

The Evolution of Body Size, Cope's Rule and the Origin of Amniotes

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Abstract.— The evolution of body size in tetrapods is assessed using a database that includes 107 early stegocephalian species ranging in time from the Frasnian (Upper Devonian) to the Tatarian (Upper Permian). All analyses use methods that incorporate phylogenetic information (topology and branch lengths). In all tests, the impact of alternative topologies and branch lengths are assessed. Previous reports that raised doubts about the accuracy of squared-change parsimony assessment of ancestral character value appear to have used datasets in which there was no phylogenetic signal. Hence, squared-change parsimony may be more reliable than suggested in recent studies, at least when a phylogenetic signal is present in the datasets of interest. Analysis using random taxon reshuffling on three reference phylogenies shows that cranial and presacral length include a strong phylogenetic signal. Character optimization of body size in stegocephalians using squared-change parsimony on a time-calibrated phylogeny incorporating branch length information is used to test a previously published scenario on the origin of amniotes and of the amniotic egg that implies that the ancestors of amniotes were small (no more than 10 cm in snout-vent length), and that their size increased subsequent to the appearance of the amniotic egg. The optimization suggests that first amniotes were somewhat larger than previously hypothesized; the estimated snout-vent length is about 24 cm, and the lower end of the 95% confidence interval of the phylogeny that yields the smallest inferred size suggests that no ancestor of amniotes measured less than 12 cm in snout-vent length. Character optimization, permutational multiple linear regressions, and independent contrast analyses show that Cope's rule of phyletic size increase applies to early reptiliomorphs but that it does not apply to early stegocephalians globally. [Amniotes; Cope's rule; early tetrapods; Paleozoic; phylogeny.]

The origin of amniotes has fascinated generations of paleontologists, and several groups have been proposed to represent close relatives of amniotes (Cope, 1880; Broili, 1904; Case 1911; Carroll, 1970a, 1982; Gauthier et al., 1988; Smithson et al., 1994), but despite this, the most interesting biological aspects of the origin of amniotes still elude us. For instance, we ignore the nature of the selective pressures that led to a shift from an aquatic to a terrestrial environment of reproduction in stem-reptiliomorphs. Hypotheses on this question can be (and have been) formulated (Romer, 1957; Laurin and Girondot, 1999), but most of them have not been tested (testing such hypotheses is difficult because we often lack the required data). Romer (1957) suggested that the ancestors of amniotes started laying eggs on land while they retained an aquatic adult lifestyle. Terrestrial egg-laying would have had two advantages: first, there were fewer predators on land (among vertebrates, at least); second, this reduced vulnerability of the eggs and juveniles to seasonal drying of the body of water (the Permian redbeds, in which some of the oldest amniotes had been found, were thought to represent a seasonally arid environment). Romer's (1957) interesting hypothesis of terrestrial egg-laying by an aquatic adult remains plausible, even though the Permian redbeds are now known to post-date by several millions of years the origin of amniotes (that took place no later than the Pennsylvanian), and there is no evidence that the ancestors of amniotes had to face seasonal drought (Carroll, 1988). Another poorly understood problem is how the selective pressures that favored the appearance of the amniotic egg may have affected other life history traits and body size in the ancestors of amniotes. The most explicit published scenario on the origin of amniotes (Carroll, 1970b) suggests answers to some of these questions and makes some explicit predictions.

Like Romer (1957), Carroll (1970b, 1991) argued that the ancestors of amniotes would have initially laid anamniotic eggs on land. Carroll's (1970b, 1991) scenario assumes that direct development (and probably the shift from an aquatic to a terrestrial site for egg-laying) occurred before the appearance of the extraembryonic membranes. This is plausible because these membranes have generally been interpreted as adaptations to terrestrial reproduction, although Laurin and Girondot (1999) examined the possibility that these membranes enabled extended embryo retention.

Carroll (1970b, 1991) suggested that the initial absence of the extraembryonic membranes that are unique to amniotes (amnion, chorion, and allantois) would have limited the size of such eggs to less than 1 cm in diameter, because of diffusion problems (the embryo would not have been able to get rid of its carbon dioxide without special respiratory surfaces, such as are provided by the chorion beyond a certain size). Furthermore, he suggested that the absence of a larval stage in amniotes limited the amount of posthatching growth. The presence of a correlation between egg diameter and snout-vent length of adult geckos and plethodontids supports this idea (Carroll, 1970b, 1991). Species of squamates whose egg is less than 1 cm in diameter have adults whose snout-vent length is less than 10 cm (Carroll, 1970b, 1991). These factors suggest that early ancestors of amniotes would have been small (no more than 10 cm in snout-vent length). Thus, early reptiliomorphs should be smaller than their ancestors (stem-tetrapods), that generally exceeded this size. After the extraembryonic membranes had appeared, egg size and body size could increase. This implies that Cope's rule of phyletic size increase should apply to early amniote evolution.

Although this scenario is accepted by some authors, such as Paton et al. (1999), it has never been subjected to

TABLE 1. Published predictions or statements about the evolution of body size in early stegocephalians and early reptiliomorphs.

Prediction	Source	
1	Depéret 1907	There is a general size increase in early stegocephalian evolution (from their origin in the Devonian, through the Lower Permian).
2	Carroll 1970b; 1991	Reptiliomorphs decreased in size prior to the origin of Amniota.
3	Carroll 1970b; 1991	Some stem-reptiliomorphs were smaller than 10 cm in snout-vent length.
4	Carroll 1970b; 1991	Reptiliomorphs and amniotes increased in size, after the origin of the amniotic egg.

a rigorous test. Admittedly, parts of this scenario can not presently be tested (the size and type of eggs laid by the immediate ancestors of amniotes, for instance) because of the lack of adequate data, but the predictions about the evolution of body size (Table 1) are tested below.

Cope's rule has been argued to apply to early stegocephalian evolution. The French paleontologist Charles Depéret, who wrote extensively about body size evolution, believed that phyletic size increase was pervasive in animal evolution, to the point that he disputed any case of body size reduction (Depéret, 1907: 209). More to the point, Depéret (1907: 204) stated that stegocephalian body size had increased steadily between the origin of the group and at least the Triassic: "L'ensemble du groupe présente une progression de taille des plus régulières depuis les petites formes du Carbonifère inférieur jusqu'aux types gigantesques du Trias supérieur de Souabe."

More recent studies cast doubt about Depéret's (1907) strong statements about the general trend towards body size increases. Cope's rule has been tested in a few groups and over a few time periods, such as Cretaceous and Tertiary foraminifera (Norris, 1991; Arnold et al., 1995), Cretaceous mollusks (Jablonski, 1997), Cenozoic mammals (Alroy, 1998), Tertiary (MacFadden, 1986), and Neogene equids (Alberdi et al., 1995), and although some groups apparently showed a predominant tendency toward size increase (MacFadden, 1986; Norris, 1991; Arnold et al., 1995; Alroy, 1998), others did not (Alberdi et al., 1995; Jablonski, 1997). Gould (1997) has even argued that Cope's rule was a psychological artifact. I have tested the hypothesis that Cope's rule applies to early (Devonian to Lower Permian) stegocephalian body size evolution (Table 1).

