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The Phylogenetic Definition of Reptilia

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Naming taxa is an important endeavor in the documentation of life by systematists, whether it is conducted in the context of traditional rank-based classification or within a phylogenetic framework. Proponents of the phylogenetic approach distinguish between the diagnosis of a group and its definition (Ghiselin, 1984; Rowe, 1987, 1988), and this distinction forms the basis for a phylogenetically based method of naming taxa formerly referred to as Phylogenetic Taxonomy (de Queiroz and Gauthier, 1990, 1992, 1994) and now called Phylogenetic Nomenclature (PN; Cantino et al., 1999; Gauthier and de Queiroz, 2001; Bryant and Cantino, 2002). Emphasis in naming has been placed on ancestry using phylogenetic definitions, and the widespread adoption of node- and stem-based definitions (apomorphy-based definitions have yet to receive as widespread acceptance, but see Gauthier and de Queiroz, 2001; Anderson, 2002; Laurin and Anderson, 2004) has led to a proliferation of new names and definitions. This shift in nomenclatural practice has, unfortunately, fostered a growth in redundant names and definitions for well-known taxa (Benton, 2000). The PhyloCode (Cantino and de Queiroz, 2003) has modified the rule of priority as used in other codes (i.e., International Code of Zoological Nomenclature) to determine which of two or more possible names with equivalent definitions is valid (Brochu and Sumrall, 2001), or which of several definitions for a given name is valid (Cantino and de Queiroz, 2003). Unfortunately, it is now apparent that some of the definitions for well-known taxon names established early in the emergence of PN were not devised following conventions now widely accepted, by either defining groups in an overly restrictive manner, or via selection of reference taxa without due consideration of the ramifications of differing tree topologies (Anderson, 2002; Laurin and Anderson, 2004).

It has become evident in broad-scale amniote taxonomy that the first published definition for Reptilia (Gauthier et al., 1988a), which would have priority under a binding PhyloCode, is problematic because of the dramatic controversies over the affinities of the specifier taxon Testudines (see Zardoya and Meyer, 2001 for review of hypotheses for turtle relationships). Recent morphological and molecular studies have challenged conventional hypotheses concerning the affinities of turtles, and this has led to unexpected and undocumented changes in the composition of the well-known taxon Reptilia, with additional ramifications for the nomenclature of some of its included taxa. We examine the consequences of the application of priority to the nomen Reptilia as our understanding of early amniote interrelationships has progressed over the past two decades, and offer a new definition that brings the phylogenetic concept of this taxon name into line with both currently accepted conventions of PN and historical usage. This new definition corrects an error created by the combination of the selection of a higher taxon (rather than a species) as a specifier, and an unexpected topology. We believe that now is an appropriate time to examine the definitions established when PN was in its earliest stages, and hope to correct what we consider to be a poorly formulated definition upon publication of a binding PhyloCode.

