

Point–Counterpoint

Syst. Biol. 53(1):68–80, 2004
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ISSN: 1063-5157 print / 1076-836X online
DOI: 10.1080/10635150490264716

Meaning of the Name Tetrapoda in the Scientific Literature: An Exchange

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This exchange stems from an on-going debate between advocates of crown clade (e.g., Gauthier et al., 1988; Rowe, 1988; Laurin, 1998) and those of apomorphy-based (e.g., Ahlberg and Clack, 1998; Lee, 1999; Padian et al., 1999; Anderson, 2001) definitions of widely used taxon names (see Table 1 for a glossary of terms). Both types of definitions have advantages: apomorphy-based definitions usually retain a composition of taxa similar to that proposed in most paleontological studies (Lee, 1999), whereas crown clade definitions correspond more closely to the usage of these names by comparative biologists working on extant taxa (de Queiroz and Gauthier, 1992; but see Bryant, 1994; Lee, 1996). Here, we concentrate on the name Tetrapoda, which has been the subject of recent discussion (Anderson, 2001, 2002; Laurin, 2002), but many of the arguments presented here could be applied to other widely used names, such as Mammalia, Aves, and Vertebrata.

Laurin (1998, 2002) adopted the crown clade definition of the name Tetrapoda (the last common ancestor of amniotes and lissamphibians, and all its descendants) proposed by Gauthier et al. (1988). Anderson (2002) objected to the crown clade definition of Tetrapoda and, following Lee (1999), advocated adoption of an apomorphy-based definition of this name (the first sarcopterygian to have possessed digits homologous with those in *Homo sapiens*, and all its descendants). The following exchange is aimed at clarifying the respective advantages of both types of definitions.

Established usage of taxon names is important because the systematic community will soon define many widely used names, and the PhyloCode (Cantino and de Queiroz, 2000) recommends, when defining a name, to disrupt current and historical usage as little as possible (Recommendations 10A, 11A). Furthermore, as stated by Anderson (2002: 824), “the PhyloCode provides mechanisms for the amendment (Article 13) or

suppression (Article 15) of definitions with priority if they should contravene long accepted usage and thus create instability in nomenclature.” These considerations are important because name definitions under the PhyloCode delimit taxa (i.e., determine their inclusiveness when applied in the context of a particular phylogenetic hypothesis), whereas definitions under traditional rank-based codes do not. Within the traditional rank-based nomenclature system, debates about the inclusiveness can go on indefinitely, whereas within the PhyloCode system, such debates will be minimized (given a particular phylogenetic hypothesis) after the International Committee on Phylogenetic Nomenclature (ICPN) determines which of two conflicting phylogenetic definitions, or names with the same definition, should be retained. The ICPN will have ruling authority (although we expect such actions will be rare if the rules of the PhyloCode are followed, similar to current practice under the International Code of Zoological Nomenclature), but it is more productive to discuss various competing definitions prior to the implementation of the PhyloCode. By ensuring that the most appropriate definition becomes established at the initiation of the PhyloCode system, much future controversy and ICPN action can be avoided.

The case of the name Tetrapoda is not unique. Similar disagreements between proponents of crown clade and apomorphy-based definitions have involved several other widely used names, such as Aves (reviewed by Gauthier and de Queiroz, 2001) and Mammalia (Rowe, 1988; Desui, 1991; Rowe and Gauthier, 1992; Wible and Hopson, 1995; Ji et al., 1999; Sidor, 2001). Thus, the current debate on the meaning of the word Tetrapoda can serve as a case study that may help with the resolution of similar disputes in the future. In this point–counterpoint, we debate four key issues related to the definition of the name Tetrapoda.

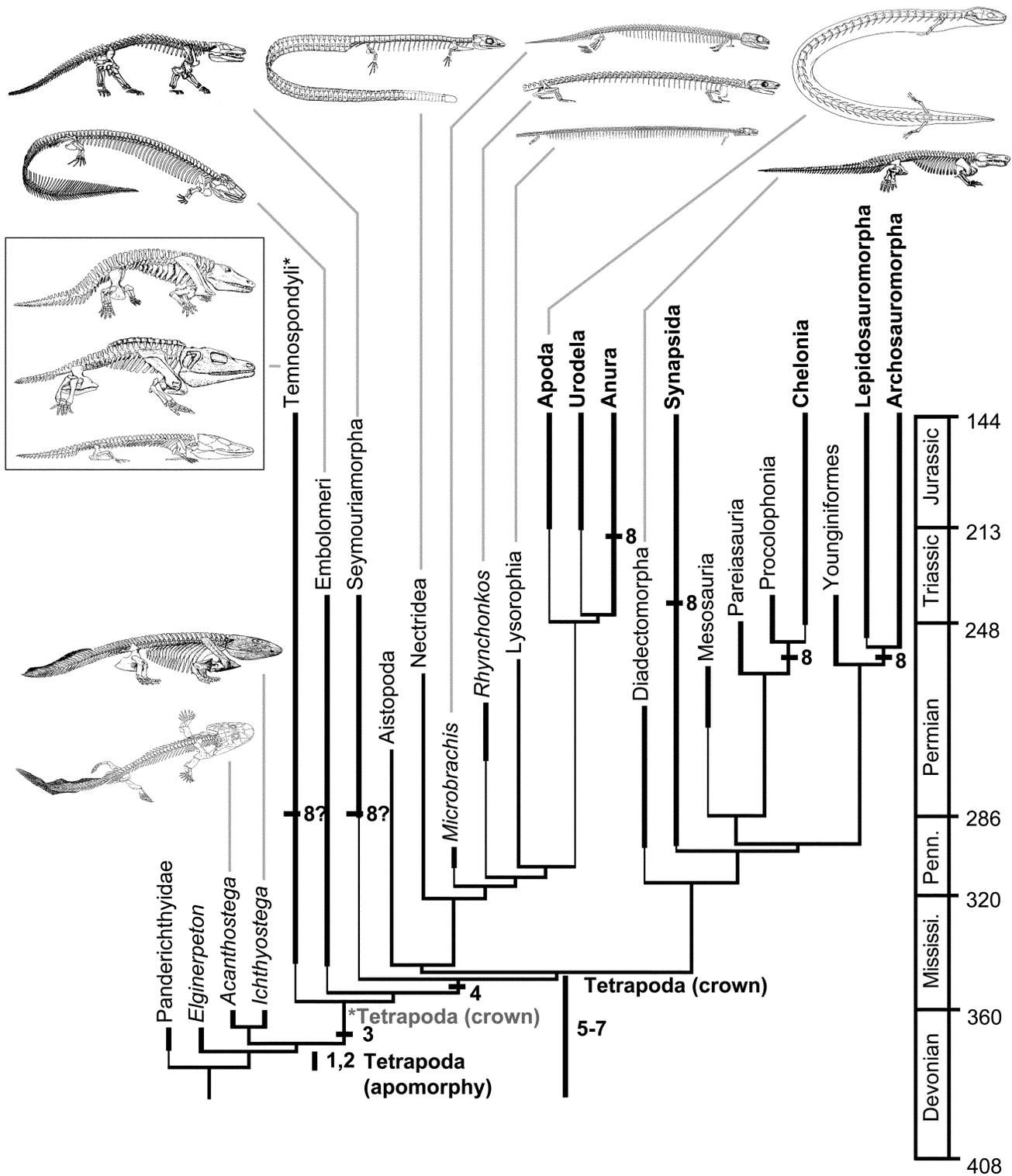


FIGURE 1. Time of appearance of various tetrapod characters that are linked to a terrestrial lifestyle. 1 = loss of the direct bony connection between the shoulder girdle and the skull (taking advantage of this newly acquired mobility of the head must have necessitated many physiological adaptations); 2 = appearance of the digits and limbs (probably accompanied by changes in posture and locomotion); 3 = loss or reduction of the internal gills; 4 = loss of the lateral-line organ, at least in the adults; 5 = complexification of the lungs and greater reliance on pulmonary respiration (the time of appearance of costal ventilation is difficult to assess and may be later than that of character 5); 6 = adaptation of the kidney to excrete most of the nitrogenous wastes, much of which was previously excreted into the water through the gills; 7 = changes in the morphology of the eye to see in air (necessitated by the lower refraction index of air) through changes in the shape of the lens and/or of the

TABLE 1. Glossary of terms used in this exchange.

| | |
|---------------------------------------|---|
| Apomorphy-based definition | A phylogenetic definition that identifies a clade's most recent common ancestor using a taxon and an apomorphy as internal specifiers. For example, Tetrapoda is the clade stemming from the first species possessing digits homologous with those in <i>Homo sapiens</i> . |
| Crown clade | A node-based clade defined using only extant taxa as internal specifiers. The example provided for the node-based definition is also a crown clade. |
| Node-based definition | A phylogenetic definition that identifies a clade's most recent ancestor using two taxa as internal specifiers. For example, Tetrapoda is the clade stemming from the most recent ancestor of <i>Rana pipiens</i> and <i>Homo sapiens</i> . |
| PhyloCode | A proposed system of nomenclature that uses clades and their relationship, not ranks, to show relative levels of inclusiveness. The current draft of the PhyloCode may be read at http://www.ohiou.edu/phylocode/ . |
| Phylogenetic definition | A statement that explicitly identifies a taxon by specifying the most recent common ancestor of that clade. A phylogenetic definition can be stem based, node based, or apomorphy based. |
| Specifier | A species, taxon, or apomorphy that anchors a name in a phylogenetic definition. |
| Stem-based definition | A phylogenetic definition that identifies a clade's most recent ancestor using an internal and an external taxon as specifiers. For example, Tetrapoda is the clade consisting of <i>Homo sapiens</i> and all species more closely related to <i>Homo sapiens</i> than to <i>Panderichthys</i> . |
| Total group | A stem-based definition that uses only extant taxa as specifiers. For example, Tetrapoda is the clade consisting of <i>Homo sapiens</i> and all taxa more closely related to <i>Homo sapiens</i> than to <i>Lepidosiren paradoxa</i> . |
| Traditional rank-based classification | A system of nomenclature that uses a series of nested ranks to show relative levels of inclusiveness. A standard identifying suffix is required for most ranks, and a system of priority establishes which name is valid within a given rank or coordinated sets of ranks. Originated by Linnaeus (and sometimes called Linnean taxonomy), current traditional rank-based classifications are regulated by three main codes: the International Code of Zoological Nomenclature, the International Code of Botanical Nomenclature, and the Bacteriological Code. |

CHARACTERS THAT HAVE TRADITIONALLY BEEN CITED AS "KEY ATTRIBUTES" FOR TETRAPODA ARE TYPICALLY RESTRICTED TO THOSE THAT FOSSILIZE WELL

LAURIN: Anderson (2002: 825, emphasis added) stated that

although there is a physiological component to other names such as *Aves* (Gauthier and de Queiroz, 2001) and *Mammalia* (Rowe, 1988) that justifies the restriction of those names to the crown, *no such component exists for Tetrapoda*. The defining feature of tetrapods is based in hard anatomy easily preservable and observable in the fossil record.

Although he did not indicate why the physiological component to the names *Aves* and *Mammalia* justifies the restriction of these names to crown groups, the reason is obvious enough: most physiological characters, as well as soft anatomical and molecular characters, can only be documented in extant forms. Thus, to decide which

definition of the name Tetrapoda best fits established usage, the key question then becomes, have any physiological (or other nonpreservable) synapomorphies been used to define the name Tetrapoda?

A survey of a dozen biology books shows that in most cases, a critical part of the definition of the name Tetrapoda (or tetrapods or even Amphibia or amphibians in the paraphyletic sense of these words) is a terrestrial lifestyle, a character that is not normally preserved. This is important because the terrestrial lifestyle is probably ancestral for crown tetrapods but not for vertebrates with digits (Coates and Clack, 1991; Laurin et al., 2000). This conclusion holds whether the phylogeny of Laurin (1998) or other phylogenies, such as those of Gauthier et al. (1988) or Ruta et al. (2003), are accepted (Fig. 1). The physiological and accompanying soft anatomical or skeletal changes associated with a terrestrial lifestyle are often difficult to date, but they probably

FIGURE 1. retina, and appearance of eyelids; 8 = acquisition of a tympanic middle ear incorporating a light stapes (accompanied by two other ossicles in mammals). Abbreviations: Mississi. = Mississippian; Penn. = Pennsylvanian. The phylogeny combines known age range data and inferred ghost lineages and follows Laurin and Reisz (1995, 1999). In many earlier phylogenies and that of Ruta et al. (2003), extant amphibians are a subgroup of Temnospondyli, but this placement does not change the sequence or timing of appearance of characters 1–8. However, this placement changes the position of the crown clade definition of the name Tetrapoda; its alternative position is indicated with an asterisk. The position of apomorphy-based Tetrapoda is also indicated. Some of the taxa in this phylogeny are (starting from the stem) *Panderichthyidae*, a poorly known group of sarcopterygians with tetrapodlike features in the skull but retaining fins; *Elginerpeton*, from the Devonian, the first vertebrate that may have had digitized limbs with fairly derived proximal limb elements, but no digits are known; *Ichthyostega* and *Acanthostega* (together *Ichthyostegalia*), the first completely known vertebrates with digitized limbs, with polydactylous manus and pes and retaining features suggestive of an obligatorily aquatic life; Temnospondyli, a very diverse assemblage of medium to large animals long considered by many workers as ancestral to modern amphibians; Aistopoda, Nectridea, *Microbrachis*, *Rhynchonkos*, and Lysorophia (together *Lepospondyli*), a very diverse assemblage of small animals, some elongate and partially to fully limbless and others short and probably fully terrestrial, considered by some workers to be ancestral to some or all modern amphibians; Apoda, Urodela, Anura (together *Lissamphibia*) are modern amphibians; Synapsida, the clade including mammals and their extinct relatives; Chelonia, the clade including turtles; Lepidosauromorpha, the clade including lizards and snakes; Archosauromorpha, the clade including crocodylians and birds. Sources of the skeletal reconstructions: *Acanthostega*, Coates (1996); *Ichthyostega*, Jarvik (1955); Temnospondyli, Gregory (1951), Williston (1910), and Watson (1958); Embolomeri, Panchen (1972); Seymouriamorpha, White (1939); Nectridea, Bossy and Milner (1998); *Microbrachis* and *Rhynchonkos*, Carroll and Gaskill (1978); Lysorophia, Wellstead (1991); Apoda, Jenkins and Walsh (1993); Diadectomorpha, Williston (1912).

did not occur simultaneously (Fig. 1), and many post-date the origin of the digits (Romer and Parsons, 1977; Laurin, 1998). The facts that the name Tetrapoda is normally closely associated with a terrestrial lifestyle and that this terrestrial lifestyle probably characterizes the crown group but not the clade of vertebrates that possesses digits argue in favor of a crown clade definition of the name Tetrapoda.

ANDERSON: I dispute that "Tetrapoda is normally closely associated with a terrestrial lifestyle" as a defining trait. In the systems predating phylogenetic nomenclature, taxa were considered classes, and membership within one class or another was decided by the possession of specific "key attributes," both primitive and derived (Ghiselin, 1966; Hull, 1976). The key attribute of Tetrapoda since its inception has been the limb with digitized manus and pes; terrestriality was invoked as the explanation for the evolution of the limb (first by Goodrich, 1930:158). Terrestriality is not reducible to a character; rather, it is a behavioral tendency with a wide range of expression that is correlated with a suite of actual characters. Systematists now draw a much clearer distinction between pattern (the characters present in a taxon) and process (the explanation for those characters) than was used in the 1930s. An advantage of an apomorphy-based definition for Tetrapoda using the feature with which it is long associated, the digitized limb, is that this definition is independent of assumptions of process (e.g., terrestriality); were it not for this independence we would not be able to test scenarios of evolution with phylogenetic hypotheses (Eldredge and Cracraft, 1979; Fisher, 1981). Additionally, as you cited above, recent fossil discoveries (Coates and Clack, 1991) indicate that the development of digitized limbs is disconnected from both terrestriality (a very exciting development in our knowledge of the early evolution of limbed vertebrates) and the origin of the crown (and thus does not represent a synapomorphy of the crown). Terrestriality is a process, not a character per se, that evolved sometime (possibly multiple times) between the acquisition of the digitized limb and the origin of the crown group. Therefore, I believe that terrestriality, although scientifically very interesting, is not relevant to the discussion at hand.

Another advantage of the apomorphy-based definition of Tetrapoda is historical continuity, a recommendation of the PhyloCode. In my previous contribution to this debate (Anderson, 2002), I placed an emphasis on historical continuity with respect to the name Tetrapoda. Taxa such as Mammalia and Aves included the key attributes of endothermy and lactation, physiological features that can only be known definitively in the crown. Thus, from the perspective of historical continuity, it could be argued that those names should be restricted to the crown, because features only known in the crown have been historically associated with the names. Tetrapoda, however, never had a key attribute that was not easily preservable in the fossil record. Its key attribute was the digitized limb (Goodrich, 1930). Therefore, from the perspective of historical continuity,

it is logical to define Tetrapoda in reference to the apomorphy of the digitized limb. Because the limb and digits are primitively ossified, one can directly observe the presence or absence of this feature in the fossil record. This character is well circumscribed and easily identified, and its homology is directly testable via phylogenetic analysis. The origin of limbs is currently the focus of much research, so the clade of limbed vertebrates requires a name for ease of communication; why not use the name that is historically strongly tied to this clade and is already in wide use with this meaning?

LAURIN: My literature survey shows that a majority of authors think that terrestriality is a defining feature of tetrapods, just as endothermy is a defining feature of mammals and birds. Of course, in all these cases, there are other defining features (hair and mammary glands for mammals; feathers, the wing, and flight for birds, the limb for tetrapods), and some of these features are behavioral (flight, lactation, terrestriality). I would not consider terrestriality to be a process or a behavioral tendency; if terrestriality created selective pressures that led to further evolution of the digitized limbs after they originated in an aquatic environment, this scenario would not be drastically different from that of endothermy creating selective pressures for the appearance and subsequent evolution of hair in mammals and feathers in birds. If you consider endothermy to be a defining feature of Aves and Mammalia, I see no reason to deny the connection between terrestriality and the name Tetrapoda.

ANDERSON: Your literature search only showed an association between tetrapods and terrestriality, which I have never denied, but terrestriality was never explicitly stated in any of your chosen texts to be a key attribute. Simply mentioning terrestrial next to tetrapod is insufficient proof of its diagnostic utility in prephylogenetic paradigms of taxonomy. How do you define terrestrial? How is terrestrial recognized in the fossil record?

Limbs, unlike terrestriality, were specifically mentioned as key attributes in the references you surveyed. For instance, Romer and Parsons (1977:63, emphasis added) stated,

Legs, the diagnostic feature of the tetrapod [the first tetrapods were identified as Ichthyostegalia on page 62], may have thus been, to begin with, only another adaptation for an aquatic life. The earliest amphibian was little more than a four-legged fish. Life on land would have been the farthest thing from its thoughts (if it had any).

Hildebrand (1982) clearly cited the limb as the key attribute; at no point in his discussion did he say that terrestriality is a key attribute of tetrapods. In the most recent edition of this text (Hildebrand and Goslow, 2001), this section has been reworded because it can no longer be argued that terrestriality is the sole explanation for tetrapody, but the limbs are still described as the key feature.

LAURIN: I agree that the first, most important cited key feature of tetrapods is the presence of two paired limbs. However, similar statements could be made for birds and feathers or the wing or for mammals and the mammary glands. There is probably a link to the

etymology of these terms. Thus, the main key character of tetrapods is the limb, but in many of the sources that I have consulted, the link between tetrapods and terrestriality was about as strong as that between endothermy and birds or mammals. As you suggest, terrestriality may be often thought of as an explanation for the presence of the limb (even though such an explanation has now been discarded), but similarly, flight has often been thought of as an explanation for the presence of endothermy in birds, as shown by the following quote (Carroll, 1988:338): "Because of the energy requirements for sustained powered flight, their body temperature and metabolic rate are higher than those of even the most advanced mammals." Thus, I still think that the association between terrestriality and tetrapods is similar to that between endothermy and birds and mammals, although it may be mentioned slightly less frequently in the literature. If there is a difference, it is in degree but not in kind.

NEONTOLOGISTS AND PALEONTOLOGISTS APPLY THE NAME TETRAPODA DIFFERENTLY

LAURIN: You argued (Anderson, 2002:825) that "for all previous uses of Tetrapoda as a taxon name, including that by Gaffney (1979), it included *Ichthyostega* and other fossils." This is obviously not the case, as an exhaustive search in the online version of Current Contents (ISI Web of Science) demonstrated. Other databases were not used to avoid getting duplicates, and the Current Contents database includes all of the life sciences, so it is probably representative of the scientific literature in which the word tetrapod can be found. A search for the word tetrapod yielded 134 references, 112 of which included the word tetrapod in a biological meaning (the other meanings described, among other things, molecular structures with four axes). The word *Ichthyostega* was present in the text of a few of these articles.

The same survey has direct bearing on your claim that to preserve continuity of usage, an apomorphy-based definition of the name Tetrapoda should be adopted. A careful reading of the abstracts indicates that in the recent literature (which reflects the current usage), the word tetrapod has been used in an ambiguous way that is neither clearly apomorphy based nor crown clade based in about half (59) of these studies (Fig. 2a). The meaning of the word tetrapod is clearly associated with a morphological concept in only 12 studies. A crown group concept was seldom unambiguously and explicitly associated with the word tetrapod (in seven abstracts), but in the studies in which the meaning of this term was not clearly stated but could be implied, it was closer to a crown clade concept in the vast majority of cases (31 of 34; see the Appendix). Examination of the entire text does not markedly change these results (Fig. 2b). This is not surprising because the literature is replete with statements about the evolution of genes, proteins, hormones, behavior, or other features of organisms that do not fossilize. Most of the authors who have discussed the evolution of such features did not apparently make

a distinction among the various meanings of the word tetrapod, and indeed most of them were probably unaware of these nomenclatural considerations, but by necessity the vast majority of such statements can only be known to apply to crown clades. Thus, if their literal (rather than intended) meaning is surveyed, most statements about tetrapods actually concern the crown group. In the following exchange, I always refer to the literal meaning.

The scientists working on nonfossilizable characters outnumber those working on the mineralized parts of hard tissues (mostly paleontologists and a few histologists). The greater part of the scientific literature dealing with any taxon is not paleontological (Figs. 2c, 2d); thus, if there are physiological (and other nonfossilizable) differences between a taxon and its closest known relative, there are advantages in restricting the name of that taxon to a crown group. Discussions of characters that cannot usually be preserved in fossils could use well-known names, rather than having to use more obscure names (when they are available) or having to explain that these characters may not have been present in the first (extinct) members of the taxon. Another solution would be to adopt new names for the crown clades and use a definition closer to the paleontological tradition for widely used names, but it seems unrealistic to expect that most physiologists, molecular biologists, and other scientists working exclusively with extant taxa would adopt the new names. This survey of the biological literature (Fig. 2; Appendix) indicates that most authors do not bother with such subtle nomenclatural considerations, as shown by the great proportion of studies in which the sense of the word tetrapod was ambiguous. The name Neotetrapoda, erected by Gaffney (1979), which coincided more or less with the crown group of tetrapods under the phylogeny that he accepted, has not been used by other workers. A search of the online Current Contents (for the period 1/1/2000 to 13/5/2003) for all variants of this name failed to yield a single reference. Other names that have been proposed for crown groups, such as Neornithes (as used by Cracraft, 1986) have not been used often. Gauthier and de Queiroz (2001:19) reported that the words Aves and birds were used in 206,238 publications listed in the *Zoological Record* for the period 1978–1999, whereas the word Neornithes was used in only seven publications for the same period. Furthermore, the adoption of new names for crown clades would not solve the problem of the numerous statements made about tetrapods, birds, mammals, amniotes, etc. (that really apply to the crown group) already in the literature; the meaning of these names cannot be retroactively changed. Whatever the proponents of Phylogenetic Nomenclature decide, the literature on extant taxa will still contain many statements about the characteristics of tetrapods, birds, and mammals, and if the definition of these names does not correspond with the crown clades, many of the statements in that literature will be inaccurate.

The meaning attributed to the word tetrapod in the paleontological literature seems to differ from that in the neontological literature. In most paleontological studies,

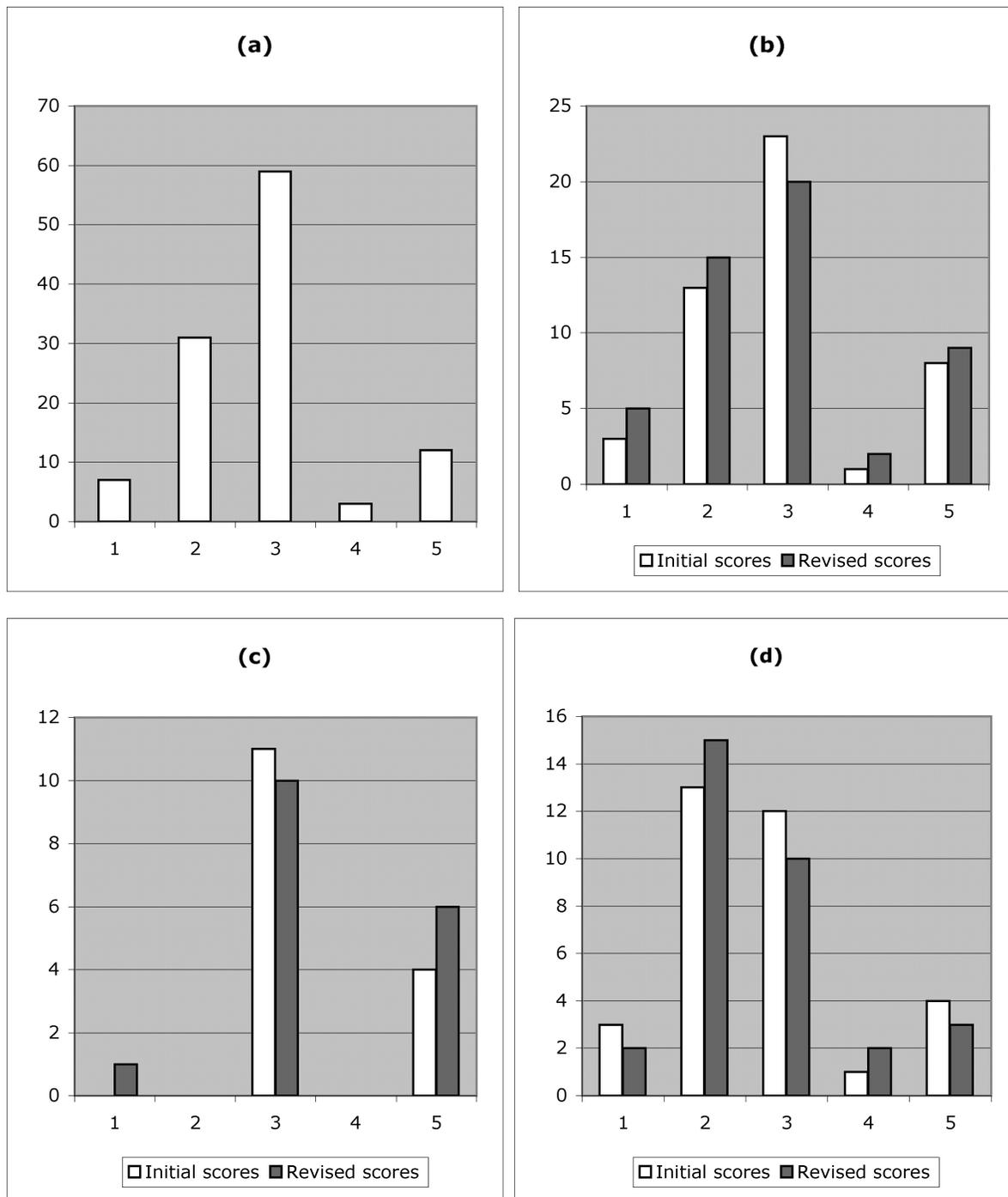


FIGURE 2. Literal meaning of the word tetrapod in the scientific literature. These articles (covering the period January 1, 2000 to August 5, 2002) included the word tetrapod in either the title, key words, or abstract. The x-axis represents the various meanings of the word tetrapod: 1 = crown group, when a statement made in the abstract about tetrapods clearly referred to the crown group; 2 = somewhat ambiguous but closest to crown group, when the author did not seem to refer explicitly to either concept but when the text focused on aspects of organisms that can only be documented in extant taxa, such as genes, proteins, etc.; 3 = ambiguous, when no clue in the text indicated to which concept of tetrapod the author referred; 4 = somewhat ambiguous, but closest to morphological, whenever a connection between the presence of limbs and the word tetrapods seemed implied or when taxa called tetrapods probably do not belong to the crown group; 5 = morphological, when a statement made about tetrapods referred to the first limbed vertebrates or seemed to imply that all limbed vertebrates were tetrapods. The y-axis indicates the number of articles. (a) Based on abstracts of 134 articles indexed in the online version of Current Contents. (b) Based on a sample of 51 (the first articles on the exhaustive list that were available in the library of the Université Paris 7, the central library of the Muséum National d'Histoire Naturelle, or the personal library of M.L.) of the 134 articles indexed in the online version of Current Contents. The initial score is based only on the abstract of these papers, whereas the revised score is based on the full text. (c) Based on 17 paleontological studies (all the paleontological studies included in sample b). Categories as in a and b. (d) Based on 33 neontological studies (all the neontological studies included in sample b).

a morphological concept of the word tetrapod is clearly dominant (Fig. 2c), but in neontological studies, it is the crown clade concept that most often corresponds to established usage (Fig. 2d). This difference has not often been discussed (Lee, 1996) because most neontologists do not appear to be concerned with the exact meaning of the word tetrapod and they probably think that early limbed stem tetrapods such as *Ichthyostega* are tetrapods, but the way that they use the name tetrapod is inconsistent with this position, as de Queiroz and Gauthier (1992:468) pointed out. Thus, although the apomorphy-based concept that you advocate appears to be widespread in paleontology, it does not appear to prevail in most biological fields. This conclusion is reached if literal, rather than intended, usage of the word tetrapod is studied (as is done here). Most neontologists seem to accept an apomorphy-based definition of the name Tetrapoda, but their use of this name is inconsistent with such a definition and reflects the widespread use of fuzzy tree-thinking (the use of a single name for more than one clade, usually two or more nested clades).

ANDERSON: First, I am not advocating the use of a term in a paleontological sense because all biologists used Tetrapoda as referring to limbed vertebrates historically; Goodrich himself, who coined the name, was a neontologist. Second, it is not just neontologists who did not adopt Gaffney's Neotetrapoda. Third, you criticize my statement about the use of Tetrapoda as a taxon name, but your entire study of current usage in biology is based upon a search of the vernacular word and not the technical nomen. It is little wonder that the vast majority of times that tetrapod is used in the literature is ambiguous because there is little dispute over what the vernacular term means—limbed vertebrates—so why should these authors define this in the abstract (let alone specifically mention *Ichthyostega*)? A search of the ISI Web of Science (formerly Current Contents) for the nomen Tetrapoda using the same parameters as your review yielded a total of seven citations. Two of these are my papers (Anderson, 2001, 2002), and one is yours (Laurin, 2002), so the reader can probably infer how the term was used given our current discussion. In one article, Tetrapoda was used parenthetically in the title of a specimen description (Reisz and Sutherland, 2001) and was not discussed further (ambiguous usage). The remaining three citations are molecular studies; however, the authors' intended meaning can be understood from the text. Lovsin et al. (2001) dated the origin of Tetrapoda to 400 million years ago (MYA), in the Lower Devonian, which refers to the timing of the emergence of limbs and not the crown. Sanchez et al. (2001) equated Tetrapoda to a larger group including amphibians, reptiles and mammals rather than solely the crown. Mezhzherin (2002) referred to superclass Tetrapoda in the traditional sense. Searches for Tetrapoda support my previous statement.

Nonetheless, you raised some ancillary issues that should be considered further. As you admit, "most neontologists . . . probably think that early limbed stem tetrapods such as *Ichthyostega* are tetrapods." I agree with

this statement, and it is borne out by my search of the use of Tetrapoda. However, to improve upon this speculation, I surveyed the corresponding authors of the 51 studies you examined in detail in your tetrapod search. After multiple studies by the same author were combined, I garnered a total of 46 currently valid e-mail addresses, to which I sent my survey of what the authors think is meant by tetrapod and Tetrapoda.

To date, I have 21 respondents: nine people who work exclusively on extant organisms, five who work exclusively on extinct organisms, two who work on both but primarily extant organisms, and five who work on both but primarily extinct organisms. The considerable overlap in taxa of interest demonstrates the difficulty of partitioning the use of names by living status (extinct or extant); many biologists work on both living and fossil taxa and presumably are sensitive to issues related to the study of either group. The vast majority of respondents (16/21) mean limbed vertebrates when they use the name tetrapod, and 15/21 mean limbed vertebrate when they use the name Tetrapoda. Only a few respondents (4/21) use tetrapod and Tetrapoda in reference to the crown group; only two more than the number of respondents who use Tetrapoda as a total group (2/21). Three of the respondents using the crown group meaning of Tetrapoda work exclusively on extant organisms, and one works primarily on extinct organisms (yourself). Most respondents (12/21; three paleontologists, five neontologists, two mostly paleontologists, two mostly neontologists) believe it is very important that Tetrapoda and tetrapod refer to the same thing, but some (3/21; one paleontologist, one neontologist, and one mostly paleontologist) think it is important only in certain contexts, and others (6/21; three neontologists, three mostly paleontologists) do not think it matters at all. This survey demonstrates that a wide majority of workers mean limbed vertebrates when they use the term tetrapod regardless of the living status of taxa studied, and a slight (but not significant) majority believes it is important that the vernacular term equate with the technical term. The ambiguous usage you found in the literature probably actually reflects a consensus among biologists of what the name means—why should they restate the obvious?

However, you intended to survey how people literally used the term, regardless of what the author intended. It is your contention, if I understand you correctly, that studies of "genes, proteins, hormones, behavior, or other features of organisms that do not fossilize" implicitly refer to the crown because the states of these characters cannot be known in fossil taxa. This view assumes that features currently unavailable for study in fossil taxa will always remain so, which is probably not correct. Cases of extraordinary preservation of ancient biomolecules have already been reported (e.g., Schweitzer et al., 1997a, 1997b). Second, the authors of the papers you searched are obviously not extending the results from, say, molecular studies to fossil taxa or they would probably more frequently use the taxon name Tetrapoda. They do frequently extrapolate their results to fossil taxa displaying

the gross feature of interest without any conceptual problem, but it is clear that their discussion is inferential or speculative. That they do not specify “extant tetrapod” when they report their results (although some do) is not surprising because it cannot be anything else; it is a trivial distinction given the context, and a good editor would recommend excising “extant.”

The more important point to make in considering your argument is the following, first offered by Lee (1996:1108), “it cannot be assumed that generalizations based upon extant forms apply only to crown clades.” Lee offered the example of diadectomorphs, which are not included in crown Amniota but nonetheless show indirect evidence for having an amniotic egg. As another two examples, there has been much recent research into the question of endothermy in nonavian theropods and nonmammalian “therapsids.” Undoubtedly, the patterns seen in gene expression related to limb development reach far stemward from crown tetrapods, but exactly how far cannot be determined; regardless, this fact makes these gene expression patterns synplesiomorphies of the crown node. I do not believe that we should decide to radically change the widely accepted meaning of an established name because the distribution of certain shared primitive traits of the crown can only be known in the crown.

An apomorphy-based Tetrapoda, however, has a synapomorphy (with explicitly stated homology) to anchor the name. The presence or absence of the apomorphy can be directly observed in the fossil record, so it is less “fuzzy” than relying on nonfossilizable features present in at least the crown but also at some undetermined distance below the crown; it is precise. Furthermore, an apomorphy-based definition for Tetrapoda is fully consistent with historical and current use of both the technical and vernacular term. Contrary to your allegation above, it is a crown clade rather than an apomorphy-based definition for Tetrapoda that will lead to widespread inaccuracy interpreting the literature of the past 70 years and to widespread confusion in communication; most biologists currently mean the same thing when they use tetrapod or Tetrapoda: limbed vertebrates.

LAURIN: You began your remarks by emphasizing that I made a search on the vernacular word tetrapod rather than on the formal name Tetrapoda and concluded them by stating that biologists give the same meaning to both words. I agree with your last argument; communication in biological sciences would be difficult if we could no longer consider vertebrates as synonymous with Vertebrata or annelids as synonymous with Annelida, to give but two examples. I also agree that most biologists mean limbed vertebrates when they use the word tetrapod, but unfortunately, that is not what they literally say; in most cases, they describe the crown while stating that they describe limbed tetrapods. This contradiction simply proves that fuzzy tree-thinking is very widespread in biology.

The dangers of fuzzy tree-thinking are shown by your interpretations of the meaning of the word Tetrapoda

in the literature, because in my opinion the intended meaning of the name Tetrapoda in at least some of the seven references that you found in the ISI Web of Science is far from clear. However, the literal meaning is clearly not limbed vertebrates, which shows how ambiguous or variable the meaning of the name Tetrapoda is in this literature. For example, you concluded that Lovsin et al. (2001) referred to the origin of the limb to define the name Tetrapoda. However, the date given for the origin of this taxon (400 MYA) is in the Lower Devonian, and it precedes by more than 30 million years the oldest known fossil limbs (<367 MYA), from the Upper Devonian. The date used by Lovsin et al. (2001:2220) was taken from (and apparently rounded off) the article by Feng et al. (1997), who reported that 405 MYA is the tetrapod/fish divergence date. Feng et al. (1997) did not mention what they meant by “fish,” but they explained that this date was taken from the fossil record. Because 405 MYA coincides with the beginning of the Devonian, presumably this event refers to the divergence between dipnomorphs (a group that includes lungfishes) and tetrapodomorphs (a group that includes tetrapods) because the oldest members of this clade date from that time. Thus, Lovsin et al. (2001) used a total (stem-based) concept of Tetrapoda, not an apomorphy-based concept. Mezhzherin (2002) referred to Tetrapoda without defining it, but he clearly was describing the crown, because all his data were from extant taxa. Sanchez et al. (2001) consistently called Tetrapoda “land vertebrates” and effectively described the crown, but the limb was not mentioned. Thus, in my opinion, statements about Tetrapoda in the papers that you mention do not appear to describe the clade of limbed vertebrates. This brief discussion also shows how difficult it is, in many cases, to know which clade is actually described under the name tetrapod or Tetrapoda in the literature.

I do not assume that features currently unavailable for study in fossil taxa will always remain so. I simply mean that statements that are made about such characters that are said to be tetrapod features apply to the crown because in the vast majority of cases the data on which such statements are based are restricted to the crown. The discovery that a character applies to a more inclusive clade than the crown would not falsify a statement that tetrapods (even if restricted to the crown) possess this character (the character would simply not be unique to tetrapods). The reverse situation is more problematic because if a character were stated to be characteristic of tetrapods (defined as limbed vertebrates) and was later discovered to be restricted to a part of that clade (the crown, for instance), the statement would be falsified. This distinction was not widely appreciated in previous studies. For instance, Lee (1996:1106) argued that “only convention makes us apply these non-osteological synapomorphies to the crown clade—the least inclusive level at which these traits might have arisen,” and Sereno (1999) proposed a similar argument. I agree that crown clades cannot be viewed as better corroborated than more inclusive clades simply because their diagnosis often includes nonosteological synapomorphies.

However, if we wish to maximize veracity of the scientific literature, there is an advantage to using well-known names for crown clades because many statements in the neontological literature can be tested for crown clades but cannot be tested for more inclusive clades. Thus, these statements are scientific in the context of crown clades but not in the context of larger clades. Worse, if some of these statements that cannot be currently tested were to become testable later (through development of new techniques or discovery of exceptionally preserved fossils) as you argue, many of them could turn out to be false if widely used names were attributed to clades more inclusive than the corresponding crown group. The presence of unpreserved characters in extinct taxa can be inferred, but inference is necessarily less certain than observation. You gave the example of the presence of an amniotic egg in diadectomorphs, inferred by Lee (1996) and further documented by Lee and Spencer (1997); however, Laurin and Reisz (1999:1250) disagreed with this interpretation.

IS FUZZY TREE-THINKING A BASIS FOR ATTACHING THE NAME TETRAPODA TO THE CROWN CLADE?

ANDERSON: Do these papers (Doolittle et al., 1990; Feng et al., 1997; Lovsin et al., 2001) demonstrate fuzzy tree-thinking, as you contend? The source of the data, Benton (1990), used Tetrapoda in a morphological (and phylogenetic) sense, even explicitly citing *Ichthyostega*. Doolittle et al. (1990) specified “fish-tetrapod” rather than Benton’s intended Dipnoi-Tetrapoda but appear not to have changed the meaning of the name; the statements are equivalent, specifying the same node. One cannot charge Doolittle et al. with fuzzy tree-thinking in this instance. Feng et al. (1997) used the same terms and divergence dates as did Doolittle et al., except for using 405 MYA (from the estimate of Benton, 1990, cited by Doolittle et al., 1990, which is an earlier version of Feng et al., 1997) rather than 400 MYA, which suggests that it was either a typographical error (not committed by Lovsin et al., 2001) or that they considered the sister taxon to tetrapods to be actinistians rather than dipnoans for some unmentioned reason. Regardless, this confusion does not stem from their specifying a clade different from that implied by Benton when using the word tetrapod and thus is not due to fuzzy tree-thinking, as you defined it.

With this new information, the usage of Lovsin et al. (2001) does become more ambiguous. Did they simply misinterpret the “fish-tetrapod” split of Feng et al. (1997) to mean “origin of Tetrapoda,” or were they really using Tetrapoda in a total group sense as you contend? The latter case seems unlikely when one considers that the total group definition has received little support in the literature. The two respondents in my survey who favor a total group definition are from the same lab and are the only workers I am familiar with who have followed the lead of Patterson (1993).

LAURIN: You are only interested in what the authors intended to describe, and I agree with you that in

most cases, this is the apomorphy-based name. However, what they actually described varies from a total group (tetrapodomorphs) to a crown group and is sometimes (usually in paleontological studies) the apomorphy-based group. Most authors use the words tetrapods and Tetrapoda indiscriminately for these three clades (total group, apomorphy-based clade, and crown clade), so that in many cases it is not clear which of these three clades they describe.

ANDERSON: I believe that precision in communication of biological ideas can be improved, but I disagree that restricting the well-known name to the crown is the best way to achieve this precision. Falsification is at the heart of science—we gain new knowledge, we test our ideas against it, and we adjust accordingly. From this discussion, it seems that one of the critical issues is accommodating current uncertainty in character coding. There are gaps throughout the Tree of Life where critical taxa are unavailable for molecular study; after all, most life forms on the tree are extinct. Some gaps are large, e.g., there is still no consensus on the question of the origin of turtles because of a large gap in the fossil record at the turtle stem. Similar to turtles, there is a large concentration of extinct taxa at the tetrapod stem. These taxa are unavailable for molecular testing, and so, you argue, we should restrict the name Tetrapoda to the crown lest we attribute a feature to tetrapods that later is found to be restricted to a less inclusive group. However, in the discussion of apomorphy-based definitions and key attributes, it seems to be forgotten that we do not name taxa by the characters they possess. I advocate using an anatomical feature but only to specify the particular ancestor that bears the name. The distribution of characters, preservable or not in the fossil record, will vary with each phylogenetic analysis, so it does not matter if new observations might render previous statements of character distribution “inaccurate,” because this happens all of the time.

LAURIN: It is true that the time of appearance of characters changes occasionally as discoveries are made, but that is not the problem. Stating that the crown possesses some features, even though the features may have appeared before the crown, is a correct statement. But stating that an apomorphy-based taxon possesses features that may be restricted to the crown is unwarranted and may be mistaken. Perhaps this is simply a difference of attitude between us; you consider that some mistakes in statements of characters of clades are unavoidable, whereas I try to minimize the number of such erroneous statements.

ANDERSON: Your argument presents a false dichotomy. The “mistakes” you refer to are unavoidable no matter which definition of Tetrapoda is accepted. Most fossil taxa at the stem probably will never provide DNA sequences, but most crown taxa have not been directly sampled either. If future work shows that a terminal subclade does not have a particular feature that previously had been attributed to the crown, then the previous statement is rendered “inaccurate” and requires a special ad hoc appeal to homoplasy. Above the crown

or below the crown, our knowledge of character evolution will change, requiring the revision of our earlier thinking.

Do neontologists intentionally attribute the distribution of nonpreservable features to all limbed vertebrates? In only three instances during the 2000–2002 period of your literature survey (of a total of 112 where the term tetrapod was used in a biological sense) did a molecular study even use the name Tetrapoda (the issue of how it was used aside); in all other cases (109/112) the vernacular word tetrapod was used, suggesting a reluctance to attribute described features to the entire clade (which has not been sampled). In the course of this discussion it has become apparent that there is a difference in how workers view vernacular words. In the case of some, such as yourself, there is a strict one-to-one relationship between informal and formal nomina so that the vernacular is used mostly to avoid monotony in technical writing. This is fine for more obscure names or names only used in phylogenetic taxonomy, but well-known names have the added burden of historical usage and some, such as tetrapod, have passed into the lay lexicon. This is presumably why the PhyloCode specifically mentions historical consistency—it avoids confusion in these instances by preventing radical changes in meaning. Your examples of the words vertebrate and annelid are appropriate because the phylogenetic definitions for Vertebrata and Annelida are consistent with historical usage. No organism that was long considered a vertebrate has been excluded from Vertebrata as defined phylogenetically, so there is no disconnect between the technical and lay use of vertebrate, unlike the situation created by adoption of a crown clade definition of Tetrapoda. I agree with you that one should be precise in biological communication and avoid using overly informal terms unless the context is clear; however, not all workers (9 vs. 12 of 21) surveyed think this is essential, so future discussion on this subject with the wider biological community might be warranted.

LAURIN: Even statements made about the crown can be falsified, but such statements usually represent the most parsimonious interpretation of character distribution. By contrast, most statements about (apomorphy-based) tetrapods in the soft anatomical, molecular, and physiological literature are not justified by parsimony. Furthermore, a statement justified by parsimony and data on character distribution in both main subgroups of a clade is far less likely to be falsified than is a statement based on a subset of optimizations and character distributions that does not span the two main subgroups of a clade. Thus, although both types of statements can be falsified, the proportion of erroneous statements will be far greater for an apomorphy-based Tetrapoda than for those for a crown clade Tetrapoda.

I do not think that the prevailing use of the vernacular term tetrapod in the neontological literature indicates reluctance to ascribe features to the entire clade. If this were so, the authors would presumably have indicated that their findings apply to most or some tetrapods, but such statements are rare. I believe that the use of vernac-

ular is preferred by scientists whose primary research focus is not systematics.

CONCLUSION: WHAT SHOULD BE THE DEFINITION OF TETRAPODA?

LAURIN: There is nomenclatural fuzziness in the current literature because at least four types of characters are called tetrapod characters: those that have appeared early on the stem before the limb appeared, those (mostly skeletal) that are known to have appeared with the limbs, those that are known in the crown but that can be inferred to have appeared with the limb (because they are involved in the development of the limb), and those that are known in the crown and for which there is no reason to suspect that they extend much beyond it. I object to calling all four tetrapod characters, and if we can get rid of such nomenclatural ambiguity, we should.

The name Tetrapoda (and the vernacular tetrapod) has been used (literal meaning) differently in the neontological and in the paleontological literature. Neontologists generally have described the crown, whereas paleontologists have described the clade of limbed vertebrates. Use of the apomorphy-based definition will allow this dual literal meaning to persist. The probability that neontologists will adopt a new name (such as Neotetrapoda) to refer to the crown is very low, judging by the restricted use of such terms (e.g., Neotetrapoda, Neornithes). However, if we adopted the crown clade definition of the name Tetrapoda, paleontologists might accept it and use another name for limbed vertebrates because most paleontologists are aware of the distinction between these two clades. This is the most realistic way to give the name Tetrapoda a single, unambiguous meaning in the scientific literature. To maximize continuity of literal meaning in the neontological literature and consistency of literal meaning in future paleontological and neontological publications, a crown clade definition would be most advantageous, despite the arguments that you have presented here. You seem happy to have the literal meaning of the word tetrapod vary among studies, but I think scientific nomenclature should be precise and unambiguous, so I prefer a solution that will give a single, unambiguous meaning to taxon names.

The current usage of the term Tetrapoda (or the vernacular term tetrapod) is sufficiently variable to leave the question of the prevailing usage of this name unresolved, especially if we consider both intended and literal usage. Thus, it will be difficult to change the meaning of a widely used taxon name once it is defined under the PhyloCode by arguing that the established definition does not correspond to the established usage, at least when that definition corresponds with the usage (intended or literal) that prevails among paleontologists or among neontologists. The same conclusions would probably hold for most widely used names (e.g., Aves, Reptilia, Mammalia) that have recently been given crown clade definitions. The ISPN may have to consider revising the recommendations (10A, 11A) and articles (13 and 15) of the PhyloCode concerning historical or established

usage of taxon names, because this exchange shows that determining the established usage of a name is far from easy.

ANDERSON: From early in the development of phylogenetic nomenclature, it has been recognized that an apomorphy-based definition best reflects the historical usage of nomen Tetrapoda (de Queiroz and Gauthier, 1992); however, concerns about the implications of apomorphy-based definitions as they were originally phrased and about perceived additionally stability led to the adoption of a crown clade definition (Gauthier et al., 1988; de Queiroz and Gauthier, 1990, 1992). The current convention of specifying the homology of the apomorphy in question has addressed previous concerns (Lee, 1999; Cantino and de Queiroz, 2000), and the claimed additional stability argument has been scrutinized and found unsubstantiated (Bryant, 1994; Lee, 1996; Lee and Spencer, 1997; Sereno, 1999). As a result, apomorphy-based definitions are being employed more frequently, even by those who initially avoided them (Gauthier and de Queiroz, 2001). I therefore believe that there is no convincing reason for maintaining the crown clade definition for Tetrapoda when there is a much better alternative.

An apomorphy-based definition for Tetrapoda maintains the historical meaning of "limbed vertebrates." Preserving historical usage, a principle incorporated into the PhyloCode, means that there is continuity in the literature, unbroken for >70 years, which will facilitate future research. An apomorphy-based Tetrapoda is a monophyletic group and adheres to all current conventions of phylogenetic nomenclature. The anchor apomorphy has had its homology (which is specifically defined) tested via phylogenetic analysis. Because the apomorphy in question is primitively ossified, it can be identified in the fossil record, and therefore we can speak specifically about the origin of limbs, a subject of intense current investigation. Furthermore, an apomorphy-based definition for Tetrapoda reflects how most workers (by their own admission) use the name, how most biologists use the vernacular (which is usually left undefined in the literature), and how the general public uses the vernacular. The specificity of the homology of the anchor apomorphy and consistency in usage fosters clear communication, which is the goal of any taxonomic system.

I believe it may be ultimately destructive to the wider acceptance of phylogenetic nomenclature if we radically alter the long-term, generally undisputed meaning of this well-known name when it can easily be incorporated into the phylogenetic system in a manner that maintains its historical integrity. Nine (all but one of whom are neontologists) of the 21 biologists I surveyed have never even heard of the PhyloCode; only a single worker, yourself, has applied its ideas in research. The real solution to the problem of fuzzy tree-thinking is to better educate all practicing biologists about the importance of precision in name use and discussions, not to change the meanings of well-known and widely understood names because we think "it seems unrealistic to expect that most physiologists, molecular biologists, and other scientists work-

ing exclusively with extant taxa would adopt the new names."

ACKNOWLEDGMENTS

J.S.A. thanks all who responded to his survey, Drs. David Dilkes, Sean Modesto, and Johannes Müller, and Mr. David Evans for many helpful conversations and criticisms, and the Natural Sciences and Engineering Research Council of Canada for supporting his portion of this discussion. M.L. thanks Drs. Harold Bryant, Michael S. Y. Lee, Fredrik Pleijel, Armand de Ricqlès, Chris Simon, Kevin de Queiroz, and Louise Zylberberg, Mr. Emmanuel de Margerie, and Mr. Damien Germain for useful suggestions to improve this manuscript. Both authors thank Drs. Chris Simon and Philip Cantino for their careful review of this exchange.

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First submitted 30 July 2003; reviews returned 18 September 2003;
final acceptance 18 September 2003
Associate Editor: Chris Simon

APPENDIX

METHOD USED IN DETERMINING THE LITERAL MEANING THAT WAS GIVEN TO THE WORD TETRAPOD

The numbering in the following discussion follows that of Figure 2. Articles that explicitly referred to a crown clade and studies that made statements that are true of the crown clade but that cannot be documented in extinct vertebrates with limbs were coded as using a crown clade definition of the word tetrapod (1).

In several cases, the meaning of the word tetrapod was more ambiguous, and determination of which concept was used was more difficult. The exact criteria used to judge such studies were numerous, but a few examples are provided here. Studies that made statements that were more appropriately considered to apply to the crown than to the morphological taxon (2) include studies such as that of Fella et al. (2002:1355), who stated that "if the axolotl TRD locus is nested within the TRA locus, as in mammals, then this organization has been present in all tetrapod vertebrates." The logical link between states present in a mammal and a lissamphibian implicitly applies to a crown group. Furthermore, comparative studies in which only extant taxa were studied but for which the word tetrapod was used to discuss these taxa or the clade that includes them were considered to use a concept closer to the crown concept than to a morphological concept, except when the discussed characters concerned pentadactyl limbs. The coding scheme that has been adopted throughout this survey does not attempt to capture what the authors intended to state but rather what they do state.

In many studies, the meaning attributed to the word tetrapod cannot be known exactly and could apply equally well to the crown concept as to the morphological concept (3). This group includes studies such as that of Fabrezi and Barg (2001:210), who stated that "the unity and diversity of developmental processes in the vertebrate limb have singular importance in the interpretation of evolutionary hypotheses of tetrapod diversification." This statement provides an ambiguous link between the presence of limbs and the taxon Tetrapoda (indeed, as in several other studies, the word limb is associated with the word vertebrates rather than with the word tetrapod), but the alluded diversity of developmental processes is only known in the crown, and the identity of the clade that is said to diversify is not specified exactly. Such statements have been considered ambiguous.

Cases of ambiguous meanings of the word tetrapod that are closer to the morphological than to the crown concept (4) include the article by Neyt et al. (2000:82), who stated that "while most fish species use the undulating contractions of the axial musculature to generate

propulsive force, tetrapods also rely on the appendicular muscles of the limbs to generate movement." Of course, we cannot be certain that the first limbed vertebrates used their limbs like extant tetrapods, but it seems reasonable to think that the appearance of digits and of other structures of the limb must be closely linked with the change in how movements were performed.

Studies that tied the appearance or presence of limbs with the word tetrapod were considered to use a morphological concept (5). Thus, the study of McGonnell et al. (2001:354) falls in this category, because they stated that "the pectoral girdle and the skull became physically dissociated during tetrapod evolution" and because the dissociation between girdle and head is approximately contemporaneous with the origin of limbs.

In some studies, the word tetrapod was used in a descriptive sense and to describe inanimate entities (6), and in yet others the word tetrapod did not appear (7) (it was probably entered only as a key word). These two categories have been excluded from Figure 2 and are not further discussed.