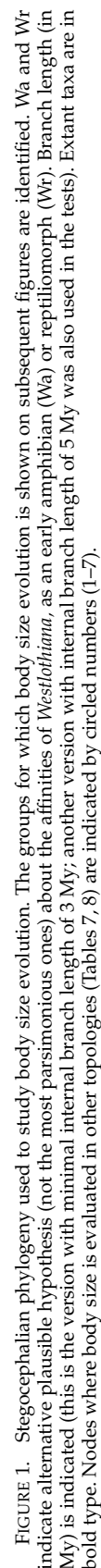
METHODS

The Reference Phylogenies

Most recent studies on the evolution of body size and Cope's rule have compared the body size of various species of the same genera in two (Jablonski, 1997) or more (Alroy, 1998) geological periods, or species and genera of presumed lineages spanning a few geological

stages (Alberdi et al., 1995). Such an approach is justified in taxa for which detailed phylogenies are not available, but for taxa for which fairly detailed phylogenies have been published, a method that incorporates phylogenetic data may be more appropriate. Using such methods (see below) to test the predictions of Carroll's (1970b) scenario about body size, a reliable phylogeny must be available, and the body size of relevant taxa must be known. Both of these requirements are somewhat limiting in this case. Our understanding of tetrapod phylogeny has been drastically altered by recent, large-scale computer-assisted phylogenetic analyses that have shown that the previously widely accepted phylogeny (Panchen and Smithson, 1988; Lombard and Sumida, 1992) is not the most parsimonious one (Carroll, 1995; Laurin and Reisz, 1997, 1999; Laurin, 1998a; Anderson, 2001). These phylogenies (and others) have been used to compile a global phylogeny of early stegocephalians (Fig. 1; Appendix 1). The phylogeny is a supertree that was simply compiled by taking various parts of published phylogenies; no new data analysis was performed. The matrix representation parsimony (MRP) method (Baum, 1992), which has been used in several recent studies (such as Bininda-Emonds et al., 1999), has not been used because this method would not take into consideration qualitative differences between the original phylogenies (i.e., whether or not they were based on a data matrix, how the matrix was analyzed, etc.). Instead, incompatibilities between the various phylogenies were resolved using the following criteria: phylogenies that were based on a computer-assisted phylogenetic analysis were preferred over phylogenies based on a manual analysis of a matrix, and the latter were preferred over phylogenies that were not based on a matrix; phylogenies with a high number of terminal taxa (OTUs) were preferred over phylogenies that included a small number of OTUs; recent phylogenies were preferred over ancient ones; phylogenies based on numerous characters were preferred over those based on few characters.

The branch lengths of the phylogenies used in this study represent millions of years of evolution (Figs. 1, 2). The oldest record of each taxon for which body size data were available were used. Minimal divergence times between taxa were established from the fossil record, by searching for the oldest member of each clade (not only among the genera and species included in this study). When several successive dichotomies (of nested clades) appeared to have taken place simultaneously (the oldest known member of the nested clades were of equal age), a minimal length of 3 My was placed at the internal branches (this pushed the age of the most inclusive clade farther into the past). In general, a taxon was considered to have been present throughout a geological epoch; the calculations assume that the data of the taxon represent its size at the end of the geological epoch in which it belongs. This was done to avoid getting spurious size trends because of size differences of taxa that are nearly contemporaneous, and whose relative age is poorly corroborated (as is frequent for fossils coming from various continents).



from these authors represents the “traditional” point of view and because it presents a great number of differences with the preferred phylogeny (Fig. 2). In this phylogeny, only the relationships between the large clades are different; the topology within temnospondyls, “microsaurs,” Nectridea, Baphetidae, Seymouriamorpha, Anthracosauria (embolomeres and *Gephyrostegus*), and Cotylosauria (Diadectomorpha and Amniota) is identical to that of the main phylogeny (Fig. 1). This reflects the fact that few phylogenies (sometimes only one) are present within these clades (temnospondyls are an exception).

The impact of internal branch length was studied by producing a phylogeny whose topology is identical to the reference phylogeny, but where the minimal length of the internal (and terminal) branches is 5 My (instead of 3 My). It was not useful to test other values of minimal branch lengths because values of less than 3 My yield artefacts that prevent a meaningful analysis of the results (see below), and a minimal branch length of more than 5 My pushes back the divergence date between the oldest clades ridiculously deep into the past. For instance, in the tree with minimal branch length set to 5 My, the divergence between *Ichthyostega* and post-Devonian stegocephalians dates from 394.4 My, in the Pragian (Lower Devonian), and this date is probably too ancient; with minimal branch lengths set to 3 My, the same divergence dates from 371.5 My, in the Frasnian, and this is perfectly reasonable. Thus, 3 and 5 My appear to represent the extremes of the plausible range of values of minimal branch lengths.

The resulting phylogenies incorporate 107 taxa that range in time from the Frasnian (Upper Devonian; some early sarcopterygians were included to provide an estimate of body size of the earliest stegocephalians) to the Tatarian (Upper Permian), but the bulk of the taxa date from the Visean (Mississippian) to the Artinskian (Lower Permian; Appendices 2, 3). Indeed, only two taxa from the Middle and Upper Permian were included because they represented the last members of clades whose greatest diversity was achieved in the Pennsylvanian or the Lower Permian. This includes the seymouriamorph *Kotlassia* and the varanopid *Varanodon*. Some relevant taxa had to be excluded because no detailed phylogeny of their group had been published. For instance, Caseosauria is represented only by three genera (*Eothyris* and two caseids) because no phylogeny of caseids is currently available. Other taxa had to be excluded because only larvae and immature postmetamorphic juveniles are known, such as branchiosaurs (Schoch, 1992) and some seymouriamorphs (Laurin, 1996b).

Throughout this study, phylogenetic definitions of taxon names (Stegocephali, Tetrapoda, Amphibia, Reptiliomorpha, Amniota, etc.) follow the first proposed definitions. A review of the relevant definitions can be found in Laurin (1998a, 2001). Stem-tetrapods include all taxa that are more closely related to Tetrapoda than to lungfishes or the coelacanth but that are not part of Tetrapoda, and similarly, stem-reptiliomorphs (or stem-amniotes) include all taxa that are more closely related

amniotes than to lissamphibians, but that are not part of Amniota.

Taxonomic Sampling

Obtaining the body size for extinct taxa is usually not problematic (although one of the several possible ways of estimating body size must be chosen), except for taxa represented by fragmentary remains. Thus, the oldest known synapsid (*Protoclepsydrops*) could not be included because its cranial and presacral lengths could not be accurately estimated and because it cannot be placed within the phylogeny of synapsids (Carroll, 1964a). The lengths used for the calculations (Appendix 2) are based on the average of all the individuals that appeared to be adults and that could be measured for each taxon.

