of the highest categories (kingdoms, phyla, classes). There are multiple new lines of evidence and sufficient numbers of clear cases in which monophyletic interpretations are, at best, labored or, in some cases, untenable. Accordingly, I believe that now is a good time to begin a reassessment of what we mean by monophyly, and of some selected situations in which the applicability of the concept may be demonstrably inappropriate.

The body of this paper has three parts. First is a discussion of issues relating to the possibility of the development of an operational definition of the concept of monophyly at the levels of both genomic structures and for the highest phylogenetic categories. Next are considerations of two of the major evolutionary developments in the history of life on earth: i) the origins of life; and ii) the origins of the vertebrate tetrapods. I have chosen these two developments because all of the available evidence relating to each of them is indirect and circumstantial. These situations are likely to persist indefinitely, if not forever. Therefore, hopefully, in these contexts the underlying theoretical and philosophical issues may be easier to identify, isolate and discuss. Under these conditions one's hypotheses are not limited by the available data.

What is monophyly?

A broadly applicable operational definition for the term monophyly remains elusive. The choice of a definition has both theoretical and practical implications. For example, it affects our perception of how many different kinds of organisms there are and have been, which is a basic statistic underlying Benton's (1995) discussion of historical variations in amounts of biodiversity. There also are ongoing arguments relating to the applicability of the concept at various levels of phylogenetic differentiation (Crisp and Chandler 1996).

What could, or should, monophyly mean in terms of evolutionary process? What do we really mean by the terms "common ancestor" or "basal form"? Two substantial issues are involved.

1) *Are ancestors single or multiple?* The answer to this question appears to be "it depends." The cladistic view of phylogeny is that ancestors do not exist as separate entities. The single species that gave rise to an array of descendant species is not the ancestor of that clade, but is instead its most primitive (plesiomorphic) member (Forey et al. 1992; Panchen 1992; Carroll 1997). Such species are perhaps best called basal forms.

This view appears generally to work well at what might be termed the micro- and meso-scales of evolutionary differentiation (from populations to the levels of genera and families). The application of molecular biological techniques has brought questions at these levels within the range of empirical science in at least some cases. Results of these types of studies have radically changed many perceptions concerning phylogenetic relationships. They have also made it apparent that there are no single, universal scenarios, even at these levels (Fitch and Ayala 1995; Smith and Szathmary 1995; Ferraris and Palumbi 1996; Hillis 1997; Huelsenbeck and Rannala 1997).

The least convincing applications of this view involve the macro-scale of evolutionary differentiation, the highest categories (kingdoms, phyla, classes). It seems certain that final determinations of the mono- or polyphyletic origins of most of these categories cannot be solely based upon morphological grounds. All these groups have relatively ancient origins. The fossil record from far back in time is either non-existent or simply too partial, fragmentary, stochastic and mosaic in nature to provide definitive answers. Questions always persist as to the nature of the relationships that may exist between known fossils and the "true" phylogenetic relationships of the groups of organisms being studied. There is, however, no doubt that strong circumstantial cases have been made, based largely upon morphological evidence, for polyphyletic origins of a number of major groups of organisms (Jablonski et al. 1996; Janvier 1996; Carroll 1997; Maley and Marshall 1998).

The extent to which the monophyly, or lack thereof, of many of the higher categories of organisms may be demonstrable at the molecular level has also become seriously problematic. This statement is based upon discoveries in recent years flowing primarily from genome sequencing projects and other aspects of molecular genetics. The genomes of living organisms are highly complex, and it is apparent that the more we learn about them the more complex we find they are.

2) *Do traceable genetic lines of descent exist that might ultimately permit characterization of the genomes of organisms basal to the clades for the highest categories?* The answer to this question increasingly appears to be no. Recent work on genomic structures demonstrates that all living organisms are genetic composites – mosaics and chimeras composed of bits and pieces of multiple genomes derived from multiple sources. Breakdowns appear to be occurring in many of the major distinctions upon which systematists and evolutionary biologists have based the system of organismic classification, most notably the distinctions between the three kingdoms of the Archaea, Bacteria, and Eukarya (Russo et al. 1996; Belfort and Weiner 1997; Henikoff et al. 1997; Tatusov et al. 1997; McDonald 1998; Pennisi 1998b). The primary literature in this area is mostly very recent, and is increasing rapidly in both numbers and variety of papers. I now present a selective summary of highlights from this literature, including also a few secondary articles that provide useful perspectives.

