THE HISTORY AND SEMANTICS OF THE "MONOPHYLY DEBATE"

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ABSTRACT: Some of the major sources of confusion in the "monophyly debate" between the cladist and gradist schools of biological systematics have been caused by the failure to distinguish between theoretical and operational definitions, the failure to understand that monophyly and polyphyly were traditionally contradictories, and the fallacious equation of the term "monophyletic" with the much more theory-dependent terms "natural" and "taxonomically acceptable."

In order to clarify this debate, distinct terms are used for three important concepts of monophyly: (1) "monophyletic group" (defined with reference to a phylogenetic tree showing the ancestor-descendant interrelationships among the members of such groups); (2) "cladophyletic group" (defined with reference to a cladogram showing the cladistic relationships among the members of a specified group of known entities; and (3) "monophyletic taxon" (the traditional, typological concept of monophyly, which deals with the single or multiple origin of the derived "defining characters" of a taxon).

There are only two types of extensionally-defined groups of entities that differ significantly in the nature of the cladistic relationships among their members: cladophyletic groups and non-cladophyletic groups. Thus, there is no need to define "paraphyly" and "polyphyly" in terms of terminal entities on a cladogram. Although often confused with paraphyly, the term "metaphyletic group" is useful for expressing unresolved cladistic relationships. The most parsimonious method for assigning fossils to a given crown clade ironically corresponds to the "typological" practice of pseudointensional definition of taxa.

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INTRODUCTION

Monophyly and the related terms holophyly, paraphyly, and polyphyly are of basic theoretical importance to the "cladist" (phylogenetic; Hennigian) and "gradist" (evolutionary; Mayr-Simpsonian) schools of biological systematics. These terms have been defined in several ways within each school, and there is still no agreement between the schools on their "correct" meanings, as evidenced by the papers of Oosterbroek (1987), Meacham and Duncan (1987), Farris (1990; 1991), and Wood (1994). Hull (1988:141) summarized the situation as follows:

"On one thing both agreed: there is one and only one "proper" use of the relevant terms- their usage- and their opponents were misusing these terms in an especially pernicious way. The dispute continues undiminished to the present. According to the parties to this feud, anyone who does not acknowledge that terms have proper uses that must be adhered to does not understand language, and anyone who does not see that the usage which the speaker prefers is the one true usage is bigoted, blind, or both."

Hull (1990:399) noted that "The term [monophyly] is sufficiently central in systematics to warrant a coherent discussion of the vagaries of its development." Accordingly, the purpose of this paper is to clarify the history and semantics of the monophyly debate by examining several prominent definitions that have been offered over the past few decades. Substantive issues relevant to this debate have been obscured by numerous logical errors, and the only way to correct them is through a detailed analysis of each. This task has obviously been attempted many times before, but it has yet to be adequately accomplished.

Of great importance to the clarification of semantic misunderstandings is the practice of stipulative definition (Robinson, 1954). Such a definition announces to the readers of a paper that an ambiguous or new term is going to be used in a specific sense, and that for the sake of logical consistency and clear communication, they are asked to suspend their own biases and accept the meaning stipulated by the author. After digesting the arguments in the paper, the readers are then naturally free to accept or reject the stipulated definition(s). In the discussions to follow, stipulative definitions will be given for several systematic terms, and a few new terms will be coined as well. This approach is necessary because many workers have labored under the false assumption that there is somehow only one valid concept of "monophyly" and related terms, when in fact there are several.

Extensional Definition of *Groups* vs. Pseudointensional Definition of *Taxa*

Before we can ask whether or not a given assemblage is monophyletic, it is necessary that we all agree on the content of that assemblage. "Extensional" and "intensional" definitions are two different methods for delineating the membership of an assemblage (e.g., Buck and Hull, 1966). With extensional definition, the content of an assemblage is delineated by the simple enumeration of the names of each member (e.g., "the group consisting of and only of Species A, B, and C"). Given an extensionally-defined group of species, two types of evolutionary relationship may exist among them, independent of any intrinsic morphological characters that they possess. These are "ancestor-descendant" and "cladistic" relationships, which correspond to two major concepts of monophyly that will be discussed in this paper.

In contrast to the members of an extensionally-defined group, the members of an intensionally-defined assemblage (class)

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must possess the attributes that define the class (Ghiselin, 1984a). The possession of such defining attributes by an individual are necessary and sufficient conditions for membership in the class. For example, taxonomists trying to decide whether or not a specimen should be assigned to Taxon Gizmomorpha have traditionally relied upon an "intensional" definition of this taxon, such as "the set of all organisms that possess a gizmo." This character-based method of taxon-definition has resulted in the third major concept of "monophyly" that will be discussed in this paper.

The terms "group" and "taxon" are often used interchangeably in systematics. For example, neontologists working on organisms without a fossil record often envision "taxon" in a purely epistemological (or phenomenological) sense, as a group consisting of and only of a specified set of known species. In this paper, however, "group" will be used for the concept of extensionally-defined sets of organisms and/or species and/or taxa, and "taxon" will be used for the concept of what I will call "pseudointensionally"-defined sets (classes) of organisms.

Group- An extensionally-defined set of organisms and/or species and/or taxa. The membership of a group is defined by enumerating the names of all and only those "entities" that are to comprise the group.
Taxon- A "pseudointensionally"-defined set of one or more organisms. A taxon is a conceptual set of organisms (known and unknown, extinct and extant) that possess (or that have at least one ancestor that possessed) a specified set of characters.

THREE CONCEPTS OF MONOPHYLY

Monophyletic Group

For the purposes of this paper, "monophyletic *group*" and related terms are used for those highly theoretical concepts defined with reference to the ancestor-descendant relationships existing among the members of such groups, as depicted on a hypothetical phylogenetic tree (I endorse the definition of "phylogenetic tree" given by Eldredge and Cracraft, 1980:113). The traditional topological distinction between monophyletic and polyphyletic groups thus involved the question of whether a given group had one, or more than one basal connection to the phylogenetic tree (Tuomikoski, 1967). My own definitions of "monophyletic *group*" and related terms will be given later, after development of relevant concepts.

Cladophyletic Group

A very different concept of "monophyly" is involved when we are interested in the cladistic relationships among a group of entities. For example, given the group of species A, B, and C, the most common question that would be asked of it in this context is: "Are A, B, and C more closely related cladistically to each other than any of them are to any other known species?" For the purposes of this paper, this concept of monophyly is assigned a new term, which may be defined immediately as follows:

Cladophyletic Group- An extensionally-defined group of organisms and/or species and/or taxa in which every member is more closely related cladistically to every other member than to any known (or otherwise specified) organisms and/or species and/or taxa that are excluded from the group.

The concept of cladistic relationship employed here is that discussed by Hennig (1966:74). A group of entities forms a cladophyletic group when every member of that group shares at least one common ancestor that is not also possessed by any known (or otherwise specified) entities that are excluded from the group. Ghiselin (1981:142) and Colless (1985:364) used the terms "merophyletic group" and "operationally holophyletic group" for essentially the same concept as cladophyletic group, but I prefer the latter because it conveys the importance of cladistic relationship. At least for the purposes of this paper, the use of an unambiguous term for this concept of monophyly will help to clarify several issues. It should be evident that the category "cladophyletic group" is a hybrid concept containing both ontological and epistemological elements. That is, while the definition of "cladophyletic group" refers to the actual historical relationship of recency of common ancestry, these relationships are necessarily considered only with respect to entities that happen to be known to humans at any given time. The latter fact bears on the question of whether cladophyletic groups are "natural," and will be discussed in more detail below.

Monophyletic Taxon

Traditionally, the memberships of particular taxa were delineated by the characters that "defined" those taxa (e.g., de Queiroz and Gauthier, 1990:308). Ghiselin (1984a) noted that particular taxa cannot be *intensionally* defined solely in terms of morphological characters, because such characters may be lost in the later history of a taxon, and so "in effect would be forbidden to evolve" (Rowe, 1988:247). Although I agree with Ghiselin's conclusion, and find Rowe's own method of taxon-definition important and compelling, no recent systematist has actually endorsed strict intensional definition of taxa (e.g., no one has recently proposed that snakes be excluded from the taxon Tetrapoda because they lack legs). Rather, particular taxa have traditionally been implicitly "defined" using a combination of morphological characters and relational attributes of organisms (compare with "apomorphy-based definition" of de Queiroz and Gauthier, 1990; see also Løvtrup, 1977; Loevtrup, 1987; and Lucas, 1992). For the purposes of this paper I will call this method of definition "pseudointensional definition." Thus, when systematists say "The taxon that is "defined" by characters x, y, and z," they have traditionally meant "the conceptual set of organisms (known and unknown, extinct and extant) that either possess or have at least one ancestor that possessed characters x and y and z" (cf. Frost and Kluge, 1994:274). Note that this definition says nothing about whether characters x, y, and z are *homologous* for all of the members of that taxon. That question is the basis of the traditional theoretical distinction between monophyletic and polyphyletic taxa, namely, whether the derived characters we use to pseudointensionally-define a given taxon evolved only once, or more than once in the evolutionary history of the organisms that possess them.

