Systematic Biology

Toward an Integrated System of Clade Names

Kevin de Queiroz [a]
[a] Department of Vertebrate Zoology, National Museum of Natural History,
Smithsonian Institution, Washington, DC, USA

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KEVIN DE QUEIROZ

Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560, USA;
E-mail: dequeirozk@si.edu

Abstract.—Although the proposition that higher taxa should correspond to clades is widely accepted, current nomenclature does not distinguish clearly between different clades in nested series. In particular, the same name is often applied to a total clade, its crown clade, and clades originating with various nodes, branches, and apomorphies in between. An integrated system of clade names is described based on categories of clades defined with respect to lineages that have survived to the present time. In this system, the most widely known names are applied to crown clades, the names of total clades are formed by adding a standard prefix to the names of the corresponding crowns, and the names of apomorphy clades describe the specific apomorphies with which they originated. Relative to traditional approaches, this integrated approach to naming clades is both more precise concerning the associations of names with particular clades and more efficient with regard to the cognitive effort required to recognize the names of corresponding crown and total clades. It also seems preferable to five alternatives that could be used to make the same distinctions. The integrated system of clade names has several advantages, including the facilitation of communication among biologists who study distantly related clades, promoting a broader conceptualization of the origins of distinctive clades of extant organisms and emphasizing the continuous nature of evolution. [Apomorphy; branch; clade; crown clade; names; node; stem; total clade.]

The clade is one of the basic concepts of systematic and evolutionary biology. Defined as complete systems of common descent or monophyletic groups—that is, entities each composed of an ancestor and all of its descendants (Hennig, 1966; Farris, 1974; Wiley, 1981)—clades are general products of the evolutionary process. The development of the clade concept has been associated with a number of changes in biology, including a shift in emphasis from the traditional ranked categories of the taxonomic hierarchy (e.g., class, order, family, genus, and species, in the sense of a rank) to the historical evolutionary categories clade and species, in the sense of a metapopulation lineage (e.g., Hennig, 1966, 1969, 1981; de Queiroz, 1997). Related to this shift in emphasis, and despite some continued resistance (e.g., Nordal and Stedje, 2005), the proposition that supraspecific taxa should correspond to clades (Hennig, 1966) has become widely accepted (e.g., Purves et al., 2001; Freeman, 2005; Futuyma, 2005).

The emerging field of phylogenetic nomenclature (e.g., de Queiroz and Gauthier, 1990, 1992, 1994; Cantino and de Queiroz, 2006; see preface of last reference for a bibliography) is one manifestation of the shift from an emphasis on ranks to an emphasis on clades. In this approach, the references of taxon names are specifically identified as clades (e.g., *Iguanidae* = the least inclusive clade containing both *Iguana* and *Oplurus*; following Recommendation 6.1A of the *International Code of Phylogenetic Nomenclature*, all scientific names, not only those associated with the ranks of genus and species, will be italicized in this paper). In contrast, under the traditional approach to biological nomenclature, the references of taxon names are identified as groups assigned to particular taxonomic ranks (e.g., *Iguanidae* = the group ranked as a family that contains the genus *Iguana*). In short, phylogenetic nomenclature is designed to govern the names of clades rather than those of ranked groups, which may or may not correspond to clades.

Under the traditional approach to biological nomenclature, an integrated system of taxon names has been developed, at least around the intermediate ranks in the hierarchy (i.e., subtribe to superfamily or order; see Jeffrey, 1989). Thus, within broad taxonomic subdisciplines (botany, zoology, bacteriology), the names of all taxa assigned to the same rank have the same ending or suffix (e.g., the names of all families end in *-idae* in zoology and *-aceae* in botany and bacteriology). In addition, the names of taxa, at least at certain ranks, are derived from those of subordinate taxa (e.g., the name of a family, such as *Iguanidae*, is based on the name of an included genus, in this case, *Iguana*).

In contrast, phylogenetic nomenclature has, up to the present time, taken a more ad hoc approach to naming. Proponents have emphasized methods for specifying the references of names (phylogenetic definitions) as well as rules for dealing with different names that refer to the same taxon (synonyms) and identically spelled names that refer to different taxa (homonyms), as seen in the draft *International Code for Phylogenetic Nomenclature*, or *PhyloCode*, hereafter *ICPN* (Cantino and de Queiroz, 2006). Although some consideration has been given to preserving the nested relationship between taxa when the name of a taxon is based on that of a subordinate taxon (e.g., *ICPN*, Art. 11.7), by and large, little attention has been devoted to developing an integrated system of clade names (but see Hennig, 1965, 1969, 1981; Jefferies, 1979; Lauterbach, 1989, de Queiroz and Gauthier, 1992; Meier and Richter, 1992; Gauthier and de Queiroz, 2001). In this paper, I discuss such a system based on theoretically and operationally significant categories of clades. Although most of the conventions of this system have been proposed previously (e.g., Lauterbach, 1989, de Queiroz and Gauthier, 1992; Meier and Richter, 1992; Gauthier and de Queiroz, 2001), they have not been widely adopted, nor have their advantages over alternative approaches been discussed in detail.

CATEGORIES OF CLADES BASED ON TREE COMPONENTS

The significant categories of clades that serve as the basis for an integrated system of clade names are related to three general categories of definitions that have been identified in the context of phylogenetic nomenclature (e.g., de Queiroz and Gauthier, 1990, 1992, 1994), which have been termed and defined with reference to the common representation of phylogeny as a tree or branching diagram. A *node-based clade* is a clade conceptualized as originating at a particular node of a phylogenetic tree (Fig. 1a), where the node represents the "instant" at which one lineage split into two, and the clade includes the node but not any part of the branch subtending the node. The name of such a clade would be defined using a node-based definition. A *branch-based clade* is a clade conceptualized as originating with a particular branch of a phylogenetic tree (Fig. 1b), where the branch represents a lineage between two splitting events, and the clade includes the entire branch but neither the node at its base nor any other branch or branches connected to that node. The name of such a clade would be defined using a branch-based definition. Finally, an *apomorphy-based clade* is a clade conceptualized as originating with a particular apomorphy (Fig. 1c), commonly represented by a bar across the branch of a phylogenetic tree. The clade includes that part of the branch tipward from and including the point where the apomorphy originated (or, alternatively, where it became fixed within the lineage) but not the part rootward of it. The name of such a clade would be defined using an apomorphy-based definition.

The definitions that are here termed *branch-based* have previously been termed *stem-based* (e.g., de Queiroz and Gauthier, 1990, 1992, 1994). This terminological change is proposed for two related reasons. First, it brings the terminology of phylogenetic definitions into line with that of phylogenetic trees (e.g., Swofford et al., 1996; Page and Holmes, 1998; Hall, 2004). In the literature on trees, the connections between nodes or vertices are termed *branches*, *internodes*, or *edges*—not *stems*. Second, the proposed change brings the terminology of phylogenetic definitions into line with that used to discuss the origins of clades bounded by extant organisms in relation to their extinct outgroups (e.g., Hennig, 1965, 1969, 1981; Jeffries, 1979; Lauterbach, 1989; Meier and Richter, 1992; Donoghue, 2005). In the literature on this subject, the term *stem* (as in *stem species*, *stem lineage*, and *stem group*) is used in association only with branches that are directly ancestral to clades bounded by extant organisms (crowns, see below). In other words, the term *stem* is not synonymous with *branch* but is used instead for a subset of branches (those that are directly ancestral to crowns). Thus, the replacement of *stem-based* with *branch-based* makes the terminology of phylogenetic nomenclature consistent with that adopted in closely related fields (compare Donoghue, 2005).

Node-based, branch-based, and apomorphy-based clades do not represent fundamentally different kinds of evolutionary entities. The members of all three categories are fundamentally similar in being conceptualized and defined as parts of phylogeny each of which is composed of an ancestor and all of its descendants. Because phylogeny is continuous, clades form continuous nested series (see de Queiroz and Donoghue, 1990: fig. 2). Thus, the three categories of clades identified above simply represent convenient ways of partitioning those continuous series using as reference points different components (nodes, branches, bars representing character state changes) of the idealized representation of phylogeny as a tree in the sense of a minimally connected graph.