At least seven sets of phenomena and processes are relevant:

- a) The abilities of many types of microorganisms to exchange genetic materials, not just interspecifically but even between kingdoms (plasmid transfers – currently invoked as a major possible source of both antibiotic resistant strains and of new infectious strains of pathogens; Bult et al. 1996; Gueiros-Filho and Beverley 1997; Hartl 1997; Mazel et al. 1998; Pennisi 1998a).
- b) The abilities of many viruses to both insinuate their own genomes into those of host organisms and also to incorporate genetic materials from their hosts into their genomes – resulting in the horizontal transfer of genetically active materials to other organisms (these elements have been identified between classes within single phyla, between phyla, and between kingdoms; Domingo et al. 1996; Tristem et al. 1996; Martin et al. 1997).
- c) The existence of ubiquitous, genetically expressed transposable elements (transposons) within eukaryotic genomes that, in some cases, can be experimentally transferred between organisms in widely

disparate lineages (Hilario and Gogarten 1993; Figueroa et al. 1995; Loukeris et al. 1995; Henikoff et al. 1997; Tatusov et al. 1997; McDonald 1998).

- d) The existence within multiple, phylogenetically widely dispersed genomes of large numbers of both protein families (over 700 known clusters of orthologous groups to date) and gene families, many of which appear to have had both different phylogenetic origins and different phylogenetic histories (Henikoff et al. 1997; Tatusov et al. 1997).
- e) The occurrence within multiple, phylogenetically widely dispersed genomes of whole-genome duplications that have subsequently had diverse evolutionary histories (Henikoff et al. 1997; Tatusov et al. 1997).
- f) The symbiotic origins of such intracellular organelles in eukaryotes as mitochondria (Lang et al. 1997; Vogel 1997; Gray et al. 1998), chloroplasts (Koehler et al. 1997), hydrogenosomes (Palmer 1997; Martin and Mueller 1998), and even nuclei (Pereira et al. 1997; Reeve et al. 1997), with each category of organelle having a different microorganismic origin (Runnegar 1992; Margulis 1993; Sogin 1997).
- g) The possible widespread occurrence of reticulate evolution, based on temporally varying amounts of broad scale hybridization, in many plants and a variety of groups of marine invertebrates, most notably the scleractinian corals (Veron 1995; Romano and Palumbi 1996).

In addition it seems probable that the history of life includes many significant occurrences of widespread homoplasy (Sanderson and Hufford 1996). These homoplasies are often difficult to detect and hard to unequivocally document.

These phenomena collectively make it appear nearly impossible that the highest categories of living organisms can be said to have had single basal species. At the macro-scale life appears to have had many origins. The base of the universal tree of life appears not to have been a single root, but was instead a network of inextricably intertwined multiple branches deriving from many, perhaps 100 or more, genetic sources (Pennisi 1998b). The traditional version of the theory of common descent apparently does not apply to kingdoms as presently recognized. It probably does not apply to many, if not all, phyla, and possibly also not to many classes within the phyla.

The origins of life

Wherever life first arose, whether here on earth or extraterrestrially (or both), the processes leading to its origins were complex and developed over extended periods of time. Prebiotic syntheses of essential organic compounds of many kinds had to develop first. Multiple theories have been advanced, both

as to how these compounds arose and as to how the right mixtures might have come together in organized ways at particular places and times to produce the first self-replicating living entities (Eigen and Winkler-Oswatitsch 1992; Kasting and Chang 1992; Bloch 1995; Bock and Goode 1996; Chela-Flores and Raulin 1996; Hirabayashi 1996; Krupp 1996; Crabtree 1997; Huber and Wächtershäuser 1997). It seems improbable that direct fossil evidence relating to these earliest events will ever be found.

Three process related general scenarios are available with respect to possible origins of life. The first postulates that these early evolutionary developments happened only at one place, at one moment in time, by one process, and produced only one kind of new organism. This plesiomorphic organism then went on to evolve into all the varieties of its descendants. The outcome of this scenario would be that all organisms belong to a single clade and that the universal tree of life is monophyletic.