I do not claim that pseudointensional definition is the best way, or even a desirable way to define particular taxa or envision taxa in general. Indeed, in the context of a realistic ontology of biological systematics, pseudointensional definition of particular taxa would be unacceptable (e.g., Griffiths, 1974; Ghiselin, 1984a, 1997; Ax, 1989; de Queiroz and Gauthier, 1990; Bryant, 1994). However, because one of the goals of this paper is the clarification (not endorsement!) of the traditional, character-based concepts of monophyletic and polyphyletic taxa, I will use the term "taxon" in the traditional, character-based sense of the "morphological archetype."

The relationships of the three major concepts of "monophyletic assemblage" discussed in this paper to the method by which these assemblages are defined are summarized as follows:

Extensional Definition:

1. Monophyletic Group- Based on the ancestor-descendant relationships among the members of the group as depicted on a hypothetical phylogenetic tree.
2. Cladophyletic Group- Based on the cladistic relationships among the members of the group, relative to certain entities that are excluded from the group.

Pseudointensional Definition:

3. Monophyletic Taxon- Based on single or multiple origin of the derived defining characters of the taxon.

Before offering my own definitions of monophyletic group, monophyletic taxon, and related terms, it will be necessary to clarify some additional semantic problems that have plagued this debate. These include the distinction between theoretical and operational definitions, the traditional relationship between monophyly and polyphyly, and the relationship between monophyly, naturalness, and taxonomic acceptability.

MISCELLANEOUS SEMANTIC ERRORS IN THE MONOPHYLY DEBATE

Theoretical and Operational Definitions

Different definitions of the same scientific term often have different purposes. A significant source of confusion in the monophyly controversy has been the lack of appreciation by some systematists of the different goals and consequences of theoretical and operational definitions. In the debate over monophyly, theoretical definitions are phrased in an ontological context, in terms of evolutionary history as it actually happened, independent of our knowledge or beliefs concerning that history. Operational definitions are phrased in an epistemological or phenomenological context, in terms of evolutionary relationships as they *seem* to be, as viewed in the sometimes very dim light of the fallible methodologies and incomplete evidence available to humans. In the context of biological systematics, some of these distinctions have been discussed by Ghiselin (1974; 1984a; 1997), Griffiths (1974), de Quieroz (1988), Szalay and Bock (1991), and Frost and Kluge (1994).

Definitions of "monophyletic group" and related terms that are phrased with reference to a phylogenetic tree showing the ancestor-descendant relationships of hypothetical species (e.g., Holmes, 1980; Meacham and Duncan, 1987) are highly theoretical in nature. Since ancestor-descendant relationships among actual, known species are rarely if ever determinable, these definitions are not meant to be practical or operational, but are only used to convey idealized concepts of these terms.

In contrast, the concept of a "cladophyletic group" is also phrased in terms of a theoretical definition, but one more amenable to practical application than the ancestor-descendant-based concept of "monophyletic group." For example, consider the question: "Do *Pan*, *Gorilla*, and *Homo* form a cladophyletic group with respect to *Pongo*?" We can make a practical (but not conclusive) attempt to answer this by searching for one or more characters shared by the former three taxa that seem likely to have been inherited from a common ancestor that is not also possessed by *Pongo*. However, even if we found some promising characters, this would not in itself *establish* that *Pan*, *Gorilla*, and *Homo* must form a cladophyletic group with respect to *Pongo*, because these characters might in fact not be synapomorphies, but symplesiomorphies or homoplasies (see Note 3 for remarks on the equivocal nature of the term "synapomorphy").

Operational definitions are employed in science when one wishes to reduce the amount of "subjectivity" involved in the use of a given term (Hull, 1968:439). The term "operational definition" is used here in the strict sense of being formulated so as to guarantee a conclusive decision as to whether the defined term will apply in an actual situation. In regard to monophyly, operational definitions have been phrased with reference to the *apparent topology* (as opposed to the *true interrelationships*) of terminal entities on a given, fully-resolved cladogram. Examples of such definitions are those of Nelson (1971), Farris (1974), and Oosterbroek (1987), which will be discussed later. Operational definitions have an important place in science, but monophyly and related terms have traditionally been theoretically-defined. Later I will give examples of the misunderstanding of these types of definitions during the history of the "monophyly" debate.

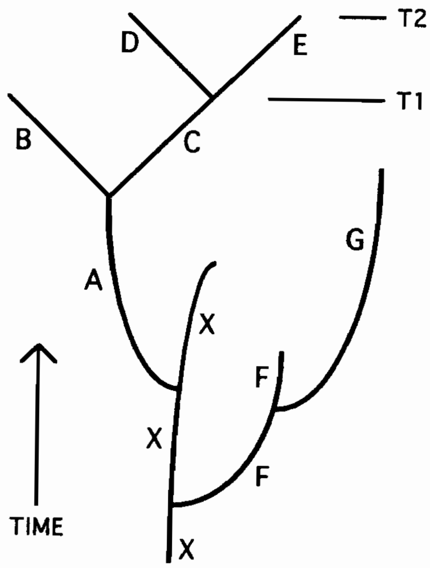

Figure 1. Hypothetical phylogenetic tree used for illustration of the concepts of "monophyletic *group* " and associated terms, as defined herein. Lettered branches represent individual species evolving and/or existing through time. Shape and slope of individual branches does not represent anything; only the topology of their mutual interconnections is relevant. See text for explanation.

The Traditional Relationship Between Monophyly and Polyphyly

There has been much debate over the "traditional" meaning of monophyly (e.g., Holmes, 1980; Wiley, 1981; Ashlock, 1984; Farris, 1985, 1990). This controversy has persisted owing to a confusion about what is being argued. There never was a single pre-Hennigian definition of monophyly; there were several, all or most of which were vague. Instead, the traditional usage of this term simply involved its logical relationship with the term "polyphyly." Holmes (1980:56, 65, 69) convincingly argued that Hennig's (1966) definition altered the well-established contradictory relationship between monophyly and polyphyly:

"...the claim made by some cladists that Hennig's concept is the traditional one definitely does not stand up under scrutiny. Traditionally, a taxon was either monophyletic or polyphyletic; it could not be anything else, since these terms were antonyms [contradictories]. In Hennig's usage, these terms are no longer antonyms [contradictories], since certain groups are no longer monophyletic nor polyphyletic; Hennig found it necessary to coin an additional term- paraphyletic- for such groups. This indicates that Hennig changed the generally undersood meaning of monophyly; this is also suggested by statements made by Hennig (1966:207)...Prior to the spread of Hennig's ideas, the validity of what are now known as paraphyletic taxa (nonmonophyletic according to Hennig), such as the class Reptilia, generally went unchallenged because they were assumed to be monophyletic. If Hennig's meaning was the "traditional" one, the class Reptilia and the numerous other admittedly paraphyletic taxa named in the literature would never have become widely accepted."[1]

Holmes (1980) has made an excellent point. Traditionally, the concept of "monophyly" was concerned only with the "mode of origin" of a given assemblage, *not* with whether all of the descendants of the "most recent common ancestor" were included in that assemblage (see also Ghiselin, 1981; Charig, 1982). For example, on the phylogenetic tree shown in Fig. 1, at time T1, the extensionally-defined group ABC is monophyletic, and specifically, "holophyletic." At time T2, the very same extensionally-defined group ABC is paraphyletic, but it is *still* monophyletic, because it still does *and always will have* a single basal connection to the phylogenetic tree (i.e., a "single origin"), which is all that the term "monophyletic" traditionally implied. Although Hennig's own concept of "monophyletic group" (cladophyletic group of this paper) was very important, it was nevertheless semantically inappropriate to apply this term to it. Hennig's (1975:247), Wiley's (1981:85), and Wyss and de Queiroz's (1984) arguments to the contrary simply miss the point; their observations of the failure of Mayr's (1974) own definition of monophyly are correct but irrelevant. When Mayr (1974:104) stated: "Hennig has created enormous confusion by adding to the traditional definition of a monophyletic taxon the following qualification: '...and which includes all species descended from this stem species'," he was *not* saying that Hennig's definition was *conceptually* illogical. He was saying that it was *semantically inappropriate* for the term "monophyletic" to be applied to this concept, simply because "monophyletic" traditionally and logically implied only "having a single basal connection to the phylogenetic tree" and not "includes all species descended from the stem species." Wiley (1981:85) stated: "Earlier definitions seem more consistent with Hennig's when all of their logical connotations are examined. For example, Wernham (1912) considered a group monophyletic if the ancestor was included in the group. This fits well with the definition of Heslop-Harrison (1958). Both definitions logically produce the same results as Hennig's definition." I disagree with Wiley. Heslop-Harrison (1958:178) stated: "To say that such a group is monophyletic is to imply that all existing plants which we place in the Angiospermae arose from a single ancestral population which, because of its possession of characteristics in common with modern angiosperms, *would itself be classified as such* [italics in original]." Contrary to the assertions of Wiley (1981), both Wernham's and Heslop-Harrison's concepts of monophyly are similar not to Hennig's, but to *Ashlock's* (1971), in that the most recent common ancestor must be "cladistically a member" (i.e., have the same derived characters common to the known members) of that taxon (see discussion of Ashlock's definitions below). Neither Wernham nor Heslop-Harrison stated nor implied that a taxon must include all of the descendants of the most recent common ancestor in order to be monophyletic. In fact, Heslop-Harrison (1958:179), unlike Hennig, clearly regarded monophyly and polyphyly as contradictories.