Although node-based, branch-based, and apomorphy-based clades represent convenient ways of partitioning nested series of clades, these general categories are not the most convenient or significant categories of clades with regard to the development of an integrated system of clade names. For one thing, there are too many of them. Indeed, for every monophyletic group inferred from a phylogenetic analysis, it would be possible to recognize a node-based clade, a branch-based clade, and one or more apomorphy-based clades. For another thing, at
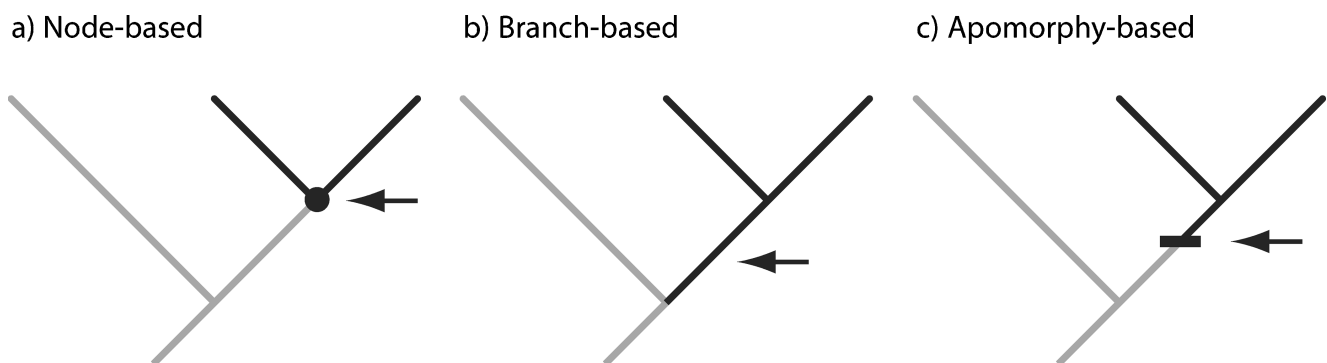
FIGURE 1. Categories of clades based on the components of phylogenetic trees (modified from de Queiroz and Gauthier, 1990, 1992, 1994). (a) Node-based, where the clade is conceptualized as originating at a particular node on a phylogenetic tree. (b) Branch-based, where the clade is conceptualized as originating at a particular branch on a phylogenetic tree. (c) Apomorphy-based, where the clade is conceptualized as originating with a particular apomorphy on a phylogenetic tree. Darker branches or segments thereof are those included within the specified clade; arrows point respectively to the node, branch, and apomorphy associated with the origin of the specified clade.
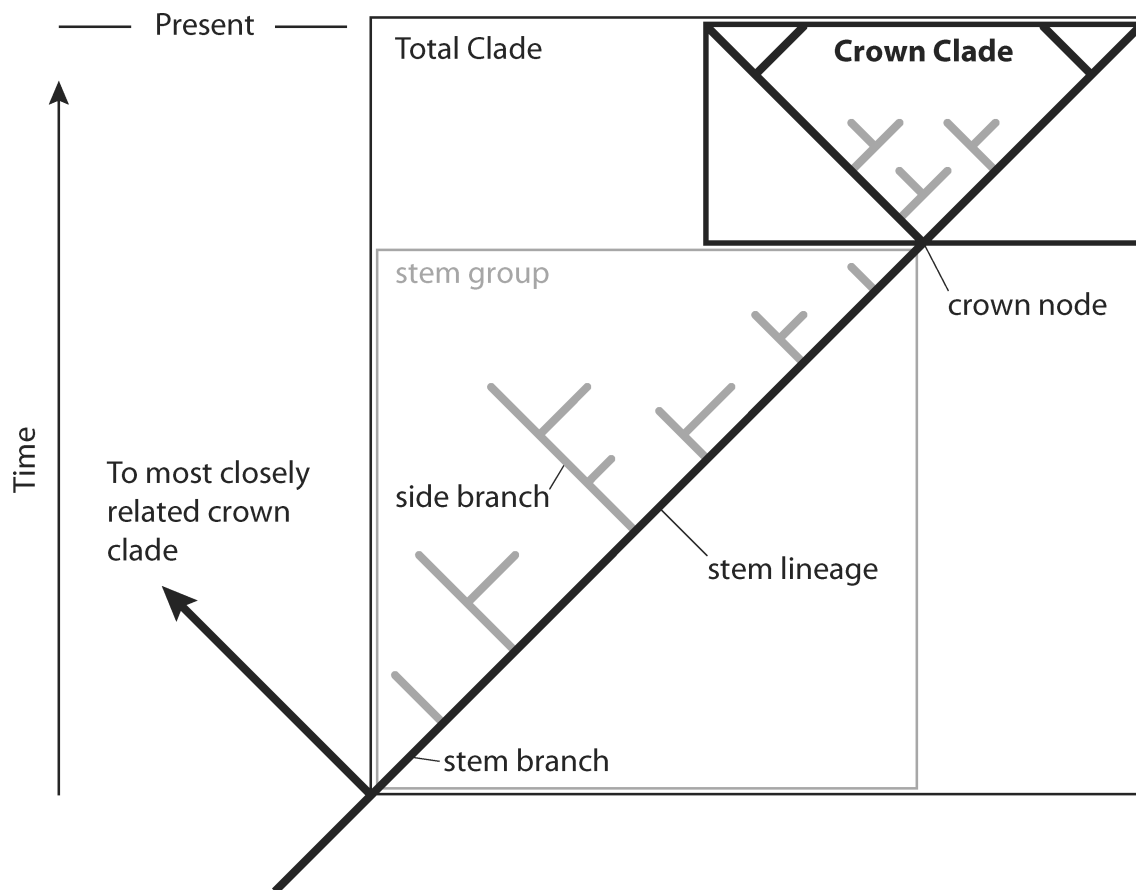
FIGURE 2.   Categories of clades and related concepts based on lineage survival (modified from Meier and Richter, 1992). Lineages lacking extant descendants (side branches) are represented by grey branches; those having extant descendants are represented by black branches. The stem lineage includes all branches that are ancestral to the crown clade, from the base of the stem branch (representing the origin of the stem species of the total clade) to the crown node (or, alternatively, to the base of the branch representing the origin of the stem species of the crown clade).

this level of resolution, the differences between the clades are relatively minor, involving only parts of species (i.e., one contains the entire ancestral species, another only that part of the ancestral species after a particular apomorphy arose, and yet another only that part of the ancestral species at the "instant" when it divided to form descendant species). Moreover, if one interprets the ancestors specified in node-based and apomorphy-based definitions as entire ancestral species, rather than parts of those ancestral species, then the distinctions between the different categories of clades break down (Gauthier and de Queiroz, 2001; see also Frost and Kluge, 1994; Sereno, 1999).

CATEGORIES OF CLADES BASED ON LINEAGE SURVIVAL

The categories of clades that seem most useful with regard to the development of an integrated system of clade names are those based on patterns of lineage survival—in particular, on the survival of lineages to the present time. These categories of clades are appropriate as the basis for an integrated system of clade names because they reflect different ways in which taxa (as clades) are com-

monly conceptualized and thus different ways in which taxon names are commonly used. The three categories of clades in question were first explicitly recognized by Hennig (1965), though he emphasized two of them in his later work (Hennig, 1966, 1969, 1981, 1983). I will adopt the following terms and definitions for these categories of clades (Fig. 2).

A *crown clade* is a clade originating from the last common ancestor of two or more extant organisms or species (Fig. 2). Hennig (1965) described this concept in terms of the age of the last common ancestor of the recent species of a group. Crown clades have also been referred to as **groups* (Hennig, 1969, 1981) and *crown groups* (Jefferies, 1979). The node at the base of a crown clade may be termed a *crown node*. For the purposes of the following discussion, it will not be critical to distinguish between the interpretation of the ancestor in which a crown clade originated as an entire species (branch) versus only part of that species (node or apomorphy), as the crown clade category will generally be used to make coarser distinctions than that between a node and part or all of its immediately subtending branch. However, regardless of whether one considers node-based, branch-based,

and apomorphy-based definitions to mark theoretically significant distinctions (see previous section), in practice, the names of crown clades are defined using definitions that are node-based in form, including branch- and apomorphy-modified variants (see *ICPN*, Art. 9). A definition that ties a name to a crown clade may be termed a *crown clade definition*, which may be either implicit (e.g., a node-based definition in which all internal specifiers are extant) or explicit (e.g., if the name is defined as "the crown clade . . . ").

A *total clade* is a clade composed of a crown clade and all species and/or organisms that share a more recent common ancestor with that crown than with any other mutually exclusive crown (Fig. 2). Hennig (1965) described this concept in terms of the age of separation of a group from its sister group. Total clades have also been called *total groups* (Jeffries, 1979), *pan-monophyla* (Lauterbach, 1989), *stem clades* (de Queiroz and Gauthier, 1992), and *panstems* (Joyce et al., 2004). The branch at the base of a total clade may be termed a *stem branch*, which represents the ancestral species in which the clade originated, that is, its stem species (see below). In practice, the names of total clades are defined using branch-based definitions, including node- and apomorphy-modified variants. A definition that ties a name to a total clade may be termed a *total clade definition*, which may be either implicit (e.g., a branch-based definition in which at least some internal specifiers and all external specifiers are extant) or explicit (e.g., if the name is defined as "the total clade . . . ").

An *apomorphy clade* is a clade originating with the ancestor in which a particular derived character state arose. Hennig (1965) described this concept in terms of the first appearance of the "typical" characters of a group, though he de-emphasized apomorphy clades in his subsequent writings (e.g., Hennig, 1966, 1969, 1981, 1983). In contrast to crown and total clades, apomorphy clades are conceptualized in terms of apomorphies rather than lineages that have survived to the present. On the other hand, some apomorphy clades are associated with the origins of apomorphies that characterize groups of extant organisms; such apomorphy clades form nested series between total clades and their crowns. The apomorphy upon with a particular apomorphy clade is based may be termed its *defining apomorphy*. The names of apomorphy clades are defined using apomorphy-based definitions.

As in the case of node-based, branch-based, and apomorphy-based clades, crown clades, total clades, and the apomorphy clades nested between them do not represent fundamentally different kinds of evolutionary entities. Again, the members of all three categories are fundamentally similar in being conceptualized and defined as parts of phylogeny each of which is composed of an ancestor and all of its descendants. Crown clades, total clades, and the apomorphy clades nested between them simply represent convenient ways of partitioning continuous nested series of clades based on lineages that have survived to the present time.

CROWNS AND STEMS

Because the crown and stem concepts are central to the proposed integrated system of clade names that will be described below, it is important to clarify these concepts. The term *crown* is commonly used to mean the highest part of an object, in the present case, a phylogenetic tree. If such a tree is conceptualized as growing upwards through time, with the older parts of lineages represented by the lower branches of the tree and the younger parts by the higher branches, then the crown of a phylogenetic tree consists of those parts that are the youngest and thus highest. The very youngest parts of a phylogenetic tree are those lineage segments surviving at the present time, which correspond to (the extant parts of) extant species. A *crown clade*, then, is a clade originating from the last common ancestor of extant species (Fig. 2).

This use of the term *crown* agrees with that of Meier and Richter (1992), who rejected Lauterbach's (1989) use of the term for taxa comprising only extinct species. Although the terms *crown* and *stem* will most commonly be used with reference to extant groups, they can be generalized so that they are applicable to entirely extinct groups (compare Monks, 2002; Donoghue, 2005). The reason is that although a clade whose component lineages are now all extinct is not a crown clade in the context of the present time, it may have been a crown clade at some earlier time. Thus, a more general definition of the term *crown clade* is a clade originating from the last common ancestor of two or more organisms or species that were extant at a specified time or interval thereof (e.g., period, series, stage). To avoid confusion, when the term is used to refer to entirely extinct clades, the temporal frame of reference should be stated explicitly.

The term *stem* is commonly used to mean an axis of the above-ground portion of a plant, in the present context, of the metaphorical tree that represents phylogeny. If the crown of such a tree consists of those parts that have survived to the present time, then the axis of the relevant part of the tree can be equated with the ancestral lineage leading up to that crown (Fig. 2). More specifically, the term *stem* will be used here to refer to the ancestral lineage of a particular crown clade from the point where that lineage separated from the ancestral lineage of the most closely related crown clade to the point where the primary lineages within the crown of interest separated from one another (represented by the crown node). The stem may also be termed the *stem lineage*. Meier and Richter (1992) used the term *ancestral lineage* for what is here termed the *stem lineage*; however, it seems preferable to use the former term in a more general sense that includes not only stem lineages but also lineages that are ancestral to wholly extinct clades.

The stem (lineage) is commonly composed of several branches in the sense of internodes, which may be termed *stem branches*, though the term *stem branch* may be used more specifically for the basal-most of those branches, which represents the ancestral species of the total clade. The branches representing extinct lineages that share a more recent common ancestor with a particular crown

clade than with any mutually exclusive crown clade may be termed *side branches* (relative to the crown clade of interest; Fig. 2). In this context, a total clade is composed of a particular crown clade, its stem lineage, and the side branches of that stem lineage.

A *stem species* (Hennig, 1966) is the ancestral species of a particular clade—the species in which the clade originated and from which it diversified (here *stem* is used only for the most basal part of the axis). Both crown clades and total clades have stem species, and except for cases in which all species resulting from successive speciation events have extant descendants, those species are different (see Meier and Richter, 1992; fig. 1). Node-based, branch-based, and apomorphy-based clades also have stem species; however, when a distinction is made between the ancestors represented by nodes (lineages at the "instant" of a divergence), branches (lineages between divergence events), and lineages at the "instant" of an apomorphy origin (or fixation), only the ancestor from which a branch-based clade originates corresponds to a stem species (in the other cases, the ancestor corresponds to only part of a stem species).