Second, organisms might have arisen by a variety of possible mechanisms or processes (including possibly arrival from extraterrestrial sources). Assume that the many different possible sequences of initial events occurred many times, in many bodies of water, at many locations on the surface of earth, over extended periods of time. Also assume that there almost certainly were multiple environmental disasters that stochastically produced widespread, but not world-wide, extinctions (a world-wide event would, of course, simply return the entire process to its start). Unless one now assumes that environmental conditions and ecological interactions all over the parts of the earth not directly affected by these disasters stringently selected for the survival of only a single, biochemically uniform type of organism [a variation on the first scenario and a possible illustration of the occurrence of widespread homoplasy (Sanderson and Hufford 1996)], this scenario should have resulted in many kinds of organisms having a variety of basic biochemistries and a variety of genetic compositions.

The multiple types of proto-organisms produced in these ways presumably then reproduced, distributed themselves over the remainder of the earth's surface over varying periods of time, and evolved into the diversity of organisms that followed. Substantial amounts of horizontal transference of genetic materials occurred by many different mechanisms, at many times and places, in many different directions, between many different groups, as did the development of various symbioses and the occurrence of widespread hybridization. Under this scenario life had multiple, polyphyletic origins, all of which have been inextricably intertwined.

The probability of the first scenario seems small. The surface of the earth is too large in extent, and the complexities of that surface, even far back in the Archaean, must have been too varied and diverse to make that sequence

plausible. There must have been proto-oceans, with a range of types of bottom sediments in different places, and with both exposed and protected coast-lines, bays, lakes and rivers, dry land terrains of many kinds, etc. All of these macro-environments, like those existing today, must have contained a diversity of micro-environments that could have permitted, and probably would have selected for, a wide range of chemical mixtures and, eventually, proto-organisms.

It also seems probable that the motilities, mobilities, and survival capacities of the proto-organisms that developed in these micro-environments were too limited (in the presence of the surrounding strongly turbulent, high energy macro-environments, almost all of which were subjected to intense ultraviolet radiation), to permit their wide dispersal, even over very long periods of time. The second scenario therefore seems much more probable, more realistic, and less arbitrary. Based upon this reasoning, life is probably not monophyletic, and any appearances that it might be are just that – appearances.

What may have occurred subsequent to these earliest events is, of course, no less conjectural. It is possible that one genetically related group of organisms may have eventually out-competed and ultimately eliminated all descendants deriving from other ancestral sources. Using this third scenario, retrospective, present-day molecular biological probes of basal relationships of the highest level evolutionary categories might be interpreted to indicate apparent monophyly of surviving descendants, but only if one ignores the horizontal genetic transfers, the transposons, symbionts, hybrids, etc. described in the preceding section. Taking into account the apparent ubiquity of these genomic processes, and the probable phylogenetically diverse origins of the genomic elements involved, this third possibility appears to be both improbable and technically impossible to demonstrate. It is also more complex than either of the other scenarios, requiring several additional basic assumptions.

Life, therefore, is probably polyphyletic in origin. The second scenario is to me the simplest, the most plausibly realistic, and the most congruent with current understanding. It also has the substantial advantage of being stimulatory of continuing research efforts to provide tests of the scenario. If taken seriously, it might stimulate reappraisals of existing lines of evidence. Might the RNA world not have preceded the DNA world, but instead have been a parallel development? There is increasing evidence to support such scenarios (Landweber and Gilbert 1994; Ding et al. 1996; Ferris et al. 1996; Biebricher and Gardiner 1997; Conrad et al. 1997; Welch et al. 1997; Jeffares et al. 1998; Poole et al. 1998).

The origins of tetrapods

Many people are actively investigating the origins of terrestrial vertebrates. The data base for discussions has expanded dramatically within the past decade. Several new, relevant, and well-preserved fossils have been found and described, and there have been major studies using molecular biological approaches. Despite the large volume of publication, however, the underlying reality remains unchanged: everything we know is circumstantial and indirect, and what actually occurred remains unknown. Janvier (1996) provides a refreshingly objective and dispassionate general commentary on this specific question, and on a series of other questions relating to early vertebrates.

Three approaches to tetrapod origins are available: i) the classical paleontological – morphological – taphonomic approach based almost exclusively upon the fossil record; ii) the molecular biological approach based upon studies of living fishes belonging to what are considered to be basal groups; and iii) an alternative approach that adds to these data bases several other, different considerations. The primary focus in this discussion is on option (iii), but fairly detailed documentation and explication of the main points deriving from the other two options are essential to make the argument accessible to non-specialists.