A BRIEF HISTORY OF TAXONOMIC CONCEPTS FOR REPTILIA

To understand the motivations of some workers and their formation of phylogenetic definitions for the nomen Reptilia, it is important to review the history of this taxon. Reptilia was erected originally as a Class by Laurenti (1768) for the inclusion of tetrapods that were neither mammals nor birds. Amphibians were included in Reptilia by Owen (1854, 1859) and other authors, but following Haeckel's (1866) work that demonstrated reptiles, birds, and mammals shared a common reproductive strategy (the amniotic egg), frogs, salamanders, and caecilians were placed unanimously in a separate taxon, Linnaeus' (1758) Amphibia. Hence, reptiles were primarily distinguished from birds and mammals by poikilothermy and lack of integumentary features such as hair and feathers (e.g., Zittel, 1902), a concept that lasted well into the succeeding century. Fossil tetrapods that satisfied this diagnosis were placed within Reptilia. However, some of the first fossils assigned to Reptilia were recognized by early workers to have conspicuously mammalian characteristics (Owen, 1860, 1884; Cope, 1878, 1898). Thus, species of the groups Pelycosauria, Dinocephalia, Dicynodontia, and Theriodontia came to be known colloquially as "mammal-like reptiles," and were eventually placed formally within their own taxon, Synapsida, which was established as a Subclass of Reptilia (Osborn, 1903). It was recognized early that synapsids were related more closely to mammals than to other fossil taxa included within Reptilia (e.g., Baur, 1887; Broom, 1914), but most early systematists had no objection to a paraphyletic Reptilia. This view became entrenched as the classic hypothesis that explained the origin of mammals from reptiles (Romer and Price, 1940; Romer, 1966). During the time that paleontologists were beginning to distinguish fossil synapsids from unequivocal reptiles, Haeckel (1866) distinguished reptiles, birds, and mammals from other tetrapods (amphibians) by placing them in a new taxon that he called Amniota, which was ignored as a taxon name (although the concept was accepted) in many subsequent published classifications (e.g., Zittel, 1902; Piveteau, 1952; Romer, 1966).

A more testable picture of amniote interrelationships appeared following the adoption of phylogenetic systematics (Gaffney, 1980; Reisz, 1981; Gardiner, 1982; Heaton and Reisz, 1986; Gauthier et al., 1988a, 1988b). The emerging consensus (Gauthier et al., 1988a; Laurin and Reisz, 1995) divided amniotes into two main groups: synapsids on one hand, and all remaining amniotes on the other (Fig. 1a and b). Synapsida was defined as a stem-based group with Mammalia as its crown (Rowe, 1988), whereas Reptilia was defined as a node-based group using extant turtles, snakes, lizards, and crocodiles as reference taxa (Gauthier et al., 1988a). Gauthier et al. (1988a) recognized a sister-group relationship between turtles and captorhinids (Fig. 1a), a relationship identified formally as Anapsida, which they defined as “extant turtles and all other extinct taxa that are more closely related to them than they are to other reptiles.” In the Gauthier et al. (1988a) tree, Anapsida is the sister group of a clade formed by the Carboniferous taxon *Paleothyris* and the diapsid groups Araeoscelidia and Sauria (crown-group diapsids, *sensu* Gauthier, 1984). The crown-based concept for Reptilia by definition omitted several Permian and Triassic taxa that, since their respective discoveries during the late 19th and early-mid 20th centuries, were regarded to be basal reptiles (mesosaurids, millerettids, procolophonians, and pareiasaurs). These taxa together formed a clade (informally designated “parareptiles”) that Gauthier et al. (1988a) identified as the sister taxon of Reptilia.

The Gauthier et al. (1988a) phylogeny was the principal reference for amniote interrelationships and taxonomy until Laurin and Reisz (1995) identified turtles as the sister taxon of procolophonid “parareptiles.” The Laurin and Reisz (1995) results expanded the content of the reptilian crown group by incorporating “parareptiles,” and thereby produced a topology in which Reptilia was divisible into turtles and their fossil relatives on one side and diapsids and their close relatives on the other (Fig. 1b). Laurin and Reisz (1995) bestowed Olson’s (1947) names Parareptilia and Eureptilia on the former and the latter groupings, respectively, as stem-based taxa. The other major departure from the work of Gauthier et al. (1988a) is that Laurin and Reisz (1995) found no support for a relationship between Mesosauridae, a group that comprises the oldest known fully aquatic amniotes, and the other “parareptiles.” Mesosauridae formed a clade with the augmented reptilian crown, a grouping that was given Huxley’s (1864) rarely used nomen Sauropsida (Gauthier, 1994; Laurin and Reisz, 1995). Gauthier (1994:137), citing “Laurin and Reisz (in press),” defined Sauropsida in stem-based fashion as “reptiles plus all other amniotes more closely related to them than they are to mammals,” whereas Laurin and Reisz (1995:180) themselves defined this taxon name as a node-based group, “the last common ancestor of mesosaurs, testudines and diapsids, and all its descendents.”

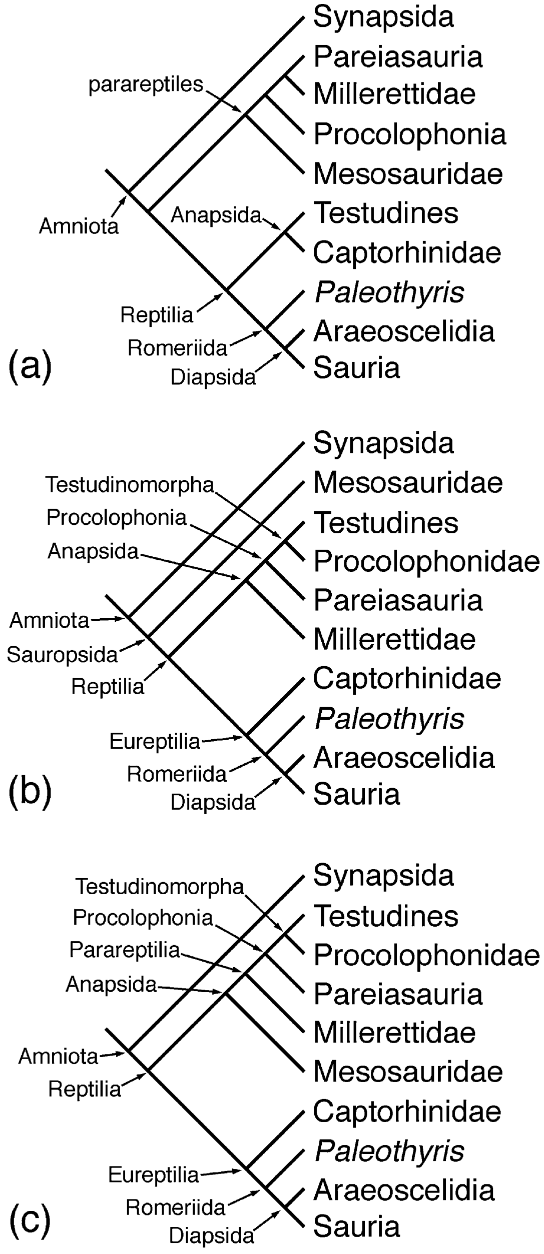

FIGURE 1. Cladograms showing the progression of ideas concerning amniote phylogeny and nomenclature that are in line with traditional ideas for reptile interrelationships (i.e., Diapsida does not include Testudines). (a) Gauthier et al. (1988a). (b) Laurin and Reisz (1995). (c) Modesto (1999). The nomenclature shown employs a strict priority among the phylogenetic definitions for taxon names. Arrows indicate taxon names for clades.

The Laurin and Reisz (1995) analysis supplanted that of Gauthier et al. (1988a) as the standard view of early amniote phylogeny. It was slightly modified by Modesto (1999) who, in work stimulated by new data on mesosaur anatomy, placed mesosaurs back in a clade with millerettids, pareiasaurs, and procolophonids (Fig. 1c), thus recovering the original content of Gauthier et al.'s (1988a) "parareptiles." Reptilia and Sauropsida, *sensu* Gauthier et al. (1988a) and Gauthier (1994), respectively, shared the exact same content (although not the same definitions), so Reptilia was recognized by Modesto (1999) as the senior synonym because it was the older, more established name. Because Parareptilia, as defined by Laurin and Reisz (1995), was equated in both definition and content with Anapsida (*sensu* Gauthier et al., 1988a) by Modesto (1999), deBraga and Reisz's (1996) definition of Parareptilia ("the most recent common ancestor of millerettids, *Acleistorhinus*, lanthanosuchids, *Macroleter*, Procolophonia, and all its descendents") was recognized as the valid definition (rendering Parareptilia a subclade of Anapsida). Anapsida, which in traditional rank-based classifications grouped several early amniote groups together on the basis of a plesiomorphy (the absence of temporal fenestrae), is an unfortunate name because it epitomizes a paraphyletic group to most students of early amniote phylogeny. Despite its phylogenetic "reinterpretation" by Gauthier et al. (1988a), this nomen has received little support in recent phylogenetic studies, as evidenced by the observation that the clade of mesosaurs and parareptiles (*sensu* deBraga and Reisz, 1996) is either left unnamed on cladograms (e.g., Berman et al., 2000: Fig. 4) or Mesosauridae is simply pruned from the amniote tree, thereby circumventing the problem of Anapsida (e.g., Zardoya and Meyer, 2001: Fig. 3). Reisz and Scott (2002) did use the term Anapsida for the clade of mesosaurs, millerettids, pareiasaurs, and procolophonids, but these authors did not include turtles in their analysis because of the ongoing controversy over turtle relationships. Reisz and Scott (2002) therefore appear to have associated the nomen Anapsida with the content of the group that was recognized by Modesto (1999), rather than with the definition of the nomen created by Gauthier et al. (1988a) insofar as the specifier taxon "Testudines" was intentionally omitted from consideration.

The amniote phylogenies of Gauthier et al. (1988a) and Laurin and Reisz (1995) may be thought of as most closely reflecting historical views of amniote classification in that turtles represent a lineage distinct from that comprising other living reptiles. In traditional rank-based classifications, turtles were grouped with several early reptile groups within Anapsida (Williston, 1917; Romer, 1966; Carroll, 1988). However, recent morphological and molecular studies suggest that turtles are instead diapsid reptiles, variously identified as lepidosauromorphs (lizards, snakes, tuataras, and their fossil relatives; Rieppel and deBraga, 1996; deBraga and Rieppel, 1997), or archosauromorphs (crocodiles, birds, and their fossil relatives; Hedges and Poling, 1999; Kumazawa and Nishida, 1999; Zardoya and Meyer, 1998, 2001). We will not go into further detail about these competing hypotheses for the diapsid affinities of turtles because they are beyond the scope of the present work, and the reader is referred to Zardoya and Meyer (2001) and Lee (2001) for detailed reviews and treatments of these hypotheses.

CONSEQUENCES OF DIFFERENT TREE TOPOLOGIES ON THE NOMENCLATURE OF MAJOR REPTILIAN CLADES

If the hypothesis that turtles are diapsid reptiles becomes the consensus view among systematists, it creates problems for the nomenclature of the reptilian side of the amniote tree. Gauthier et al. (1988a: 142) defined Reptilia as "the most recent common ancestor of extant turtles and saurians, and all its descendents." This has been interpreted to mean Reptilia can be regarded to be a crown group (Laurin and Reisz, 1995). However, if a diapsid identity for turtles is accepted, the Gauthier et al. (1988a) definition renders Reptilia and Sauria (*sensu* Gauthier, 1984) as competing names for the exact same clade. According to priority by date of first publication of a name, the former nomen should be recognized as the senior synonym, although the phylogenetic definition of Sauria has priority over that of Reptilia. It seems apparent to us that no systematist would regard the name "Sauria" to have priority over the older, more widely used name "Reptilia." Of greater concern is the fact that, if turtles are saurians, Gauthier et al.'s (1988a) definition for Reptilia is redundant, because it uses Sauria and a saurian group (turtles) as specifiers. Questions of historical continuity aside, the definition for Reptilia must be emended because of its now circular construction. Unfortunately, definitions of Reptilia published subsequent to Gauthier et al. (1988a) offer no viable alternative. The definition provided by Laurin and Reisz (1995: 183, "the most common ancestor of testudines and diapsids, and all its descendents") and deBraga and Rieppel (1997: 228, "the most common ancestor of diapsids and all its descendents"), renders Reptilia synonymous with Diapsida if turtles are nested within Diapsida. The deBraga and Rieppel (1997) definition is clearly a *lapsus calami*, because the content outlined in the definition is not consonant with the placement of Reptilia on their tree; their definition of Reptilia can be rejected for this reason. The definition of Laurin and Reisz (1995) suffers the problem of internested specifiers if it is applied to phylogenies in which turtles are diapsids; this includes most recent studies of reptile interrelationships (deBraga and Rieppel, 1997; Zardoya and Meyer, 1998; Hedges and Poling, 1999; Kumazawa and Nishida, 1999; Rieppel and Reisz, 1999). Lee (2001) is the only recent worker who espouses a parareptilian origin for turtles. Given the lack of consensus on the phylogenetic position of turtles, a phylogenetic definition of Reptilia that is not sensitive to the lability of this specifier taxon is clearly desirable.

A corollary problem caused by a diapsid origin for turtles is that Anapsida (*sensu* Gauthier et al., 1988: "all

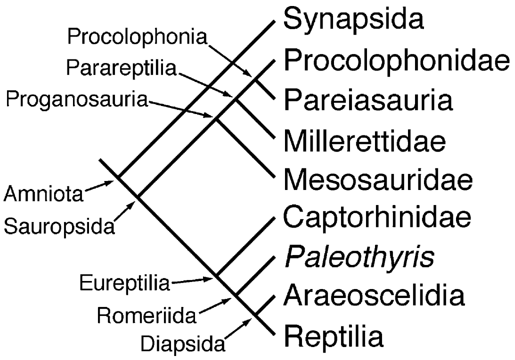

FIGURE 2. Amniote phylogeny illustrating revised nomenclature assuming the diapsid identity of Testudines as hypothesized by Zardoya and Meyer (1998), Hedges and Poling (1999), and Rieppel and Reisz (1999), and employing strict priority for phylogenetic definitions. The use of Reptilia here assumes the original crown group definition for the nomen (Gauthier et al., 1998a), not the definition provided by Laurin and Reisz (1995).

amniotes closer to turtles than to diapsids") also becomes a recursive (and therefore problematic) definition requiring amendment or abandonment. Gauthier's (1994: 138) updated definition for Anapsida ("chelonians (turtles) and all other amniotes more closely related to them than they are to saurians") connotes the same meaning as Gauthier et al.'s (1988a) definition. Despite its phylogenetic reconception by Gauthier et al. (1988a), it is probably best that Anapsida is abandoned as a formal name in light of its long precladistic usage as the name of a paraphyletic group of amniotes, and our observation that most workers associate the taxonomic term "anapsid" with its morphological connotation (the absence of temporal fenestrae; e.g., Lee, 2001:Fig. 2). Our reasoning with Anapsida does not necessarily translate to other taxonomic entities that have been recognized as paraphyletic in traditional classifications, such as Amphibia, Osteichthyes, and even Reptilia, because it is only with Anapsida that a single primitive morphological structure is strongly associated with the name.

A NEW PHYLOGENETIC DEFINITION FOR REPTILIA

The name Reptilia is one of the oldest names in the history of classification, and is known to both the general public (albeit possibly only from the vernacular term "reptile") and biologists. The multiple phylogenetic definitions that have been devised for Reptilia (Gauthier et al., 1988a; Laurin and Reisz, 1995; deBraga and Rieppel, 1997) indicate a desire among systematists to conserve it as a taxonomic entity. These phylogenetic definitions, however, are not satisfactory for reasons discussed above. In addition, the view that Reptilia, like many familiar, established taxon names, should be defined as a crown group is not compulsory (Bryant, 1994; Lee, 1996; Lee and Spencer, 1997; Sereno, 1999; see Anderson, 2002 and Laurin and Anderson, 2004 for a more detailed discussion). The main objective for using crown-group definitions is that some workers believe such definitions are more stable than other phylogenetic definitions. Paleontologists such as Lucas (1992), Patterson (1993), Lee (1996), Lee and Spencer (1997), and Benton (2000) have been particularly vocal in their opposition to crown-group definitions for well-known names because they appear to have the greatest impact on classifying fossil taxa. For instance, several basal amniote groups (mesosaurs, procolophonoids, pareiasaurs, millerettids, captorhinids, "protorothyridids" such as *Paleothyris*, and stem diapsids), recognized traditionally as reptiles, would be regarded as "nonreptilian sauropsids" if one uses a crown-group definition for Reptilia in conjunction with phylogenies that place turtles within extant diapsids. Given that the justification for originally restricting the name Reptilia to crown taxa, increased stability, is not defensible, the question becomes simply, "what definition best captures the historical meaning of the taxon name?" A less inclusive Reptilia (e.g., Fig. 2) does not seem to be the answer. The removal of "pelycosaurs" and therapsids (the "mammal-like reptiles" of previous parlance) from Reptilia was accepted long ago because these taxa clearly form a lineage (leading to mammals) separate from the other groups of amniotes ("reptiles": e.g., Baur, 1887: 104). However, it seems unlikely that the current biological community will be receptive to an even less inclusive Reptilia, essentially a subset of Diapsida, in which traditionally recognized "reptiles" (including stem diapsids) can no longer be recognized as reptiles. This situation is similar to the controversy surrounding the crown-group definition for Aves, in which many workers reject the idea that *Archaeopteryx* is not a bird because it falls outside of a crown-defined Aves (Chatterjee, 1997; Chiappe, 1995; Padian, 1997, 2001; but see Gauthier and de Queiroz, 2001). Evidence that most workers are loathe to accept a less inclusive Reptilia is illustrated in recent cladograms that portray the interrelationships of basal amniotes and assume diapsid affinities for turtles: most identify Reptilia as the sister group of Synapsida (deBraga and Rieppel, 1997: 286; Modesto, 1999:fig. 4b; Rieppel and Reisz, 1999:fig. 1; Sumida and Modesto, 2001:fig. 1; Zardoya and Meyer, 2001:fig. 4).

There are two cases in which Sauropsida is used in preference to, or interchangeably with, Reptilia. Benton (1991), following his previous usage (Benton, 1990a), applied Sauropsida to the clade of Diapsida plus Testudines, making his Sauropsida a crown taxon (Benton, 1990b). In his figured phylogeny, Sauropsida is a subset of the sister taxon to Synapsida, a clade (Sauropsida + "parareptiles") that Benton (1991) did not name; Benton (1991) appears to have adopted the phylogeny of Gauthier et al. (1988a), but used Sauropsida in preference to Reptilia. In his concluding remarks, however, Benton (1991: 327) describes Sauropsida and Synapsida as sister taxa, a statement that is not consistent with the clade names in his figure. This statement is an error, because the figured phylogenies in both Benton (1990b) and Benton (1991) both use Sauropsida as a crown clade, whereas later Benton (1997) uses Sauropsida as a total group, as do Gauthier (1994) and Laurin and Reisz (1995). Benton's (1990a, 1990b, 1991, 1997) use of the name Sauropsida changed as the concept of this group evolved in the literature (personal communication, 2004). Lee (2001) used the names Sauropsida and Reptilia interchangeably in his paper; this appears to be due to the fact that Lee (2001), following deBraga and Rieppel (1997), excluded Mesosauridae from his consideration of reptilian phylogeny, which resulted in the content of the stem-based nomen Sauropsida being equated with that of the node-based Reptilia.

Gauthier et al.'s (1988a) definition for Reptilia has generated uncertainty due to the current controversy over the phylogenetic position of turtles within the synapsid sister taxon. Under traditional rank-based nomenclature, Testudines would merely be considered *sedis mutabilis*, and it is doubtful that this uncertainty in the placement of turtles with respect to squamates, sphenodontians, and crocodiles would precipitate the growing perplexity of what is and what is not a reptile that has been wrought by Gauthier et al.'s (1988a) definition. Our concerns outlined here are not offered as a criticism of the theory and practice of PN, but as a critique of what time has revealed to be an improperly formed definition devised in the early stages of PN.

A definition for Reptilia that is less sensitive to changing tree topologies is clearly desirable, especially one that retains the spirit of traditional concepts for Reptilia (e.g., does not dispense with extinct taxa that consensus has failed to ally with synapsid amniotes) and the emerging phylogenetic synthesis of reptilian nomenclature (e.g., the widespread recognition of stem [*sensu* Jefferies, 1979] reptiles). We offer a new stem-based definition for Reptilia: the most inclusive clade containing *Lacerta agilis* Linnaeus 1758 and *Crocodylus niloticus* Laurenti 1768, but not *Homo sapiens* Linnaeus 1758. Species are used as specifiers to avoid the assumption of monophyly that the use of higher taxa entails (which led to the difficulties of the original definition), following the suggestions of Article 11.1 of the PhyloCode (Cantino and de Queiroz, 2003). We have also used three specifier taxa in order to restrict the application of the nomen, following the suggestion of Article 11.9 of the PhyloCode. This definition restricts the name Reptilia to the group that includes all members of the synapsid sister group, regardless of the interrelationships of turtles and other extant nonsynapsid amniotes (Fig. 3). The new definition is also more consonant with traditional classifications than the crown-group hypothesis for Reptilia, and consistency with traditional taxonomy is recommended by the PhyloCode (e.g., Articles 10 and 11; Cantino and de Queiroz, 2003).

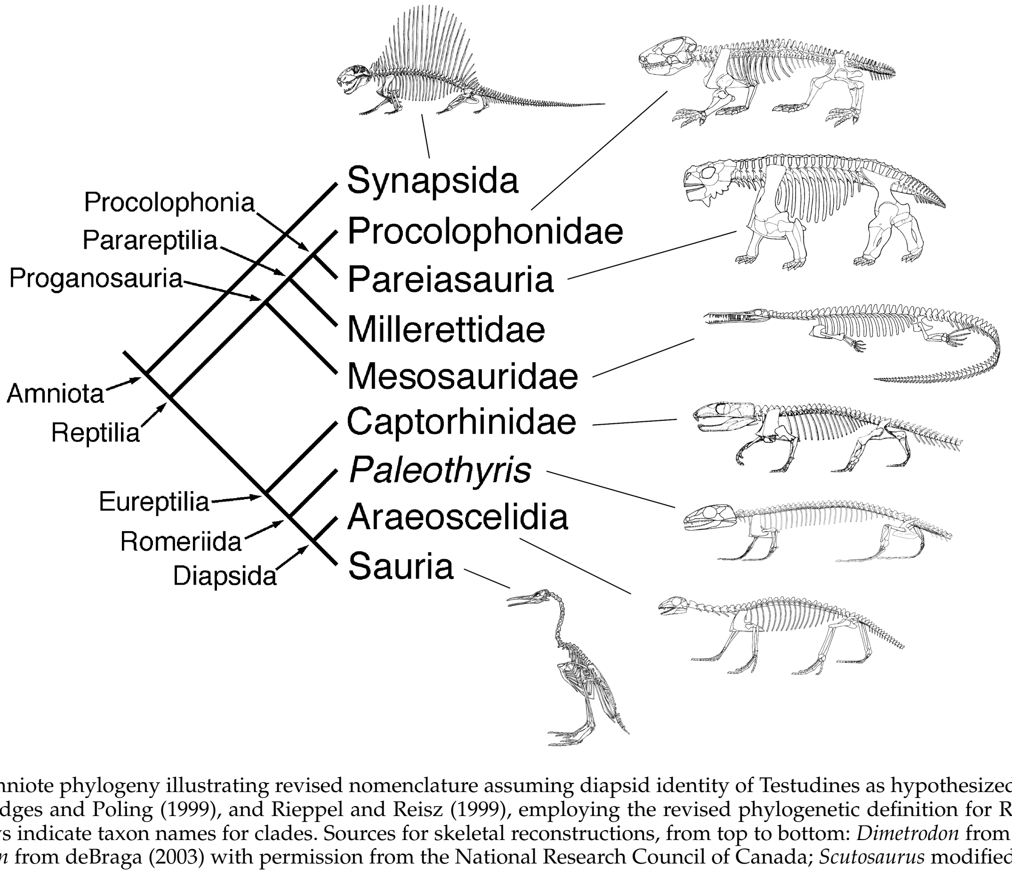

FIGURE 3. Amniote phylogeny illustrating revised nomenclature assuming diapsid identity of Testudines as hypothesized by Zardoya and Meyer (1998), Hedges and Poling (1999), and Rieppel and Reisz (1999), employing the revised phylogenetic definition for Reptilia suggested in the text. Arrows indicate taxon names for clades. Sources for skeletal reconstructions, from top to bottom: *Dimetrodon* from Romer and Price (1940); *Procolophon* from deBraga (2003) with permission from the National Research Council of Canada; *Scutosaurus* modified from Lee (1997); *Mesosaurus* original reconstruction by S. P. Modesto; *Captorhinus* (= *Eocaptorhinus*) from Heaton and Reisz (1980) with permission from The Paleontological Society; *Paleothyris* from Carroll (1969) with permission from The Paleontological Society; *Araeoscelis* reproduced from Reisz et al. (1984) with permission from R. R. Reisz and the Society of Vertebrate Paleontology; and *Hesperornis* from Marsh (1880).

Our new definition creates a logically consistent nomenclatural system, with the well-known taxa Reptilia and Synapsida forming stem-based components of a "stem-node triplet" (Sereno, 1999) with the node-based Amniota. Whereas our definition is equivalent to Gauthier's (1994) for Sauropsida ("reptiles plus all other amniotes more closely related to them than they are to mammals," p. 137), we believe that the use of the well-known Reptilia is preferable to the more obscure Sauropsida because it captures the traditional meaning of the taxon being named, as the concept has evolved.

CONCLUSION

The idea of extending the rule of priority to phylogenetic definitions is a recent one. In the years following the publication of Gauthier et al. (1988a) and the definitions for many long-established taxon names found therein, investigators of amniote phylogeny have published their own definitions for the same and new taxa. This has led to a superfluity of definitions. For example, Reptilia has four definitions of which we are aware (Gauthier et al., 1988a; Gauthier, 1994; Laurin and Reisz, 1995; deBraga and Rieppel, 1997), Diapsida has five (Gauthier et al., 1988; Laurin, 1991; Gauthier, 1994; Laurin and Reisz, 1995; deBraga and Rieppel, 1997), and Parareptilia has three (Laurin and Reisz, 1995; deBraga and Reisz, 1996; deBraga and Rieppel, 1997). In some cases later authors refer to the definitions created in previous publications, but proceeded to draft their own definitions without providing an explanation as to why earlier definitions required replacement, nor did later authors provide justifications for why their definitions represented improvements over the earlier definitions. We anticipate that the adoption of the PhyloCode will end this practice, and hope it will lead to more critical initial definition formulations.

Some systematists have criticized the tenets of PN on the grounds that it disposes traditional rank-based systematics and replaces it with a system that has led to unwieldy numbers of names for groups and unsubstantiated promises of taxonomic stability (Benton, 2000; Dyke, 2002). There are advantages and drawbacks to both systems (Bryant and Cantino, 2002). We recognize that the multiplication of names in PN is a thorny problem because of the nearly inexhaustible number of potentially namable clades, but we wonder if anyone truly laments the diminished art of suffix conformation that is demanded by mandatory taxon ranking in traditional rank-based systematics? It is our opinion that most of the criticisms of PN will be addressed upon publication of the PhyloCode, by ensuring a standard for the establishment and usage of definitions among all workers using PN.

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