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THE ONTOGENETIC METHOD FOR DETERMINING CHARACTER POLARITY AND ITS RELEVANCE TO PHYLOGENETIC SYSTEMATICS

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Abstract.—In an attempt to clarify the relevance of ontogenetic transformations for systematics, the ontogenetic method for determining character polarity (the biogenetic law of Nelson, 1978) is analyzed from the perspective of phylogenetic systematics. In phylogenetic systematics, as defined here, the relationships sought are those of common ancestry and, thus, the concept of phylogeny is taken as an axiom from which systematic methods are deduced. This perspective has a number of consequences concerning the role of ontogenetic transformations in systematics, among which are the following: (1) Von Baer's second law, which states that less general characters are developed from the most general, is not universally true. (2) The validity of Nelson's biogenetic law (not to be confused with other concepts of similar name) does not depend on the validity of von Baer's law. (3) As a theory about the relationship between ontogeny and phylogeny, Nelson's biogenetic law can only be tested by known character phylogenies. However, outgroup, paleontological, and ontogenetic methods of polarity determination need not be interpreted as scientific theories; instead, they can be interpreted as theorems deduced from the axiom of phylogeny and certain auxiliary assumptions. (4) The usefulness of the ontogenetic method rests on an assumption of ancestral character retention. If ancestral characters are retained in descendant ontogenies, then ancestral characters will be more general than their phylogenetic derivatives. (5) The sequence of ontogenetic transformation is irrelevant to the usefulness of the ontogenetic method; generality is the critical factor. (6) An "ontogenetic" method based on generality may be useful for determining evolutionary polarity when characters are instantaneous morphologies, but ontogenetic transformations rather than instantaneous morphologies are more appropriately considered characters when attempting to determine phylogenetic relationships among organisms. When ontogenetic transformations are viewed as characters, there can be no ontogenetic method for determining evolutionary character polarity; however, the comparative phylogenetic method properly involves a comparison of ontogenetic transformations. (7) Ontogenetic polarities are different than phylogenetic polarities; the two have the relationship of part to whole, respectively. (8) For characters that exhibit ontogenetic transformation, homology is distinct from synapomorphy. (9) Finally, there is no threefold parallelism in phylogenetic systematics. Comparative anatomy, paleontology, and embryology are not three separate disciplines within systematics; rather, the three form a single comparative method unified in the organism by the concept of evolution. [Biogenetic law; von Baer's law; cladistics; character; evolution; generality; homology; ontogenetic method; ontogeny; outgroup method; paedomorphosis; parsimony; paleontological method; phylogenetic systematics; phylogeny; polarity; semaphoront; synapomorphy; threefold parallelism.]

I consider neoteny an apparent falsifier of a more general principle [than the biogenetic law], that of character phylogeny But I consider neoteny an apparent falsifier in a narrow sense. At times I have suspected that it is not a falsifier at all, but a reflection of lack of information. One may doubt, for example, that any characters are truly lost, rather than transformed. Apparent loss may be an indication that the characters and transformations are merely poorly understood and, consequently, wrongly defined. The problem may be amenable to investigation through analysis of the nature of characters and their comparison—tasks which I do not undertake here [Nelson, 1978: 344].

The rise of phylogenetic systematics (Hennig, 1966) has been accompanied by an increasing concern about one of its essential components—methods for determining the evolutionary polarity of characters. Although many different kinds of evidence have been advocated towards this end (reviewed by de Jong, 1980; Stevens, 1980), the two most popular form the bases of the outgroup method (Watrous and Wheeler, 1981; Farris, 1982; Maddison et al., 1984) and the ontogenetic method

(Nelson, 1978; Nelson and Platnick, 1981; Patterson, 1982, 1983).

The initial evolutionary basis of cladistics sparked the current interest in methods of polarity assessment. Curiously, some advocates of the ontogenetic method, called pattern cladists by Beatty (1982), suggest that a belief in, or knowledge of, evolution is superfluous to cladistics (Platnick, 1979; Nelson and Platnick, 1981; Patterson, 1982, 1983). I agree with Patterson (1982) that the use of cladistic methods does not require any assumption about evolution; however, if systematics is an attempt to reconstruct evolutionary history, then this assumption will dictate which cladistic methods are useful. Such a perspective reveals that, although the ontogenetic method may be satisfactory for pattern cladism, it is not satisfactory for phylogenetic systematics. The reason for this concerns one of the most fundamental concepts of systematics, namely, the nature of characters.

The goals of systematics are important considerations in evaluating the appropriateness of systematic methods and concepts. Consequently, I must first consider the role of the theory of evolution in systematics, for this is central to the difference between the goals of pattern cladism and those of phylogenetic systematics. In order to expose the inadequacies of the ontogenetic method in phylogenetic systematics and to highlight the need for a change in character concepts, I next explore some consequences of polarity determination under traditional character concepts. These traditional concepts are subsequently rejected in favor of a character concept chosen to reveal phylogenetic relationships among organisms.

THE ONTOGENETIC METHOD

The ontogenetic method of polarity assessment has been articulated by Nelson (1978:327) as a restatement of the biogenetic law: "given an ontogenetic character transformation, from a character observed to be more general to a character observed to be less general, the more general character is primitive and the less general ad-

vanced." This method is said to depend not on Haeckelian recapitulation but only on the validity of von Baer's second law (Patterson, 1982, 1983), which states that "less general characters are developed from the most general, and so forth, until finally the most specialized appear" (Gould, 1977:56).

Nelson (1978; repeated in Nelson and Platnick, 1981) knew of no evidence against his version of the biogenetic law and concluded that it may be generally valid. He also argued that among the ontogenetic, outgroup, and paleontological methods of polarity determination, ontogeny was the decisive criterion because it was least easily protected from falsification by ad hoc means. I do not dispute these claims within the context of pattern cladism; however, I argue that their force is lost from a phylogenetic perspective. I also argue that, although it may be possible to divorce evolution and systematics, according to the view of science adopted by many systematists, a phylogenetic perspective is preferred if systematics is to bear a scientific relationship to the theory of evolution.

THE ROLE OF THE THEORY OF EVOLUTION IN SYSTEMATICS

A central difference between pattern cladism and phylogenetic systematics is the role that the theory of evolution plays in systematics. According to Nelson (1978: 336, 337), "systematics and comparative anatomy (applied to fossils, too) are possible only to the extent that ontogeny is orderly," and "the theory of evolution itself is an extrapolation of ontogeny." In other words, the hierarchical relationships among characters in ontogeny form the basis of an internested hierarchical system of taxa, from which one can generalize the theory that evolution (used throughout this paper in the sense of descent with modification without regard to its mechanism) explains this hierarchy of groups within groups.

Under this view of the relationship between evolution and systematics, cladism bears no scientific relationship to the the-

ory of evolution, at least under the Popperian view of science advocated by many systematists (Bock, 1974; Wiley, 1975; Platnick and Gaffney, 1977; Nelson, 1978; Gaffney, 1979; Nelson and Platnick, 1981). Although my view of science differs, I will adopt the Popperian view of science for the purpose of evaluating the relationship between evolution and cladistic systematics. According to Popper (1968), falsifiability is the demarcation criterion separating scientific and nonscientific theories. Under this view of science and the pattern cladists' view of evolution as a generalization from systematics, cladistic systematics cannot serve as a falsifier of evolution. The general pattern of a systematic hierarchy of interested sets cannot be used to corroborate the theory that evolution explains this pattern unless alternative patterns (e.g., intersecting sets, nonhierarchical) are tested for a better fit to the data. Furthermore, if evolution is generalized from systematics, then systematics can hardly be inconsistent with evolution.

Another consequence of adopting a Popperian view of science is that there is no logical basis for generalizing evolution from systematics. According to Popper (1968), there is no inductive logic; that is, there is no justification for inferring general statements from specific observations. Therefore, in addition to the lack of potential falsification of evolution by pattern cladistics, there is no justification for generalizing evolution from pattern cladistics. Although some may view this as a problem with the theory of evolution, the potential to falsify this theory by other means (see below) suggests otherwise. According to Popper (1968), the manner in which a theory is conceived is unimportant as long as the theory is falsifiable.

Alternatively, one can view evolution as the basis of systematics, as did Hennig (1966). Under this view, systematics might be used in conjunction with other data, such as stratigraphy or biogeography, to test the theory of evolution. For example, a deduction from the theory of evolution is the prediction that more inclusive clades will precede less inclusive ones in the

stratigraphic sequence. This prediction is upheld; all recognized clades do not arise simultaneously in the stratigraphic sequence. Failure to pass this test would surely be strong falsification, for if all clades appeared simultaneously in the stratigraphic sequence, I doubt that anyone would seriously entertain the theory that evolution accounted for the pattern of organic diversity.

Although pattern cladists remove the evolutionary basis from systematics, they replace the theory of evolution with another, the theory that "there is order in nature" (Nelson and Platnick, 1981:9). As the basis for systematics, I question whether this theory is preferable to the theory of evolution. If the theory of natural order claimed *only* that nature is orderly, then it might be preferable because of its greater universality. Falsification of such a theory (if possible) would rule out any kind of natural orderliness, not only orderliness resulting from evolution. However, the theory of natural order as conceived by pattern cladists is not so universal as this, for they entertain only one kind of order in systematics, specifically, a hierarchy of groups nested within groups. This is the kind of order expressed by cladograms. It is also the kind of order that evolution is supposed to produce. But the theory that evolution has produced a hierarchy of groups nested within groups makes more claims about the world than does the theory that such a hierarchy merely exists (for example, evolution claims that the hierarchy has a temporal component), and theories that make more claims have more potential falsifiers (Popper, 1968).

Finally, an evolutionary basis justifies the use of cladistic methods in biological systematics. If systematics is not based on evolution, then one must ask: "Are cladistic methods preferable to (for example) phenetic ones and, if so, why?" Accepting the theory of evolution as the basis for systematics provides a reason for preferring cladistic methods. Unlike phenetic methods, cladistic methods were formulated by Hennig (1966) with an explicit evolutionary basis. I conclude that if a falsification-

ist perspective is adopted, and if systematics is to bear a scientific relationship to evolution, then systematics should be based on evolution.

Of course, this consideration of falsifiability is superfluous if one considers evolution to be a "fact." However, acceptance of such a proposition combined with an interest in testing theories about particular evolutionary processes provides an even better reason for basing systematics on evolution. This is because phylogenetic relationships have direct bearing on many theories about evolutionary processes (Eldredge and Cracraft, 1980; Wiley, 1981). Therefore, if systematics is to hold a central role in modern comparative biology, which is said to be unified by the concept of evolution, then systematics should be based on this unifying concept but minimize assumptions about its underlying processes.

No one has specified what it means to say that systematics is "based on" the concept of evolution. I will do this by defining phylogenetic systematics as that systematics in which the relationships sought are phylogenetic relationships and, thus, the concept of evolution, or phylogeny (and by this I mean only that organisms are related through common ancestry), serves as an *axiom* from which systematic methods are *deduced*. Attempting to reformulate systematic methods as deductions from the axiom of evolution should help to clarify whether a given method is useful in phylogenetic systematics. The present paper is an evaluation of the ontogenetic method from this perspective.

My analysis of the ontogenetic method is strictly from the perspective of phylogenetic systematics, as I define it, with no claim that this perspective is the only valid one. However, I have just presented reasons for thinking that it is the appropriate one for modern comparative biology.

GENERALITY AND THE BIOGENETIC LAW

I wish to consider the meaning of the term "general" as it is used in von Baer's second law and Nelson's biogenetic law (i.e., the ontogenetic method). This neces-

sitates a brief consideration of the nature of scientific laws. There are at least two possible interpretations of scientific laws: (1) they may be theorems, that is, necessary truths deduced from axioms; or (2) they may be theories, that is, falsifiable hypotheses. As necessary truths, laws can serve to define certain of their component terms, such as "general" in the case of the two laws under consideration here. Because Nelson (1978) stressed the falsifiability of his biogenetic law, he clearly viewed it as a scientific theory rather than a necessary truth. If von Baer's law is viewed similarly, then the meaning of "general" is not given by these laws and must be established.

Von Baer's second law states that the less general characters are developed from the most general. As a scientific theory about development this seems to mean that the characters of less inclusive groups arise in development from the characters of more inclusive groups. However, if the hierarchy of groups is determined by the sequence of character transformations in ontogeny, then this law is an unfalsifiable tautology. Von Baer's law is testable only if the hierarchy of groups and, thus, the generality of characters is determined according to some other criterion. Nelson (1978) did this by defining generality as follows: a character is more general if it occurs in both members of a pair of species; it is less general if it occurs in only one of them. I will generalize this definition according to the suggestion of W. P. Madison (pers. comm.): character x is more general than character y if and only if all organisms possessing y (at some stage in ontogeny) also possess x and in addition some organisms possessing x do not possess y .

According to this definition of general, von Baer's law is not a law; that is, it is not universally true (Fink, 1982). De Beer (1940) cited various cases ("embryonic and larval adaptations") in which less general characters develop into more general ones. For example, the dorsal nerve cord of teleosts arises as a solid rod and later hollows out; however, many other chordates develop a hollow dorsal nerve cord by

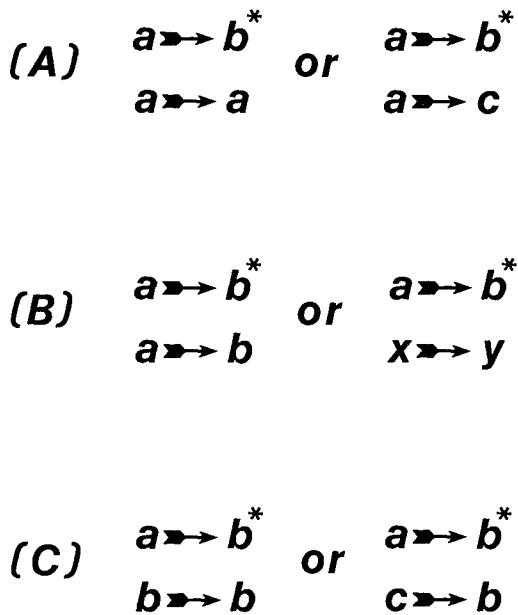


FIG. 1. Possible relationships between a character and its ontogenetic precursor: (A) precursor is more general; (B) precursor is equally general; (C) precursor is less general. An asterisk marks the character in question. See text for relevance to von Baer's law.

folding a plate of ectodermal tissue. Hence, less general characters (solid rod and unfolded plate) develop into a more general one (hollow cord).

Patterson (1983:25) claimed that "the embryonic membranes of amniotes, as developments (outgrowths) or [of?] more widely distributed structures, are consistent with this law [von Baer's second], as is, so far as I know, every other observation in vertebrate morphology." Perhaps the reason that Patterson and I disagree about the validity of von Baer's law is that we interpret it differently. One might view von Baer's law as a statement about the ontogenetic precursors of less general characters that says nothing about those of more general characters. Under this interpretation, von Baer's law is not falsifiable. There are only three possible situations concerning the generality of the ontogenetic precursor of a given character (Fig. 1): the precursor can be more general, it can be equally general, or it can be less general. If the precursor is more general,

von Baer's law is confirmed. However, if the precursor is of equal or lesser generality, there is no reason to reject von Baer's law. In the former case, the transformations either involve the same characters or wholly different ones, and there is little reason to compare them. In the case where the precursor is less general than the character under consideration, one has simply asked the question "What is the generality of the precursors of less general characters?" about the wrong character. Von Baer's law is falsifiable only if it is interpreted as stating that ontogenetic transformations always go from more general to less general. If this interpretation is accepted, von Baer's law is falsified.

Overemphasizing the importance of ontogeny with respect to the way in which characters are conceived can bias our views about evolution and the validity of von Baer's law. For example, some consider similar development to be the decisive criterion of homology. However, this should not allow us to conclude that otherwise similar characters that differ in their mode of development are not homologous. By doing this one rules out the possibility of detecting cases in which the mode of development of a structure is modified during the course of evolution without modification of the structure's final form (e.g., the development of the hollow nerve cord described above). Perhaps such occurrences are rare because a form is often influenced by the forms of its ontogenetic precursors. However, if we define away the possibility for a character to remain unmodified in phylogeny when its ontogenetic precursors are modified (e.g., the hollow nerve cords of teleosts are not homologous with those of other chordates because they develop differently), then von Baer's law is not only true, it is a tautology and cannot be otherwise.