Major recent evaluations of basal tetrapod origins and relationships, based primarily upon the fossil record, include: Ahlberg and Milner (1994); Schultze (1994); Ahlberg (1995); Carroll (1995); Clack and Coates (1995); Coates and Clack (1995); Long (1995); Cloutier and Ahlberg (1996); Coates (1996); Carroll (1997); and Graham (1997).

Current knowledge supports the following positions: Cladistic analyses of the most complete data sets of osteological characters so far gathered indicate that the Tetrapoda are a subclade of the clade Sarcopterygii (lobe-finned fishes). Their sister-group is the subclade Elpistostegalia, which is the group containing *Panderichthys*, the genus of Devonian fossil fishes generally regarded by paleontologists as closest to the main evolutionary line that led to the tetrapods. The living lungfishes (Dipnoi) are the Recent sister-group of the tetrapods. The living coelacanth (*Latimeria*) is in another, more distant, subclade (Cloutier and Ahlberg 1996, which is a major effort at developing a global consensus analysis of all available morphological data sets).

It is important to note that several recent discussions of sarcopterygian-tetrapod similarities and differences are based on the more extensively studied upper Devonian fish genus *Eusthenopteron*, rather than on *Panderichthys* (e.g. Carroll 1997). The fishes within these two genera are morphologically quite similar. According to Cloutier and Ahlberg (1996) these two genera are

phylogenetically close to each other, but it is still uncertain whether or not they belong to different subclades.

Cladistic analyses of different molecular biological data sets from living fishes have produced more varied results. Meyer and Dolven (1992), studying the 12S rRNA mitochondrial gene, concluded that lungfishes are the Recent sister-group of the tetrapods. Their data excluded the coelacanth from the tetrapod clade. Yokobori et al. (1994) studied the mitochondrial cytochrome oxidase subunit I gene sequence and also concluded that lungfishes and tetrapods form a clade, but so do lungfishes and the coelacanth. Their data also excluded the coelacanth from the tetrapod clade. Zardoya and Meyer (1996b) sequenced the large 28S nuclear ribosomal gene and concluded that lungfish and the coelacanth form a clade, and that both subclades are equally closely related to tetrapods. Zardoya and Meyer (1996a, 1997) sequenced the entire mitochondrial DNA genomes of both the coelacanth and a lungfish and reached a similar conclusion. Thus there are significant variations regarding conclusions derived from molecular biological data sets, and differences between various parts of the morphological and molecular data sets.

Two important points must now be made concerning all of these analyses:

First, since the analyses were all done cladistically, the underlying phylogenetic model in all cases was monophyletic. A single "main line" of tetrapod evolution is assumed to have existed in all cases. Possible polyphyletic scenarios were methodologically and philosophically excluded as implausible.

Second, these analyses of relationships serve as the springboards for extensive discussions of the possible ways in which mid- to late Devonian sarcopterygian fishes (*Eusthenopteron* is the principal exemplar, though *Panderichthys* is considered closer to the postulated main line of evolutionary change; the fossils are Frasnian in age, from about 375 mya) may have evolved to become highly differentiated amphibians (*Acanthostega* is the model genus) like those found, after an almost fossil-free gap in time of about 10 million years, in the Famennian period of the Upper Devonian (from about 365 mya). These latter discussions are based primarily upon morphology, with the origins of lungs and limbs being central concerns. Speculative inferences about physiology and behavior are also included, as are considerations of the local environments of the fossil animals, of inferred general topographies of the continents, and of aspects of global climates at the times when they lived. The basal assumption is that the properties of the known fossils, combined with what can be inferred about their environments, determine the parameters and the limits of possible, plausible evolutionary scenarios and trajectories.

There is adequate justification, I believe, for both questioning and substantially changing these perspectives. Several of the underlying assumptions deserve reevaluation, and additional relevant lines of evidence should be included. The “conventional wisdom” just described *may* be correct, but it also may not be. If it is not, or if at least the possibility of alternative interpretations is seriously entertained, then the subject area may become both more complex and more interesting.

The late E.C. Olson and I recently presented evidence and arguments for a different, more varied set of possible scenarios for tetrapod origins (Gordon and Olson 1995, Chapters 9 and 10; Gordon 1998). Basing our evaluation upon biogeographic, population genetic, and other life-history considerations, and arguing by analogy from evidence from living amphibious fishes, we concluded that it is more likely than not that tetrapods were polyphyletic in origin. Homoplasys may also have been important in this transition.