Ashlock's (1984) defense of his definition structure of monophyly was criticized by Farris (1985:296), who stated: "[Ashlock's] claim that systematists after Haeckel but before Hennig and Simpson were unanimous in using monophyly in the way that Ashlock now prefers is simply false. "Simpson's" definition was already in use in the early 20th century (see, for example, Bather, 1927; Gilmour, 1940) ... Ashlock's argument seems to consist of no more than revising history in order to provide the appearance of precedent for a usage that has no other merits." However, the fact that "Simpsonian" (categorical rank-based) definitions of "monophyly" and "polyphyly" were in use in the early 20th century is irrelevant to Ashlock's premise, namely, that these terms were traditionally *contradictories*, and that under Hennig's definition, they are not. Indeed, even under Bather's, Gilmour's, and Simpson's vague definitions, "monophyly" and "polyphyly" appear to be used as contradictories.

Finally, Farris (1990) acknowledged that "Haeckel often referred to monophyly and polyphyly as differentiated by single and multiple origins," but disputed the contention that monophyly ("single tribe") means nothing but "single-origin." Farris cited Haeckel's (1868) definition of "tribe," which specifies that a tribe consists of all of the descendants of its common ancestor, and so paraphyletic groups cannot be called tribes, and therefore cannot be "monophyletic." This is a valid point, but the debate between cladists and gradists about "monophyly" did not arise over Haeckel's definition of the term "tribe." Farris' (1990) suggestion that Simpson's and Mayr's definitions of "monophyly" were chosen largely to admit their own preferred taxa may be correct, but the same claim can be made against Hennig. Hennig accepted only "holophyletic" taxa, but he still wanted to equate the term "monophyletic" with "acceptable." In order to do this, he had to destroy the traditional contradictory relationship between monophyly and polyphyly, and *that* is what started the controversy.

A good argument for maintaining the contradictory status of monophyly and polyphyly may be made by means of analogy with the definition structure currently used for the four main types of characters that can be shared by a given set of species, and with recent attempts to change this definition structure. The terms "homology" and "homoplasy" are generally regarded as contradictories (Simpson, 1961:78; Wiley, 1981:121-122). That is, at the simplest level, a given character (e.g., "hair") shared by a given extensionally-defined group of known species (e.g., *Homo sapiens* and *Rattus rattus*) was either inherited from the most recent common ancestor of those species (and thus is homologous for them) or it was not (and thus is homoplastic for them). Among others, Hennig (1966) in particular realized that there were two aspects of homology. Thus, assuming that "hair" is homologous for *Homo sapiens* and *Rattus rattus*, this character was either inherited by them from a common ancestor *possessed by no other known species* (in which case they would form a cladophyletic group), or it was not (in which case they would not form a cladophyletic group). To his credit, Hennig coined *two new terms* for these concepts ("synapomorphy" and "symplesiomorphy"), and retained the term "homology" for what by then was its generally understood meaning (Hennig, 1966:94).[2]

HOMOLOGY	MONOPHYLY
Synapomorphy	Holophyly
Symplesiomorphy	Paraphyly
HOMOPLASY	POLYPHYLY

Thus, while "hair" is homologous for *Homo sapiens* and *Rattus rattus* (their most recent common ancestor presumably had hair), it is not a synapomorphy for them. This explicit terminological clarification increased conceptual precision, and helped lead to significant methodological advance. But Patterson (1982), Stevens (1984), and de Pinna (1991) want to change this logical definition structure. They want to assign the term "homology" to Hennig's concept of "synapomorphy,"[3] just as Hennig misguidedly assigned the term "monophyly" to the concept of "holophyly." In the context of the above example, therefore, the symplesiomorphous character "hair" would no longer be homologous (and thus homoplastic?!) for *Homo sapiens* and *Rattus rattus*. If the ill-advised suggestion to equate homology with synapomorphy is accepted, then "homology" and "homoplasy" would no longer be contradictories, the distinction between "homoplasy" and "symplesiomorphy" would become muddled, and we would have to coin a new term for the generally accepted concept of "homology" (synapomorphy + symplesiomorphy). These consequences are precisely analogous to what occurred when Hennig assigned the term "monophyly" to the concept of "holophyly"- "monophyly" and "polyphyly" were no longer contradictories, the distinction between polyphyly and paraphyly became muddled, and a completely unnecessary new term was coined for the traditional concept of "monophyly" ("convex"-

see Estabrook, 1978). If Hennig had simply coined a new term for his concept of "monophyly," and had let this term retain its traditional meaning, much of the polemics between cladists and gradists could have been avoided. Unfortunately, Ashlock's (1971) appropriate term "holophyly" was universally ignored by cladists, probably for the scientifically irrelevant but socially important psychological and political reasons discussed below.

Monophyly, Naturalness, and Taxonomic Acceptability

Systematists have traditionally equated "monophyletic" with "natural" and "taxonomically acceptable," probably because the acceptance of "clearly" polyphyletic taxa has been regarded as anti-evolutionary. However, this equation has led to logical errors in the debate over paraphyly. For example, the various reasons with which Oosterbroek (1987:103) purports to demonstrate the untenability of Ashlock's (1971) definition structure are in fact never given. Instead, Oosterbroek states that paraphyletic groups are unnatural, and seems to imply that this is sufficient grounds for cladists to call them non-monophyletic. In contrast, some gradists (e.g., Cronquist, 1987:2) seem to think that just because paraphyletic groups are logically monophyletic, they are automatically acceptable in formal classifications. However, paraphyletic groups were traditionally monophyletic merely and only by virtue of the contradictory relationship between the terms monophyly and polyphyly. Therefore, the fact that paraphyletic groups are logically a type of monophyletic group is *completely irrelevant* to the question of whether or not they are "natural," or "acceptable" in formal classifications.

The above confusions result from the fallacious equation of what should be a term that merely describes phylogenetic topology ("monophyletic group") with two inherently controversial, theory-dependent terms ("natural" and "taxonomically acceptable"). To clarify, consider the false premise "All automobiles (a descriptive term) are "stylish" (a much more theory-dependent term). Oosterbroek's (1987) position would be analogous to saying "I believe that the Edsel is not stylish. Therefore, the Edsel cannot be an automobile." Cronquist's (1987) position would be analogous to saying "Of course the Edsel is an automobile, therefore, it *must* be stylish." Given a specified group of species on a hypothetical phylogenetic tree, all systematists should be able to agree on whether that group is monophyletic, holophyletic, paraphyletic, or polyphyletic, because such terms merely describe the objectively determinable topological relationships exhibited by the members of that group. In contrast, terms such as "natural" and "taxonomically acceptable" will always be controversial, because depending on their purpose, systematists differ greatly in the criteria used for deciding whether a given group is "natural" or "acceptable" (e.g., Hull, 1988).[4]

A final point involves the fallacious equation of "natural group" with "cladophyletic group." To illustrate, Fig. 2 shows a hypothetical phylogenetic tree consisting of 25 species. Species known to humans are represented by thick branches. Suppose that the clade consisting of Species 2-14 is extinct, but that Species 7, 9, and 13 are known from fossils. It can be seen that the group consisting of Species 7, 9, and 13 is a cladophyletic group relative to all other known species on this tree. However, the group {7, 9, 13} is certainly not "natural," because it does not "exist in nature, independently of man's ability to perceive it" (Wiley, 1981:72), but rather is united by humans precisely because they are ignorant of the existence of Species 2-6, 8, 10-12, and 14. Similarly, of the clade composed of Species 15-25, only Species 19, 21, 24, and 25 are extant, and 25 is currently unknown to humans. While Species 19, 21, and 24 form a cladophyletic group with respect to all other known species on the tree, this group is again not "natural." Even if we discover Species 25 during next year's expedition to the rain forest, the new cladophyletic group {19, 21, 24, 25} would still not be "natural" according to Wiley's (1981:72) definition. As will become clear later, the group {19, 21, 24, 25} is in fact a polyphyletic group.

In summary, cladists and gradists should stop equating "monophyletic" with "natural" and "taxonomically acceptable." This error has been extremely damaging in the history of the monophyly debate, because its emotional overtones have drowned out the mutual understanding of more substantive issues.