Since von Baer's law is not universally true, it is fortunate, contrary to Patterson's (1982, 1983) view, that the ontogenetic method of Nelson (1978) does not depend on this law. As stated by Nelson (1978), the biogenetic law concerns only those cases in which the ontogenetic transfor-

mation is from more general to less general. Since the exceptions to von Baer's law (transformations from less general to more general) are not considered, whether or not these exceptions exist is irrelevant to the validity of Nelson's (1978) biogenetic law.

Unlike von Baer's law, Nelson's (1978) biogenetic law is a statement about phylogeny rather than ontogeny (which is given). Specifically, it concerns the evolutionary polarity of characters. Nevertheless, use of the ontogenetic method in (nonphylogenetic) systematics does not require assuming evolution. One might use the polarity (not necessarily evolutionary) inherent in ontogeny to construct an interested hierarchical system of taxa. Alternatively, one might use the polarity inherent in differences in the relative generality of characters to do likewise. According to von Baer's law, ontogenetic polarities are identical with those based on generality (and, thus, so are the resulting hierarchical systems). This is false. According to Nelson's (1978) biogenetic law, when exceptions to von Baer's law are removed from consideration, ontogenetic polarities and hence those based on generality are identical with evolutionary polarities (character phylogenies). As a scientific theory, this law can *only* be tested against known character phylogenies, Nelson's (1978:327) first class of potential falsifiers. However, Nelson (1978:327) asserted "that paleontologists are the only folk who claim to know the truth of any evolution relevant in the present context." He also claimed that the paleontological argument is fallacious. Thus, Nelson (1978) seemed to reject the only evidence that could falsify his biogenetic law as a theory.

Although Nelson (1978) claimed that his biogenetic law is falsifiable, he did not contradict himself by dismissing phylogeny as a potential falsifier. This is because he accepted a second class of potential falsifiers, conflicting character transformations. For example, in one pair of taxa character x is more general than character y and x transforms into y , while in another

pair of taxa y is more general than x and y transforms into x . Contrary to Nelson's (1978) claim, such conflicts do not falsify the hypothesized relationship between ontogeny and phylogeny. Instead, they falsify either hypotheses about particular character phylogenies (e.g., that x is ancestral to y based on the first pair of taxa, but see below) or the hypothesis that characters are not shuffled around haphazardly within ontogenies during phylogeny (i.e., that ontogenies evolve in an orderly fashion). Nelson (1978) knew of no instances of such conflicting transformations, suggesting that ontogenies do not evolve through haphazard shuffling of characters.

COMPARISON OF OUTGROUP, PALEONTOLOGICAL, AND ONTOGENETIC METHODS OF POLARITY DETERMINATION

I have argued that Nelson's (1978) biogenetic law is unfalsifiable if one rejects the possibility of testing it against phylogeny. What then is the biogenetic law? Within the domain of phylogenetic systematics (as defined in this paper) and under traditional character concepts, Nelson's biogenetic law is interpretable as a law in a different sense. In phylogenetic systematics, the biogenetic law is not a theory about the relationship between ontogeny and phylogeny, but a theorem about the evolutionary polarity of characters (which I will call the ontogenetic method) that can be deduced from the axiom of phylogeny. I will illustrate this by comparing the ontogenetic method with two other methods for determining evolutionary character polarity—the outgroup and paleontological methods. When referring to "alternative" characters in the following discussion I mean either that one is a modification of the other or that both are modifications of a third character. The three methods of polarity determination are designed to reveal the ancestral and derived conditions of two (for simplicity's sake) homologous characters and can be stated as follows.

The outgroup method.—Given the existence of a monophyletic group within

which occur alternative characters, a phylogenetic character transformation must have occurred within the group. (This logic applies only to cases in which the characters vary among the taxa whose interrelationships are being investigated, not within them.) Thus, the character found both inside and outside of the group is ancestral; the character found only inside of the group is derived.

The paleontological method.—Given alternative homologous characters whose existence is documented in fossils, the character found in the oldest fossil is ancestral, the alternative derived. By definition, the ancestral character must precede the derived character in time. Therefore, the oldest fossil will exhibit the ancestral condition if it represents either (1) an ancestor that existed before the phylogenetic character transformation occurred, or (2) a lineage that diverged before the phylogenetic character transformation occurred.

The ontogenetic method.—“Given an ontogenetic character transformation, from a character observed to be more general to a character observed to be less general, the more general character is primitive [ancestral], the less general advanced [derived]” (Nelson, 1978:327). If the definition of generality proposed in this paper is accepted, then the justification for the ontogenetic method depends on the persistence of ancestral characters in organisms with modified (derived) ontogenies. As long as this condition is met, ancestral characters will always be more general, derived ones less general. Additionally, as stated by Nelson (1978), use of the ontogenetic method is restricted to cases in which the temporal sequence of ontogenetic transformation is from more general to less general. Nelson’s ontogenetic method might also be deduced from an assumption of recapitulation, but since Nelson (1973a) considered the recapitulationist argument to be fallacious, I assume that his method does not have a recapitulationist basis.

Given that systematics attempts to reconstruct evolutionary history, all three methods gain their usefulness from as-

sumptions additional to the axiom of phylogeny. Denying the validity of these additional assumptions permits one either to reject the method or, given conflicting results, to evade “falsification” of the method (i.e., to account for the conflict). The second form of denial is clearly ad hoc, since the validity of the assumptions must have been accepted in order to use the method in the first place.

Nelson (1978) viewed the three methods of polarity determination as theories and evaluated them in terms of their falsifiability. He concluded that the ontogenetic method was decisive, because it was less easily protected from falsification by ad hoc means. From the perspective of phylogenetic systematics, such an emphasis on falsifiability would be misplaced. Although hypotheses about the polarities of particular characters are falsifiable theories, the various procedures for determining character polarities are more appropriately viewed not as theories but as methods (theorems) deduced from the axiom of evolution. The value of the various methods results not from their falsifiability but from the correct results that they must produce given the validity of certain other assumptions. Their “falsifiability” can be viewed alternatively as our willingness to accept the validity of these additional assumptions. The less willing we are to do so, the less adequate the method. Explaining away inconsistencies with ad hoc propositions that contradict the assumptions necessary for the use of a particular method amounts to an unwillingness to accept these assumptions. Therefore, the extent to which ad hoc propositions are used to explain away conflicts can still be viewed as a criterion for judging the adequacy of various methods.

As noted by Nelson (1978), conflicting evidence in all three methods can be sidestepped by calling seemingly equivalent characters nonequivalent (nonhomologous, homoplasious). The outgroup method allows for a second option in questioning the assumption of monophyly; perhaps certain outgroups are really ingroups. The paleontological method allows for a sec-

ond option in questioning the completeness of the fossil record. The incompleteness of the fossil record raises doubts about the validity of the assumption that the oldest fossil represents either an ancestor that existed or a lineage that diverged before the phylogenetic character transformation in question occurred. Although this assumption could potentially be supported by other characters, such a practice reduces the paleontological method to a form of the outgroup method.

Interpretation of the ontogenetic method as a deduction from the axiom of evolution has consequences that bear on the use of this method under traditional character concepts. First, and contrary to Nelson (1978), the ontogenetic method allows for a second means (in addition to the ad hoc hypothesis of homoplasy) of explaining away conflicting data and is similar to the outgroup and paleontological methods in this respect. The example of conflicting ontogenetic data used by Nelson (1978) relies on an arbitrary separation of data, otherwise no conflict occurs. Nelson considered two pairs of species. In one pair, character x_A does not transform in species A, but x_B transforms into y_B in species B. In the second pair, y_C transforms into x_C in species C, but y_D does not transform in species D. If the two pairs are examined independently of one another, the data from one pair suggest that x is ancestral while those from the other suggest that y is ancestral; however, when all four species are examined together no polarity decision can be made since both characters have equal generality (Voorzanger and Van Der Steen, 1982). A similar inability to use the ontogenetic method results if one of the two transforming species (B or C) does not exist. A more interesting case would be the existence of both transforming species but only one of the nontransforming species. In this case, the characters differ in generality so that polarity can be established.