Another limitation (but not specific to this study) is that not all taxa are equally well-represented in the fossil record. This problem is especially acute in stem-reptiliomorphs, at least if the recently proposed phylogenies of Laurin and Reisz (1997, 1999) and Laurin (1998a, b) are accepted because these imply that many taxa formerly thought to be closely related to amniotes are in fact stem-tetrapods. Thus, on the main phylogeny used for this study (Fig. 1), only two clades of stem-reptiliomorphs are recognized: *Solenodonsaurus* and diadectomorphs (but on the alternative topology [Fig. 2], six clades of stem-reptiliomorphs are known). *Westlothiana* is a possible third clade of stem-reptiliomorph. This fossil was initially described as a Lower Carboniferous amniote (Smithson, 1989; Smithson and Rolfe, 1990), making it by far the oldest known amniote. This animal is small, with a cranial length under 2 cm and an estimated snout-vent length of 11.2 cm, more or less consistent with Carroll's (1970b) prediction of the small size of some stem-amniotes. A more recent study *Westlothiana* has shown that it was not an amniote, and it was reinterpreted it as a reptiliomorph (Smithson et al., 1994). However, this conclusion was based on a phylogenetic analysis that included only presumed reptiliomorphs in the context of a classical phylogeny. A more recent study concluded that the affinities of *Westlothiana* were uncertain. The most parsimonious tree placed *Westlothiana* among stem-tetrapods, but only one extra step was required to place this taxon in a basal position within amphibians or reptiliomorphs (Laurin and Reisz, 1999). Ruta et al. (2003) made *Westlothiana* the sister-group of “lepospondyls” (that appear to be reptiliomorphs, in their phylogeny), and this raises further doubts about the affinities of this taxon. Because of its potential importance to assess body size evolution in early reptiliomorphs, *Westlothiana* was included and the impact of its three plausible positions in the phylogeny is assessed (Fig. 1).

The enigmatic taxon *Casineria*, described as a small, amniote-like, early Carboniferous reptiliomorph (Paton et al., 1999) was not included, for two reasons. First, its affinities are uncertain; it was only placed in an unresolved polytomy that included three amniotes and the equally enigmatic *Westlothiana*. Given the uncertainties about the position of *Westlothiana*, it would have been

difficult to place *Casineria* in the phylogeny. Second, no cranial remains were found, and even the presacral length of this animal is difficult to establish. To these two problems could be added that of the ontogenetic stage represented by the holotype (and only known specimen). Its great ossification suggests that it is not a very young individual, but given the indeterminate growth of most stegocephalians, it is difficult to know how mature this specimen is.

Estimating Body Size in the Terminal Taxa

With these limitations in mind, the available data can be used to test the scenario of Carroll (1970b). However, several choices must be made. The first choice concerns the estimator for body size. It is difficult (perhaps impossible) to obtain reliable and accurate estimates of body mass of most extinct vertebrates because the soft tissues are not usually preserved, and body volume is not easy to estimate, among other reasons (Gunga et al., 1998). Therefore, it is probably better to use linear measurements of skeletal remains, which can at least be measured with reasonable accuracy. In this study, both cranial length (from tip of premaxilla to posterior edge of the skull table) and presacral length (measured from the anterior edge of the atlantal centrum to the anterior edge of the first sacral pleurocentrum) are used. The second measurement may be more tightly correlated with body mass, but it is less frequently available than cranial length because a fairly complete articulated axial skeleton is required. Thus, the cranial length of 107 taxa has been obtained, but the postcranial length of only 63 of these taxa is available. I have used these variables because they can be determined reliably fairly often. For instance, skull tables of extinct taxa are often preserved articulated, from the premaxilla (or at least the nasal) to the postparietal (when present). In contrast, the braincase and the cheek are often disarticulated. Therefore, a measurement of skull length using the occipital condyle or the quadrate condyle as a posterior limit would have been less reliable. Similarly, total body length (including the tail) would not have been reliable because the tail is often incompletely preserved, if at all. When skeletal reconstructions were available, they were used to measure presacral length. Even when the reconstruction is a composite, it was generally obtained from similarly-sized individuals or individuals of different sizes that were scaled to provide a reconstruction with the right proportions. The cranial lengths obtained from such reconstructions are generally less accurate than those that can be obtained from cranial reconstructions (especially when the skeletal reconstruction is in lateral view) because the skull is often drawn fairly small on such reconstructions, so cranial lengths were usually obtained from tables of measurements, drawings of fairly complete skulls, or cranial reconstructions. In any case, I cross-checked for consistency the cranial dimensions obtained by these methods, and generally, the discrepancies were small (always less than 10%, and generally less than 5%). Considering that the cranial length of the taxa

analyzed vary from less than 1 cm to about 60 cm, that the data are log-transformed prior to analysis, and that there is no reason to believe that the errors create a time-related bias in the reported sizes, the errors introduced by using various types of reconstructions probably do not bias the analysis. Similarly, the small errors introduced by the process of reconstructing a skeleton are probably not time-dependent and should not bias the analysis.

Detecting a Phylogenetic Signal in the Studied Characters

Before optimizing body size on a phylogeny, the presence of a phylogenetic signal in this character was assessed. Indeed, the value of optimizations of characters that show no phylogenetic signal is dubious. If the distribution of the character values on the terminal taxa cannot be distinguished from a random one, there is no reason to think that parsimony provides a reliable estimate of the hypothetical ancestors because the distribution of character values of the ancestors may also be random. Therefore, determining whether or not body size (as assessed by cranial and presacral length) included a phylogenetic signal appeared to be a required preliminary step in this analysis. Recent reports that suggest relatively low precision of ancestral character value estimation using squared change parsimony and other optimization algorithms (linear parsimony, maximum likelihood, generalized least squares) also imply that assessing the presence of a phylogenetic signal in a character should be performed (Martins, 1999; Oakley and Cunningham, 2000; Webster and Purvis, 2002). A thorough reappraisal of these works is beyond the scope of this study, but the original data on virus phenotype and the phylogeny of Oakley and Cunningham (2000: Table 1, Fig. 1) have been used to determine whether or not a phylogenetic signal is present. Similar analyses were performed on the data on Neogene foraminifera of Webster and Purvis (2002). Absence of a signal could explain why these authors found that nodal value estimates were relatively imprecise. The phylogenetic signal in the dataset of Polly (2001), that yielded a good match between inferred and observed node values, is also assessed.

A straightforward approach to determine the presence of a phylogenetic signal in a character is to perform tree simulations to generate trees randomly and to look at the number of steps of the character of interest on these trees (for a continuous character, the squared length of the character over the tree is used). If the number of steps of the character of interest is less on the chosen phylogeny than in at least 95% of the randomly generated trees, we can conclude (using a 5% threshold) that the evolution of this character is associated with this tree (i.e., there is a phylogenetic signal in this character). In other words, this character has fewer steps than we should expect if it showed only random (nonphylogenetic) variation in the sample of taxa. These simulations were performed by the TreeFarm package of modules of Mesquite (Maddison and Maddison, 2002; Maddison et al., 2002). Two main tree-simulation algorithms are

available in Mesquite: uniform speciation (Yule model) and equiprobable trees. The uniform speciation model required the tree depth to be specified (this corresponds to the path length between the root and the terminal taxa, that are all contemporaneous in this model). This model was unsuitable to simulate my data because the taxa in my tree are of various ages. The equiprobable trees model yields uniform branch lengths, which does not correspond to my data either. Thus, I used another simulation algorithm of the TreeFarm package of Mesquite that was developed for this study, and that randomly permutes the terminal taxa (along with their character values) on the tree, while holding the topology (as well as the branch lengths) constant.

A second test that is often used to detect a phylogenetic signal (e.g., Morand, 1997; Böhning-Gease and Oberrath, 1999; Castanet et al., 2001) is a permutational linear regression analysis as described by Legendre et al. (1994) that can determine whether or not there is a relationship between the phylogenetic distance (here estimated by the sum of the branch lengths that link two taxa; this is the independent character) and a dependent character (here, the difference in size). The test (which is a modified Mantel test) was performed using PERMUTE 3.4 alpha 9 (distributed by P. Casgrain at <http://www.fas.umontreal.ca/biol/casgrain/en/labo/permute/>). PERMUTE performs classical multiple linear regressions on distance matrices (calculated character by character), but then tests the significance of the regression by randomizing the data of the dependent character to create a null distribution that yields a probability that the observed pattern is random (Legendre et al., 1994). The randomization procedures used by PERMUTE and Mesquite are thus comparable (in that they hold topology and branch lengths constant, but randomly reshuffle the terminal taxa and their associated character value). The main limitation of this approach is that if the relationship between phenotypic and phylogenetic distance is not linear (and there is no reason to believe that it is), no relationship may be detected, even if one is present. Thus, this type of test is probably conservative. This test has the advantage of yielding an estimate of the proportion of the variance of a character that can be explained by the phylogeny, although the estimate will underevaluate the proportion of explained variance if the relationship between phylogenetic and phenotypic distances are not linear, and if data transformation fail to linearize adequately this relationship. In all cases, the probabilities reported are those that the b coefficient (mathematically akin to a slope, but because it is calculated on distance matrices, it is not the regression coefficient on the original variables) is significantly different from 0. Permute also gives a probability associated with the r^2 but this was not used because when there is more than one independent variable, only the probabilities associated with the b coefficient can be compared. The character values (lengths and geological ages) were transformed into distance matrices using Progciciel R (Casgrain and Legendre, 2001) and the phylogenetic distance matrices were generated using

TreeEdit 1.0a9 and 10.a10 (Rambaut and Charleston, 2001).

The Time Scale

The age of the taxa was compiled to allow a test of Cope's law. A standard geological time scale was used (Harland et al., 1990), with some modifications to reflect recent developments (Jin et al., 1997). The time scale of Harland et al. (1990) has unfortunately not been systematically used by vertebrate paleontologists, often because of correlation problems between local strata and the global time scale. Therefore, I have used, whenever necessary, the literature to determine these correlations. Hentz (1988) was particularly useful for correlations and a recent revision of the Lower Permian of Texas. The ages of several taxa were already compiled by Carroll and Winer (1977), Benton (1993), and Milner (1993); these compilations provided parts of the data. I have chosen to use geological epochs (Appendix 3) because such a scale was fine enough to discriminate between early and late representatives of most clades, and because it is coarse enough to enable intercontinental correlations of terrestrial species. Had I tried using geological stages, the age of many of the species included in this study would have been uncertain.

This study enables me to test a few evolutionary hypotheses about body size evolution in stegocephalians (Table 1), three of which are linked to the scenario formulated by Carroll (1970b) about the origin of amniotes, and one of which is derived from Depéret (1907). Of course, testing prediction 4 (that reptiliomorphs increased in size after the origin of the amniotic egg) requires knowing at least approximately the date of origin of the amniotic egg. This is not so problematic because we know that this event took place among reptiliomorphs, prior to amniote origins, so if we see a significant size increase in reptiliomorphs or early amniotes, we can consider that a confirmation of prediction 4. This approach is conservative because it will lead to a rejection of prediction 4 only if there is no size increase in late reptiliomorphs or early amniotes.

Studying Body Size and Testing for Body Size Increase

I have studied body size evolution by three methods: squared-change parsimony optimization (Maddison, 1991) on a phylogeny incorporating branch length (as assessed by geological age and minimal divergence times), by multiple linear regression analysis using random permutations to test the statistical significance of the regression (Legendre et al., 1994), and by independent contrast analysis (Felsenstein, 1985). The optimizations were performed using Mesquite. Confidence intervals for nodal values were estimated using the PDAP module for Mesquite, that can generate confidence intervals for the root using independent contrasts (Midford et al., 2003). To get the confidence intervals on all the nodes other than the root, the tree had to be re-rooted (once for each node) as close to that node as possible. To do this, after the tree was re-rooted on one of the branches

stemming from the node whose confidence interval was to be established, branch length was adjusted so that the branch leading from the root to the node to evaluate was 0.0001. The length of the other branch stemming from the new root was readjusted to correspond to the entire length of the (original) branch on which the tree had been re-rooted. This procedure gave root values identical to those of the evaluated node in the first six significant digits.

The regression analysis was done using *Permute* 3.4 alpha 9 using the “matrix” permutation algorithm. In all cases, *Permute* works on distance matrices of the terminal taxa. The dependent variable was body size (i.e., differences in size between the terminal taxa), whereas the independent variables were the phylogenetic position (the taxon-to-taxon distances or path lengths, using the reference phylogeny) and geological time (the difference in geological age between terminal taxa). This method can reveal the effect of geological time on size while controlling for the phylogeny (which is necessary to compensate for the nonindependence of character values of various species).

An independent contrast analysis was performed by regressing standardized contrasts of body size against standardized contrasts of geological time elapsed since clade origin (Appendix 2). The time of the origin of the clade is defined as the divergence time between the two main clades of analyzed taxa. In this case, this divergence is between the finned stem-tetrapods *Eusthenopteron* and *Panderichthys*, and probably took place in the Givetian. However, the assumptions of independent contrasts were not met with the first compiled tree, which had minimal branch lengths set to 1 My; there

was a negative correlation between estimated contrast of cranial length and height of the nodes and between absolute value of standardized contrasts of cranial length and standard deviation (square root of sum of corrected branch lengths). The presence of such correlations suggests that the rate of evolution was heterogeneous (in this case, it decreased with time) or that some internal branch lengths were poorly estimated (which is possible because in the case when two or more nested clades seem to appear simultaneously in the fossil record, there is no direct evidence about these internal branch lengths). Branch length transformation would not have been entirely justified because it would have implicitly changed the age of the taxa, which was used to study change in size through time. Instead, to determine if the very short internal branches (minimal length of 1 My, which is much shorter than the terminal branches) were responsible for this, minimal length was increased to 3 My, and this eliminated the observed correlations (the intermediate value of 2 My was also tested, but there were also artefacts so it was not used). Thus, the main analysis is based on a tree with minimal lengths set to 3-My. In that tree, some correlations remained for the geological age (between absolute contrasts and standard deviation, and between absolute value of the contrasts and estimated value of the base nodes), but this comes from the fact that branch lengths are involved in calculating all these values and should not bias the analysis (P. Midford, personal communication from 26-8-2003). It should be noted that enforcing a 3-My minimal internal branch length means that the divergence times of many clades studied here are somewhat older than the oldest fossils known from these clades. This is not a problem because the fossil record is

TABLE 2. Probability that the character length on the preferred tree (data and tree from Oakley and Cunningham, 2000) results from chance alone. Random terminal taxon reshuffling on the tree was performed by the *TreeFarm* package of *Mesquite* (1000 random trees were examined for each test). Because of the low number of terminal taxa (eight), several random trees had the same length; the random trees that had the same length as the reference tree were added to the shorter trees to compute the probability, thus making the test conservative, but excluding these trees does not change substantially the results (shown in parentheses). Permutational multiple linear regression analyses were performed using *Permute* (999 random permutations were performed for each test). For logarithmic transformation, the following equation was used: $\ln(10 \times \text{original value})$.

Character	Random taxon reshuffling				Permutational multiple linear regression		
	Square length of reference tree	Squared length of shortest random tree	Average squared length of random trees	Probability	B coefficient	Probability	R ²
Plaque diameter (original value)	0.005072	0.003245	0.005746	0.288 (0.285)	−0.0551	0.360	0.0030
Plaque diameter (log-transformed)	0.005896	0.003378	0.006883	0.276 (0.272)	−0.0576	0.357	0.0033
Plaque shape (original value)	1.731E − 4	9.905E − 5	2.138E − 4	0.243 (0.239)	−0.0208	0.513	0.0004
Plaque shape (log-transformed)	4.631E − 4	2.622E − 4	5.767E − 4	0.244 (0.243)	−0.0193	0.516	0.0004
Lysis efficiency (original value)	0.01980	0.005809	0.01740	0.632 (0.631)	−0.1131	0.289	0.0128
Lysis efficiency (log-transformed)	0.03336	0.009367	0.02977	0.622 (0.621)	−0.1407	0.235	0.0198
Liquid fitness (original value)	0.1739	0.06259	0.2010	0.258 (0.257)	0.0575	0.336	0.0033
Liquid fitness (log-transformed)	0.05408	0.02711	0.08262	0.136 (0.135)	0.0608	0.315	0.0037

TABLE 3. Probability that the character length on the preferred tree (data and tree from Webster and Purvis, 2002) results from chance alone. Random terminal taxon reshuffling on the tree was performed by the TreeFarm package of Mesquite (10 000 random trees were examined for each test). Permutational multiple linear regression analyses were performed using Permute (999 random permutations were performed for each test).

Character	Random taxon reshuffling				Permutational multiple linear regression		
	Square length of reference tree	Squared length of shortest random tree	Average squared length of random trees	Probability	B coefficient	Probability	R ²
Area	0.022156	0.006946	0.030318	0.220	-0.0468	0.303	0.0022
Length	0.063551	0.024353	0.100671	0.100	-0.0085	0.515	0.0001
Width	0.050292	0.017476	0.072308	0.168	-0.0159	0.467	0.0003
Width/length	0.009163	0.004290	0.019427	0.050*	0.0424	0.301	0.0018

known to be incomplete (Smith, 1994). Therefore, the divergence dates shown in the figure may be reasonable estimates of the actual divergence times.

RESULTS

Phylogenetic Signal in Data previously Used to Assess the Accuracy of Optimizations

Random taxon reshuffling and multiple linear regression analysis of the data set of Oakley and Cunningham (2000), which had reported that squared-change parsimony yielded inaccurate results, failed to detect a phylogenetic signal (Table 2). The probabilities of obtaining similar patterns due to chance alone are fairly high (from 0.243 to 0.632). Logarithmic transformation did not noticeably decrease the probabilities, except for one variable, but the probability did not approach significance (0.136). Comparable analyses of the data of Webster and Purvis (2002) also fail to reveal a phylogenetic signal (Table 3), except for one of the four characters, where there is a marginally significant signal according to one of the tests. Similar analyses on the dataset of Polly (2001), which reported fairly accurate results using squared-change parsimony, yield much lower probabilities (Table 4) that are marginally significant (0.043 to 0.056).

Phylogenetic Signal in the Size Data

Random taxon reshuffling in Mesquite indicate the presence of a strong phylogenetic signal in both the cranial and the postcranial lengths (Table 5). Permu-

tational regression analysis yield higher probabilities (Table 6). All the analyses suggest that there is less phylogenetic signal in body size among stem-tetrapods than in Tetrapoda, especially for the presacral length. Thus, optimization of presacral length of stem-tetrapods on the preferred phylogeny may not yield reliable estimates of the dimensions of hypothetical ancestors, so these results are not shown. Random taxon reshuffling for other parts of the tree indicate the presence of a strong phylogenetic signal for both characters in tetrapods, amphibians and reptiliomorphs.

Body Size Evolution in Early Stegocephalians as Assessed by Character Optimization

Cranial length optimization on the preferred phylogeny.—Early stegocephalians were not particularly small, with a skull length of about 12 cm (Fig. 3). The first temnospondyls were apparently smaller, with a cranial length of about 10 cm (Fig. 4). An important size reduction occurred in dissorophoids, most notably in *Doleserpeton*, a taxon that have been argued to be the closest known relative of lissamphibians (Bolt, 1969). No growth series is available for *Doleserpeton*, and the postcranial anatomy of this animal has not been described, but its great ossification suggests that the known specimens are fairly mature. If *Doleserpeton* is accepted as closely related to lissamphibians, the greatest size reduction associated with the origin of lissamphibians may have occurred between the Moscovian (in the Pennsylvanian) and the Artinskian (in the Lower Permian), much later than if lysorophians are the sister-group of lissamphibians (see below).

TABLE 4. Probability that the character length on the preferred tree (data and tree from Polly, 2001) results from chance alone. These calculations were performed by the TreeFarm package of Mesquite, using a random reshuffling of terminal taxa (1000 random trees were examined for each test) and by Permute. As in Polly (2001), branch length is expressed in inferred number of generations. Because of the low number of terminal taxa (five), several random trees had the same length; the random trees that had the same length as the reference tree were added to the shorter trees to compute the probability, thus making the test conservative, but excluding these trees change only marginally the results (shown in parentheses).

Character	Random taxon reshuffling				Permutational multiple linear regression		
	Square length of reference tree	Squared length of shortest random tree	Average squared length of random trees	Probability	B coefficient	Probability	R ²
Molar area (log-transformed)	9.721E - 7	5.933E - 7	5.036E - 6	0.056 (0.047)*	0.6431	0.043*	0.4136

*Significant at a 0.05 level.

TABLE 5. Probability that the character length (body size in early stegocephalians) on the preferred tree results from chance alone. These calculations were performed by the TreeFarm package of Mesquite, using a random reshuffling of terminal taxa (10000 random trees were examined for each test). All lengths were log-transformed (ln of the dimensions, in mm) prior to optimization. Tree 1 represents the main reference phylogeny (Fig. 1); tree 2 has the same topology as tree 1, but all branches have a minimal length of 5 My, rather than 3 My; tree 3 has a topology between the main clades taken from Panchen and Smithson (1988) and a minimal branch length of 5 My (Fig. 2).

Character	Taxon or group	Probability (tree 1)	Probability (tree 2)	Probability (tree 3)
In cranial length	All	<0.0001***	<0.0001***	<0.0001***
	Stem-tetrapods	0.0028**	0.0036**	—
	Tetrapoda	<0.0001***	<0.0001***	<0.0001***
	Amphibia	0.0073**	0.0060**	<0.0001***
	Reptiliomorpha	<0.0001***	<0.0001***	<0.0001***
In presacral length	All	<0.0001***	<0.0001***	<0.0001***
	Stem-tetrapods	0.1047	0.1644	—
	Tetrapoda	<0.0001***	<0.0001***	<0.0001***
	Amphibia	0.0357*	0.0688	0.0032**
	Reptiliomorpha	0.0001*	0.0001*	0.0141*

*Statistically significant at a 0.05 threshold; **statistically significant at a 0.01 threshold; ***statistically significant at a 0.001 threshold.

Early anthracosaurs (sensu Laurin, 2001) seem to have been slightly larger than early temnospondyls (Fig. 5), and the moderate size of the first anthracosaur (about 11 cm) results from the small size of *Gephyrostegus*, which may be the sister-group of embolomeres (Laurin and Reisz, 1999). Embolomeres are fairly large animals, and the skull of their last common ancestor seems to have measured about 12 cm.

Early batrachomorphs seem to have been smaller (about 6 cm long), but this results partly from the position of *Westlothiana* (a very small animal) near the base of this group.

The presence of *Westlothiana* near Tetrapoda and the small size of amphibians cause a sharp reduction in size

near the base of the tetrapod crown. The first tetrapod seems to have been small (cranial length of about 4.5 cm). Size then decreases again in early amphibians (Fig. 6), and especially in the closest relatives of lissamphibians proposed by Laurin (1998a) and Laurin and Reisz (1999); the last common ancestor of brachystelechids, lysorophians (and lissamphibians) may have had a cranial length of just over 1 cm. Thus, under this phylogeny, the size decrease related to the origin of lissamphibians would have taken place from the Visean (Mississippian) to the Moscovian (Pennsylvanian).

Reptiliomorphs increased in size, compared to the first tetrapod (Figs. 5, 7). A cranial length of about 6 cm is present along the stem of Amniota, even though the known stem-amniotes (*Solenodonsaurus* and diadectomorphs) are all larger than this. The origin of amniotes does not seem to be associated with a reduction in size. Thus, only the very first stem-reptiliomorph may have approached the small size predicted by Carroll's scenario (but remained significantly larger, about 4.5 cm in cranial length). This is not fully consistent with prediction 3. If we admitted that Carroll's scenario was more or less correct by relaxing the size restriction of the first animal that laid amniotic eggs, we would have to conclude that the amniotic egg appeared very soon after the differentiation of reptiliomorphs because this lineage seems to have increased in size sharply and quickly (cranial length may have reached 6 cm by the Visean). Thus, diadectomorphs and *Solenodonsaurus* would be predicted to have laid amniotic eggs. Diadectomorphs have already been suggested to have had amniotic eggs, based on other arguments, by Berman et al. (1992), Lee and Spencer (1997), and Berman (2000). Thus, prediction 2, according to which reptiliomorphs decreased in size prior to the origin of Amniota, is tentatively refuted. The fragmentary fossil record of stem-reptiliomorphs precludes a more definitive statement on this point.

Contrary to what a literal interpretation of the fossil record suggests, most lineages of early amniotes do not seem to have increased in size (prediction 4). Size seems

TABLE 6. Probability that the character length on the preferred tree results from chance alone. These calculations were performed by the permutational multiple linear regression analysis in Permute (999 permutations were performed for each test). All lengths were log-transformed (ln of the dimensions, in mm) prior to calculating the distance matrices. The tests were performed by regressing the distance matrix of cranial or presacral length (dependent variable) against phylogenetic distance matrix (independent variable). Tree 1 represents the main reference phylogeny (Fig. 1); tree 2 has the same topology as tree 1, but all branches have a minimal length of 5 My, rather than 3 My; tree 3 has a topology between the main clades taken from Panchen and Smithson (1988) and a minimal branch length of 5 My (Fig. 2).

Character	Taxon or group	Probability (tree 1)			Probability (tree 2)			Probability (tree 3)		
		B coefficient	Probability	R ²	B coefficient	Probability	R ²	B coefficient	Probability	R ²
In cranial length	All	0.0865	0.029*	0.0075	0.0925	0.012*	0.0086	0.1343	0.001***	0.0180
	Stem-tetrapods	0.0473	0.316	0.0022	0.0164	0.418	0.0003	—	—	—
	Tetrapoda	0.3018	0.001***	0.0911	0.3110	0.001***	0.0968	—	—	—
	Amphibia	0.2169	0.039*	0.0470	0.2120	0.027*	0.0450	0.1984	0.001***	0.0394
	Reptiliomorpha	0.0838	0.132	0.0070	0.1081	0.070	0.0117	0.01586	0.387	0.0003
In presacral length	All	0.1229	0.044*	0.0151	0.0857	0.106	0.0073	0.2260	0.001***	0.0511
	Stem-tetrapods	0.0844	0.255	0.0071	-0.1196	0.185	0.0143	—	—	—
	Tetrapoda	0.3252	0.001***	0.1058	0.3241	0.001***	0.1051	—	—	—
	Amphibia	0.1185	0.178	0.0140	0.0823	0.232	0.0068	0.1199	0.090*	0.0144
	Reptiliomorpha	0.1426	0.074	0.0203	0.1526	0.058	0.0233	0.0085	0.481	0.0001

*Statistically significant at a 0.05 threshold; **statistically significant at a 0.01 threshold; ***statistically significant at a 0.001 threshold.

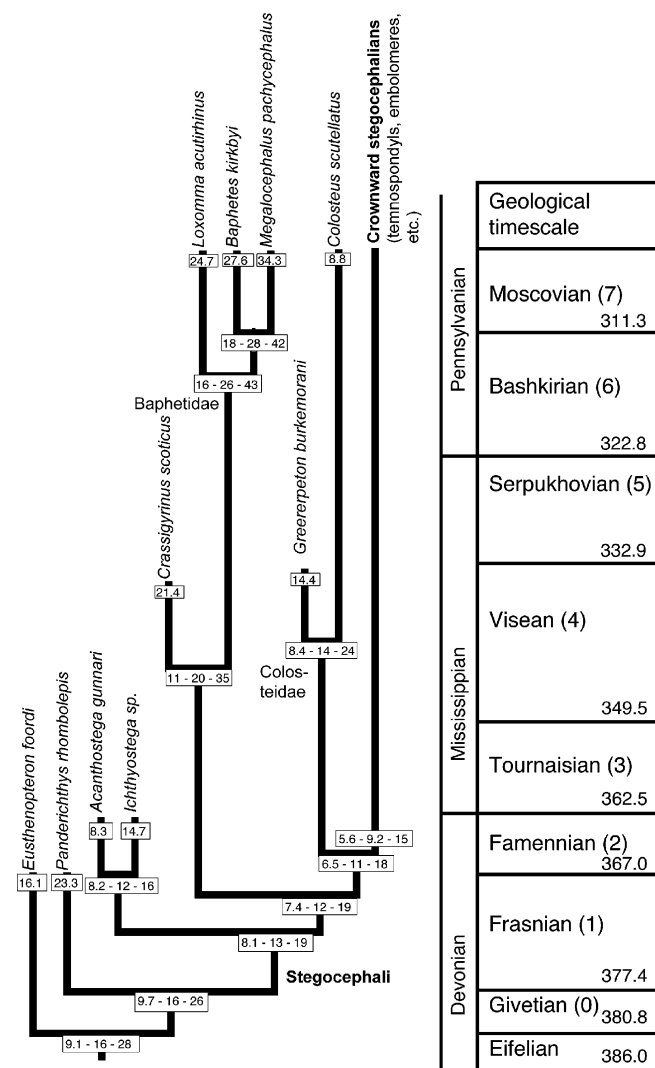


FIGURE 3. Cranial length evolution in early stem-tetrapods. All lengths (averages for adult specimens of each taxon) are expressed in cm, and represent the distance from the anterior tip of the premaxilla to the posterior end of the skull table. In this figure, and in all the subsequent ones, the size estimates of the hypothetical ancestors are reported with two significant numbers. Three values are given for every node: the lower limit of the 95% confidence interval, the estimated value, and the upper limit of the 95% confidence interval. The estimated value is not in the middle of the confidence interval because all calculations were performed on log-transformed values, and the results were converted back to cm. Extant taxa are in bold type.

to have increased in synapsids (Fig. 8) and to have decreased in some sauropsids (Fig. 7), but neither trend is obvious. Thus, prediction 4 is not unambiguously supported.

The impact of internal branch length and topology on cranial length optimization.—The position of *Westlothiana* has a moderate impact on the evolution of body size near the base of Tetrapoda. To evaluate the impact of alternative phylogenetic hypotheses, separate optimizations have been performed (Table 7). Placing *Westlothiana* at the base of Amphibia increases slightly the size of the first

tetrapod and of stem-reptiliomorphs. However, placing *Westlothiana* at the base of Reptiliomorpha implies that its ancestor with other reptiliomorphs measured about 4 cm (tree 1, with minimal branch length of 3 My) or 5 cm (tree 2, with a minimal branch length of 5 My), or no less than 2.5 cm, if the lower end of the 95% confidence intervals are used. This is followed by a substantial size increase preceding the origin of amniotes. Placing *Westlothiana* among reptiliomorphs is the most consistent with Carroll's scenario, although it also has the least bootstrap support (Laurin and Reisz, 1999). This hypothesis would suggest a fairly early appearance of the amniotic egg (if Carroll's premises are accepted), probably during the Visean or the Serpukhovian. Indeed, enforcing a 3-My minimal branch length also leads to infer an appearance of amniotes in the Visean, and the amniotic egg would have been present by then.

The traditional phylogeny (Fig. 2) is much less favourable to Carroll's scenario because it leads to infer a minimal cranial length of 3.7 cm in stem-reptiliomorphs. This was to be expected because in this phylogeny, many clades of stem-reptiliomorphs are present, and all except *Westlothiana* are at least moderately large.

Presacral length optimization.—Using the presacral length of the vertebral column, a similar pattern emerges, even though there are a few differences and less information (because there are fewer taxa in these optimizations). The following discussion will emphasize the differences. There is still a size decrease in amphibians (Fig. 9), especially those closely related to lissamphibians, but the sister-group of Lissamphibia (the lysorophian *Brachydectes*) is not small because this animal has a long, slender body. However, the long body of lysorophians is probably an autapomorphy of this taxon, so the actual ancestors of lissamphibians in the Lower Permian were probably small, perhaps about 7 cm long, in the Moscovian, like the last common ancestor of *Brachydectes* and brachystelechids. There seems to be no decrease in body size in early reptiliomorphs; presacral length grows slightly from 19 cm at the base of Tetrapoda (Table 8, tree 1) to 22 cm at the base of Cotylosauria. This is inconsistent with prediction 2. Early stem-reptiliomorphs appear to have been much larger than Carroll predicted, with a presacral length of more than 18 cm. This is inconsistent with prediction 3. Within amniotes, there seems to be at least a moderate size increase, especially noticeable in synapsids (Fig. 10). Thus, prediction 4 is supported.

The impact of internal branch length and topology on presacral length optimization.—Placing *Westlothiana* at the base of Amphibia results in few changes; this increases the size of the first reptiliomorphs somewhat (Table 8, trees 1Wa, 2Wa).

Placing *Westlothiana* at the base of Reptiliomorpha causes a small size reduction (to 15 or 17 cm) associated with the origin of reptiliomorphs, followed by an increase in size in cotylosaurs (Table 8, trees 1Wr, 2Wr). However, even under this phylogenetic hypothesis, which is the most favorable to Carroll's scenario, the presacral length remains well above the prediction; the minimal size in stem-reptiliomorphs is near 9.5 cm

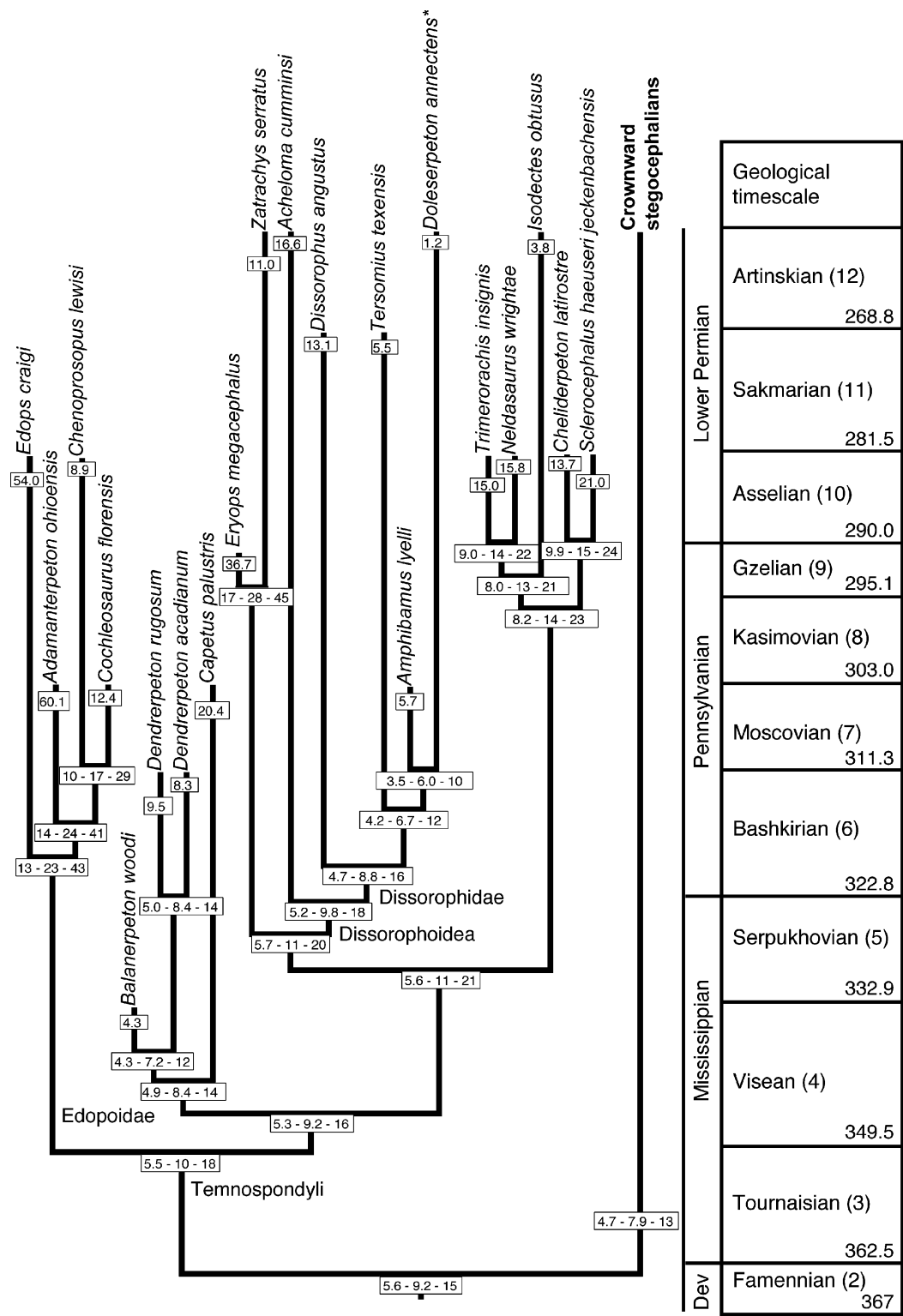


FIGURE 4. Cranial length evolution in temnospondyls. The taxon (*Doleserpeton*) marked by an asterisk (*) has been argued to be closely related to lissamphibians, or to at least anurans. All lengths are expressed in cm, and represent the distance from the anterior tip of the premaxilla to the posterior end of the skull table. Extant taxa are in bold type.

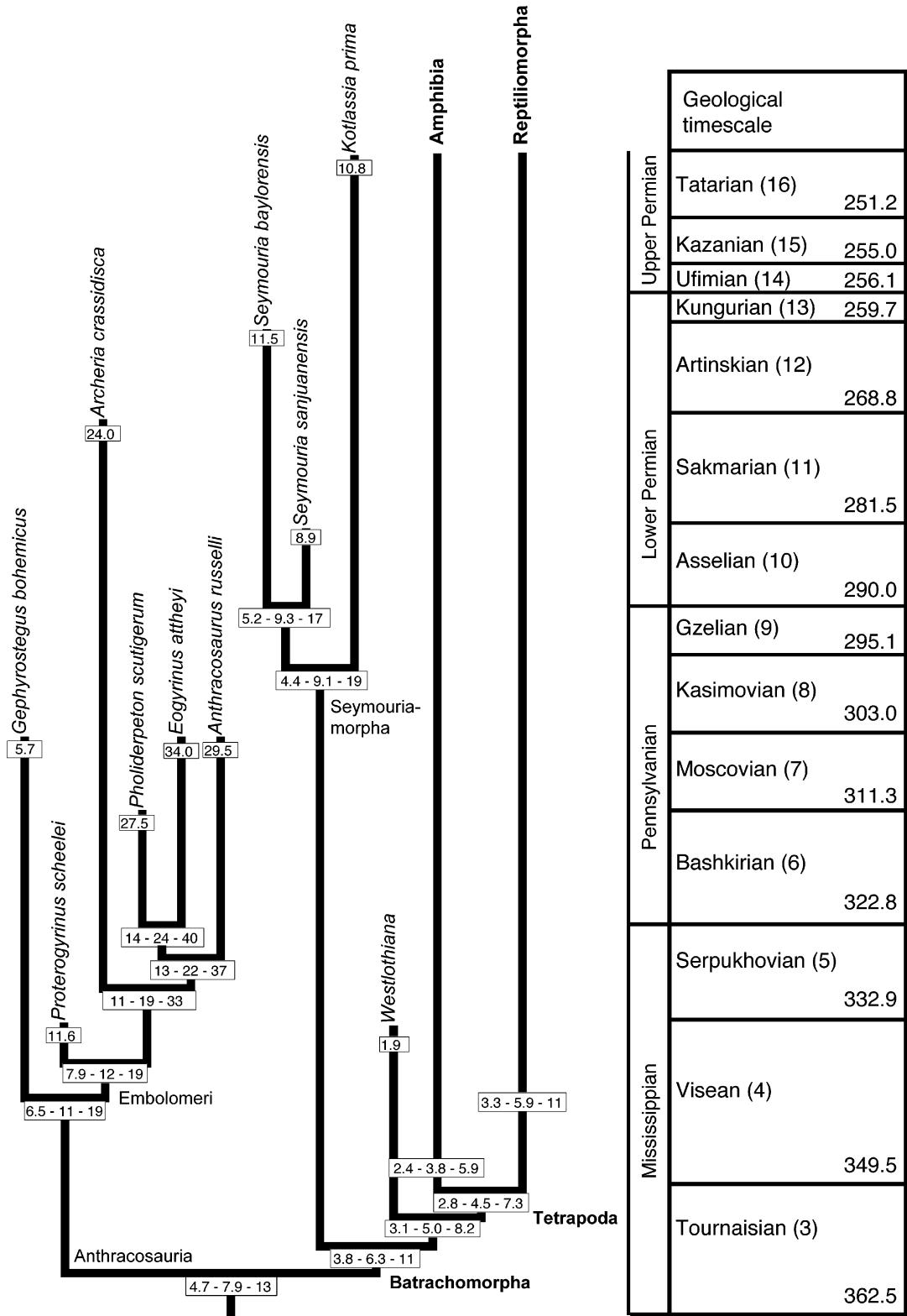


FIGURE 5. Cranial length evolution in anthracosaurs and seymouriamorphs. All lengths are expressed in cm, and represent the distance from the anterior tip of the premaxilla to the posterior end of the skull table. Abbreviations: M. Per, Middle Permian; U. Per, Upper Permian. