

Points of View

Syst. Biol. 45(4):559–568, 1996

Application of Phylogenetic Taxonomy to Poorly Resolved Crown Clades: A Stem-Modified Node-Based Definition of Rodentia

ANDRÉ R. WYSS¹ AND JIN MENG^{2,3,4}

¹Department of Geological Sciences, University of California, Santa Barbara, California 93106, USA;
E-mail: wyss@geology.ucsb.edu

²Department of Vertebrate Paleontology, American Museum of Natural History, Central Park West at 79th Street,
New York, New York 10024, USA; E-mail: meng@amnh.org

³Institute of Vertebrate Paleontology and Paleoanthropology, P.O. Box 643, Beijing, China

Phylogenetic taxonomy (de Queiroz and Gauthier, 1990, 1992) entails the naming of clades, a procedure distinct from and secondary to the process of clade recognition. Current procedures for defining taxon names in terms of common ancestry were developed in the context of well-resolved (usually dichotomously branching) phylogenies. Because of the recent discovery of a fossil bearing importantly on the origin of rodents (Meng et al., 1994), we introduce here a new way of stating phylogenetic definitions for the names of clades having poorly understood internal relationships. Our concern here is the usage and definition of taxon names (which labels/names are used to identify which taxa/clades) rather than the diagnosis of taxa themselves (the manner in which the entities designated with names are themselves recognized) (de Queiroz and Gauthier, 1990, 1992).

Of the three basic forms of phylogenetic definitions previously proposed (de Queiroz and Gauthier, 1990), we emphasize here only the node-based type. In node-based phylogenetic definitions (de Queiroz and Gauthier, 1990), a taxon name refers to

the clade stemming from the immediate common ancestor of two specified descendants, e.g., the name "Mammalia" might be defined as the clade stemming from the most recent common ancestor of monotremes and therians (Rowe, 1988). Consistent with this example, the application of widely employed and familiar names (such as "mammal" or "rodent") to crown clades (clades stemming from the most recent common ancestor of sister taxa, i.e., taxa with extant representatives) is a convention being increasingly affirmed in phylogenetic taxonomy (Gauthier et al., 1988; de Queiroz and Gauthier, 1992; Bryant, 1994). Such crown-clade-restricted definitions, which are intended to standardize the usage of such commonplace names (Gauthier et al., 1988; de Queiroz and Gauthier, 1992), are thus node based in their formulation.

Recent discovery of a new early Cenozoic fossil taxon (Meng et al., 1994) prompted a consideration of relationships among various clades of eutherian mammals, including rodents, lagomorphs, and several extinct forms. This new taxon, *Tribosphenomys*, was identified as the nearest outgroup of a diverse, extant eutherian clade conventionally but not consistently termed "Rodentia" (clade needing a name, Fig. 1); a name for this clade has not pre-

⁴ Present address: Department of Biology, University of Massachusetts, Amherst, Massachusetts 01003, USA.

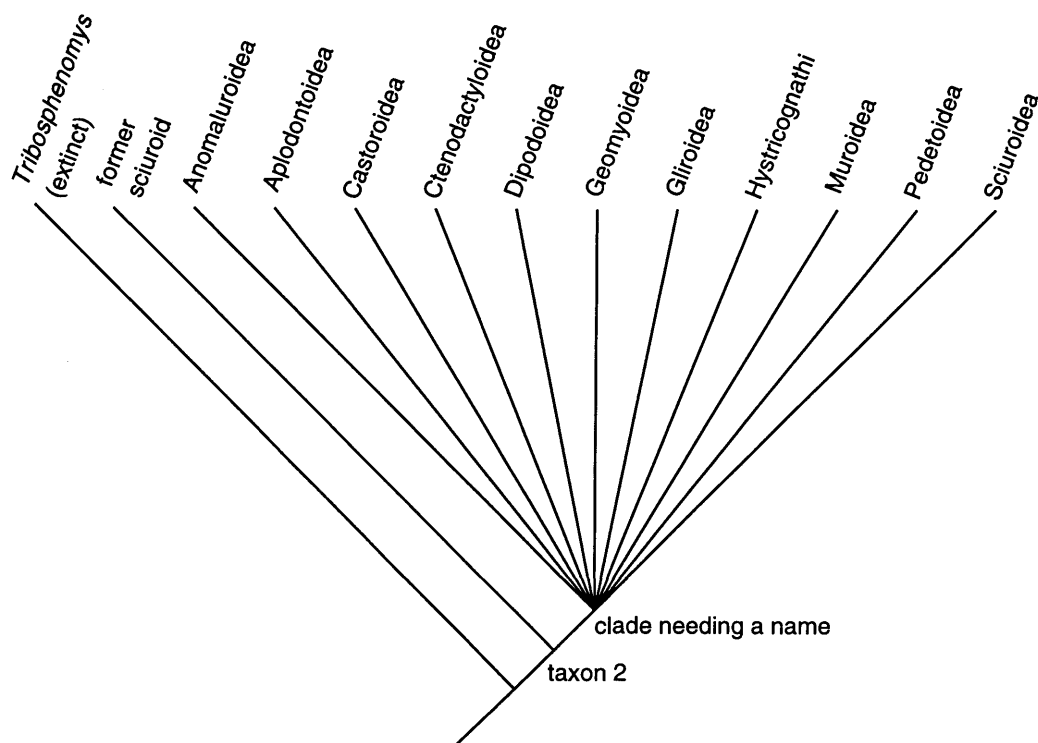


FIGURE 1. Consensus cladogram depicting poorly resolved relationships within a diverse clade of extant eutherian mammals. The polytomy (clade needing a name) is traditionally termed rodents, although no association between this name and clade has previously been formally proposed. The fossil taxon *Tribosphenomys* (Meng et al., 1994) represents the nearest known outgroup of this polytomy. "Former sciuroid" illustrates what would occur if an extant mammal formerly considered well nested within the crown polytomy actually represented a basal divergence.

viously been defined phylogenetically, however. The following considerations stem from our effort to apply a phylogenetically defined name to this crown clade, the internal relationships of which are poorly resolved. This situation contrasts with that of "Mammalia" (and most other examples around which phylogenetic taxonomic procedures were developed), where the crown clade consists of two monophyletic subcomponents (monotremes and therians) with securely established relationships. Our aim, therefore, is to devise a way of stating crown-clade-restricted definitions for the names of clades whose internal relationships are poorly understood (i.e., best represented as a basal polytomy). Ideally, the definitions of names of polytomies (1) must not be tau-

logical (e.g., the name "Rodentia" cannot be defined as the clade stemming from the most recent common ancestor of extant rodents) and (2) should make use of widely understood associated terms. An ability to withstand certain anticipated future changes in understanding of relationships among major lineages within the crown clade might be regarded as an additional worthy attribute of such a definition.

The most direct way of naming a polytomous crown clade using a node-based definition is to make reference to the common ancestor of all the maximally inclusive taxa within that clade for which there is reasonable evidence of monophyly. With reference to the nearest outgroup of *Tribosphenomys*, a phylogenetic definition might refer to the clade stemming from the

most recent common ancestor of Anomaluroidae, Aplodontoidea, Castoroidea, Ctenodactyloidea, Dipodoidea, Geomyoidea, Gliroidea, Hystricognathi, Muroidea, Pedetidae, and Sciuroidea (AACCDGGHMPS) (usages of these names follow Hartenberger, 1985); for historical reasons, a name available to be linked with this clade is "Rodentia." Although a crown-clade-based definition stated in this manner is unwieldy, de Queiroz (1994) pointed out that this is precisely the function of nominalist definitions (the substitution of a short term for a longer expression). Moreover, in referring to multiple subtaxa, this expression highlights the uncertain relationships within the clade being named.

A potential drawback to this way of stating this definition concerns its "behavior" in the face of changing views of internal relationships of the clade. For example, future studies might demonstrate some living taxon currently considered a member of the Sciuroidea to instead be sister taxon of the AACCDGGHMPS clade (Fig. 1). Unless "Sciuroidea" had been defined with explicit reference to that taxon as a descendant, this former sciuroid would be excluded from "Rodentia" by definition (not being a member of the clade stemming from the most recent common ancestor of AACCDGGHMPS). Now two crown groups would require names, the clade stemming from the most recent common ancestor of AACCDGGHMPS (clade needing a name, Fig. 1) and the clade stemming from the most recent common ancestor of the former sciuroid plus the clade including AACCDGGHMPS (taxon 2, Fig. 1). Principles of priority would dictate that the name "Rodentia" remain tied to the polytomy, necessitating a new (and hence unfamiliar) name for taxon 2. This outcome would be problematic, given that this former sciuroid had always previously been known as a rodent, and would force comparative biologists to learn a new name for a clade (taxon 2) with which they are already thoroughly familiar (albeit with different assumed internal relationships). Our aim in defining "Rodentia" is to make this name of maximum utility to the greatest

number of comparative biologists; part of that utility is derived from a correspondence between this definition and the way this name is generally used. Maximal utility requires either (1) periodic adjustments to definitions as needed after changes of relationship are established or (2) "buffering" definitions against possible future changes in phylogeny (e.g., ensuring that the precise wording of the definition of "Rodentia" preserves the relationship between this name and the clade encompassing all living taxa generally considered rodents, even if internal relationships alter).