OPERATIONAL DEFINITIONS OF PARAPHYLY AND POLYPHYLY

Nelson (1971) proposed operational definitions of "monophyletic group" and related terms that were based on the hypothesized cladistic relationships among extensionally-defined groups of terminal species. Nelson's definition of a "monophyletic group" is an operational analog to the theoretical concept of a cladophyletic group. However, Nelson's definitions of paraphyly and polyphyly have been justifiably criticized by Farris (1974, 1991), Platnick (1977b), and Holmes (1980). Nelson (1971:471) stated: "In my opinion, the concepts of monophyly, paraphyly, and polyphyly are best understood with reference to a theory of relationships, i.e., a sister-group system, and can be defined only with reference to such a system- either in general or in particular." Nelson's opinion is false. As shown below, theoretical definitions of monophyly, holophyly, paraphyly, and polyphyly are easily phrased in terms of the ancestor-descendant interrelationships among the members of such groups, as represented on phylogenetic trees.

Farris' (1974) operational definitions of what I prefer to call "algorithmic holophyly," "algorithmic paraphyly," and "algorithmic polyphyly" provide a method for distinguishing three different topologies of terminal entities on cladograms. Given an assumption of relationships as expressed by a fully-resolved cladogram, Farris' definitions will result in a conclusive assignment of either "monophyly," "paraphyly," or "polyphyly" to any group of entities on that cladogram, but precisely because these definitions are operational and not theoretical, this is so even if the relationships indicated by that cladogram are in fact false.

A misunderstanding of the nature of these definitions is evident in the comments of Wiley (1981: 92), who stated: "In

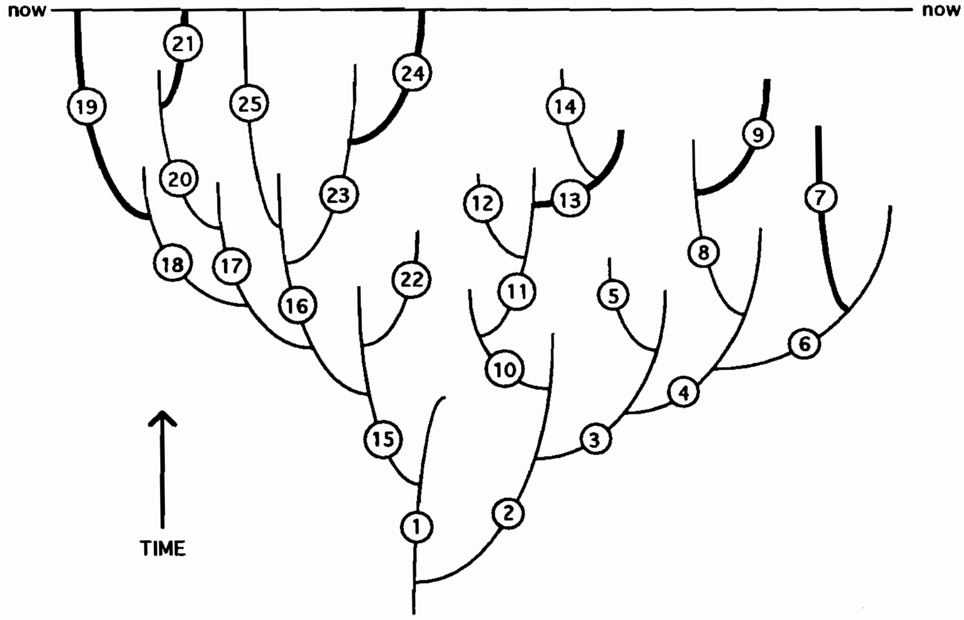

Figure 2. Hypothetical phylogenetic tree showing why cladophyletic groups are not necessarily "natural." See text for discussion.

conclusion, Farris's definitions lead to unambiguous results concerning the nature of particular supraspecific groupings...More importantly, they provide a method for distinguishing natural and non-natural groups." Wiley's first statement is correct, precisely because Farris' definitions are operational and not theoretical. However, Wiley's second statement is false, for the same reason; he has confused ontology with epistemology. Farris' definitions were not designed to distinguish between hypotheses of relationship that are true (i.e., "natural" groups) and those that are false (i.e., "non-natural" groups); indeed, they were specifically phrased in order to avoid those theoretical notions. Farris (1974) stated that "...we should not attempt to use real characters in deciding the paraphyly or polyphyly of a group...." However, as discussed later, the terms paraphyletic and polyphyletic *taxon* can indeed be "defined" with reference to real characters.

Oosterbroek's (1987) concepts of paraphyly and polyphyly are similar to those of Nelson's (1971) in that they are operationally-defined, phrased with reference to a given cladogram showing terminal entities, and distinguished on the basis of alleged differences in cladistic structure. Unfortunately, I can see neither theoretical nor practical significance in Oosterbroek's distinction between these terms. Detailed criticisms of Oosterbroek's definitions are given by Farris (1991). However, I disagree with Farris' (1991:304) claim that "without characters, paraphyly and polyphyly mean nothing." Again, as shown below, "monophyletic *group*" and related terms can be theoretically-defined solely on the basis of the ancestor-descendant relationships among the members of such groups, without any reference to characters.

There are only two types of extensionally-defined groups of entities that differ significantly in the nature of the cladistic relationships among their members- cladophyletic groups and non-cladophyletic groups (in this respect I agree with Hennig, 1975:247). It seems pointless to try to define "paraphyly" and "polyphyly" with reference to terminal entities on a cladogram. That is, a given extensionally-defined group of species is either one in which every member species is more closely related cladistically to every other member species than to any known species that is excluded from the group, or it is not. If it is not a cladophyletic group, *who cares* about what else it might be?

Farris' (1974) operational definitions rob the terms monophyly, paraphyly, and polyphyly of any theoretical significance. For example, in Fig. 2, the group {7, 9, 13} would be "monophyletic" according to Farris. If Species 14 were then discovered, the very same group {7, 9, 13} would be "paraphyletic," and if Species 5 and 12 were discovered, the very same group {7, 9, 13} would be "polyphyletic." Thus (by design), the status of a group under Farris' operational definitions is dependent largely on the magnitude of the ignorance of systematists. In contrast, the conceptual distinction between paraphyletic and polyphyletic groups is fundamental when these terms are defined with reference to a phylogenetic tree showing the ancestor-descendant interrelationships among the members of such groups (in this respect I disagree with Hennig, 1975:247).

PREVIOUS CONCEPTS OF "MONOPHYLETIC *GROUP* " AND RELATED TERMS

To reiterate, I am using "monophyletic *group*" and related terms in this paper to refer to those idealized concepts that are defined with reference to a hypothetical phylogenetic tree showing the ancestor-descendant relationships existing among the members of such a group. Mayr's (1942) traditionally vague definition of monophyly ("descendants of a single species") has been adequately criticized by Hennig (1966:72), and Simpson's (1961:124) equally vague concept ("Monophyly is the derivation of a taxon through one or more lineages...from one immediately ancestral taxon of the same or lower rank") has been adequately criticized by Holmes (1980:61). My discussion begins with Hennig (1966:73), who offered the following theoretical definition:

"A monophyletic group is a group of species descended from a single ("stem") species, and which includes all species descended from this stem species."

If taken literally, Hennig's definition requires that *all* species descended from the stem species be included in a group in order to make it monophyletic. This concept would then be similar to that of a "clade" (i.e., an ancestor and all of its descendants, known and unknown, extinct and extant). However, as noted by Tuomikoski (1967:140) and Bonde (1977:757), Hennig's definition was probably meant to apply mainly to extensionally-defined groups of known or extant species. In other words, the neontologist Hennig was probably trying to communicate the concept of a cladophyletic group (i.e., all of the *known* descendant species of a usually *unknown* stem species). This is probably why Hennig's definition neither explicitly requires nor logically implies that the stem species is to be included in a monophyletic group.

Hennig (1965:104) made the following distinction between the paraphyly and polyphyly of extensionally-defined groups of known species: "If, in a system, one associates in a group species whose agreement rests on convergence, a polyphyletic group is thereby formed, as has been established above and is generally recognized. If one associates species whose agreement rests on symplesiomorphy, then a paraphyletic group is formed." Hennig (1975:248) reaffirmed this view and suggested that "The terminological distinction between paraphyletic and polyphyletic groups is valid, therefore, only when attention is drawn to the particular kind of mistake made in the process of character analysis that led to the formation of the groups." Platnick (1977b:197) pointed out that the problem with this distinction is that if recognized on the basis of both homoplastic and symplesiomorphic characters, a given extensionally-defined group of species could be both paraphyletic and polyphyletic at the same time. Indeed, a group of extant species actually forming a cladophyletic group with respect to all other extant species (a "monophyletic group" according to Hennig's usage) but unknowingly united by systematists on the basis of what in fact were homoplastic characters, would necessarily also be a polyphyletic group according to Hennig's statements. This situation will be discussed further below.

Eldredge and Cracraft (1980:10) suggested that a "monophyletic taxon" is: "...a taxon composed of two or more species consisting of an ancestral species and all its known descendants" (Eldredge and Cracraft use the term "taxon" here as I use the term "group"). Eldredge and Cracraft have attempted to combine two concepts into one definition, with the result that neither concept is clear. A "clade" (i.e., an ancestor and *all* of its descendants, known and unknown, extinct and extant) is very different from a "cladophyletic group" (i.e., all and only the *known* descendants of a usually *unknown* ancestor). These two concepts must be kept distinct.

Holmes (1980:83) offered the following theoretical definitions:

MONOPHYLETIC- Pertaining to a group of species that includes the most recent common ancestral species of the entire group plus all more recent justifiably inferred ancestors of each species of the group.

Holophyletic- Pertaining to a group of species comprising a single ancestral species and all its descendants.

Paraphyletic- Pertaining to a monophyletic group that excludes one or more discrete groups descended from the most recent common ancestral species of the entire group.

POLYPHYLETIC- Pertaining to a group of species that does not include both the most recent common ancestral species of the entire group and all more recent inferred ancestors of each species of the group.

These definitions were formulated with reference to a phylogenetic tree showing the ancestor-descendant interrelationships among the members of each type of group. Unfortunately, Holmes' definitions suffer from his use of the nebulous phrase "justifiably inferred." Furthermore, these definitions imply that a group consisting only of the two daughter species of a dichotomously-splitting stem species (e.g., group DE in Fig. 1) is polyphyletic, because such a group obviously excludes the most recent common ancestral species of the entire group. Although my own concepts of "monophyletic group" and related terms are very similar to those of Holmes, the definitions offered below will be more rigorously formulated. Oosterbroek's (1987:107) criticisms of Holmes' (1980) definitions are invalid, because he mistakenly assumed that they were meant to apply only to terminal species. Again, Holmes' definitions were theoretical in nature, phrased with reference to a phylogenetic tree and not a cladogram. As such, they dealt not only with terminal species, but with all species (extinct and extant, terminal and ancestral) descended from the "common ancestor."

Wiley (1981:84) presented a set of definitions that he identified as those of Farris (1974):

MONOPHYLY- A group that includes a common ancestor and all of its descendants.
PARAPHYLY- A group that includes a common ancestor and some but not all of its descendants.
POLYPHYLY- A group in which the most recent common ancestor is assigned to some other group and not to the group itself.

These definitions have been endorsed by several cladists (Schoch, 1986; de Queiroz, 1988). In view of their explicit reference to ancestors and descendants, these definitions were apparently intended to be theoretical interpretations of the operational definitions of Farris (1974). However, when applied in the theoretical context of a phylogenetic tree showing ancestry and descent, several flaws become evident. For example, the presence in these definitions of the imprecise word "includes" enables a group to be both monophyletic and polyphyletic at the same time. Thus, the group ABCDEFG in Fig. 1 is "monophyletic," because it "includes a common ancestor" (e.g., C) "and all of its descendants" (D and E). The same group is also "polyphyletic," because the most recent common ancestor of the group (X) is not assigned to the group itself. These definitions could be improved if the phrase "is composed only of" were substituted for the word "includes," but they would still be unacceptable. First, like those of Holmes (1980), these definitions imply that a group consisting of the two descendant species of a dichotomously-splitting stem species is polyphyletic. Second, as noted by Holmes (1980:69-70), the mere inclusion of "the most recent common ancestor" of a group does not automatically make that group nonpolyphyletic. For example, the group XEG in Fig. 1 "includes a common ancestor" (X) "and some but not all of its descendants" (E and G), but it is not a paraphyletic group; it is a polyphyletic group, as will become clear later. For those who would undoubtedly accuse me of nitpicking here, I suggest that they read Wiley's (1981:258-260) own microscopic (but largely irrelevant) examination of Ashlock's (1971) definitions. It is necessary to point out the flaws in Wiley's definitions precisely because they have been widely accepted.

Meacham and Duncan (1987) offered yet another set of theoretical definitions of "monophyletic group" and related terms, formulated with reference to a hypothetical phylogenetic tree. Unfortunately, owing to their questionable redefinition of the term "ancestor," Meacham and Duncan's definitions lead to the conclusion that all of the descendant species of a dichotomously-splitting stem species form a non-holophyletic group. For example, the most recent common ancestral species of the group DE in Fig. 1 is species C. By Meacham and Duncan's definition, C is both an ancestor and descendant of itself. But, by extensional definition, the group DE excludes species C; therefore, not all of the descendants of the most recent common ancestor of DE are included in DE, and so this group is not holophyletic, but "paraphyletic." Although my own concepts of "monophyletic group" and related terms are similar to those of Meacham and Duncan, their unnecessary redefinition of the term "ancestor" has not clarified the monophyly issue.

NEW THEORETICAL DEFINITIONS OF "MONOPHYLETIC *GROUP*" AND RELATED TERMS

In the following phylogenetic tree-based definitions, the term "group" will refer to an extensionally-defined assemblage of two or more species, although in principle there is no reason why we could not apply monophyly and related terms to single species and groups of organisms or cells (Tuomikoski, 1967; de Queiroz and Donoghue, 1988; 1990a, b, and references therein). I use the term "species" here for the concept of "species as individuals," whether those particular species be members of a species-category called "biological species," "evolutionary species," or any other species-category for which particular species are regarded as ontological individuals (e.g., Ghiselin, 1974, 1987, 1997; Eldredge and Cracraft, 1980; Wiley, 1981; de Queiroz and Donoghue, 1988).

MONOPHYLETIC GROUP- A group of species consisting of a one-piece section of the phylogenetic tree, with a single basal connection to the rest of the tree.

Holophyletic Group- A monophyletic group that contains all of the descendant species of the oldest-appearing species in the group.

Paraphyletic Group- A monophyletic group that does not contain all of the descendant species of the oldest-appearing species in the group.

POLYPHYLETIC GROUP- A group of species consisting of two or more unconnected sections of the phylogenetic tree, or a group with two or more basal connections to the rest of the tree.

The term "oldest-appearing species" in these definitions refers either to the *single* species that originated the earliest, or to two or more oldest-appearing species that originated simultaneously, via, for example, dichotomous speciation. "Oldest" is used instead of "ancestral" or "stem" species in order to avoid the contradiction of a stem species being its own ancestor, a problem discussed by Platnick (1976; 1977a) and Wiley (1977). To illustrate these definitions, refer to Fig. 1. Suppose that the diagram represents an actual phylogenetic tree of descent. Each lettered branch represents a species evolving and/or existing through time. Both dichotomous speciation (C -> D + E) and multiple, non-simultaneous speciations of a single ancestral species (X -> F; X -> A) are shown (e.g., Eldredge and Cracraft, 1980, fig. 3.1).

Consider the group ABCDE. Since it consists of a one-piece section of the phylogenetic tree and has a single basal connection to the rest of the tree, ABCDE is a monophyletic group. Furthermore, ABCDE is a holophyletic group, because it contains all of the descendant species of A. Other examples of holophyletic groups are BCDE, CDE, and XABCDEFG. Note that groups such as DE whose two equally-oldest members are the sister species of a dichotomously-splitting parent species are also monophyletic.

The group ABC, although monophyletic (it consists of a one-piece section of the phylogenetic tree, with a single basal connection) is also paraphyletic, because it does not include all of the descendant species of A (it excludes D and E). Other examples of paraphyletic groups are CE, BCD, XFG, and XABCDE.

The group BAD is polyphyletic because it consists of two separate sections of the phylogenetic tree, even though the oldest-appearing species in the group (A) gave rise to all of the remaining species in the group. Other examples of polyphyletic groups are BE and ABCDEFG.

The above definitions of monophyletic group and polyphyletic group are based on the intuitively obvious characterizations of Tuomikoski (1967), and are also topologically consistent with those of Charig (1982) and de Queiroz and Gauthier (1990). Finally, it should be noted that the terms "clade" and "holophyletic group" are almost, but not quite synonyms. By definition, a clade is an ancestor and all of its descendants. Thus, a group such as DE in Fig. 1 is a holophyletic group, but it is not a clade.

"MONOPHYLETIC *TAXON*" AND RELATED TERMS

Before reviewing character-based concepts of "monophyletic *taxon*" and related terms, it is necessary to explain what I mean by "character," and then distinguish between two types of characters. First, I regard a character as any morphological or other genetically-based condition of an organism, such as "eye present," "shaft of femur square in cross-section," or "tail absent" (cf. Hennig, 1966:95). A "character" shared by two or more organisms is thus simply an operational "similarity," subject to additional theoretical interpretation of the true nature of that similarity, e.g., homologous (apomorphous + plesiomorphous) and homoplastic characters. Second, I will use the words "primitive" and "derived" in the following explicitly typological sense: A character is derived for a taxon if it occurs in no organism that is immediately ancestral to the most recent common ancestor of all of the pseudointensionally-defined members of that taxon. Conversely, a character that is primitive for a given taxon would be one that *is* present in an organism immediately ancestral to the most recent common ancestor of all of the pseudointensionally-defined members of that taxon.

To illustrate, suppose we define the taxon Amniota by the character "presence of amniote egg," the taxon Aves by the character "presence of feathers," the taxon Mammalia by the character "presence of hair," and (assuming the amniote egg evolved only once) the paraphyletic taxon "Reptilia" by the characters "presence of amniote egg and absence of hair and feathers." The character "presence of amniote egg" would be derived for both Amniota and "Reptilia" (because, by definition, the organisms immediately ancestral to these taxa cannot have this character), while the characters "absence of hair" and "absence of feathers" would be primitive for "Reptilia," because the organisms immediately ancestral to "Reptilia" presumably already had these characters. Similar views of the roles of "derived" and "primitive" characters in defining paraphyletic taxa have been expressed by Tuomikoski (1967:142), Ashlock (1972:431-433), and de Queiroz (1988:252).

Again, solely for the purposes of this paper, the concepts to which I assign the terms "monophyletic *taxon*" and "polyphyletic *taxon*" are the traditional, typological concepts of these terms, which dealt with the question of whether the "essential" derived defining characters of a given taxon arose in only one lineage in the genealogical history of the members of that taxon, or whether those characters evolved independently in two or more distinct lineages. Ashlock (1971) offered theoretical definitions of these character-based concepts as follows (Ashlock used the term "group" in his definitions, but for consistency I will use "taxon"):

MONOPHYLETIC TAXON- One whose most recent common ancestor is cladistically a member of that taxon.

Holophyletic Taxon- A monophyletic taxon that contains all of the descendants of the most recent common ancestor of that taxon (monophyly of Hennig).

Paraphyletic Taxon- A monophyletic taxon that does not contain all of the descendants of the most recent common ancestor of that taxon.

POLYPHYLETIC TAXON- One whose most recent common ancestor is not cladistically a member of that taxon.

Regarding the phrase "cladistically a member," Ashlock (1971:66) stated: "Cladistic membership of an individual in a taxon requires that the individual share apomorphous characters, that is, unique evolutionary innovations, with the taxon." Thus, Ashlock used the phrase "cladistically a member" for the concept of "has the same derived characters that are common to the known members of the taxon." Ashlock's use of the ambiguous term "cladistic membership" was unfortunate, and his definitions have been widely misunderstood. For example, Farris' (1974) and Platnick's (1977b) criticisms are invalid because they supposed Ashlock's definitions were meant to be practical or operational rather than theoretical in nature, while Wiley's (1981:258-260) criticisms are invalid because he mistakenly assumed that Ashlock's concept of "cladistic membership" in a *taxon* was meant to be synonymous with "actual assignment to an extensionally-defined *group*." In his recent discussion of monophyly and related terms, Wood (1994) also did not make these distinctions. Nevertheless, with suitable modification of Ashlock's concept of "cladistic membership," his definitions are acceptable as theoretical characterizations of monophyletic and polyphyletic *taxa*.

Holmes (1980:58) described the traditional character-based concept of "monophyletic taxon" in reference to Mammalia: "The generally understood meaning (prior to 1950) of the question as to whether the class Mammalia is monophyletic or polyphyletic has been whether or not mammals evolved from reptiles once or more than once- in other words, whether or not all members of the class Mammalia descended from a single ancestral mammalian species [emphasis in original]." A very similar concept of "monophyletic taxon" was expressed by Haeckel (1897; quoted in Rowe, 1988:241). However, this traditional typological concept is extremely vague. By the phrase "single ancestral mammalian species," it was implied that this ancestral species was *morphologically* a "mammal." But what exactly is required of this ancestral species for it to be "morphologically a mammal"? Must it have had all of the derived characters that we use to unite extant mammals? Or, would possession of most, a few, or perhaps just one of these characters be sufficient for "morphological mammalness"?

The character-based concept of monophyletic taxon has probably never been precisely defined, but is often implicit in discussions of the contradictory term "polyphyletic taxon." For example, in reviewing the possible polyphyly of the Cyclostomata, Romer (1965:144) stated: "...it is difficult to believe that the total set of characters [of the Cyclostomata] could have been achieved [polyphyletically] by two distinct lines of descent from ancestral types far removed from one other." Similarly, Takhtajan (1969:7), arguing against a polyphyletic origin of the angiosperms, stated: "The independent origin of the whole complex of angiosperm characters in several different lines of higher plants...would be comparable to the so-called 'dactylographic miracle', whereby given enough time, a work of literature, such as a Shakespearian sonnet, would be produced by chance alone." Implicit in these statements is the conclusion that if the *entire set* of derived characters of a given taxon did *not* all originate independently more than once, then that taxon would *not* be polyphyletic. Another way of saying this is that if *at least one* of the derived characters of a given taxon originated *only once* in the genealogical history of the members of that taxon, then that taxon would be *monophyletic.*

To illustrate these concepts, consider the hypothetical phylogenetic trees in Fig. 3. Each oval represents a species. Letters inside the ovals represent the relevant derived (and independent) characters of the species whose mutual ancestor-descendant relationships are indicated. Species without letters possess characters that are irrelevant to this discussion. Suppose that three "derived" characters, x, y, and z, are found only in the extant species 1, 2, 3, and 4, and we define a Taxon Xyzmorpha using these three characters. Although we obviously hope that these characters are homologous for species 1-4, we will probably never know whether all, some, or none of them actually are. Suppose, as shown in Fig. 3A, that all three characters originated only once in the genealogical history of species 1-4. Then, the most recent common ancestor of species 1-4 (species 5) would also have all of these characters; it would be what I will call a "full apomember" of Taxon Xyzmorpha, because it has *all* of the defining derived characters of this taxon (I suggest that the term "apomember" is more appropriate and less confusing than Ashlock's term "cladistic member").

Suppose however, as shown in Fig. 3B, that character x originated only once in the genealogical history of species 1-4, but that characters y and z both originated twice, independently, "by parallelism." Then, the most recent common ancestor of species 1-4 (species 8) would possess character x, but would necessarily lack characters y and z; it would be what I will call a "minimal apomember" of the Taxon Xyzmorpha, because it has at least one, but not all of the defining derived characters of that taxon. Nevertheless, the Taxon Xyzmorpha in this case would still be monophyletic according to Romer's (1965) and Takhtajan's (1969) concept of this term (even though it would no longer be composed of a monophyletic *group* of species). For a given taxon to be polyphyletic under Romer's and Takhtajan's concept, *all* of the defining derived characters of that taxon must have originated more than once in the genealogical history of the members of that taxon. For example, in Fig. 3C, two distinct lineages of species independently developed the entire set of defining derived characters of Xyzmorpha. Thus, the most recent common ancestor of species 1-4 (species 11) necessarily lacks all of these characters; it is a non-apomember of the Taxon Xyzmorpha.

Variations of Romer's (1965) and Takhtajan's (1969) character-based concepts of monophyly and polyphyly may be found in the literature. For example, Heslop-Harrison (1958) would require that all of the defining derived characters of a taxon originate only once in order for that taxon to be monophyletic. Under such a definition, however, the slightest amount of parallelism would render a taxon polyphyletic. Evidently, Romer's and Takhtajan's more liberal concept of "monophyletic taxon" was (vaguely) shared by many systematists before the Hennigian revolution. I therefore offer the following characterizations as clarifications of these traditional typological concepts of "monophyletic taxon" and related terms:

MONOPHYLETIC TAXON- A conceptual assemblage of organisms (known and unknown, extinct and extant), that possess (or that have at least one ancestor that possessed) a specified suite of characters in which at least one derived character originated only once in the genealogical history of the organisms that possess this character suite.

Holophyletic Taxon- A monophyletic taxon consisting of all of the organisms that possess (or that have at least one ancestor that possessed) a specified set of derived characters.

Paraphyletic Taxon- A monophyletic taxon consisting of all of the organisms that possess (or that have at least one ancestor that possessed) a specified set of derived characters, *and* that possess one or more specified primitive characters.

POLYPHYLETIC TAXON- A conceptual assemblage of organisms (known and unknown, extinct and extant) that possess (or that have at least one ancestor that possessed) a specified suite of characters in which each derived character originated more than once in the genealogical history of the organisms that possess this character suite.

These characterizations are not called definitions for several reasons. First, I have not explained what I mean by the phrase "origination of a character"; a precise explanation would involve a long discussion of the concepts of "homology" and "character" that is beyond the scope of this paper. Second, the above characterization of paraphyletic taxa does not take into account the possibility of character reversals in the more derived members of their corresponding holophyletic taxa. For example, if the taxon "Reptilia" is defined in the manner previously discussed, then certain birds and mammals that have lost their feathers or hair would have to be considered members of "Reptilia."

Although the conceptual flaws present in the above characterizations of the traditional character-based concepts of monophyletic taxon and related terms might be correctable, the resulting definitions would be extremely cumbersome, and there is little point in pursuing what seems like a typological dead end. Nevertheless, using these characterizations, it is possible to clarify the traditionally vague concept of a "monophyletic taxon" ("one whose members were all descended from a single ancestor") as follows: "A monophyletic taxon is one whose members were all ultimately descended from a single *apomember*

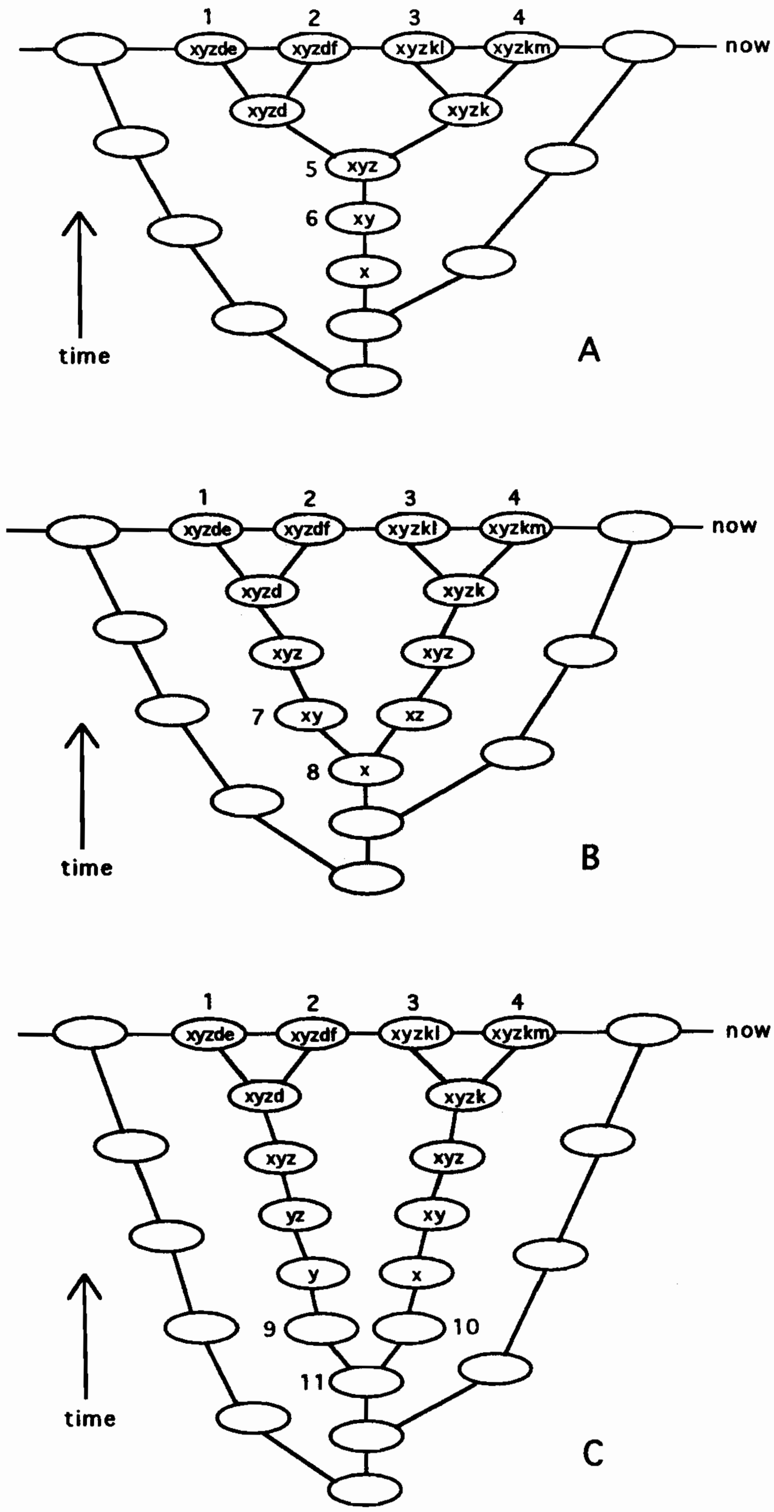

Figure 3. Hypothetical phylogenetic trees illustrating the traditional, character-based concepts of monophyletic and polyphyletic *taxon*. Each oval represents a species, and the letters inside certain ovals represent different characters evolving and accumulating in each lineage over time. See text for explanation.

(full or minimal) of that taxon." The corresponding concept of polyphyletic taxon can also be given: "A polyphyletic taxon is one whose members were all ultimately descended from two or more *non-apomembers* of that taxon."

Gosliner and Ghiselin (1984:270) stated: "The worst symptom of contemporary typology is the tendency to confuse the polyphyly of taxa with the polyphyly of characters- in consequence dismembering perfectly good, natural (genealogical) groups." What Gosliner and Ghiselin are saying is that even if the derived characters that characterize the known members of a given taxon did originate more than once in the genealogical history of these members, these known members may still form a cladophyletic group. I agree. For example, in Fig. 3C, the fact that characters x, y, and z all originated twice in the genealogical history of species 1-4 has no necessary bearing on whether or not species 1-4 form a cladophyletic group with respect to all other extant species. As shown in Fig. 3C, they do! However, this fact is irrelevant to the question of whether Taxon Xyzmorpha in Fig. 3C would traditionally have been called polyphyletic, simply because the traditional concept of a polyphyletic taxon was one defined with homoplastic characters, *whether or not* its known members form a cladophyletic group.

Of course, if the typological thinking inherent in the traditional concepts of "monophyletic taxon" and related terms is damaging to the progress of systematics (as I believe it has been; e.g., Ghiselin, 1984a; Rowe, 1988; Rowe and Gauthier, 1992; de Queiroz, 1988; 1994; Bryant, 1994), then so much the worse for such thinking. Again, my purpose in discussing the traditional character-based concepts of "monophyletic taxon" and related terms is not to endorse their use, but merely to clarify them, so that they can be separated from and compared with the very different concepts of "monophyletic group" and "cladophyletic group."

METAPHYLETIC GROUPS

Separation of the concepts of "cladophyletic group" and "monophyletic taxon" discussed above allows clarification of certain aspects of the "metataxon" concept (Donoghue, 1985; Gauthier et al., 1988). This concept will here be called "metaphyletic group" (cf. Mishler and Brandon, 1987) for consistency with my own usage. The controversial aspect of this concept involves the question of whether "metaphyly" is just a synonym of "paraphyly" (cf. Kluge, 1989; Wheeler and Nixon, 1990), or whether "metaphyletic groups" are a useful category in their own right (e.g., de Queiroz and Donoghue, 1990b). My own definition of "metaphyletic group" is as follows:

Metaphyletic Group- An extensionally defined group of organisms and/or species and/or taxa for which (in the context of a given hypothesis of relationships) there is no character evidence to suggest that the group is either cladophyletic or non-cladophyletic.

The term "metaphyletic group" is useful for indicating uncertainty about cladistic relationships. Kluge (1989:293) questioned its validity by stating that "Being unresolved is not an objective property of natural entities." As discussed above, however, even cladophyletic groups are not necessarily "natural entities," so Kluge's point seems irrelevant. Furthermore, we need to distinguish cladophyletic groups, metaphyletic groups, and non-cladophyletic groups for the same reason that we need to separate the concepts of "innocent person," "suspected criminal" (who may be innocent or guilty; we just don't yet have sufficient evidence to say), and "true criminal." For the same reason, I disagree with de Queiroz and Gauthier's (1990:313) view that the concept of a metaphyletic group may eventually become superfluous. See Archibald (1994), Frost and Kluge (1994:281-282), and McKenna and Bell (1997:28) for further discussion.

Previous definitions of "metataxa" have not emphasized that metaphyletic groups are *extensionally* defined. This omission has led some to regard "metaphyly" to be the same as "paraphyly," because they fail to appreciate the difference between extensional definition of a *group*, and pseudointensional definition of a *taxon*. To illustrate, consider Fig. 4. It shows a cladogram with six terminal species (1-6). All six species belong to the presumably holophyletic taxon Holoabcmorpha, defined by the putative autapomophies a, b, and c. Species 4-6 are also united by the putative synapomorphies d, e, and f, which are definitely absent in Species 1-3. Furthermore, no character evidence currently exists to indicate whether the group consisting of and only of Species 1-3 is cladophyletic or non-cladophyetic; it is therefore a metaphyletic group. Tomorrow, we might find a putative synapomorphy that would support the cladophyly of Species 1-3, or we might find a new putative synapomorphy shared by, say, Species 2 and 4-6 that would seem to render Species 1-3 non-cladophyletic (see de Queiroz and Donoghue, 1988, fig. 7). These issues are however completely distinct from the decision of whether or not to typologically define a paraphyletic *taxon* to include Species 1-3. Thus, if we deliberately defined the paraphyletic grade taxon "Paraabcmorpha" as "all organisms that possess characters a, b, and c, but lack characters d, e, and f," then, by definition, Species 1-3 would belong to this paraphyletic taxon, whether or not the extensionally-defined *group* of Species 1-3 is eventually determined to be cladophyletic or non-cladophyletic.

PHYLOGENETIC DEFINITIONS OF CROWN CLADES

The method of phylogenetic definition of "crown clades" (in terms of the ancestor of a specified group of extant species and all of its descendants) was advocated by Rowe (1988), de Queiroz (1988), and Gauthier et al. (1988), and is being discussed extensively in the current literature (e.g., Bryant, 1996; Wyss and Meng, 1996; Dominguez and Wheeler, 1997). Phylogenetic definitions are phrased with reference to a hypothesis of cladistic relationships among known entities, and their use seems compelling for certain higher-level taxa whose extant species can indeed be confidently assumed to form a cladophyletic group (e.g., Mammalia; see Rowe, 1988; Rowe and Gauthier, 1992; Bryant, 1994). Nevertheless, such crown clade definitions present

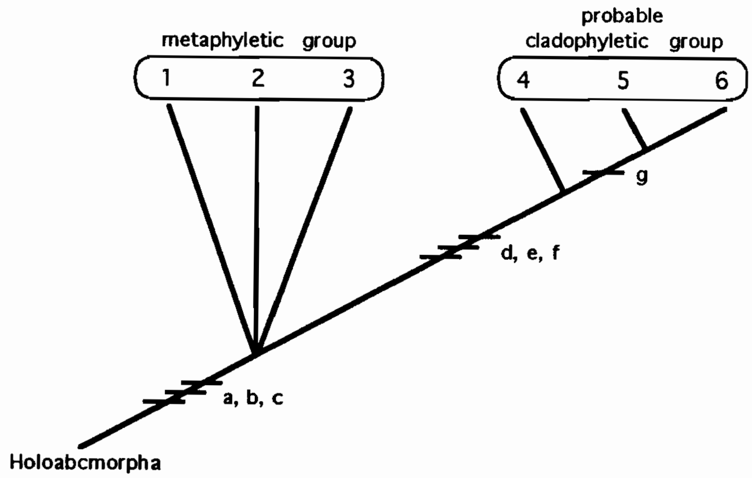

Figure 4. Hypothetical cladogram illustrating the difference between an extensionally-defined metaphyletic *group* and a pseudointensionally-defined paraphyletic *taxon*. See text for explanation.

some interesting practical problems in the actual classification of fossils. These problems arise from the fact that we can rarely if ever know whether all or any of the *putative* synapomorphies we use to unite a given group of extant species are *in fact* synapomorphies. This point seems to have been overlooked by Patterson and Rosen (1977:158), Ax (1984; 1989) and Böger (1989) in their discussions of this general subject.

In Fig. 3, suppose that the indicated characters of the various species are skeletal (preservable in fossils), and that the extinct species are represented by complete skeletons, such that the presence or absence of characters x, y, and z in each species can be definitely established. The crown clade Xyzmorpha would be defined as the most recent common ancestor of Species 1, 2, 3, and 4, and all of its descendants. Now suppose that we find a complete skeleton of Species 6, which has characters x and y but not z. Should this species be assigned to crown clade Xyzmorpha or not? In the case of Fig. 3A, all three characters originated only once in the genealogical history of Species 1-4, and therefore Species 6 is not a part of the crown clade Xyzmorpha. In Fig. 3B, however, Species 7 (which is morphologically identical to Species 6) would by definition belong to crown clade Xyzmorpha, simply because (unbeknownst to us) characters y and z originated twice in the genealogical history of Species 1-4. Finally, in a pronounced case of parallelism (Fig. 3C), although Species 9-11 have none of the putative synapomorphies that diagnose Xyzmorpha, all of them nevertheless belong to this crown clade.

Ironically, the most parsimonious approach to the classification of actual fossil specimens to crown clades would equate operationally with the practice of pseudointensional definition of taxa previously discussed. That is, we would assign a given fossil to a particular crown clade if and only if it shows all of the putative synapomorphies that diagnose the clade (or can be inferred on the basis of other characters to have descended from a species that did have all of them). Again, owing to parallelism (or reversal), this approach will sometimes exclude species that do in fact belong to the crown clade (Figs. 3B-C). However, the alternative method of classification would be less parsimonious, simply because in order to assign a fossil not possessing all of the putative synapomorphies of a given crown clade to that crown clade, one must make the ad hoc assumption that some homoplasy has occurred.

SUMMARY

In order to clarify the history of the monophyly debate, I have used distinct terms for the three concepts to which monophyly and related terms have most often been applied. These are: (1) "monophyletic group " (defined with reference to a phylogenetic tree showing the ancestor-descendant interrelationships among the members of such groups); (2) "cladophyletic group" (defined with reference to a cladogram showing the cladistic relationships among the members of a specified group of organisms and/or species and/or taxa); and (3) "monophyletic taxon " (the traditional, typological concept of monophyly, which deals with the single or multiple origin of the derived "defining characters" of a taxon).

Theoretical and operational definitions of terms have different purposes in science. The criticism that a given theoretical definition of monophyly is impractical or non-operational is irrelevant to the conceptual validity of that definition. Similarly, while some operational definitions of "monophyly" and related terms may be internally valid, this has no bearing on the fact that these definitions do not communicate the concepts to which these terms have traditionally been applied.

Some arguments concerning the traditional meaning of monophyly and polyphyly have confused particular definitions of these terms with a much broader concept, namely, the definition *structure* by which they were conceptually related. Ashlock's (1971) definition structure is justifiable because monophyly and polyphyly have traditionally been and logically are contradictories. That is, as delineated on a phylogenetic tree, a given group of entities can only form either one, or more than one basal connection with the rest of that tree.

HISTORY AND SEMANTICS OF MONOPHYLY

The traditional equation of the term "monophyletic" with the terms "natural" and "taxonomically acceptable" is improper. The fact that paraphyly is logically a form of monophyly does not mean that paraphyletic taxa are "natural," nor that cladists must accept them in formal classifications, nor that this justifies their use by gradists. Paraphyletic taxa should be accepted or rejected solely on the basis of their own merits or faults.

There are only two types of extensionally-defined groups of entities that differ significantly in the nature of the cladistic relationships among their members: cladophyletic groups and non-cladophyletic groups. Thus, there is no need to try to distinguish between "paraphyly" and "polyphyly" with reference to terminal entities on a cladogram. The distinction between paraphyly and polyphyly is meaningful only in terms of ancestor-descendant relationships as shown on a phylogenetic tree ("monophyletic group" and related terms) and in terms of characters ("monophyletic taxon" and related terms). Although many workers continue to confuse metaphyly with paraphyly, the term "metaphyletic group" is useful for expressing uncertainty about cladistic relationships. Phylogenetic definitions of crown clades are conceptually attractive. Ironically, however, the most parsimonious method for assigning fossil species to a given crown clade corresponds operationally to the "typological" practice of pseudointensional definition of taxa.

The goal of this paper was to clarify three historically significant concepts of monophyly. The terms that I have chosen for this purpose seem appropriate to me, but are unimportant in themselves; others might prefer different terms. I merely contend that these three different concepts have at one time or another been viewed by different workers as being valid for different conceptual purposes, and that they must be assigned three different terms if we wish to communicate with each other. Substantive issues can be logically debated only when both sides agree on the semantic groundrules.

NOTES

1. Holmes (1980) used "antonym" for the concept of the logical term "contradictory." However, "antonym" is most often used for the concept of the logical term "contrary," i.e., "opposite." For example, in a monochromatic world, the *contrary* of "black" is "white." However, the *contradictory* of "black" is "not black," the domain of which would be "white and every shade of gray."
2. The term "homology" was traditionally used only when referring to organs or structures (or parts thereof). However, Hennig (1966:95) also applied this term to characters such as the absence of a structure (e.g., "legs absent") and the different attributes of a structure (e.g., "eye color blue"). In other words, if any particular condition shared by two given species could originate once or more than once in their evolutionary history, then that character could be homologous or homoplastic. However, if we restrict the term "homologue" only to organs or structures or parts thereof (cf. Ghiselin, 1984b:217), then the character "absence of legs" in snakes cannot be homologous for snakes, even though it is (presumably) a synapomorphy for snakes. Similarly, the character "eye color blue" found in two given species could be a synapomorphy for them, but not a homology, since the latter term would only apply to "eye" (e.g., Rodrigues, 1986). Further discussion of this important topic is beyond the scope of this paper.
3. Unfortunately, "synapomorphy" is also equivocal. Contrary to Roth's (1988:4) view that it "has been precise and unambiguous since its inception," this term continues to be used in both operational and theoretical contexts. For example, Wiley (1981:82) and McKitrick (1994:8) used "synapomorphy" to designate a shared derived character, whether homologous or not. As discussed by Tuomikoski (1967:139), workers who employ the term in this operational sense will thus often speak of "true synapomorphy" when they mean "homologous shared derived character." In contrast, Bock (1977:888) and Eldredge and Cracraft (1980:37) used "synapomorphy" in a theoretical sense, to designate "*homologous* shared derived character," and so in practice must speak of "putative synapomorphy," or "hypothesized synapomorphy." This situation exists because Hennig (1966) generally used the term synapomorphy in the theoretical (homologous) sense (e.g., pp. 89-90 and 144), whereas the logical etymological meaning of synapomorphy is simply "shared derived character," with no implication that such characters must also be homologous for the stipulated entities that have them.
4. These remarks may seem paradoxical in that they imply that evaluation of an entity as natural or unnatural is itself a subjective process. However, this seems to be a consequence of the many different ways in which the term "natural" has been used in systematics (e.g., Van Valen, 1978, footnote 20). My own view would be that only individual populations, species, and holophyletic groups can be considered natural in the phylogenetic sense, but I would prefer to avoid this loaded term.

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