A *stem group* (Hennig, 1969, 1981, 1983) is the group of extinct species that belong to a particular total clade but not to its crown (Fig. 2). It includes both extinct species that are directly ancestral to the crown (those of the stem lineage) and those that are not directly ancestral (side branches), but it does not include species that are ancestral to, or side branches of, more inclusive crowns (Hennig, 1969, 1981, 1983; Meier and Richter, 1992). A stem group is paraphyletic, and for that reason some authors have argued that the concept itself should be rejected (e.g., Wiley, 1979; Ax, 1985). The utility of the stem group concept, however, is not as the basis for a formally recognized taxon. Instead, its utility is providing a convenient means of referring to the collection of ancestral species and side branches that are members of a particular total clade but not of its crown. The stem group concept provides a means of referring to such a collection that both avoids using a formal scientific name (or a vernacular equivalent) for a paraphyletic group (e.g., *Synapsida* or mammal-like reptiles *sensu* Carroll, 1988) and also is more straightforward than the terminology that might be used in its absence (e.g., stem group mammals versus non-mammalian theropsids).

HENNIG'S APPROACH TO CLADE NAMES

Hennig (1965, 1966) initially treated the categories that I am here calling crown, total, and apomorphy clades as three different meanings of the age of origin of a group, and later (Hennig 1969, 1981) as three different ways of delimiting (i.e., conceptualizing) a particular group. He argued against conceptualizing a group in terms of an apomorphy on the grounds that such an approach requires distinguishing essential characters from nonessential ones (Hennig, 1981: 26), and even assuming that the essential characters could be defined objectively, they may not be preserved in fossils (one of Hennig's primary concerns was referring fossils to groups containing

their living relatives). Moreover, conceptualizing a group in this manner ultimately requires emphasizing only one of the many apomorphies that may be characteristic of the extant members of the group.

For these reasons, Hennig restricted further considerations to conceptualizing groups as crown versus total clades, both of which he considered "compatible with the aims of phylogenetic research" (1981:29)—that is, with "recognizing groups of recent species and assigning individual fossils or groups of fossils to these groups" (1981:28). Hennig (e.g., 1981:29) considered it undesirable to give different names to corresponding crown and total clades, which was perhaps related to the common (if misguided) criticism of "cladistic classification" as resulting in the proliferation of names and ranks (e.g., Colless, 1977; Heywood, 1988; Mayr and Ashlock, 1991). Therefore, Hennig preferred to conceptualize (and name) groups as total clades, which permitted him to refer extinct species to the same clades as their extant relatives (Fig. 3a). In contrast, conceptualizing (and naming) groups as crowns would require coining additional names for the total clades to accommodate fossils lying outside of the crowns (Fig. 3b). Nonetheless, Hennig recognized the importance of distinguishing between crown and total clades, which he accomplished by appending an asterisk to the name when referring to the crown (e.g., *Trichoptera* for the total clade; **Trichoptera* for the crown; Fig. 3a).

Despite the importance of Hennig's insight in identifying different categories of clades, his conventions for distinguishing between the members of those categories leave much to be desired. Hennig's approach hinders biologists from making important distinctions related to what he identified as "the first task of phylogenetic research," namely, "to reveal the genealogical relationships that exist between all known species" (1981:3). The problem is that biologists need to be able to do more than merely refer a fossil to a (total) clade containing its extant relatives. At the very least, they also need to be able to determine and communicate whether that fossil lies inside or outside of the crown clade. Although Hennig made that distinction with an asterisk, this convention seems ineffective in that, first, the same symbol is used to designate several other things (e.g., uncertain monophyly, footnotes) and, second, it is unclear whether and how the asterisk would be pronounced. And in many cases, biologists may want to convey even more precise information about the phylogenetic positions of fossils than simply whether they are inside versus outside of the crown. For groups with good fossil records, nomenclatural distinctions conveying such precise phylogenetic information are already being made by naming clades originating with various intermediate nodes, branches, and apomorphies (e.g., Craske and Jefferies, 1989: fig. 6).

Another problem with Hennig's approach is that it emphasizes the meanings of names rather than the naming of clades (see de Queiroz, 1994). By treating the different categories of clades as different possible ways to delimit the group designated by a particular name (e.g., *Trichoptera*), those categories are implicitly treated as
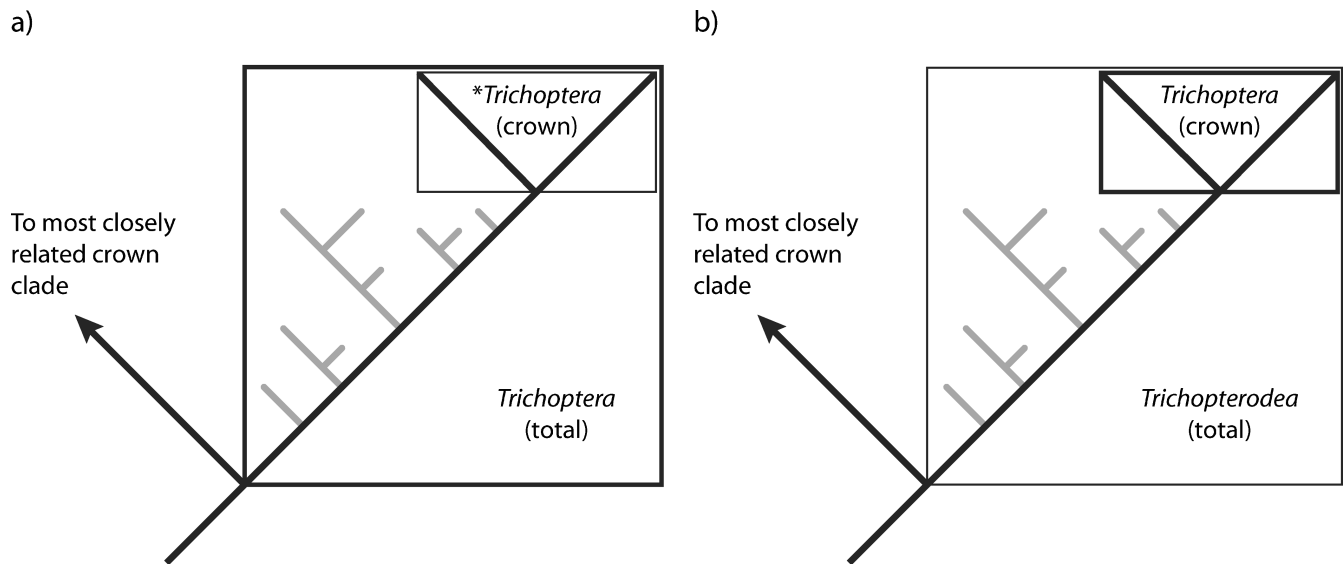
a)

b)

FIGURE 3. Hennig's (1981) reason for conceptualizing taxa (and associating names) with total clades rather than crown clades. (a) If a taxon, in this case *Trichoptera*, is conceptualized as a total clade, then fossils representing the stem group (grey branches) are members of that taxon. (b) If *Trichoptera* is conceptualized as a crown clade, then fossils representing the stem group are not members of that taxon, and a second taxon (e.g., *Trichopterodea*) must be recognized to permit assigning those fossils to a taxon containing their nearest living relatives. Note, however, that if the distinction between crown and total clades is considered important under the total clade approach (a), then a convention to distinguish the two clades is required. Hennig accomplished this by appending an asterisk when the name refers to the crown clade (e.g., *Trichoptera*).

different possible meanings of a single name. The problem is that once a decision is made to associate a name with one of several possible clades, the other clades tend to be neglected. Thus, once Hennig decided that names should refer to total clades, the other categories of clades and the distinctions that they embodied were largely ignored. Apomorphy clades were not named at all, and crown clades were given the same names as the corresponding total clades, distinguished only by an appended asterisk.

Evolutionary biology in the 21st century can no longer tolerate the ambiguities of naming systems that seemed adequate in the 1960s. Contemporary evolutionary biology in general, and systematic biology in particular, needs a system for naming clades that conveys the important distinctions in a precise and unambiguous way. To do this, biologists must question Hennig's position that a single name is adequate, or rather preferable, for a nested series of no fewer than three different clades (de Queiroz and Gauthier, 1992). We need to adopt a system that highlights the distinction between crown clades and total clades, in particular, as well as their nested relationships. We need to shift our nomenclatural emphasis from a primary concern about the meanings of particular names to a primary concern about the naming of theoretically and operationally significant categories of clades. The remainder of this paper is an attempt to outline such a system under the view that a more precise, less ambiguous, and therefore more useful nomenclature requires different names for different clades. Although the proposed system differs from the approach adopted by Hennig, it is nevertheless based on the categories of clades that he first identified.

AN INTEGRATED SYSTEM OF CLADE NAMES

An integrated system of clade names involves some general rules for naming clades in the three categories discussed above. The general goal is to develop a system in which taxon names distinguish precisely and unambiguously between the different categories of clades, and it is easy to remember and/or infer the associations of names with particular clades, while at the same time causing minimal disruption to the existing nomenclature. The proposal itself revolves around four primary issues: (1) the one-to-one relationship between crown and total clades, (2) the greater familiarity of certain names, (3) the etymological meanings of names, and (4) the current uses of names. It is important to recognize that the development of an integrated system requires that these issues be considered simultaneously, and a consequence of doing so is that there will necessarily be compromises. That is, although certain conventions may not be optimal according to any of the four above issues considered individually, when all four issues are considered together, those conventions seem best for achieving the overall goal of an integrated system relative to similarly constrained alternatives.

In attempting to develop an integrated but minimally disruptive system of clade names, the ambiguities of the existing nomenclature turn out to be advantageous. That is, when considering whether to apply an existing name to a crown, an apomorphy, or a total clade, most of the best-known names (in particular, those used originally for distinctive groups of extant organisms) will have been applied to clades in more than one of these categories, and some will have been applied to clades in all of them, as well as to additional nodes, branches, and

apomorphies. For example, Rowe and Gauthier (1992) have documented such a diversity of previous uses for the name *Mammalia*. More generally, Hennig (1981) noted that paleontologists have tended to associate such names with key apomorphies (e.g., Lee, 1999, 2001; Anderson, 2002), though Hennig (1981) himself used those names for total clades (see also Patterson and Rosen, 1977; Ax, 1987; Patterson, 1994), and neontologists often use them, at least implicitly, for crown clades (see also Rowe, 1988; de Queiroz and Gauthier, 1992; Meier and Richter, 1992; Laurin, 2002). As a consequence of this ambiguity, selecting any one of these alternative references is to some degree consistent with the traditional use(s) of many widely known names.

Allowing etymological meanings to influence the selection of clade names does not violate the general principle of both rank-based and phylogenetic nomenclature that the primary function of a name is to provide a means of referring to a taxon—that is, as opposed to indicating its characters, relationships, or membership (e.g., *ICBN*, Preamble 1; *ICPN*, Principle 1). According to this prin-

ciple, once a name has been established, it cannot be rejected solely on the grounds that it is descriptively inaccurate. This principle does not require, however, that the etymological meanings of names be ignored prior to establishment. On the contrary, when the etymological meanings of names are congruent with the properties of the taxa to which those names refer, the names are easier to remember, thus enhancing their primary function of referring to taxa. In other words, the functions of referring to taxa and indicating characters, relationships, or membership need not be in conflict, and when they are in agreement, names are easier to remember and use.