STEM-MODIFIED NODE-BASED WAYS OF STATING A DEFINITION FOR "RODENTIA"

The above goal seems best attained through a kind of crown-clade-restricted phylogenetic definition proposed here, termed a stem-modified node-based definition (K. de Queiroz, pers. comm.). Such definitions have the effect of pointing to clades encompassing Recent members of a stem-based taxon by making reference to a particular node. Here, we explore several alternative ways of stating this kind of phylogenetic definition, using "Rodentia" as an heuristic example.

One way of linking the name "Rodentia" to the "clade needing a name" of Figure 1 is by defining "Rodentia" as the clade stemming from the most recent common ancestor of *Mus* and all Recent simplicitates more closely related to it than to any other eutherian order (sensu Simpson, 1945) (=the clade stemming from the most recent common ancestor of Recent simplicitates). A disadvantage of this alternative is the unfamiliarity of "Simplicitata" to most comparative biologists (used here as the stem-based companion to Rodentia, i.e., rodents plus all eutherians more closely related to them than to other eutherian orders: see Table 1, Fig. 2). We refer to *Mus* because of its familiarity and cosmopolitan distribution.

To avoid referring to the unfamiliar name "Simplicitata," another way of stating a stem-modified node-based definition for "Rodentia" would be to asso-

TABLE 1. A phylogenetic taxonomy of Glires (following conventions of de Queiroz and Gauthier, 1992; K. de Queiroz, pers. comm.) Unnamed clades excluded. Plain text is used for stem-based names; ALL CAPS are used for node-based names; **BOLD** is used for crown clades; † = extinct. (a) Skeleton taxonomy for neontologists. (b) Detailed taxonomy for paleontologists.

(a) Gliriformes

GLIRES

Duplicidentata

LAGOMORPHA

Ochotonidae

OCHOTONA

Leporomorpha

LEPORIDAE

Simplicidentata

RODENTIA

APLODONTOIDEA

HYSTRICOGNATHI

GLIROIDEA

GEOMYOIDEA

MUROIDEA

PEDETOIDEA

CTENODACTYLOIDEA

CASTOROIDEA

SCIUROIDEA

ANOMALUROIDEA

(b) Gliriformes

GLIRES

Duplicidentata

LAGOMORPHAMORPHA

†MIMOTONA

LAGOMORPHA

Ochotonidae

OCHOTONA

Leporomorpha

LEPORIDAE

Simplicidentata

†EURYMILUS

†MATUTINIA

†RHOMBOMYLUS

RODENTIAMORPHA

†HEOMYS

RODENTIAFORMES

†TRIBOSPHEMOMYS

RODENTIA

APLODONTOIDEA

HYSTRICOGNATHI

GLIROIDEA

GEOMYOIDEA

MUROIDEA

PEDETOIDEA

CTENODACTYLOIDEA

CASTOROIDEA

SCIUROIDEA

ANOMALUROIDEA

ciate this name with the clade stemming from the most recent common ancestor of all Recent mammals more closely related to *Mus* than to Lagomorpha (or slight variants thereof). A potential shortcoming of this way of stating the definition is its dependence on the assumption that the rodent sister group is Lagomorpha; if this were to prove incorrect, all Recent mammals more closely related to *Mus* than to lagomorphs would (by definition) be rodents. In general, however, such stem-modified node-based definitions, in which the sister taxon is specified, are potentially useful for polytomous crown clades having securely established sister taxa, e.g., "Eutheria" (the name generally associated with the next most inclusive crown clade of which rodents are unquestionably members). Given current uncertainty about relationships among major lineages of eutherian mammals (Novacek, 1992), an efficient crown-clade-restricted definition of "Eutheria" might be that this name refers to the clade stemming from the most recent common ancestor of *Homo* and all Recent mammals more closely related to it than to Marsupialia.

A final alternative way of phrasing a stem-modified node-based definition of "Rodentia" would be to attach this name to the clade stemming from the most recent common ancestor of *Mus* and all Recent mammals more closely related to it than to other eutherian orders (sensu Simpson, 1945). This version offers the following potential advantages: (1) it avoids reference to names known generally only to paleontologists (e.g., Simplicidentata); (2) it is insensitive to future changes in understanding of higher level relationships within Rodentia; (3) it would not be perturbed by possible future extinctions (due to inclusion of the geologic term "Recent") (see Lucas, 1992; Bryant, 1994); and (4) it would be stable if a new living basal member of the crown clade were discovered. Given our aim of linking the name "Rodentia" to the clade stemming from the most recent common ancestor of the extant mammals traditionally termed rodents, the main vulnerability of this definition is

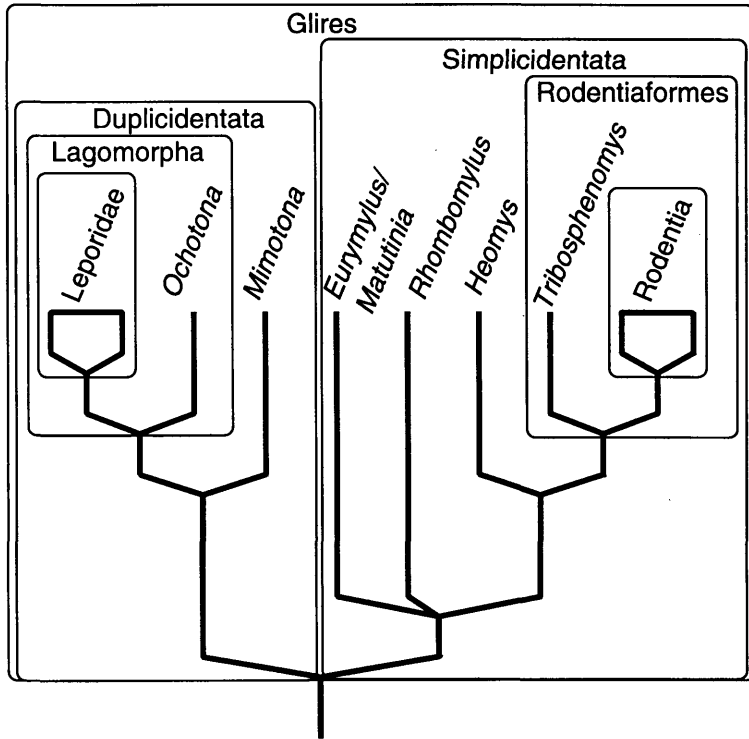


FIGURE 2. Proposed phylogenetic relationships of major groups of gliiriform eutherians (from Meng et al., 1994), with node-, stem-, and stem-modified node-based taxon names for a few of the major clades superimposed. The poorly understood internal relationships within crown clade rodents are represented by a polygon. Widely known names are applied to crown clades; less familiar names are applied to more inclusive stem- and node-based taxa. Glires is defined as the clade stemming from the most recent common ancestor of Lagomorpha and Rodentia. Simplicidentata is defined as all gliiriform eutherians sharing a more recent common ancestor with Rodentia than with Lagomorpha. Rodentiaformes is defined as the clade stemming from the most recent common ancestor of *Mus* and *Tribosphenomys*. Rodentia is defined as the clade stemming from the most recent common ancestor of *Mus* and all Recent mammals more closely related to *Mus* than to Lagomorpha or members of any other eutherian "order." Duplicidentata is defined as all gliiriform eutherians sharing a more recent common ancestor with Lagomorpha than with Rodentia. Lagomorpha is defined as the clade stemming from the most recent common ancestor of *Ochotona* and *Leporidae*. Leporidae is defined as the clade stemming from the most recent common ancestor of *Lepus* and all Recent lagomorphs more closely related to it than to *Ochotona*.

the unlikely possibility that *Mus* is not closely related to other mammals currently termed rodents (or some other profound error in our understanding of mammalian phylogeny). If either of these eventualities came to pass, the name "Rodentia" would probably require redefinition, as would much of the nomenclature of living synsids.

In short, complete definitional stability cannot be guaranteed, nor should it necessarily be sought. Trade-offs occur among the stability of definitions of well-known names of crown clades, the degree to

which these definitions retain essentialistic elements, and the practicality of their use. The optimal wording of any phylogenetic definition is particular to the taxon in question, e.g., how well its living diversity is known and how securely its internal phylogeny and relationship to sister taxa are established, and must be determined on a case-by-case basis.

The third alternative (among numerous others we do not have the space to consider here) best assures a useful degree of future stability for the name "Rodentia." Thus, we choose to define the name "Ro-

dentia" as the clade stemming from the most recent common ancestor of *Mus* and all Recent mammals more closely related to *Mus* than to Lagomorpha or members of any other eutherian "order," sensu Simpson (1945). ("Lagomorpha" is included for referential purposes, suggesting that this is the likely sister taxon of Rodentia but keeping this assumption independent of the definition.)

ARE "STANDARD" NODE-BASED DEFINITIONS STILL USEFUL?

The potential benefits of stem-modified node-based definitions might seem to call into question whether the "standard" node-based format remains the preferred way to state crown-clade-restricted phylogenetic definitions. For example, why not define "Mammalia" as the clade stemming from the most recent common ancestor of *Mus* and all Recent amniotes sharing a more recent common ancestor with it than with *Iguana*? This way of stating a definition for "Mammalia" offers a potential advantage over its standard node-based counterpart: stability in the face of newly discovered extant taxa and changing views of internal relationships of the clade.

Suppose a living *Morganucodon* were discovered and its currently favored phylogenetic position remained unchanged (i.e., still viewed as having diverged prior to the divergence between monotremes and therians). There would be two crown clades needing names, *Morganucodon* + monotremes + Theria and monotremes + Theria. A stem-modified node-based form of the definition of "Mammalia" would accommodate this discovery.

A second way in which a stem-modified node-based form of the definition of "Mammalia" would behave differently than its node-based counterpart relates to possible future changes in ideas about internal relationships. Suppose synapsids previously considered therians, e.g., flying lemurs, were shown to be the sister group of monotremes + remaining therians. Under a stem-modified node-based definition, flying lemurs would remain mammals, whereas under a node-based

definition they would not (unless "Theria" were defined with specific reference to flying lemurs, in which case "Theria" and "Mammalia" would identify the same clade and would therefore become synonyms). Stability against such profound phylogenetic perturbations is not necessarily desirable, however.

Both of these scenarios (living *Morganucodon*; flying lemurs as the sister group of other mammals) are too far fetched to abandon a simple node-based definition of "Mammalia" in favor of a stem-modified node-based definition. For other taxa, however, such as those whose living diversity is poorly documented or whose internal relationships are uncertain, these concerns might be more valid. Thus, node-based definitions are far from obsolete; they offer a clear, nominalistic, and stable means of defining crown clades, particularly when relationships within these clades are reasonably well understood. The essentialistic overtones of stem-modified node-based ways of stating definitions, plus the additional abstraction they entail, do not justify the weak insurance of stability provided for names founded on well-understood phylogenies.

Returning to our proposed definition of "Rodentia," some fossils previously called "rodents" (e.g., *Tribosphenomys*) are not members of the clade here designated by that name. We therefore anticipate resistance to our proposed definition; others may be tempted to propose more inclusive alternatives, for example defining "Rodentia" as the clade stemming from the most recent common ancestor of the crown group and *Tribosphenomys*. Linking the name "Rodentia" to some taxon other than the crown clade, however, has the unfortunate effect of forcing the minting of a new term for the crown clade (de Queiroz and Gauthier, 1990, 1992).

Our proposed crown clade definition will not end, nor is intended to end, debate about whether certain fossils are or are not "rodents" (as here defined). Rather, our proposal provides an unambiguous, concrete, and unvarying method of defining this widely used name in the first place (a

problem that has no objective biologic solution). As such, it is hoped that this definition will promote stable usage of the name "Rodentia," helping to focus attention on the important issues of character distribution and phylogenetic placement by diverting concern from the secondary issue of which clade is associated with a particular name.

OTHER POTENTIAL CRITICISMS

Restricting "Rodentia" to the Crown Group Simply Redirects Debate to the Usage of Other Names Referring to More Inclusive Clades

This concern is valid; nonetheless, many more biologists use the name "Rodentia" than use any of the more inclusive terms proposed in Table 1 and Figure 2. Paleomammalogists will continue to modify the content of the clade here designated by the name "Rodentia" and the content of more inclusive clades. They will also invent new names for as yet undiscovered clades as needed. Through all this, however, the definitions of the various names themselves would remain unchanged.

This Definition Does Not Solve the Problem of Diagnosing Rodentia

Diagnosing a taxon (documenting its existence) and naming it (definition) are separate issues (de Queiroz and Gauthier, 1990, 1992). This proposal addresses only the issue of which mammalian clade, of the myriad to choose from, should be designated by the name "Rodentia." For a diagnosis for the taxon here designated by the name "Rodentia," see the lists of apomorphic features provided by Luckett and Hartenberger (1993) or Meng et al. (1994).

Why Not Invent a New Name for the Crown Group and Use "Rodentia" for a More Inclusive Clade?

No useful purpose is served by proposing unfamiliar new names to replace those already widely understood and employed. It is preferable to stabilize familiar and widely used names, leaving paleontologists to contend with more specialized terms.

There Are Relatively Few Fossilizable Features Diagnostic of the Clade Here Given the Name "Rodentia," Making It Difficult to Establish Whether Certain Fossils "Are Rodents"

Our proposed definition may cloud the taxonomic status of certain poorly known fossils. This problem stems partly from the relatively good fossil record of near rodent outgroups. Were various fossil forms (e.g., "eurymylids," *Heomys*, *Tribosphenomys*) not known, numerous additional osteological apomorphies would be diagnostic of the taxon here termed "Rodentia." Furthermore, as de Queiroz and Gauthier (1992) noted, this difficulty refelects more a debility of fossils (their incomplete preservation) than a problem with the definition. Although it may be uncertain whether certain fossil forms traditionally termed "rodents" are in fact members of the taxon here given that name, standardization of an otherwise ever vacillating nomenclature more than compensates for this inconvenience.

Stem-Modified Node-Based Definitions Are Unnecessarily Essentialistic

A more general potential criticism of stem-modified node-based definitions is that they are overly essentialistic (de Queiroz, 1994) in seemingly placing greater logical priority on the defined term ("Rodentia") than on the entity described by the definition (a particular clade of eutherian mammals). We defer a more complete rebuttal of this point with two brief observations. First, such criticism applies to any instance where one seeks to link a widely used name with the clade biologists usually associate with that name; it is not unique to the stem-modified node-based case. Second, previously proposed forms of phylogenetic definitions were developed around well-resolved phylogenies. Tacit in these methods is the notion that identification of a clade automatically dictates a description of that system of common ancestry. Phylogenetic definitions are thus generally seen as following a two-step protocol: (1) identify a clade and (2) designate a name by which this clade is to be known.

Experience with a clade having poorly resolved internal relationships suggests that the details of clade description are not a simple mechanical outcome of clade identification, and there is usually considerable flexibility in how particular clades are described. Step 1 thus consists of two sub-steps: (1a) identify a clade and (1b) determine how best to describe that clade. Because a particular system of common ancestry can be described in numerous ways, additional criteria are needed to select among the various alternatives for use in the actual definition. The familiarity of subsidiary terms, clarity, stability of relationships, and therefore future stability of the defined name all bear on the decision of how the clade of interest is most appropriately described.

In sum, fashioning a precise clade description for use in the definition of a taxonomic name (whether in a node-based or stem-modified node-based manner) involves a logical step distinct from the initial identification of that clade; the details of this description govern the name's "behavior" given changing ideas about relationships. Presented with various equally accurate and clear ways of describing a particular clade, we see no point in deliberately ignoring considerations about the future stability of names, even though such concerns retain essentialistic elements. However, the best way to describe a clade is not necessarily the one that provides a maximally buffered definition. We suggest only that in attempting to choose among alternative ways of describing a particular clade, buffering against probable future phylogenetic changes is one factor to consider, all other qualities of those descriptions being equal. Whether "all other qualities" among our various versions of describing the clade stemming from the most recent common ancestor of Recent mammals generally termed rodents are in fact equal is open to debate. Others might think that the stem-modified node-based style of formulating definitions relies on an unsatisfactorily vague concept of the entity being named.

NOMENCLATURAL STABILITY

Much of this discussion presupposes the desirability of some degree of nomenclatural stability, yet it is also possible for definitions to be overly "buffered" (K. de Queiroz, pers. comm.). There are instances, such as following major phylogenetic rearrangements, where periodic redefinition of particular names might be preferred over unchanging, heavily buffered definitions. Consider again flying lemurs being discovered to represent the sister group to monotremes plus therians. This major phylogenetic change would be highly unanticipated, given that flying lemurs are currently placed several nodes removed from a basal position within Mammalia, and would fundamentally alter our concept of the ancestor of Recent synapsids. Definitions of "Mammalia" should not attempt to cover such a contingency. In fact, proposing a stem-modified node-based definition of "Mammalia" (which would let flying lemurs as the sister taxon to monotremes plus therians continue to be considered mammals without further intervention) might be counterproductive in that it would obscure the fact that our concept of the taxon Mammalia had undergone a fundamental shift, i.e., our ideas about its common ancestor have been altered. Such a phylogenetic change under the current node-based definition of "Mammalia" would warrant either (1) formal redefinition of "Mammalia" (e.g., as the clade stemming from the most recent common ancestor of flying lemurs, monotremes, and therians), which would call attention to this change in clade concept while preserving agreement between the definition of this term and its most commonly employed usage, or (2) the coining of a new name for the clade stemming from the most recent common ancestor of flying lemurs and Mammalia.

There is a distinction, however, between the degree of buffering provided by a stem-modified node-based definition for the name "Rodentia" and the flying lemur example just cited; this difference stems from the poorly resolved relationships

within "Rodentia." Relationships among taxa currently comprising the basal rodent polytomy are likely to become more resolved with time. Because the monophyly of many of the taxa in this polytomy is not well established, it is not inconceivable, for example, that some taxon currently considered a sciuroid might eventually prove to be the sister group of the remaining members of the clade (Fig. 1). Moreover, these new phylogenetic views might well leave our concept of this clade's most recent common ancestor unchanged (the diagnosis of taxon 2 in Fig. 1 might be no different from the one characterizing the original polytomy, the increased resolution perhaps simply reflecting discovery of a new feature diagnosing the clade needing a name [Fig. 1]). Thus, a definition might be regarded as optimally buffered if it withstands changes in ideas about internal relationships of the taxon of interest but is sensitive to those phylogenetic changes substantially altering our concept of its most recent common ancestor.

As noted by de Queiroz (1994), strict adherence to nominalist ideals in taxonomy (redefining existing names and inventing new ones freely) often conflicts with the needs of biologists, i.e., a stable and universal nomenclature. Many pragmatic issues in taxonomy such as the stability, recognizability, priority, and common usage of names or the informativeness of diagnoses of the clades designated by those names are at odds with nominalistic concerns, even crown clade restriction of commonly used names. A compromise emphasizing a moderate degree of nomenclatural stability while minimizing essentialistic underpinnings must be sought. We leave it to others to decide whether the benefits gained by our stem-modified node-based definition of "Rodentia" are worth its essentialistic price. If we have erred on the side of essentialism, then at least we hope this will initiate further discussion of how best to describe clades in the definitions of taxon names.

CONCLUSIONS

"What, if anything, is a rabbit?" (Wood, 1957) is doubtless the most memorably ti-

tled work about extinct gliriform eutherians. As elegantly discussed by de Queiroz (1994), however, scientists are interested in what names such as "rabbit" denote rather than in the names per se. More fully expressed, Wood's query would read, "What entity should be known by the word 'rabbit'?" Hence a more appropriate form for such questions is, "Among the many identified clades of eutherian mammals, which is best designated with the name 'rabbit,' 'rodent,' etc.?"

No taxa seem more appropriately or usefully designated by such widely used names than crown clades (Gauthier et al., 1988; de Queiroz and Gauthier, 1992). Stem-modified node-based methods offer an expedient means of formulating crown-clade-based definitions of names for taxa in which internal relationships are poorly understood. We hope that these proposals will hasten, at least for rodents, the close of an era where "different authors use the same name for different clades and different names for the same clade" (de Queiroz and Gauthier, 1992:465).

ACKNOWLEDGMENTS

We thank Harold Bryant for his thoughtful commentary on an early version of the manuscript. Kevin de Queiroz's enlightening suggestions greatly influenced many of the ideas presented and the form of Table 1. Four reviewers contributed materially to the final form of the manuscript. J.M. was supported by a Frick Research Fellowship from the AMNH and by NSF grant DEB-9508685, and A.R.W. was supported by NSF grant DEB-9318126.

REFERENCES

- BRYANT, H. N. 1994. Comments on the phylogenetic definition of taxon names and conventions regarding the naming of crown clades. *Syst. Biol.* 43:124-130.
- DE QUEIROZ, K. 1994. Replacement of an essentialistic perspective on taxonomic definitions as exemplified by the definition of "Mammalia." *Syst. Biol.* 43:497-510.
- DE QUEIROZ, K., AND J. GAUTHIER. 1990. Phylogeny as a central principle in taxonomy: Phylogenetic definitions of taxon names. *Syst. Biol.* 39:307-322.
- DE QUEIROZ, K., AND J. GAUTHIER. 1992. Phylogenetic taxonomy. *Annu. Rev. Ecol. Syst.* 23:449-480.
- GAUTHIER, J., A. G. KLUGE, AND T. ROWE. 1988. Amniote phylogeny and the importance of fossils. *Cladistics* 4:105-209.
- HARTENBERGER, J.-L. 1985. The order Rodentia: Major

- questions on their evolutionary origin, relationships and suprafamilial systematics. Pages 1–33 in *Evolutionary relationships among rodents* (W. P. Luckett and J.-L. Hartenberger, eds.). Plenum, New York.
- LUCAS, S. G. 1992. Extinction and the definition of the class Mammalia. *Syst. Biol.* 41:370–371.
- LUCKETT, W. P., AND J.-L. HARTENBERGER. 1993. Monophyly or polyphyly of the order Rodentia: Possible conflict between morphological and molecular interpretations. *J. Mammal. Evol.* 1:127–147.
- MENG, J., A. R. WYSS, M. R. DAWSON, AND R.-J. ZHAI. 1994. Primitive fossil rodent from Inner Mongolia and its implications for mammalian phylogeny. *Nature* 370:134–136.
- NOVACEK, M. J. 1992. Mammalian phylogeny: Shaking the tree. *Nature* 356:121–125.
- ROWE, T. 1988. Definition, diagnosis, and origin of Mammalia. *J. Vert. Paleontol.* 8:241–264.
- SIMPSON, G. G. 1945. The principles of classification and a classification of mammals. *Bull. Am. Mus. Nat. Hist.* 85:1–350.
- WOOD, A. E. 1957. What, if anything, is a rabbit? *Evolution* 11:417–427.

Received 7 September 1995; accepted 19 July 1996
Associate Editor: Brian Farrell

Syst. Biol. 45(4):568–575, 1996

Constraints on Protein Evolution and the Age of the Eubacteria/Eukaryote Split

MICHAEL M. MIYAMOTO¹ AND WALTER M. FITCH²

¹Department of Zoology, University of Florida, Gainesville, Florida 32611-8525, USA; E-mail: miyamoto@zoo.ufl.edu

²Department of Ecology and Evolutionary Biology, 321 Steinhaus Hall, University of California, Irvine, California 92717-2515, USA; E-mail: wfitch@uci.edu

Doolittle et al. (1996; see also Doolittle et al., 1989) recently concluded that modern eubacteria versus archaeobacteria and eukaryotes last shared a common ancestor (the cenancestor) ~2 billion years ago (Ga), a figure that is ~50% less than the alternative estimate of ≥ 3.5 Ga from micropaleontology and paleo geochemistry (Schopf, 1983, 1993, 1994; Schidlowski and Aharon, 1992; Nisbet and Fowler, 1996). This date of ~2 Ga was based on their molecular clock calculations with 531 protein sequences for 57 different enzymes. Their protein clocks were calibrated by the estimated divergence times from the fossil records for seven groups of vertebrates and echinoderms (Doolittle et al., 1996: table 2). In contrast, the ≥ 3.5 -Ga estimate is based on microfossils of the earliest known forms of life from this period (Schopf, 1993, 1994). These fossils show surprising structural diversity that is remarkably similar to that of modern photosynthetic cyanobacteria and their fossil representatives from the Precambrian Proterozoic (~0.6–2.1 Ga). Confirmation of this older diver-

gence time from micropaleontology comes from paleo geochemical analyses of stable isotopes in rocks and metasediments from ~3.5–3.8 Ga (Schidlowski and Aharon, 1992; Nisbet and Fowler, 1996). These paleo geochemical data strongly support an ancient separation between eubacteria and eukaryotes (≥ 3.5 –3.8 Ga), with some estimates approaching the age of the earth itself (~4.2 Ga vs. ~4.6 Ga, respectively). Resolution of the divergence time for eubacteria versus eukaryotes is of great importance because of its relevance to questions about the inevitability of life arising on earth (and possibly elsewhere [McKay et al., 1996]) and about the nature of the cenancestor and of the environment in which it evolved (Balter, 1996; Doolittle et al., 1996; Mooers and Redfield, 1996; Nisbet and Fowler, 1996).

Doolittle et al. (1996) were well aware that the accuracy of their protein clock calculations depended on the reliability of their estimates of evolutionary distances among taxa. Thus, these authors used the PAM-250 and BLOSUM-62 matrices to