Suppose that species A, B, and C exist, but species D does not. As stated, Nelson's (1978) formulation of the ontogenetic method applies only to situations in which

the ontogenetic transformation is from more to less general (in this case from x to y). Thus, transformations such as that occurring in species C (y to x) would be ignored. This is an unnecessary restriction (see below). If we remove this restriction there is a conflict. The relative positions of the characters in different transforming ontogenies suggest one or more of three possibilities: (1) seemingly equivalent characters in different ontogenies are not equivalent; or (2) ancestral characters have not been retained in descendant ontogenies (Fig. 2); or (3) ontogeny does not evolve in an orderly manner (see section on generality and the biogenetic law). The ad hoc hypothesis of homoplasy is available to all three methods of polarity determination discussed herein. However, rejection of the assumption that ancestral characters have persisted in organisms with modified character ontogenies provides another ad hoc means of explaining conflicting ontogenetic data (Fig. 2). The ontogenetic method has no fewer options for ad hoc protection than do the other methods of polarity determination.

MISUNDERSTANDINGS ABOUT THE ONTOGENETIC METHOD

Commonality.—Adopting a phylogenetic perspective clarifies several other misunderstandings about the ontogenetic method. The first concerns the difference between ontogenetic and commonality methods. Kluge (1985) claimed that Nelson's law is a special form of ingroup analysis that uses commonness as the estimator of polarity. The definition of generality necessitates that more general characters are also more common than less general ones (Fig. 3A). Nevertheless, the ontogenetic method is not the same as the commonality method, for more common characters are not necessarily more general (Fig. 3B). Since commonality bears no necessary relationship to relative time of phylogenetic appearance, there is no reason to infer that common characters are ancestral to less common ones (compare Van Valen, 1978; de Jong, 1980; Stevens, 1980; Arnold, 1981; Watrous and Wheeler,

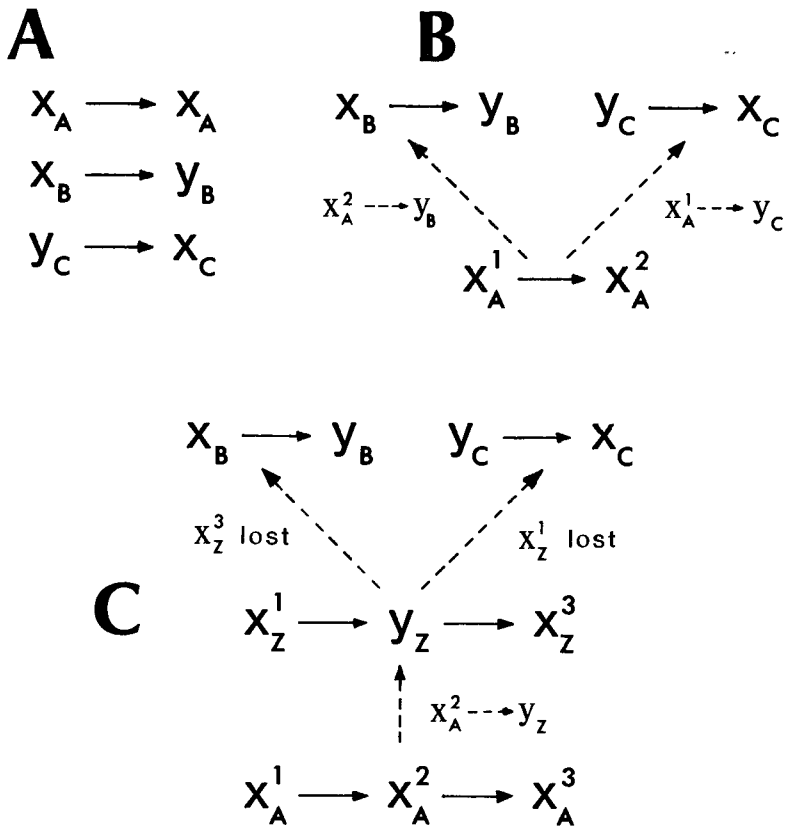


FIG. 2. Ad hoc protection for the ontogenetic method. (A) Character ontogenies of three organisms which it is inferred (by generality) that x is ancestral and y is derived. (B) Provided that ancestral characters have persisted in organisms with modified ontogenies, homoplasy must be invoked to explain the known patterns of ontogenetic character transformation, that is, either $x_B \neq x_C$ or $y_B \neq y_C$. (C) If loss of ancestral characters is admitted as possible, then no homoplasy is required; y_B and y_C may stem from the same character in the common ancestor. Thus, homoplasy is not the only ad hoc means of accounting for conflicting ontogenetic data. Arrows on solid lines represent ontogenetic transformations; those on dashed lines represent phylogenetic transformations. Certain nontransforming ontogenies have been expanded redundantly in order to facilitate comparison.

1981; Wheeler, 1981; Wiley, 1981). In contrast, given that ancestral characters are retained in modified ontogenies, ancestral characters are necessarily more general than their derivatives.

Sequence versus generality.—A more interesting result of the present analysis is that the sequence of ontogenetic transformation is irrelevant to the ontogenetic method. The critical factor is generality. As long as ancestral characters are retained in descendant ontogenies, ancestral characters will always be more general than their derivatives. Even when the on-

ontogenetic transformation is from less general to more general one can infer that the more general character is ancestral, the less general derived. In fact, the logic that characters arising earlier in phylogeny will be more general than those arising later in phylogeny applies even to characters that are parts of different ontogenetic or phylogenetic transformations. For example, one can infer that backbones arose earlier in phylogeny than did feathers from the observation that every organism that has feathers has a backbone but not every organism that has a backbone has

feathers. A corollary of this proposition is that the ontogenetic method relies neither on Haeckelian nor on "von Baerian" recapitulation. The notion that the sequence of character transformation in ontogeny mirrors that in phylogeny is central to both of these concepts (Løvtrup, 1978), but the sequence of character transformation in ontogeny is irrelevant to the ontogenetic method.

Given that the sequence of ontogenetic transformation is irrelevant to the usefulness of the ontogenetic method, it is curious that so much emphasis is placed on this sequence. Nelson's (1978) restriction of the ontogenetic method to cases in which the ontogenetic transformation is from more to less general places unnecessary limitations on the applicability of this method, for generality alone is sufficient to establish polarity (see Nelson, 1978:339). Furthermore, if one is unwilling to dismiss the possibility that modifications of nonterminal ontogenetic stages can occur without resulting in the modification of terminal stages, then knowledge of the ontogenetic sequence without knowledge about generality does not provide evidence about evolutionary character polarity. Thus, it is useful to distinguish between different versions of the ontogenetic method (see Nelson, 1973a). The first of these is the traditional version, which is of dubious value since it is based on the universal occurrence of phylogenetic change through the modification of terminal ontogenetic stages (including Haeckelian and "von Baerian" recapitulation). I largely ignore this traditional version in the present paper. A second formulation of the ontogenetic method is Nelson's (1978), which is based on generality but is unnecessarily restricted to cases in which the ontogenetic transformation is from a more general character to a less general one. A third version of the ontogenetic method is presented in this paper. It too is based on generality but considers the sequence of ontogenetic transformation to be irrelevant. This third version of the ontogenetic method can be stated as follows: *given that ancestral characters are*

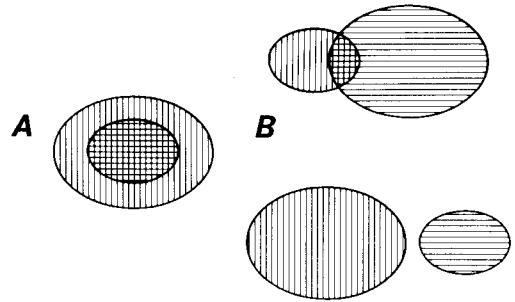


FIG. 3. The relationship between generality and commonality. (A) Since a more general character occurs in all those organisms (or taxa) that possess a relatively less general character as well as in some organisms that do not possess the less general character, a more general character will always be more common than a less general one. (B) In cases where organisms (or taxa) bearing the characters in question either form intersecting sets (above) or do not overlap (below), more common characters are neither more general nor less general than less common ones. The size of the ellipses is proportional to the number of organisms (or taxa) included within them.

retained in descendant ontogenies, ancestral characters are more general than derived characters.

Because these last two versions of the ontogenetic method are based on generality, the validity of each depends on the retention of ancestral characters in descendant ontogenies. Unfortunately, the universal occurrence of ancestral character retention is a dubious proposition, and thus the usefulness of these methods is questionable. By itself, the failure of ancestral characters to persist in descendant ontogenies will result in characters of equal generality (Figs. 4 and 5) and, thus, will only render the methods inapplicable; it will not lead to incorrect results. However, when coupled with incomplete sampling, the loss of ancestral characters can result in derived characters having greater apparent generality than ancestral ones (Fig. 5), thus leading to incorrect inferences about evolutionary character polarity. Furthermore, although ancestral characters are more general than derived characters given ancestral character retention, it does not follow that more general characters are necessarily ancestral, even with complete sampling. If two characters

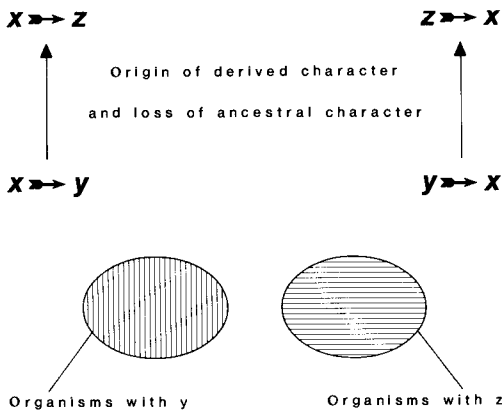


FIG. 4. Effect of the loss of ancestral characters on generality and the determination of evolutionary character polarity. In cases where the origin of the derived character (z) coincides with the loss of the ancestral character (y) in phylogeny, ancestral and derived characters occur in nonoverlapping sets of organisms and thus have equal generality. Therefore, character polarity cannot be determined on the basis of generality. Horizontal arrows represent ontogenetic transformations; vertical arrows represent phylogenetic transformations.

arise simultaneously in phylogeny (i.e., within the ontogeny of a single organism), then the phylogenetic loss of one of these characters results in the alternative character having greater generality even though it is not ancestral.

Paedomorphosis.—Another result of the present analysis is that, contrary to concerns stated by some authors (Rieppel, 1979; Stevens, 1980; Arnold, 1981), paedomorphosis is not particularly problematic for either Nelson's or my version of the ontogenetic method (Fig. 6). Use of this method depends on the retention of ancestral characters in descendant ontogenies, while paedomorphosis involves the elimination of terminal characters, which may or may not be ancestral. If terminal addition or the modification of terminal ontogenetic stages are the common patterns in phylogeny, as is suggested by the "laws" of Haeckel and von Baer, then paedomorphosis will rarely cause problems in application of the ontogenetic method. This is because derived rather than ancestral characters will be eliminated. Never-

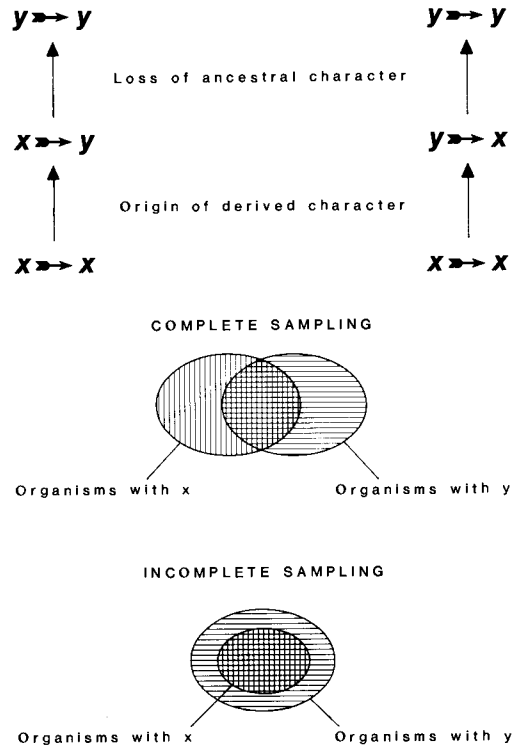


FIG. 5. Effect of the loss of ancestral characters on generality and the determination of evolutionary character polarity. In cases where the origin of the derived character (y) precedes the loss of the ancestral character (x) in phylogeny, ancestral and derived characters occur in partially overlapping sets of organisms and thus have equal generality. Therefore, if organisms having each of the three classes of character ontogenies are sampled, evolutionary character polarity cannot be determined. However, if organisms having character ontogeny $x \rightarrow x$ are not sampled, the derived character (y) will appear to be more general than the ancestral character (x), and an incorrect polarity inference will result.

theless, if a terminal character lost through paedomorphosis also happens to be ancestral, then paedomorphosis coupled with incomplete sampling can lead to erroneous inferences about evolutionary character polarity (Fig. 7).

The confusion surrounding the supposed problem that paedomorphosis poses for the ontogenetic method results from an inappropriate extrapolation of the ontogenetic method to cases that it does not claim to cover. As stated, Nelson's bioge-

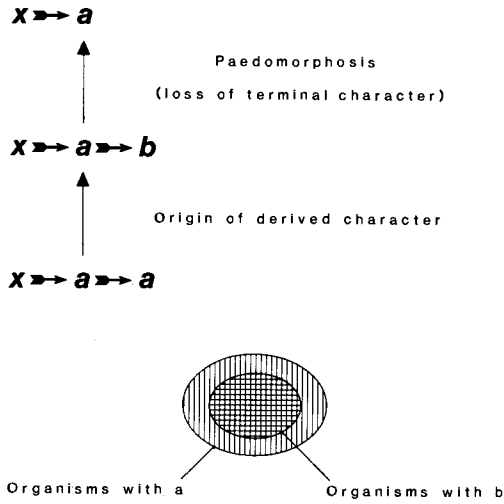


FIG. 6. Paedomorphosis involving loss of a derived character and the ontogenetic method. When phylogeny involves terminal addition or the modification of terminal ontogenetic stages, subsequent paedomorphosis causes loss of a derived character (*b*). As long as the ancestral character (*a*) is retained, it will never be less general than the derived character, even with incomplete sampling. Therefore, incorrect polarity inferences will not result.

netic law describes the relationships between instantaneous morphologies. (Instantaneous here means brief enough so that only a single morphological character is recognized.) Given an ontogenetic character transformation from morphology *x* to morphology *y* in some organisms and the presence of only morphology *x* in others, it is concluded that morphology *x* is ancestral and morphology *y* is derived. That paedomorphosis is responsible for some of the nontransforming ontogenies does not invalidate this conclusion in any way, for the ontogenetic method makes a statement about the relationship among instantaneous forms, not among ontogenies.

Implicit or explicit in the writings of various authors who consider paedomorphosis to be a source of problems for the ontogenetic method is the notion that comparisons are made among adults (Gould, 1977; Van Valen, 1978; Rieppel, 1979; de Jong, 1980; Stevens, 1980; Arnold, 1981). Comparison of adult stages is an at-

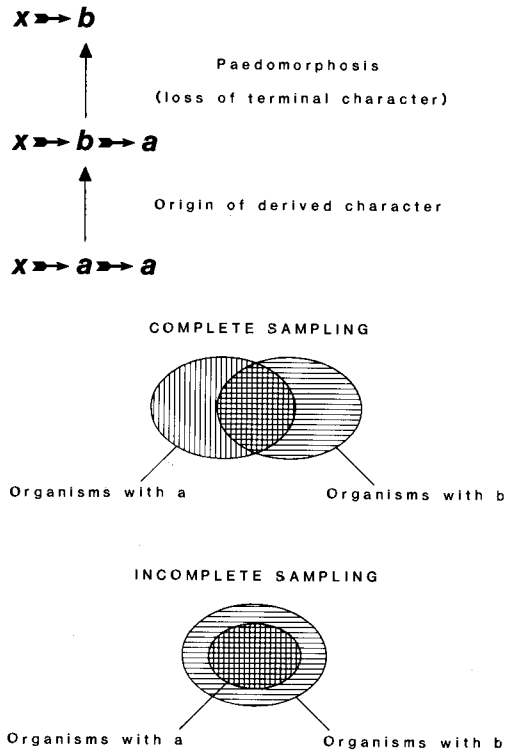


FIG. 7. Paedomorphosis involving loss of an ancestral character and the ontogenetic method. When phylogeny involves the modification of nonterminal ontogenetic stages without modification of terminal stages, subsequent paedomorphosis can cause the loss of an ancestral character (*a*). If organisms with all three classes of character ontogenies are sampled, the characters have equal generality and no polarity inference can be made. However, if certain organisms (i.e., those having $x \rightarrow a \rightarrow a$) are not sampled, then the ancestral character (*a*) will appear to be less general than the derived character (*b*), and evolutionary polarity will be incorrectly inferred.

tempt to compare organisms (ontogenies) at a standard stage, and paedomorphosis will cause problems when instantaneous morphologies whose polarities have been inferred using the ontogenetic method are used to determine phylogenetic relationships among organisms (Stevens, 1980; Kluge, 1985). Thus, there appear to have been at least two misunderstandings involved when Stevens (1980) and Arnold (1981) criticized Nelson (1978) on the grounds of paedomorphosis. First, since Stevens (1980) considered Nelson (1978)

to have included some form of outgroup analysis in his reformulation of the biogenetic law, Stevens misconstrued Nelson's meaning of generality. Second, both Stevens (1980) and Arnold (1981) criticized Nelson (1978) from the perspective of organism phylogenies, while the ontogenetic method, as stated, elucidates not the phylogeny of organisms but that of instantaneous morphologies. Of course, most systematists (but not necessarily most comparative anatomists) study organism phylogenies, and they commonly base these organism phylogenies on inferences about the phylogeny of instantaneous morphologies (character polarities). Nelson (1978) did not discuss the relationship between such character phylogenies and organism phylogenies, and he also mixed instantaneous and transformational character concepts in his discussion of paedomorphosis (e.g., "If neoteny [paedomorphosis] is assumed, the transformation from x to y is primitive, not character x alone . . ." [Nelson, 1978:340]). Part of the confusion about the ontogenetic method apparently stems from a failure to clearly distinguish between organism phylogenies and the phylogenies of instantaneous morphologies.

AN ALTERNATIVE CHARACTER CONCEPT

Instantaneous morphologies and ontogenetic transformations as characters.—The source of the confusion about paedomorphosis and the ontogenetic method resides in the basic assumption of what constitutes a character. Under the ontogenetic method, as stated by Nelson (1978) and adopted by Nelson and Platnick (1981) and Patterson (1982, 1983), characters are instantaneous morphologies that make up ontogenetic transformations. This character concept is used widely among systematists and is what I have referred to above as the traditional character concept. However, biological systematics has generally been concerned with the relationships among organisms rather than those among instantaneous morphologies, and organismal morphology is ontogenetically dynamic. Consequently, as Patterson (1983:

27) and others have indicated, "phylogeny differs from ontogeny in that it is a sequence of ontogenies, or life cycles." Therefore, if we attempt to determine the phylogenetic relationships among organisms as life cycles (Danser, 1950), and if we do not wish to bias ourselves against the possibility of paedomorphosis, then instantaneous morphologies whose polarities are determined by the ontogenetic method should not be the characters of the phylogenetic systematist; ontogenetic transformations, or the lack thereof, should be the characters instead (see Nelson and Platnick, 1981:353). This does not mean that all characters are properly ontogenetic transformations, for many attributes of organisms do not transform during ontogeny.

Acceptance of the view that ontogenetic transformations are characters clearly reveals the inappropriateness of the ontogenetic method in phylogenetic systematics. Under the (dubious) assumptions of ancestral character retention and the non-simultaneous phylogenetic appearance of the characters in question, the ontogenetic method might be used to argue that character (y) in the previous example is derived from character (x). Nevertheless, it cannot justify the conclusion that an organism bearing character ($x \rightarrow y$) was derived from one bearing character ($x \rightarrow x$), for both of these characters have equal generality. In fact, if one accepts ontogenetic transformations as characters then the phrase "ontogenetic character transformation" is redundant. Instantaneous morphologies, often treated as characters, are parts of ontogenetic transformations and are thus only parts of characters. Under this view of characters, there can be no ontogenetic method for polarity determination; the ontogenetic transformations within a character tell nothing about the evolutionary polarity of that character relative to others.

At this point I want to reemphasize the difference between two different kinds of polarity. Characters (as ontogenetic transformations) have both ontogenetic and evolutionary polarities (Nelson, 1985).

Ontogenetic polarities exist *within* characters and, in doing so, they exist between instantaneous morphologies, which are parts of characters. In contrast, evolutionary polarities exist *between* characters. When speaking of methods of polarity determination, I refer only to evolutionary polarities. I suspect that much confusion has resulted from a failure to distinguish between different kinds of polarity, a failure that is not surprising under traditional character concepts. When instantaneous morphologies are treated as characters, both ontogenetic and evolutionary polarities exist at the same hierarchical level (i.e., both exist *between* characters), and it is easy to confuse them. When ontogenetic transformations are treated as characters, ontogenetic and evolutionary polarities are clearly distinguishable since they exist at different hierarchical levels: ontogenetic polarities exist within characters, evolutionary polarities between them.

Given the validity of the arguments presented above, one gains some insight into possible reasons that proponents of the ontogenetic method adopt certain other positions. Some proponents of the ontogenetic method suggest that an evolutionary basis for systematics is superfluous (Platnick, 1979; Nelson and Platnick, 1981; Patterson, 1982, 1983). This view stems from a confusion of ontogeny and phylogeny, a confusion that can only result when instantaneous morphologies rather than ontogenetic transformations are used as characters. When one bears in mind that ontogenetic polarities differ from phylogenetic polarities, it is evident that, although ontogenetic transformations provide direct evidence about ontogenetic polarities within characters, they are uninformative about the phylogenetic polarities between characters. The reliance of at least some systematists on the ontogenetic method in the first place seems related to other aspects of their character concepts. Although they accept instantaneous morphologies as characters, they see a transformational relationship among these characters (Platnick, 1978; Nelson and Platnick, 1981; Nelson, 1985). But if one

removes the evolutionary basis from systematics, then ontogeny is the only context in which a transformational relationship among characters is meaningful. The development of pattern cladistics was obviously complex, and the end result may be internally consistent. However, as a system for illuminating only the ontogenetic relationships among instantaneous morphologies, there is little reason to interpret its results in the context of organism phylogenies.

Viewing ontogenetic transformations rather than instantaneous morphologies as characters also has consequences for phylogenetic systematics. Under this character concept, the outgroup method is still applicable. The paleontological method is most profitably viewed as a special case of the outgroup method, and one in which the characters (transformations) are generally poorly known. Although there is no longer an ontogenetic method for polarity determination, ontogenetic transformations lose none of their importance since they now form the basis of characters.

I do not attempt to work out all the implications that viewing ontogenetic transformations as characters has for the practice of phylogenetic systematics. Nevertheless, I want to discuss some points in anticipation of criticism. For organisms with ontogenies, every morphological character can potentially be traced back to the zygote. This does not mean that the entire organism must be treated as a single character, for branching in developmental pathways allows one to recognize separate characters just as one is able to recognize separate lineages of organisms even though they too stem from a single common ancestor. The question then is "How large a segment of ontogeny constitutes a systematic character?" If systematic characters are defined as features of organisms that are used to determine the relationships among these organisms, then the answer to the question is "large enough to encompass variation that is potentially informative about the relationships among the organisms being studied." Therefore, there is no need for the character to in-

clude all the parts common to the ontogenies of all the organisms under study.

The criticism might be raised that now we are back where we started—comparing parts of ontogenies. But my point is not that we must know the ontogenies fully before we can do systematics. Instead, I want to emphasize that acceptance of the proposition that phylogeny is a sequence of ontogenies should affect our views about what kinds of attributes of organisms provide information about phylogenetic relationships among these organisms. This perspective reveals that although a knowledge of ontogeny is of the utmost importance in phylogenetic systematics (since ontogeny is what is modified during the course of phylogeny), the sequence of ontogenetic transformation is uninformative about phylogenetic character polarities. Using the previous example (some organisms exhibiting an ontogenetic transformation from x to y , others exhibiting x but no further transformation), it is unclear whether organisms lacking y exhibit an ancestral or a derived condition (see Lundberg, 1973). Given the possibility of paedomorphosis, the absence of a feature can be a derived character (contrast with Nelson, 1978:340). If the absence of a feature can be a character, then it is valid to use instantaneous morphologies as characters in phylogenetic systematics. The reason I have chosen to use ontogenetic transformations as characters instead is that this position embraces the distinction between ontogeny and phylogeny. I next explore some further consequences of the view that ontogenetic transformations are characters.

Homology and synapomorphy.—Patterson (1982), developing an idea implicit or explicit in the writings of many previous authors (references cited in Eldredge and Cracraft, 1980:36; Patterson, 1982), equated homology and synapomorphy. In a phylogenetic context, the logic behind this equivalency is as follows: Homology, as similarity inherited from a common ancestor, includes symplesiomorphy and synapomorphy. But plesiomorphy and apomorphy are relative concepts; a symplesiomorphic homology is a synapomor-

phy when viewed at a more inclusive hierarchical level. Therefore, the concept of synapomorphy subsumes the concept of symplesiomorphy, and homology equals synapomorphy.

Although equating homology and synapomorphy may at first seem a logical consequence of adopting a phylogenetic definition of homology, I feel that a strict equation of these two concepts (in the case of characters that have ontogenies) is based on a confusion of ontogeny with phylogeny, a confusion rooted in traditional character concepts. Homology, as used by most authors, describes a relationship among instantaneous morphologies. Such instantaneous forms are parts of ontogenetic transformations, which are in turn parts of organism phylogenies. For this reason, ontogenetic transformation of one instantaneous form into another establishes their homology. Synapomorphies, on the other hand, are the characters of monophyletic groups; that is, synapomorphies are characters placed on cladograms or phylogenetic trees where they exist as evolutionary novelties. But if my previous argument is accepted, then (regardless of what has been done in practice) ontogenetic transformations, rather than instantaneous morphologies, are the characters of monophyletic groups. Therefore, in contrast with homology, which describes a relationship between instantaneous forms, synapomorphy describes a relationship between ontogenetic transformations. Homology does not equal synapomorphy.

This perspective should clarify what inferences can and cannot be made about organisms whose ontogenies are poorly known. For example, suppose that a fossil possesses instantaneous morphology y . The ontogenetic transformation $x \rightarrow y$ establishes the homology of x with y . If the transformation $x \rightarrow y$ is determined to be derived relative to the ontogeny in which x does not transform (on the basis of out-group comparison), then it is reasonable to consider the fossil to be the remains of an organism that possessed the transforming ontogeny or a modification of it. However, if the fossil possesses instantaneous

morphology x , it cannot be determined whether this fossil represents an organism that belongs to the clade diagnosed by the transforming ontogeny, for both ontogenies contain this instantaneous morphology.

Ontogeny and parsimony.—Nelson and Platnick (1981; see also Nelson, 1973a, b; Lundberg, 1973; Maddison et al., 1984) justified the ontogenetic method on the grounds of parsimony:

Suppose . . . that we study the ontogeny of species A and B, and discover that early in development both species have pharyngeal gill slits, which subsequently either remain as slits (species A) or close (species B). The young stages of these species obviously share a . . . general character (gill slits); in a phyletic context, the presence of gill slits in young stages can be considered primitive for the two species. But what about the adults? There are two possibilities: (1) the presence of gill slits in adults, as in young stages, is primitive, or (2) the presence of gill slits in adults is derived. With reference to species A and B, possibility (1) requires that species B has gained an attribute (closed gill slits in adults) that was lacking in the common ancestor, whereas possibility (2) requires that species A has lost an attribute (closed gill slits in adults) that was present in the common ancestor. But of course, for species A to have lost the attribute, it must first have been acquired by the common ancestor, and that required prior gain of the attribute is equivalent to the entire change implied by possibility (1). Thus these possibilities can be diagrammed: [diagram in text redrawn here as Fig. 8] and it can be seen that possibility (2) involves both character transformations required by possibility (1): the acquisition of gill slits, and the acquisition of closed gill slits in adults, plus a third character transformation, the acquisition of open gill slits in adults. Possibility (1) is more parsimonious, and can be preferred on that basis [Nelson and Platnick, 1981:37–38].

This justification rests on a confusion between ontogeny and phylogeny, which in turn rests on a concept of instantaneous morphologies as characters. The validity of Nelson and Platnick's argument rests on the assumption that the occurrence of gill slits must precede the closure of these slits. In ontogeny, this is obviously true. In phylogeny, however, it is true only in the most trivial sense: the first organism that closed its gill slits must have had them open earlier in its own ontogeny. When the organism, or life cycle, is considered as a whole, there is no reason to assume that a given structure must be preceded in

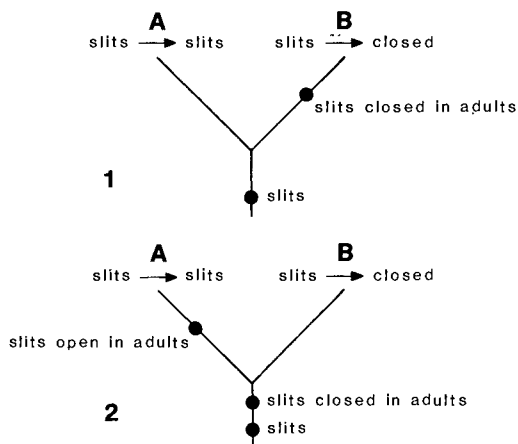


FIG. 8. Dendrograms used to illustrate justification for the ontogenetic method on the grounds of parsimony (redrawn from Nelson and Platnick, 1981: 38).

phylogeny by its ontogenetic precursor. In other words, there is no reason to assume that the first organism to bear gill slits could not have closed them later in its ontogeny. Thus both hypotheses require an equal number of changes (Fig. 9)

Although the preceding argument undermines Nelson and Platnick's (1981) parsimony justification for the ontogenetic method in the context of organism phylogenies, parsimony can still be used to justify this method in the context of the phylogenies of instantaneous forms. Suppose that organisms in taxon A have a nontransforming ontogeny for character (instantaneous form) x and those in taxon B exhibit an ontogenetic transformation from x to y . (I avoid the example of gill slits and closed gill slits since the very description of the character "closed gill slits" prohibits exceptions to von Baer's second law.) We wish to know which character, x or y , came first in phylogeny. The two possibilities are diagrammed in Figure 10 (A, B). If x is ancestral to y , a single phylogenetic transformation is required to account for the observed ontogenies (Fig. 10A). If y is ancestral to x , two changes are required (Fig. 10B). Thus, it is more parsimonious to consider x ancestral to y in that this hypothesis requires fewer phylogenetic transformations (or in that it does

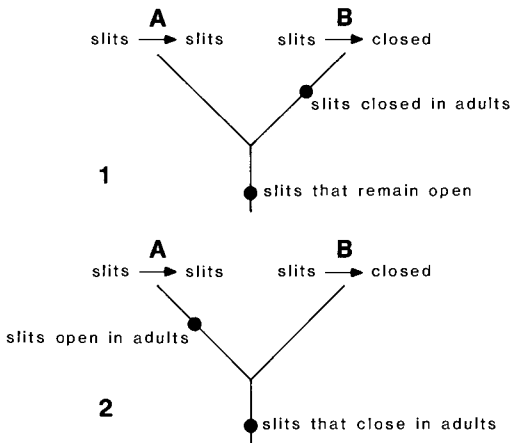


FIG. 9. Parsimony and the ontogenetic method. Since there is no reason to assume that the first organism that had gill slits could not have closed them later in its ontogeny, possibilities (1) and (2) require an equal number of phylogenetic transformations.

not require the postulation of hypothetical organisms). However, as noted earlier, this conclusion results not from the sequence of ontogenetic transformation but from the generality of characters. It is more parsimonious to consider x ancestral to y even if the ontogenetic transformation in taxon B is from y to x (Fig. 10C, D).

Such a parsimony justification for the ontogenetic method applies only to determining the polarities of instantaneous morphologies and not to the polarities of ontogenetic transformations, the appropriate characters for examining phylogenetic relationships among organisms. To attempt such an extrapolation is to confuse ontogeny with phylogeny. Since the origin of x and y in phylogeny is potentially simultaneous (i.e., within the life cycle of a single organism), there is no need to postulate the first step ($y \rightarrow y$) in Figure 10B and D. Simply by asking whether x or y came first in phylogeny one has ruled out the possibility that they arise simultaneously, and of course in ontogeny they do not.

Under the ontogenetic character concept advocated in this paper, such parsimony justifications involving only two taxa are simply not applicable. Using the above example, taxon A and taxon B have differ-

ent ontogenetic transformations and thus different characters. Given this information alone, parsimony provides no reason for inferring that either character (transformation) is ancestral to the other. Of course, additional information may be available. This is where outgroups and parsimony are relevant.

Semaphoronts.—Hennig (1966:6) defined the semaphoront as "the organism . . . during a certain, theoretically infinitely small, period of its life." He considered the semaphoront, rather than the organism, to be the basic element of systematics. According to Wiley (1981:119), systematics should involve the comparison of "comparable semaphoronts," that is, specimens at similar stages in their life history. This is similar to Gould's (1977:212) suggestion that phylogeny be depicted as a sequence of organisms at comparable stages of development, traditionally adults.

What are "comparable" stages? To a systematist, the attainment of adulthood (maturation of the gonads) is itself a character, and one whose timing can presumably change during phylogeny (e.g., progenesis of Gould [1977] and Alberch et al. [1979]) much like others. Furthermore, many developmental changes occur after the maturation of the gonads, so that even adults may not be comparable. If one *must* choose a single transformation as the standard for comparison, attainment of adulthood is a convenient reference point, especially for those studying paedomorphosis. This is the one character that would seemingly never be paedomorphic itself. Paedomorphosis in the character "attainment of sexual maturity" would be the ultimate evolutionary mistake. Nevertheless, choosing any one transformation as the standard for comparison is artificial, and given that all transformations have the potential to change their timing relative to others, this practice gives no guarantee of designating comparable semaphoronts.

The very practice of using semaphoronts (whether comparable or not) as the basic units of systematics necessitates using instantaneous morphologies as characters—a practice that I argue against. But even under the view of ontogenetic trans-

formations as characters, the semaphoront is a valuable concept. It serves to remind us that although the phylogenetic systematist attempts to determine relationships among organisms as ontogenies, or life cycles, in practice only semaphoronts are available for study (compare Danser, 1950). I disagree with Patterson's (1983) claim that ontogenetic transformations are empiricisms while phylogenetic transformations are generalizations. Although some ontogenetic transformations are potentially amenable to direct observation, in practice nearly all "observations" of ontogenetic transformations are generalizations from semaphoronts.

HISTORY AND THE RELEVANCE OF ONTOGENETIC TRANSFORMATIONS

After submission of this paper, Gareth Nelson brought to my attention three manuscripts, which have now been published, dealing with ontogeny and character polarity. Brooks and Wiley (1985) and Kluge (1985) criticized the ontogenetic method, and Nelson (1985) responded to the criticisms. Except for the addition of scattered references, I have not been able to address these papers without drastically modifying my own. Nevertheless, many of the disagreements raised in the papers by Brooks and Wiley, Kluge, and Nelson embody problems that I have attempted to clarify. I hope that my paper will be seen as a means of understanding the bases of the disagreements and perhaps reconciling divergent opinions.

On the surface, my position may appear more critical of the position taken by Nelson (1985) than of those taken by Brooks and Wiley (1985) and Kluge (1985). However, I feel that most of the differences between Nelson's position and mine stem from a single basic philosophical difference, for if I accept his view of the relationship between evolution and systematics I find little to disagree with. This view that evolution is a generalization from systematics (Nelson, 1978, 1985) coupled with a view of science that rejects inductive methods (Popper, 1968) may explain why Nelson, Platnick and others attempt to dissociate systematics from evolution.

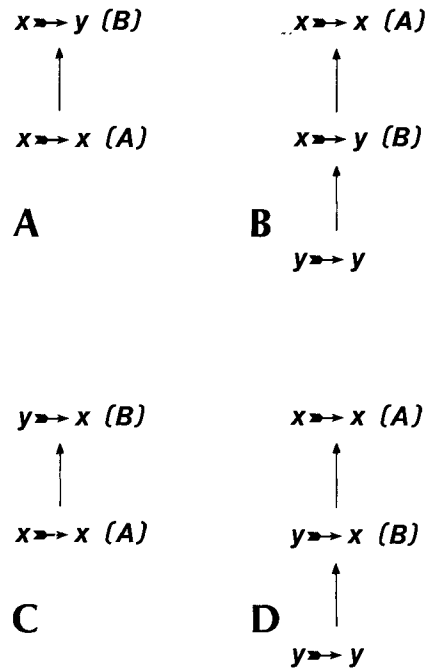


FIG. 10. Parsimony and the phylogeny of instantaneous morphologies. If it is assumed that x and y do not originate simultaneously in phylogeny, then it requires fewer phylogenetic transformations to suppose that the less general morphology is derived—regardless of the sequence of ontogenetic transformation. Parenthetical taxa next to ontogenetic transformations mean only that such taxa possess the specified ontogeny, not that they are actual ancestors. Horizontal arrows represent ontogenetic transformations; vertical arrows represent phylogenetic transformations.

My own philosophy of science is somewhat different, finding a role for induction (in generating theories) as well as deduction (in testing them). In this light, I would like to address two issues raised by Nelson (1985) that were apparently not treated to his satisfaction by Brooks and Wiley (1985) or by Kluge (1985): history; and the relevance of ontogenetic transformations.

I agree with Nelson (1973a; see also Gould, 1977; Patterson, 1983) that knowledge of the sequence of ontogenetic transformations played an important role in the history of systematics. I also agree that the theory of evolution was developed partly as a generalization from systematics (compare Nelson, 1978, 1985; Patterson, 1983).

Nevertheless, some theories resist falsification so persistently or their explanatory power is so great that their roles change during the course of history. For the case of evolution and its relationship to systematics, Ghiselin (1969:83) described this change as follows:

Darwin solved the problem [inherent in defining the term "natural" solely on the basis of metaphysical posits] by redefining "natural" as derivative of the mechanism which underlies what was previously a mere empirical generalization about observed properties of organisms. The change he made exemplifies a basic shift in attitude. Instead of finding patterns in nature and deciding that because of their conspicuousness they seem important, we discover the underlying mechanisms that impose order on natural phenomena, whether we see that order or not, and then derive the structure of our classification systems from this understanding. The difference, then, lies with the decision as to what is important. It reflects a basic gulf in attitude separating idealists given to the older forms of induction, on the one hand, and empiricists who employ the hypothetico-deductive method, on the other. Classification ceased to be merely descriptive and became explanatory.

Ghiselin's optimism notwithstanding, the transition of evolution from theory to axiom in the context of systematics is far from complete. Two notable exceptions come to mind: first, the attempt during the evolutionary synthesis to redefine species as evolutionary units (e.g., Simpson, 1961; Mayr, 1969); and, second, Hennig's (e.g., 1966) attempt to redefine various systematic terms and formulate systematic methods as deductions from the concept of evolution. My paper is an attempt to make this deductive approach explicit.

I am now prepared to answer Nelson's (1985) question: "What is the relevance for systematics of ontogenetic character transformations?" Once the axiomatization of evolution in systematics is accepted, the answer is simple: characters do not transform in ontogeny; ontogenetic transformations are themselves the characters.

CONCLUSION

I have argued that certain problems in polarity determination are related to current character concepts. Perhaps these character concepts are tied to an emphasis on the explanation of adult form, an em-

phasis that predates acceptance of evolution as the explanation for organic diversity. Griffiths (1974:99) traced it back to Aristotle. An emphasis on adult form tends to focus attention on terminal ontogenetic stages and thereby encourages the use of instantaneous morphologies as characters. Another part of the problem may result from the long common history shared by systematics and comparative anatomy. These two disciplines overlap one another extensively, but perhaps not enough attention has been paid to their differences. An example of this neglect is the failure of comparative biologists to distinguish between two different goals—reconstructing the relationships among organisms, and reconstructing the relationships among certain instantaneous morphologies, usually those of particular organs or organ systems. Both kinds of studies are commonly carried out in three different ways: (1) through the comparison of the adult stages of organisms belonging to different taxa, (2) through the study of fossils, and (3) through the study of ontogeny. This tripartite approach is embodied in Agassiz's threefold parallelism among comparative anatomy, paleontology, and embryology.

Unfortunately, the traditional emphasis on adult form is at odds with the goals of phylogenetic systematics. An axiom of this methodology is phylogeny itself, and phylogeny is a sequence of ontogenies, of which the adult is but a segment. If the current emphasis on adult form can be replaced with a more complete acceptance of the ontogenetically dynamic nature of organismal morphology, our character concept will also change. Then it will be seen that the threefold parallelism is based on an artificial separation of disciplines, for comparative anatomy, paleontology, and embryology along with systematics make up a single comparative method unified in the organism by the concept of evolution.

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