The core of the proposed integrated approach is a standard way of naming crowns and their corresponding total clades that highlights the one-to-one relationship between those two categories of clades (Fig. 4). Apomorphy clades will also be considered; however, because their relationships to both crown and total clades are often many-to-one, it is more appropriate to develop an integrated system around crown and total clades. In describing this system, I will also consider the types of
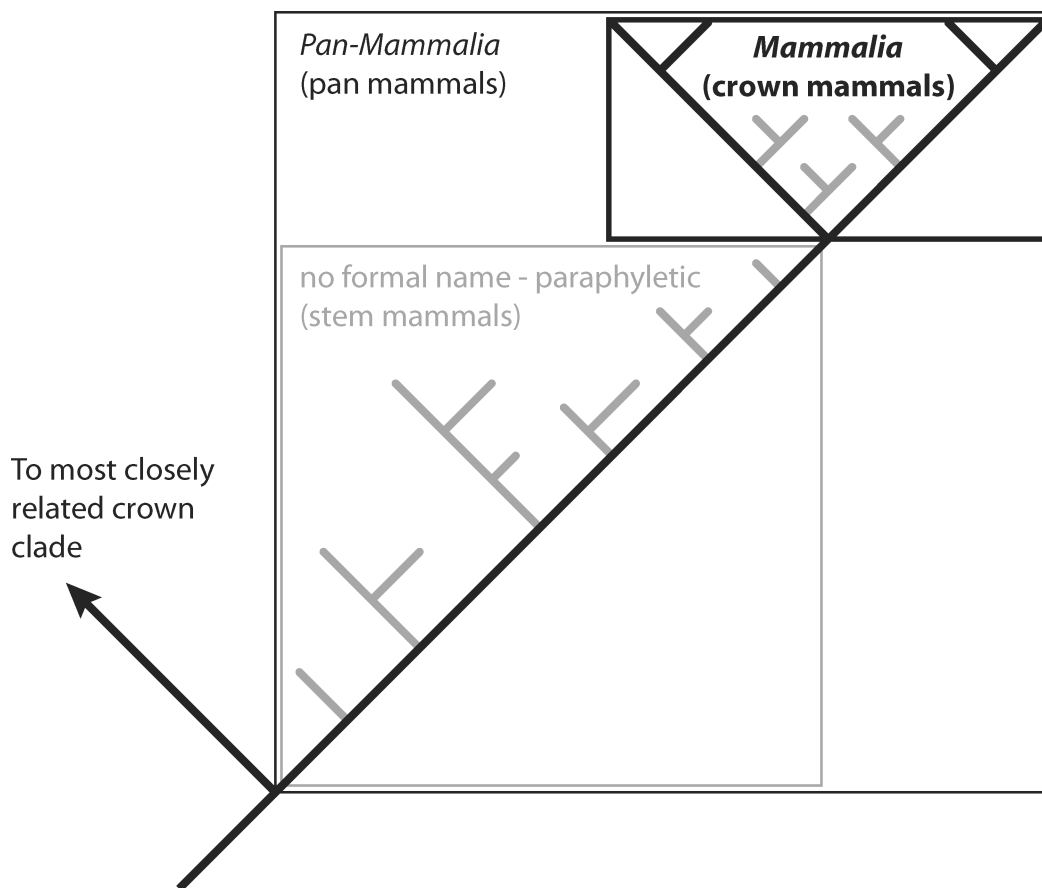
FIGURE 4. An example of the proposed approach to naming crown and total clades. *Mammalia* (crown mammals) is used for the crown clade, and *Pan-Mammalia* (pan mammals) is used for the corresponding total clade. As a paraphyletic group, the stem group does not receive a formal scientific name; however, the vernacular term "stem mammals" may be used to refer to the set of organisms that are the members of the total clade *Pan-Mammalia* but are not members of the crown clade *Mammalia*. Other names may be used for various node-based, apomorphy-based, and branch-based clades between *Pan-Mammalia* and *Mammalia*, such as *Synapsida* (apomorphy), *Therapsida*, *Cynodontia*, *Mammaliamorpha* (node), *Mammaliaformes* (node), *Mammalignatha* (apomorphy), and *Apo-Mammalia* (apomorphy).

names that are best suited etymologically for clades in the different categories.

Crown Clades

The first component of the proposed integrated system is to give crown clades the best-known names commonly (if inconsistently) used to refer to those clades (Fig. 4)—for example, names such as *Mammalia*, *Cephalopoda*, and *Angiospermae*. This approach was proposed by Gauthier (1984, 1986) and has been advocated by several subsequent authors (e.g., Gauthier et al., 1988a, b; Rowe, 1988; de Queiroz and Gauthier, 1992; Meier and Richter, 1992; Gauthier and de Queiroz, 2001; Laurin, 2002; Donoghue, 2005). The primary reason behind it is that the best known names will refer to the clades about which the most can be known. Given that many aspects of organismal biology (e.g., molecular biology, biochemistry, cell biology, genetics, embryology, physiology, endocrinology, neurobiology, behavior) are rarely preserved in fossils, and that the vast majority of biologists study extant organisms, the best-known clades will generally be crowns. Consequently, applying the best-known names to crown clades is the most effective use of those names. If biologists are to adopt a more precise nomenclature concerning the series of clades from stem to crown, then they should use the name of a crown when discussing features that have been surveyed only in extant organisms. They should not use the name of a more inclusive clade. Given that most biological features are surveyed only in extant organisms, the names of crowns should be the most widely used names, and thus it makes sense to select the names that are already most widely used for the crowns.

In addition, for many crown clades, stem group fossils are currently unknown. As a consequence, the widely known names are, in those cases, effectively used for the crowns. Thus, to achieve an integrated system in which clade names are used similarly across all taxa regardless of the quality of their stem group fossil records, the most widely known names must be applied to crown clades.

Another important reason for applying the best-known names to crowns is the one-to-one relationship that exists between crowns and total clades. One of the basic components of the proposed integrated system of clade names (as will be described further below) is that the name of a clade belonging to one of the relevant categories is based on the name of a clade belonging to another such category (the name upon which another name is based is termed the *base name*, ICPN Art. 10.3). Because of the one-to-one relationship between crown and total clades, the names of these two categories of clades are the logical choices for such a convention. That is, either the name of the crown should serve as the base name for the name of the total clade (as proposed), or vice versa. In contrast, the many-to-one relationship between apomorphies and both crowns and total clades makes the names of apomorphy clades less well suited as the base names from which the names of crowns and total clades are to be formed (see ALTERNATIVES, below). On the other hand, that relationship does not preclude forming the name of

an apomorphy clade from the name of a crown (or total) clade (see *Apomorphy Clades*, below).

An advantage of using the best-known names for crown clades is that it prevents the trivialization of those names that tends to occur as stem lineage histories becomes better known under the alternative convention of applying the best-known names to apomorphy clades. Under that alternative, the best-known names are commonly associated with key apomorphies—character states that differ markedly from antecedent conditions, at least among extant taxa—for example, the limbs of tetrapods. One of the great successes of paleontology, however, has been the discovery of intermediate fossil organisms that demonstrate the step-by-step evolution of many key apomorphies, thus decomposing those apomorphies into their component parts (Gauthier and de Queiroz, 2001).

For example, the complex character "limbs" (of extant tetrapods) consist of at least the following component apomorphies: convex proximal articular surface of the humerus, humeral deltoid and supinator processes, radius and ulna of approximately equal length, loss of lepidotrichia, distal elements arranged in rows (but still bound together ancestrally), digits (separate fingers and toes), and reduction of digit number to five (see Cloutier and Ahlberg, 1996; Shubin et al., 2006). In order to achieve a precise nomenclature, the association of the name (in this case, *Tetrapoda*) must then be restricted to one of these steps or component apomorphies. The problem is that the well-known name is thereby trivialized in the sense that it no longer refers to the key apomorphy as a whole but only to one of its less distinctive component parts. Moreover, that name is likely to become just one in a series of names along the stem lineage (J. Gauthier, personal communication, 2006), some of which mark the various stages in the assembly of the complex apomorphy, others of which are tied to different apomorphies or to nodes or branches. In contrast, when widely known names are used for crown clades, they remain associated with the complex apomorphies both when considerations are restricted to extant organisms (as they commonly are) and in the sense that members of the crown possess the complex apomorphy in its "fully assembled" state.

It should also be noted that using the best-known names for crown clades represents the element of broadest agreement across prior uses of those names concerning included species and organisms. For example, if a name such as *Tetrapoda* has been used for a series of nested clades from a total clade to its corresponding crown, then everyone will agree that members of the crown are members of *Tetrapoda*, but the same will not be true for various members of the stem group that are considered members of *Tetrapoda* under alternative definitions. Those alternative definitions represent a range in degrees of disagreement about which species are included in the taxon, with the total clade definition representing the case of maximal disagreement in that some of the extinct forms included under that definition will not be included under any of the alternative definitions (on the other hand, the total clade definition represents

the case of maximal agreement with regard to excluded species).

Although the proposal to use the best-known names for crown clades differs from Hennig's (e.g., 1969, 1981) preference for associating those names with total clades, it is nonetheless highly congruent with his position that "the modern animal kingdom and its classification are the fixed reference point for all phylogenetic research" (1981:31). Hennig's reason for associating the best-known name with the total clade was to avoid the need for two names (e.g., *Trichoptera* for the crown clade and *Trichopterodea* for the total clade; see Fig. 3) when referring fossils to groups containing their closest living relatives. In the context of the perspective adopted in this paper, his decision placed too much emphasis on assigning a fossil to a previously named taxon (e.g., *Trichoptera*) and not enough on distinguishing between the position of that fossil inside versus outside of the crown clade. Moreover, the approach advocated in this paper rejects the premise that phylogenetic research is best served by minimizing the number of named clades.

Certain types of names are particularly appropriate for crown clades. Among existing scientific names, the most appropriate ones are those derived from the vernacular names for particular kinds of organisms (e.g., *Aves*, *Arachnida*, *Plantae*, which are based on Greek and Latin vernacular names), those derived from proper names (e.g., *Lachesis*, *Nereidae*, *Iridaceae*, which are based on the names of ancient Greek deities), and those formed by combining the names of component crowns (e.g., *Galloanserae* for the clade composed of *Galliformes* plus *Anseriformes*). Part of the reason that these kinds of names are particularly appropriate for crowns is that they do not describe characters (apomorphies).

Other names that are well suited for crown clades are those that describe apomorphies present in members of the relevant crowns but are unlikely to be preserved in fossils (e.g., *Mammalia*, *Deuterostomia*, *Embryophyta*). The reason is that it will be rare to have direct evidence that these characters occur in fossil taxa outside of the crown. Names that describe characters that are commonly preserved in fossils (e.g., *Tetrapoda*, *Arthropoda*, *Spermatophyta*) may also be appropriate for crown clades if those names are much better known than the alternatives. To acknowledge the fact that names in these last two categories describe apomorphies, it may be appropriate to define them using apomorphy-modified node-based definitions rather than standard node-based definitions (see *ICPN*, Art. 9). For example, *Mammalia* could be defined not as the least inclusive clade containing *Ornithorhynchus anatinus* and *Homo sapiens* but as the least inclusive crown clade containing all extant organisms that possess mammary glands (homologous with those of *Homo sapiens*).

Total Clades

The second part of the proposal is to form the names of total clades by combining the names of their crowns with a standard affix (prefix or suffix) (Fig. 4). The prefix *Pan-* was proposed by Lauterbach (1989) and adopted by several subsequent authors (e.g., Walossek and Müller, 1990; Meier and Richter, 1992; Gauthier and de Queiroz, 2001; Joyce et al., 2004; Cantino et al., 2007). Thus, the names of the total clades of the crown clades *Aves*, *Deuterostomia*, and *Spermatophyta* would be *Pan-Aves*, *Pan-Deuterostomia*, *Pan-Spermatophyta*, respectively. This prefix is derived from the term "pan-monophylum" of Lauterbach (1989), which is another name for "total clade." The Greek word *pan* means "all," "the whole," or "every." So people who might otherwise prefer to associate the widely known names with total clades can interpret *Pan-Aves* (for example) as meaning "all avians (birds)." The intent, however, is to refer to the pan-monophylum; thus, *Pan-Aves* is intended to mean "the pan-monophylum or total clade of (the crown clade) *Aves*."

Most authors who have formed the names of total clades in this manner have capitalized the first letter of the prefix, included a hyphen between the prefix and the name of the crown, and capitalized the first letter of the name of the crown. An advantage of the second and third conventions is that they distinguish the names of total clades from other names that begin with *Pan-* (e.g., *Pantopoda*), though using both conventions is redundant. They have been adopted in the current (2006) version of the *ICPN*, where the names of total clades formed according to these conventions are termed *panclade names*. However, because some members of the Committee on Phylogenetic Nomenclature (CPN) objected to using panclade names in cases where alternative names had previously been explicitly defined as referring to total clades, the *ICPN* does not require that the names of all total clades be formed in this manner. That is, the *ICPN* has not fully adopted an integrated approach to the names of crown and total clades.

With the exception of a few panclade names that have already been proposed (e.g., in Lauterbach, 1989; Walossek and Müller, 1990; Meier and Richter, 1992; Gauthier and de Queiroz, 2001; Joyce et al., 2004; Cantino et al., 2007), most panclade names would be new. Nevertheless, adoption of the panclade name convention would not necessarily result in a great number of name changes. The reason is that the references of most names that could be argued as having traditionally been associated with total clades are sufficiently ambiguous that they could just as easily be interpreted as having been associated with nearby nodes or apomorphies. For example, while it is certainly true that use of the name *Synapsida* for the total clade of *Mammalia approximates* the historical use of that name (particularly because it was traditionally used for a paraphyletic group that did not include *Mammalia*), an equally good or perhaps even better case could be made for the historical association of *Synapsida* with the clade originating with the synapsid apomorphy—a particular type of fenestra in the temporal region of the skull and the bony arch that is formed as a consequence (*syn + apsis* = together + arch).

On the other hand, some existing names have been used unambiguously for total clades. Even prior to the

advent of explicit phylogenetic definitions, the references of a few names were clearly described as referring to total clades—for example, Goodrich's (1916) use of *Sauropsida* for the total clade of *Aves* + all extant "reptiles" and *Theropsida* for the total clade of *Mammalia*. Moreover, the proposal of methods for formulating explicit phylogenetic definitions led to a number of names being explicitly defined as referring to total clades (including *Synapsida*, see de Queiroz and Gauthier, 1992). In the interest of developing an integrated system of clade names, these names would have to be replaced by panclade names. The *ICPN* will use as a starting point a future date corresponding with the publication of the *ICPN* itself and a volume containing a number of names defined in accordance with its rules (*ICPN*, 2006). Consequently, none of the previously published definitions will be established under the *ICPN*, which will permit (but not require) the establishment of panclade names for the clades in question.

Apomorphy Clades

The third part of the proposal is that apomorphy clades are to be given names that describe their defining apomorphies. Conversely, names that describe apomorphies are to be applied to apomorphy clades, provided that those names are not sufficiently well known that they are applied to crown clades according to the first part of the proposal (see above). For example, *Synapsida* (together + arch) would be used for the clade originating with the first ancestor possessing the synapsid temporal arch configuration (homologous with that in *Cynognathus crateronotus*). Other examples of names that are appropriate for apomorphy clades are *Xiphosura* (sword + tail), which describes the long, pointed caudal spine of some chelicerate arthropods (assuming that another name, such as *Limulidae*, is used for the crown), and *Polysporangiophyta* (many + seed + case + plant), which describes the multiple sporangia of some land plants.

In some cases, a name that describes an apomorphy will be widely known and therefore used for a crown clade. If so, then the clade stemming from the ancestor in which that apomorphy originated is to be given a name formed by combining the prefix *Apo-* with the name of the crown clade (*ICPN*, Art. 10.9). As in the case for the names of total clades, the hyphen is to be retained and the first letter of the rest of the name is to be capitalized (e.g., *Apo-Mammalia*), though these specific conventions are less important than the general convention of forming the name using a standard affix. The prefix *Apo-* is not intended to mean "from" or "away," its meaning in Greek; instead, it is intended to suggest that the name refers to the clade corresponding to the origin of the apomorphy described by the rest of the name.

When the name of an apomorphy clade is formed by adding the prefix *Apo-* to the name of a crown clade, the apomorphy used to define the name should be the one described by the base name (i.e., the name of the crown clade); it should not be some other apomorphy that has been associated with that name. For example,

the name *Apo-Mammalia* should be used for the clade stemming from the first ancestor (of *Homo sapiens*, for example) to possess mammary glands. Although paleontologists have commonly associated the name *Mammalia* with a character that is more likely to be preserved in fossils, such as a jaw articulation formed by the dentary and squamosal bones (Simpson, 1960) or a petrosal promontorium (Lucas, 1992), the name *Apo-Mammalia* should not be tied to either of these apomorphies. If the clades associated with the origins of these apomorphies are to be named, they should be given names that describe (or otherwise refer to) the apomorphies in question. For example, the clade associated with the origin of the dentary-squamosal jaw articulation might be named *Mammalignatha* (mammal + jaw), whereas that associated with the origin of the petrosal promontorium might be named *Mammalauridoma* (mammal + ear + house; the inner ear is contained within the petrosal promontorium).

The prefix *Apo-* would not be combined with the names of crown clades that do not describe apomorphies. For example, the name *Apo-Aves* would not be used, because the name *Aves* does not describe an apomorphy (it is simply the Latin vernacular for birds). Although paleontologists have commonly associated the name *Aves* with particular apomorphies, such as wings/flight and feathers (reviewed by Gauthier and de Queiroz, 2001), it is once again more appropriate to use names that refer (etymologically) to the apomorphies in question. Thus, following Gauthier and de Queiroz (2001), the clade associated with the origin of wings/flight (homologous with that in *Passer domesticus*) could be named *Avialae* (bird + wings), and the clade associated with the origin of feathers could be named *Avipluma* (bird + feather).

"Vernacular" Names

In keeping with the proposal for increased precision in scientific clade names, it is useful to consider how precision might also be increased in so-called vernacular names. The names in question are often termed *vernacular* or *common names* because they are the ones most commonly used by non-scientists. The same names, however, are also used extensively by scientists, whether as strict equivalents of scientific names or as names for the sets of organisms that belong to the clades designated by the corresponding scientific names (de Queiroz, 1995). For example, a mammal is an organism that is a part or member of the clade *Mammalia*. In either case, vernacular names (clade member set names) play an important role in the scientific literature, and therefore it is useful to develop more precise ways of using those names.

Previously, researchers have used vernacular names for the same clades (or organisms thereof) to which they applied the corresponding scientific names, and just as in the case of scientific names, different authors have preferred different associations. In the case of many of the best-known names (those that were originally based on extant organisms), some authors have preferred to associate those names with crowns, others with total clades,

and still others with apomorphies. For such names, a more precise vernacular nomenclature can be developed without favoring any of these different traditional uses by treating each vernacular name (e.g., tetrapods, cephalopods, angiosperms) as a general name—that is, one that is not specifically associated with any of the three categories of clades. A precise vernacular terminology can then be achieved by adding a modifier to the general name to specify precisely which clade is the intended referent (Fig. 4).

In the case of crown clades, or the parts or members thereof, the term *crown* is to be combined with the general vernacular name; for example, crown tetrapods, crown cephalopods, crown angiosperms. Similarly, in the case of total clades, the term *pan* is to be combined with the general vernacular name; for example, pan tetrapods, pan cephalopods, pan angiosperms. Because the total clade includes the crown clade, any member of the crown clade is also a member of the total clade. Any crown tetrapod, for example, is also a pan tetrapod. Authors may wish, however, to distinguish those members of the total clade that are not members of the crown clade from the members of the crown clade. For this purpose, the term *stem* is to be combined with the general vernacular name, for example, stem tetrapods, stem cehalopods, stem angiosperms. Under this convention, the term "stem tetrapod" would refer to an organism that is a member of the total clade but not of the crown clade—that is, to a member of the tetrapod stem group. For those people are uncomfortable with the idea that some organisms that possess fins rather than limbs (i.e., "fishes") would be considered stem tetrapods, the name is not meant to imply that the organisms possess limbs (are tetrapodous) but only that they share a more recent common ancestor with the extant organisms that possess limbs than they do with any other extant organisms.

In the case of apomorphy clades, of which there may be several for a given crown-total clade pair, the most informative vernacular names are to be formed by combining the general name with a modifier describing the apomorphy in question. This is particularly true for vernacular names that do not themselves describe apomorphies (e.g., birds, bugs, oaks), including those derived from scientific names that are based on Latin and Greek vernacular names (e.g., crocodilians, arachnids, lilies). For example, in the case of birds, some of the vernacular names that might be used for the members of the clades originating with various apomorphies that arose along the stem lineage are bipedal birds, feathered birds, winged birds, carinate birds, pygostyled (short-tailed) birds, and toothless birds. Even when the vernacular name is based on a scientific name that describes an apomorphy, the apomorphy in question is often sufficiently complex that it is useful to form vernacular names by combining the general name with a modifier that describes the apomorphy of interest more specifically. For example, in the case of tetrapods (where the vernacular name is derived from the scientific name *Tetrapoda* that refers to the complex apomorphy "limbs"), some of the vernacular names that might be used for the members of the clades originating with various components of the complex apomorphy are dispectoral (referring to the free pectoral girdle) tetrapods, alepidotriciate (referring to the absence of lepidotrichia) tetrapods, digitate tetrapods, and pentadactyl tetrapods.

This proposal for increasing the precision of vernacular names is not entirely congruent with the corresponding proposal for scientific names; however, there are reasons why allowing the references of certain names to be general (and therefore ambiguous) is more appropriate for vernacular names than for scientific ones. For one thing, the same level of precision expected of scientific names is not necessarily expected of vernacular names. That is, we may be willing to allow a vernacular name to be vague and general with regard to the crown versus apomorphy versus total clade distinction, particularly in the non-scientific literature and given that the name can be made precise by adding a modifier. In contrast, allowing any scientific name to have a highly ambiguous reference seems undesirable. Moreover, given that the scientific names in question are the best known and most used, leaving those names vague and general would tend to undermine the development of a more precise scientific nomenclature in that the best known and most used names would be the very ones that would have ambiguous references.