I now refine, expand, and add to this argument. Some additional facts and perspectives are needed:

The crucial role that statistically inadequate sampling of Devonian faunas has played in the development of our perceptions must explicitly be acknowledged. The numbers and diversity of known fossil taxa are insufficient to permit a definitive resolution, based on the fossil record, of the central questions relating to either monophyly or polyphyly of tetrapod origins, or to the relationships between the known groups of basal fishes and tetrapods. The mathematical issues involved are closely related to those discussed by Nee and May (1997) and Myers (1997).

Comparable problems exist with respect to the molecular biological evidence. The living lungfishes and the coelacanth represent tiny, randomly selected remnants of ancient groups that were numerous, varied, and widely distributed in the Devonian. One can only wonder at how accurate, or even relevant, the relationships that we estimate to exist between these organisms today may be with respect to the actual phylogenetic relationships of their basal groups.

The known fossil record of late Devonian basal fishes and tetrapods, while significantly augmented in recent times, remains limited and partial. It is also the case that, while a few forms are now represented by well-preserved, near complete remains (notably *Eusthenopteron*, *Panderichthys* and *Acanthostega*), many of the fossils are literally fragments. The animals found represent only a small, stochastically selected, possibly quite unrepresentative, sample of the biodiversity that existed in these groups at those times. There is no way of knowing to what extent, if at all, those specific organisms were relevant to later developments, or what their relationships might have been to each other. They may all have been parts of lineages that died out,

making no contributions to the overall flow of vertebrate evolution. Using these specific animals as models is a problematic basis for generalizations about how and when tetrapods might have arisen, what they might have been like, where they might have lived, etc.

The geographic distribution of the relatively contemporaneous (within a few million years) known late Devonian tetrapods (east Greenland, eastern North America, northern Europe, Russia, Australia), in the context of the distribution of the continents during the late Devonian, indicates high probability of genetically independent parallel origins of the different groups in multiple regions separated from each other by very long distances (varying from a few thousand km to, in the most extreme case, about 20,000 km). The chances that intervening environmental discontinuities and barriers were present seems very large. If both the early amphibians and their presumed sarcopterygian progenitors respectively had relatively limited geographic ranges, and also had limited capacities for geographic dispersal, this far-flung distribution makes probable both genetic isolation and at least species level differentiation of distant populations. A probable scenario is one of separate independent origins of multiple groups of tetrapods, each deriving from a different basal fish species.

Panderichthys (found in Latvia, northern Europe) and other late Devonian sarcopterygians are presumed to have been oviparous. Living lungfishes are also oviparous, but they are fresh water forms and have no larval stages adapted for widespread geographic dispersal. The coelacanth is marine, but ovoviviparous. The indications are that all of the late Devonian amphibians known were not very active animals as adults. The postulation is that, like modern amphibians, they developed from larvae that metamorphosed. It seems improbable that any of those animals were capable of significant dispersals over long distances, crossing a variety of hostile environments.

The living amphibious fishes are instructive in several respects. Applying the principle of uniformitarianism, these fishes provide a series of possible keys to the past. Similar reasoning leads to the position that levels of environmental diversity and complexity, and of biodiversity, were comparable in the latter Devonian to what they are now.

Living amphibious fishes are all much more recent evolutionary developments and have no known phylogenetic relationships to the ancient basal sarcopterygians. They all, however, to varying extents and in many different ways, are successfully coping with a wide variety of amphibious habitats and lifestyles (Gibson 1993; Gordon and Olson 1995; Martin 1995; Ultsch 1996; Graham 1997). They therefore represent an evolutionarily successful array of morphological, physiological, behavioral and ecological methods for living transitional lives. They are collectively an envelope of possibilities with

respect to both where and how the mid- to late Devonian transitions might have occurred.

There are more than 200 species of living amphibious fishes. These species are widely dispersed over the surface of the planet. Arrays of species live from the tropics to the subarctic, from low to high elevations, from a range of freshwater habitats through estuarine environments to purely marine habitats, and from open rocky coasts subjected to the full force of oceanic waves to protected mudflats, mangrove environments and inland waters. They demonstrate that varied amphibious lifestyles can evolve almost anywhere where there is water next to land. They also demonstrate that amphibious capacities may evolve at almost any life history stage – eggs, juveniles and adults all have abilities in this direction.

Adults of many amphibious fishes do perfectly well out of water for extended periods of time (up to days) without specialized limbs for locomotion or lungs or accessory respiratory organs for breathing. Thus many of the basic assumptions made in the literature (both older and more recent) concerning the morphological properties required for successful land invasions by fishes seem to be contravened. The starting points for the major anatomical features of tetrapods need not necessarily have been what they have conventionally been postulated to have been.

Based on all of these considerations the case seems strong that the tetrapods were polyphyletic in origin. The putative resemblances between the different groups of amphibians from the late Devonian seem largely homoplasys (parallelisms and convergences). These greatly evolved and diversified organisms shared some morphological and life history characteristics which probably developed as results of widespread, strongly similar, natural selective pressures working on various life history stages of a variety of different amphibious fish species that lived in many different habitats in widely scattered localities in different parts of the earth. It is plausible that these fishes were sarcopterygians. It is also plausible that at least some of the basal forms may have been geographically widely dispersed different species within a genus much like *Panderichthys*.

There may possibly have been a plesiomorphic basal species of all *Panderichthys*-like sarcopterygians. Whatever that species may have been like, given the biogeographic and dispersal-related considerations discussed earlier, it seems probable that multiple separate (genetically differentiable) populations of this fish were ultimately basal to the different tetrapod groups in each of the far-flung regions involved.

Concluding remarks

The evidence cited and the arguments made in this essay indicate that the applicability of the concept of monophyly at the macro-scales of evolutionary differentiation increasingly appears to be severely limited. An operational definition of the concept does not seem possible at the macro-level. Indeed, the phenomenon of a monophyletic origin for the universal tree of life probably did not occur.

However, these considerations do not necessarily diminish either the general validity or the utility of the concept as a beginning, default assumption in the consideration of micro- and meso-scale evolutionary events and processes. They do, however, appear to strongly justify critical thinking about the applicability of that assumption in carefully chosen cases at those levels of scale. There is good reason to believe that at least some major groups of organisms at the meso-scale had polyphyletic origins. In considering these questions it clearly is desirable to consider all possible relevant lines of evidence. The database should not be restricted solely to morphological, taphonomic, and molecular evidence. It is also desirable to avoid restricting frameworks for the evaluation of relevant data to only cladistic models.

At the macro-levels it is clear that the new insights coming from molecular genetics, including genome sequencing, must be applied to many other important evolutionary developments and transitions in addition to those considered here. One possible application could be an attempt to clarify the bases for the strikingly large differences in ages (in excess of one billion years) estimated for major evolutionary developments in the early history of life from, on the one hand, the fossil record itself (Schopf 1993) and, on the other, calculations based on modern molecular data used as molecular clocks (Doolittle et al. 1996; Wray et al. 1996).

Bringing conceptually and ideologically less constrained perspectives, including new types of information and different ways of approaching the problems involved, into discussions of important evolutionary biological topics (such as the origins of life, of higher phylogenetic categories, and of the tetrapods), may result in more nuanced and more biologically realistic sets of applications of the concept of monophyly. This may then facilitate the development of a consensus among evolutionary biologists that will promote improved understanding of both evolutionary process and of actual evolutionary events.

The author's hope is that this essay may contribute in a small way to the mitigation of the strong trend toward more and more reductionism that pervades much of modern biology. I think biologists should try to avoid what I call "physics envy." The search for the simplest, most inclusive explanations for biological phenomena certainly must continue. However, that search

should be tempered with the realization that over-generalization (including efforts to force everything in entire fields of study into single conceptual molds, such as the cladistic mold in evolutionary biology) is also a hazard along the path to understanding of the natural world.

Acknowledgments

The ultimate origin of this essay dates back to the early 1950s. I then had the privilege of occasionally participating in a seminar on evolutionary biology organized by Ernst Mayr at the American Museum of Natural History, New York. This raised my consciousness concerning evolutionary issues. I thank Prof. Mayr and the many other participants for having done that. Multiple other influences have intervened since, however, so this essay has polyphyletic origins. Early drafts of the paper were commented on by M.J. Benton, R.M. Burian, D.G. Buth, C.R. Marshall, E. Mayr, J.W. Schopf, and three anonymous reviewers. I thank them all. All errors of fact and interpretation remaining are my responsibility.

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