Despite allowing certain vernacular names to be imprecise, the imprecise use of those names (i.e., without the modifier) should be avoided. In the scientific literature, it should be allowed only for cases in which it truly makes no difference which of the nested clades (crown versus apomorphy versus total clade) is the intended reference. In all other cases, the vernacular names should be used with the appropriate modifier. On the other hand, by associating the widely known scientific names with the best known and most commonly discussed clades (i.e., the crowns), even when vernacular names are used without modifiers (e.g., mammals), they will most commonly be used in a way that is consistent with their treatment as equivalents of their scientific counterparts (e.g., *Mammalia* in the sense of a crown clade).

ANTICIPATED OBJECTIONS

People form attachments to names and their uses, and for this reason nomenclatural proposals are often controversial. In this section, I will address anticipated objections to both general and specific aspects of the proposed integrated system of clade names, beginning with more general issues and ending with more specific ones.

Nomenclatural Distinctions

The most general anticipated objection to the proposed integrated system is that it is unnecessary, or even undesirable, to distinguish nomenclaturally between crown, total, and apomorphy clades. Thus, Hennig (1981:29) asserted that using different names for crown and total clades "would lead to unimaginable nomenclatorial complications—and in some cases has already done so!" (see also Patterson and Rosen, 1977:158; Patterson, 1994:65). Although it is true that two names are more

complicated than one, both names are necessary to make the relevant phylogenetic distinctions (see HENNIG'S APPROACH TO CLADE NAMES, above). The alternative favored by the aforementioned authors—using a single name for both the total clade and the crown—has a more serious nomenclatural drawback: It creates nomenclatural confusion because the reference of the name is ambiguous. Moreover, under the approach advocated here, nomenclatural complications are minimized by forming the names of total clades by adding a standard prefix to the names of their crowns (Meier and Richter, 1992), an alternative not considered by Hennig. If *n* is the number of names that must be learned under Hennig's approach, then under the approach advocated here, the number that must be learned is, in effect, not 2*n* names but only *n* names plus one prefix. Learning the meaning of a single prefix is a very small cost relative to the benefit in added information (a doubling). Finally, it should be noted that despite rejecting the use of different names for crown and total clades, Hennig still distinguished between those clades by appending an asterisk to the name when referring to the crown (Hennig, 1969, 1981, 1983). The next logical step in developing a more precise nomenclature is to incorporate the distinguishing feature (in this case, a standard prefix) into the names themselves.

Clade Categories and Rank Categories

Advocates of rank-free taxonomy, which should not confused with phylogenetic nomenclature (de Queiroz, 2006), may object to forming the names of clades in one category (e.g., total clades) by adding a standard affix to the names of clades in another category (e.g., crown clades). To such people, this practice may smack of the rank-based convention in which the names of taxa at certain ranks are formed by adding a standard suffix to the word stem of the name of an included taxon. For example, the names of zoological families (e.g., *Iguanidae*) are formed by adding the suffix *-idae* to the stem of the name of an included genus (in this example, *Iguana*).

Although there is a rough parallel between the two methods for forming names, the proposal concerning the names of clades is in no way connected to ranks, let alone based on then. Although crown clade and total clade are categories, they should not be confused with the rank categories (e.g., family and order) of the traditional taxonomic hierarchy. The former are defined based on the survival of lineages to the present time, while the latter are most commonly are defined subjectively and less commonly based on time of origin (e.g., Hennig, 1966; Avise and Johns, 1999). That the categories total clade and crown clade are not ranks should be obvious from the occurrence of both categories at numerous different levels within a single hierarchy of nested clades (e.g., *Pan-Metazoa*, *Pan-Vertebrata*, *Pan-Tetrapoda*, *Pan-Mammalia*, etc.). In contrast, under traditional nomenclature, a given rank may be used only once within a series of nested clades. For example, although all of the taxa listed in the previous example are total

clades, only one of them would be properly ranked as a subphylum.

It should also be noted that phylogenetic nomenclature does not propose to eliminate everything associated with traditional nomenclature (if that were even possible). On the contrary, phylogenetic nomenclature retains many ideas from its rank-based predecessors, including similar goals (e.g., unambiguous application of names in the context of a given taxonomic hypothesis) as well as analogous concepts (e.g., synonymy, homonymy, precedence) and mechanisms (e.g., precedence based on priority of publication; conservation to promote stability) (see de Queiroz and Cantino, 2001; *ICPN*, 2006, for more extensive lists). Most of the differences between the alternative systems stem from a single fundamental difference in their theoretical foundations—namely, whether the references of taxon names are specified in terms of phylogenetic relationships versus taxonomic ranks. In this context, the parallel between methods for forming certain kinds of names under the alternative systems can be seen as a manifestation of differences between the categories of taxa that are (explicitly or implicitly) considered significant under those systems: crown and total clades versus genera, families, etc.

Traditions

Probably the most common objection to the conventions advocated in this paper will be to the use of the most widely known names for crown clades, which conflicts with the traditions of using those names for either total clades (e.g., Hennig, 1969, 1981; Ax, 1987; Patterson, 1994) or apomorphy clades (e.g., Lee, 1999, 2001; Anderson, 2002) and the related fact that sometimes alternative names have already been proposed for the crowns (e.g., *Neornithes* rather than *Aves*; *Neotetrapoda* rather than *Tetrapoda*). Because most of the names in question have been used to refer to several different clades from the total clade to the crown (see Rowe and Gauthier, 1992), *any* restriction to one of the several different clades for which it has been used traditionally is likely to raise objections, yet a restriction of one kind or another is necessary to achieve a more precise nomenclature. The decision to use the best-known names for crown clades is based primarily on the reason that these are also the best-known clades. More detailed arguments for this decision and against alternatives are presented in the sections AN INTEGRATED SYSTEM OF CLADE NAMES (above) and ALTERNATIVES (below).

Aesthetics

Another anticipated objection is to the use of the specific prefix *Pan-* for forming the names of total clades (and/or *Apo-* for the names of certain apomorphy clades). Some people may object to the connotations of this prefix, while others may object to some of the individual names that will result from its use. For example, the name *Pan-Pan* for the total clade of chimpanzees (*Pan*) was used to criticize this proposal on the *PhyloCode* Internet discussion group. Because variation exists in human

aesthetic preferences, it is unlikely that any single pre-fix will be favored by all biologists. The choice of *Pan-* is based on the facts that, first, it is derived from the term *pan-monophylum*, which designates the category of clade that it signifies (pan-monophylum = total clade) and, second, it has been used and/or advocated by several previous authors (Lauterbach, 1989; Walossek and Muller, 1990; Meier and Richter, 1992; Gauthier and de Queiroz, 2001; Joyce et al., 2004; Cantino et al., 2007). Similarly, the choice of *Apo-* is based on its derivation from the term *apomorphy*, which designates the category of clade that it signifies. Regarding objections to individual names (e.g., *Pan-Pan*), the odd or ill-sounding names that would result from using the *Pan-* prefix would likely represent a small fraction of all total clade names, and it is unlikely that any single prefix or suffix could be found that would not create some names with similar undesirable properties. Moreover, the existence of a few such names is a small price to pay for the advantages of an integrated system (see ADVANTAGES OF AN INTEGRATED SYSTEM, below).

ALTERNATIVES

Assuming that the distinctions between crown, apomorphy, and total clades are sufficiently important to warrant nomenclatural distinction, and that there are advantages to basing the names of clades belonging to one category on those of clades belonging to another, it seems appropriate to consider alternatives to the specific proposal in which the widely known names are used for crown clades and the names of total clades (as well as those of some apomorphy clades) are formed from the names of their crowns (i.e., by adding a standard affix). There seem to be five main alternatives: (1) using the widely known names for total clades, and forming the names of crown clades from those of the corresponding total clades; (2) using the widely known names for apomorphy clades, and forming the names of both total and crown clades from those of the apomorphy clades; (3) using the widely known names for apomorphy clades only when they describe apomorphies and otherwise using them for crowns; (4) using the widely known names for apomorphy clades only when they describe apomorphies and otherwise using them for total clades; (5) leaving the widely known names ambiguous and forming the names of crown, apomorphy, and total clades from the more general names. I will next describe why each of these alternatives is less satisfactory.

Alternative 1

As noted above, Hennig (1969, 1981, 1983) and others (e.g., Patterson and Rosen, 1977; Ax, 1987, 1996–2003; Patterson, 1994) have applied the widely known names to total clades. If so, then a standard prefix or suffix could be added to the names of total clades to form the names of crown clades. One prefix that has been used previously is *Neo-*, as in *Neotetrapoda* (Gaffney, 1980). However, even authors who explicitly advocate using the best-known names for total clades seem unable to follow

this approach consistently. Thus, when they list the diagnostic apomorphies of taxa ostensibly conceptualized as total clades, those lists often include both characters whose occurrence is unknown outside of the crown (i.e., characters not normally preserved in fossils) and those that are *known* to be absent in the early members of the stem group. For example, Hennig (1983) listed as apomorphies of *Aves* a uropygial gland and reduction of the right ovary, characters that generally cannot be observed in fossils, as well as a pygostyle and the absence of an ectopterygoid, characters that are known *not* to occur in early members of the total clade (for additional examples, see Hennig, 1983; Ax, 1987, 1996–2003).

Hennig's (1981) primary concern was "recognizing groups of recent species and ...assigning ...fossils to these groups" (p. 28). The apomorphies in question do indeed allow the referral of organisms possessing them to total clades, as would any apomorphy of a clade nested within that total clade (Gauthier and de Queiroz, 2001). Those apomorphies, however, are not apomorphies of the total clade itself. Strictly speaking, the origins of total clades (as a subset of branch-based clades) have to do with lineage splitting rather than with character state transformations. Consequently, for an apomorphy to be present in the earliest members of a total clade, that apomorphy would have to have arisen and become fixed simultaneously with the lineage-splitting event in which the clade originated. Even speaking more loosely, the apomorphies that are associated with the origin of a total clade include only those that originated within its basalmost branch. They do not include transformations that originated later in the stem lineage. Treating such later-arising apomorphies as apomorphies of the total clade reflects an emphasis on assigning fossils to groups containing their living relatives rather than identifying the apomorphies of the total clade per se. Whether involving characters that are unknown outside of the crown or those known to be absent in early members of the stem, this practice is at odds with applying widely known names to total clades and instead reinforces arguments for applying those names to crowns.

Although most of the apomorphies that originated in a long stem lineage are apomorphies of neither the stem nor the crown per se, there is an important sense in which they are apomorphies of the crown: they are apomorphies of the crown clade *relative to other crowns*. In the case of apomorphies that are not preserved in fossils, attributing them to one crown relative to another is as precisely as their origins can be determined. The very existence of such characters highlights the fact that crowns are the clades about which the most is generally known, given that some species on both sides of the basal split are extant. This is precisely the reason that some authors have advocated using the best-known names for crowns. Even apomorphies that are known not to have been present in early members of the stem lineage are still apomorphies of the crown relative to other crowns. Given that so much more can generally be known about the origin of a crown clade than about that of its corresponding total clade, particularly in terms of apomorphies, using the best-known

names for total clades is probably not the most effective use of those names. Moreover, the practice of attributing the entire set of apomorphies that arose along a particular stem lineage to the clade associated with the widely known name argues for associating that name with the crown.

Alternative 2

Another common tradition is to use the widely known names for apomorphy clades (e.g., Lee, 1999, 2001; Anderson, 2002)—or for nodes or branches that approximate apomorphy clades (see Gauthier and de Queiroz, 2001 concerning the "*Archaeopteryx* node"). If so, then standard affixes could be added to the names of apomorphy clades to form the names of both crown and total clades (e.g., *Neo-* and *Pan-*). A problem with this alternative is that either the names of the total clades or those of the crowns would be cumbersome, depending on which one was to serve as the base name. For example, if the names of total clades were to be formed from those of crown clades, and *Mammalia* were to be used for an apomorphy clade, then the crown would be named *Neo-Mammalia*, and the total clade would bear the cumbersome name *Pan-Neo-Mammalia*. If the roles were reversed, then the cumbersome name would be that of the crown, *Neo-Pan-Mammalia* in this example.

Alternatively, the names of both crown and total clades could be formed from the names of apomorphy clades, rather than one from the other, in which case both names would be simpler (e.g., *Pan-Mammalia, Neo-Mammalia*). However, this alternative is also unsatisfactory because in contrast to crowns and stems, which have a one-to-one relationship, there are potentially many apomorphies for every crown–total clade pair. Thus, if the best-known name is to be associated with an apomorphy, attaching the standard prefix to that name would be based only on the fact that it is the best-known name, given that it corresponds to only one of the many apomorphies that evolved along the stem lineage. For example, if the names *Synapsida, Therapsida, Cynodontia*, and *Mammalia* were associated with different apomorphies that arose along the stem lineage of crown clade mammals, then the total clade could logically be named *Pan-Synapsida* or *Pan-Therapsida* or *Pan-Cynodontia* just as legitimately as it could be named *Pan-Mammalia*. Similarly, the crown clade could logically be named *Neo-Synapsida* or *Neo-Therapsida* or *Neo-Cynodontia* just as legitimately as it could be named *Neo-Mammalia*. In contrast, under the conventions advocated in this paper, if *Mammalia* is the name of the crown, then the name of the total clade can only be *Pan-Mammalia*.

Another problem with associating the widely known names with apomorphy clades is related to the decomposition of complex apomorphies that occurs as extinct intermediates from the stem group are discovered (see *Crown Clades* in AN INTEGRATED SYSTEM OF CLADE NAMES, above). One consequence of such discoveries is that a given name must be continually redefined to ensure that its reference is precise enough to allow the newly discovered fossils to be placed unambiguously either inside or outside of the named clade. Furthermore, as noted above, this situation results in the widely known names, which often originally marked major differences between extant forms (i.e., those belonging to mutually exclusive crown clades), becoming associated with increasingly smaller differences. Specifically, a name that was once associated with a complex apomorphy ends up being used to designate just one of the many small steps in the assembly of that apomorphy. For example, the name *Tetrapoda*, which was originally associated with the complex apomorphy "limbs" (Goodrich, 1930), has come to be associated with one of the numerous smaller components of that apomorphy, such as having the distal skeletal elements of the appendages arranged in longitudinal rows (i.e., skeletal structures resembling digits, but not necessarily separate fingers and toes; see Coates and Clack, 1990).

An alternative method for defining names as applying to crown clades preserves the connections of certain names to complex apomorphies, thus providing another advantage of using the best-known names for the crowns. An *apomorphy-modified node-based definition* is a method for attaching a name to a crown clade (i.e., a type of crown clade definition) that takes the following form: [name] = the most inclusive crown clade exhibiting character (state) M homologous with that in *A*, where *A* is an extant species or organism included in the crown clade to be named (*ICPN*, Art. 9). When such a definition is used to tie a name to a crown clade, the ambiguities related to the use of apomorphies as specifiers (e.g., Rowe and Gauthier, 1992; Bryant, 1994; Schander and Thollesson, 1995; Padian et al., 1999; Sereno, 1999; but see Gauthier and de Queiroz, 2001) are less problematical than in the case of standard apomorphy-based definitions. Because the definition ties the name to a crown clade, the critical issue with regard to specimen (or species) referral is whether that specimen is part of the specified crown clade, rather than possession of the apomorphy itself. As a consequence, even a vaguely specified apomorphy will suffice as long as it is specified precisely enough that it can be scored unambiguously in extant taxa.

For example, if the name *Tetrapoda* were to be defined as the name of the most inclusive crown clade characterized by limbs (homologous with those in *Homo sapiens*), then even if the precise meaning of "limbs" were left unspecified, fossil taxa of the tetrapod stem group (e.g., *Osteolepis, Eusthenopteron, Panderichthyes, Tiktaalik, Acanthostega, Ichthyostega*) would pose no problem for the definition. Regardless of whether these taxa are considered to possess limbs (their appendages exhibit some but not all of the derived features seen in the limbs of extant tetrapods), they appear to lie outside of the crown clade (Laurin and Reisz, 1997; Ruta et al., 2003). Even if the phylogenetic position of certain fossils were to be disputed, such a dispute would have to do with the coding and scoring of characters (including the components of the complex apomorphy) rather than whether the appendages of the fossils deserve to be considered limbs.

Thus, attaching the name *Tetrapoda* to the crown using an apomorphy-modified node-based definition allows the character "limbs" to remain a complex apomorphy, rather than becoming restricted to but one of the many stages in the assembly of that apomorphy. In short, it seems that using the best-known names for crown rather than apomorphy clades might be the best way to preserve the relationships between complex apomorphies and names that refer etymologically to those apomorphies.

Alternative 2 has the additional disadvantage of using names that do not describe apomorphies (e.g., *Aves*, *Arachnida*, *Plantae*) for apomorphy clades.

Alternative 3

This alternative is similar to the previous one, except that a widely known name would only be used for an apomorphy clade when the name itself describes (etymologically) the relevant apomorphy; otherwise, it would be used for a crown clade. For example, the name *Mammalia*, which is based on the word for (the apomorphy) mammary glands, would be used for an apomorphy clade, but the name *Aves*, which is based on a Latin vernacular name that does not describe an apomorphy, would be used for a crown clade. (Related words associated with flight, such as the English "aviation," represent later derivations from the Latin vernacular name.) This alternative has the same disadvantages as the previous one, though for fewer names, in terms of leading to cumbersome names for total clades (e.g., *Pan-Neo-Mammalia*) or an arbitrary choice regarding those names (e.g., *Pan-Synapsida* versus *Pan-Therapsida* versus *Pan-Cynodontia* versus *Pan-Mammalia*) as well as the continual need to redefine those widely known names that describe apomorphies, along with their concomitant restriction to ever smaller evolutionary transformations as intermediate fossils are discovered.

Alternative 4

This alternative is similar to the previous one, except that when the widely known name does not describe an apomorphy, it is used for the total clade rather than the crown. When the widely known name describes an apomorphy and is used for an apomorphy clade, this alternative has similar disadvantages to Alternatives 2 and 3 in terms of leading to cumbersome names, in this case for crown clades (e.g., *Neo-Pan-Mammalia*), or an arbitrary choice regarding those names (e.g., *Neo-Synapsida* versus *Neo-Therapsida* versus *Neo-Cynodontia* versus *Neo-Mammalia*). As in the case of Alternatives 2 and 3, it would also result in the continual need to redefine those widely known names that describe apomorphies, along with their concomitant restriction to ever smaller evolutionary transformations, as intermediate fossils are discovered. When the widely known name does not describe an apomorphy and is used for the total clade, this alternative has the same disadvantages as Alternative 1 in terms of using the best known name for the clade whose origins and apomorphies are the most poorly known.

Alternative 5

The last possibility that I want to consider is analogous to the proposal for vernacular names (see VERNACULAR NAMES, above). Under this alternative, the widely known names would be treated as general (ambiguous) names that are not specifically associated with clades in any of the three categories (total, apomorphy, crown). The names of clades in all three categories, at least for those cases in which the general name describes an apomorphy, would then be formed by adding standard prefixes to the general (ambiguous) names. For example, *Mammalia* could be used in a general ambiguous way for the whole set of nested clades from a particular total clade to its crown, with *Pan-Mammalia* used for the total clade, *Apo-Mammalia* for the clade associated with the origin of mammary glands, and *Neo-Mammalia* for the crown clade. For cases in which the widely known name does not describe an apomorphy, only the names of crown and total clades would be formed in this manner. For example, *Aves* could be used in a vague and general sense for any or all of the nested clades from the total clade to the crown, with *Pan-Aves* being used for the total clade and *Neo-Aves* for the crown (*Apo-Aves* would not be used because the name *Aves* does not describe an apomorphy).

This proposal has the advantage of not favoring any of the three different traditions concerning the references of the widely known names (i.e., crowns versus apomorphies versus total clades); however, it has a major disadvantage. Certain scientific names would have the undesirable property of being vague and therefore ambiguous in terms of their references. Moreover, this alternative risks defeating its own purpose in that it potentially undermines the development of a more precise and unambiguous nomenclature. The reason is that the ambiguous names would be the very ones that are the most widely known and used. If one of the main reasons for developing an integrated system of clade names is to promote nomenclatural precision and clarity, then leaving the best known and therefore the most used names with imprecise and ambiguous references seems a questionable means to achieve that end.

In sum, the five alternatives considered above all have significant disadvantages relative to the approach in which the most widely known names are used for crown clades and the names of total clades (and some apomorphy clades) are formed by adding a standard affix to the name of the crown. It may be, however, that some people simply will not accept the use of widely known names for crowns. If so, I suggest that they achieve a precise nomenclature by combining Alternative 5 with the proposal for vernacular names as follows: The widely known scientific names, like their vernacular counterparts, are to be treated as applying to whole ranges of clades from stem to crown (as in Alternative 5), with precision achieved by adding the same modifiers used for the vernacular names (which differ from the prefixes used in Alternative 5)—for example, pan *Tetrapoda*, digitate *Tetrapoda*, crown *Tetrapoda*, etc. In the scientific literature, the unmodified

versions of such names should be used *only* if that use is consistent with the author's intended meaning no matter which of the nested clades is interpreted as the reference.

ADVANTAGES OF AN INTEGRATED SYSTEM

An integrated system of clade names has several important advantages over the approach currently adopted, in which the names of corresponding crown and total clades, unlike the clades themselves, often have no obvious relationship to one another. In this section, I discuss three important advantages (in addition to increased nomenclatural precision) of the integrated system of clade names described above.

Cognitive Efficiency and Communication

The primary function of names is communication, and the integrated system of clade names discussed here facilitates communication by virtue of its cognitive efficiency. Because the names of total clades are derived from the names of the corresponding crown clades by adding a standard prefix, the number of names that must be learned for the various crown–total clade pairs is effectively reduced by half compared to an approach in which the name of the total clade is not based on that of the crown (or vice versa). Put another way, the overall number of names that must be learned or memorized (i.e., including those of intermediate clades) is reduced at least by the number of named total clades. The system is cognitively efficient because once the rule for forming the names of total clades is understood, knowing the name of a crown automatically means knowing the name of its total clade, and vice versa.

A direct benefit of this increased cognitive efficiency is that it facilitates communication, particularly among biologists who specialize on distantly related taxa. More specifically, biologists who know only the best known names within particular groups will have a much easier time understanding discussions of the origins of those groups. For example, in the absence of an integrated system, a biologist who specializes on *Vertebrata* is unlikely to know the names of the total clades of even such familiar crowns as *Insecta* and *Angiospermae*. In contrast, under an integrated system, the names of those total clades (*Pan-Insecta* and *Pan-Angiospermae*) would be immediately recognizable.

Describing Clade Origins

Another advantage of the integrated system of clade names is that it provides sets of names that are better suited to describing the origins of distinctive groups of extant organisms (Fig. 5). Traditionally, the tendency has been to emphasize a single name, whether it was used for crown, apomorphy, or total clade, which resulted in the origin of the distinctive clade being conceptualized in a more limited way than is appropriate. Lee (2001) has advocated conceptualizing the origin of a distinctive clade of extant organisms as the series of transformations that accumulated along its entire stem lineage, from the divergence of the stem lineage of the clade in question from that of its nearest living relatives (stem branch) to the basal-most divergence among the extant representatives of the clade (crown node). The origin of *Tetrapoda*, for example, is not just the evolution of whatever feature we use to draw the arbitrary and ever-narrowing line between fins and limbs; instead, it is the entire history of evolutionary transformations, not only in the appendages but in the whole organism, from the base of the stem to the crown. However, when the widely known name (and the corresponding vernacular name) is tied to but one of the many nested clades in this series, and the other significant clades either are not named at all or are given names that bear no obvious (i.e., etymological) connection to the widely known name, undue attention tends to be focused on the relatively short segment of the stem lineage associated with the widely known name. This approach tends to focus attention on the evolution of one or a few characters, thus diverting attention from the numerous other characters that generally separate distinctive groups of extant organisms from their closest living relatives.

For example, Lee (2001), despite arguing that the origin of a clade of extant organisms be conceptualized as the history of its entire stem lineage, advocated using both the well-known scientific names and their vernacular counterparts in ways that agree with subjective judgments about whether intermediate fossils ought to be considered part of the clade designated by the name in question (Fig. 5a). By adopting an approach in which those names are restricted to one of the many nested clades along the stem lineage, conceptualization of the origin of the clade will tend to emphasize the part of the stem lineage immediately subtending the clade with which the name is associated. Moreover, when the decision about which clade should be associated with the name is based on subjective judgments about the assignments of intermediate fossils, conceptualization of the clade's origin will tend to emphasize areas where knowledge is lacking—that is, gaps in the fossil record—as it clearly did in the snake example discussed by Lee. This situation will tend to obscure the fact that considerable knowledge may exist regarding changes along the stem lineage. Thus, Lee's (2001) proposal to conceptualize the origin of a distinctive extant group as the history of its entire stem lineage is at least partly undermined by his adoption of a traditional approach to naming.

In contrast, by basing the names of total clades (and in certain cases, those of apomorphy clades) on the names of the corresponding crowns, the widely known names are effectively associated with both ends (and sometimes also the middle) of the stem lineages (Fig. 5b), albeit with a prefix in the case of the total (and apomorphy) clades. Similarly, by treating the vernacular counterparts of widely know names as general names and forming the vernacular names of clades in all three categories by adding the appropriate modifiers (e.g., pan snakes, forelimbless snakes, crown snakes), those vernacular names
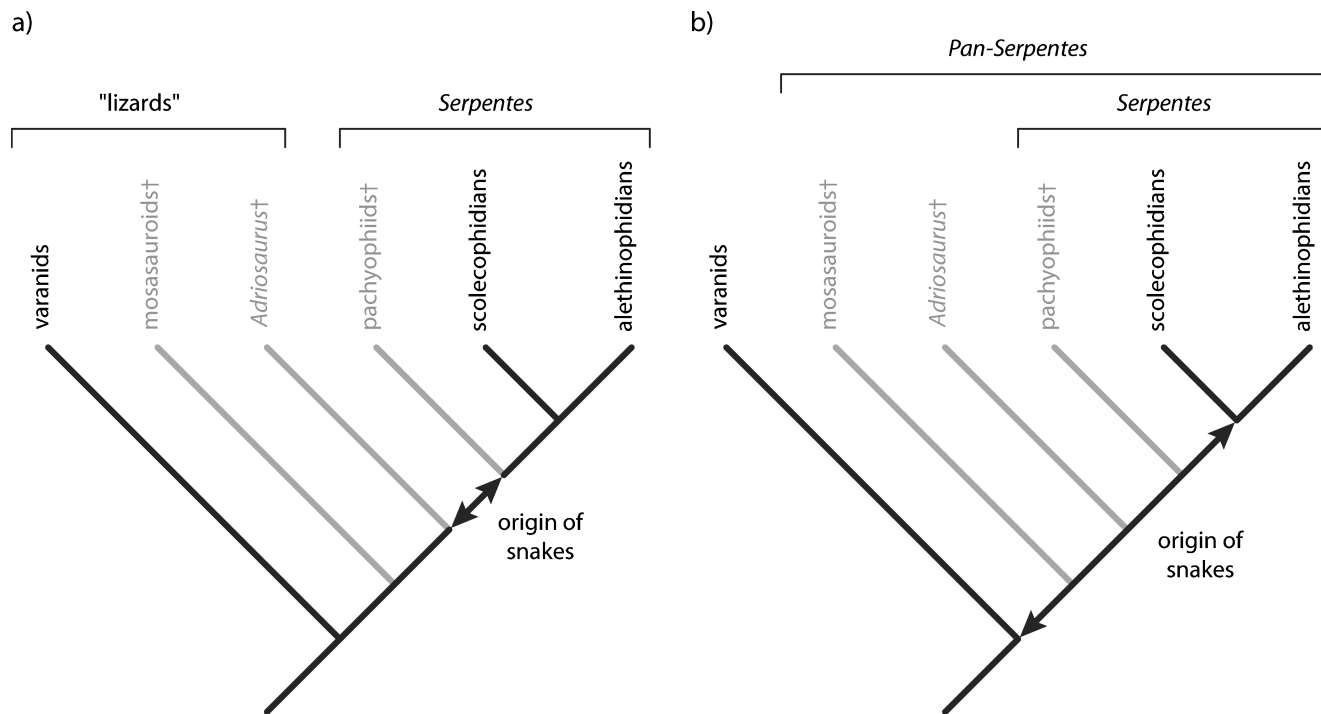
FIGURE 5. An example of the benefits of an integrated system of clade names in describing taxon origins. (a) Under traditional approaches, the name *Serpentes* (alternatively *Ophidia*) is used for a group of organisms subjectively judged to be snakes, and the origin of *Serpentes* (snakes) tends to be associated with the part of the stem lineage immediately subtending the node above which all taxa are judged to be members of *Serpentes* (branch with arrows at both ends). (b) Under the integrated system of clade names advocated in this paper, the name *Serpentes* (crown snakes) is used for the crown clade and *Pan-Serpentes* (pan snakes) is used for the total clade (along with "stem snakes" for members of the total clade that are not members of the crown), thus promoting conceptualization of the origin of *Serpentes* as being associated with the entire stem lineage (branch with arrows at both ends). Extinct lineages are indicated by grey lines; extant lineages by black ones. The argument does not depend on the correctness of the phylogeny, which is redrawn from Lee (2001).

are also associated with the entire stem lineage. These methods for forming both scientific and vernacular clade names should help to reinforce the conceptualization of the origins of distinctive groups of extant organisms as the histories of their entire stem lineages, thus discouraging the tendency to emphasize one or a few of the many evolutionary transformations that make the groups distinctive.

Emphasizing the Continuous Nature of Evolution

Yet another advantage of the integrated system of clade names is that it highlights the continuity of phylogeny, which is particularly relevant in this time of renewed political attacks on the principle of evolution (common descent). Traditional nomenclatural practices tend to obscure the continuous nature of evolution by focusing attention on but one of the many clades in a nested series, thereby playing into the hands of those who wish to cast doubt on evolution as an explanation for biological diversity. For example, if the concept embodied in the name "bird" is tied to a single character, such as flight (or a morphological correlate), then most of the organisms we know of, whether fossil or living, either possess or do not possess that character, and therefore they either are or are not to be considered birds. In

this context, it is not altogether unreasonable to claim that there are no intermediate forms between non-birds and birds—or more specifically, that *Archaeopteryx* is not an intermediate form but an unequivocal bird. Although it would be erroneous to conclude from this type of argument that the fossil record provides no evidence corroborating the principle of evolution, the simplicity of the argument works in its favor. Of potentially greater concern is the fact that the argument takes advantage of the way that scientists themselves have traditionally used taxon names.

In contrast, forming the scientific names of total (and sometimes apomorphy) clades from the names of the corresponding crowns, and forming the vernacular names of clades (or the sets of their included organisms) in all three categories from the same general name, emphasizes the nested relationships among those clades and thus the continuous nature of evolution. For example, if the name "bird" is to be treated as a general term, and distinctions are to be made among pan birds, bipedal birds, feathered birds, flying birds, short-tailed birds, toothless birds, and crown birds (to name only a few of the relevant groups), then whether a particular fossil is or is not a bird can no longer be reduced to a simple yes or no question. Because "birdness" is conceptualized as emerging along the entire stem lineage, any member of the bird

stem group is a bird in some respects but not in others—in other words, it is an intermediate form. In this context, intermediate forms are no longer restricted to a few fossils close to the origin of a particular character, such as *Archaeopteryx* and similar organisms. Instead, intermediate forms between organisms that are unequivocal birds (members of the crown) and those that are unequivocal non-birds (e.g., pan crocodilians and more distantly related taxa) are seen to be represented by a vast array of fossils, including taxa both much farther from and much closer to the crown than is *Archaeopteryx* (for taxa and phylogenies see Sereno, 1991; Pisani et al., 2002; Clarke, 2004). Although this approach to naming groups (clades) is based on the principle of evolution (common descent), it is nevertheless neutral with respect to the question of intermediate forms: if intermediates do not exist, then total and crown clades will be identical in composition. Moreover, if evolution is truly the central principle that scientists so often claim it is, then embracing that principle by adopting a system of nomenclature that highlights stem lineages is highly appropriate.

CONCLUSION

The adoption of an integrated system of clade names will undoubtedly require people to make concessions regarding the definitions of particular names and the names of particular clades. Some people will almost certainly object to using a name for a crown clade that they have previously used for a total or an apomorphy clade, or to replacing a name that they have previously used for a total clade with a name formed by adding a standard prefix to the name of its crown. Such concessions, however, are expected to involve relatively few names for each person (those in that person's particular area of taxonomic expertise) and to be distributed more or less equitably across all of biology (though those who study the stem groups of clades with good fossil records will have to make the greatest concessions). Moreover, the costs of adopting an integrated system are expected to be greatly outweighed by the benefits, including increased nomenclatural precision and cognitive efficiency as well as increased congruence between neontological and paleontological usage. Biology in general, and systematic biology in particular, can no longer afford the limitations inherent in traditional approaches to naming clades. These disciplines will be well served by adopting an integrated system of clade names that conveys clearly and efficiently the distinction as well as the relationship between crown and total clades.

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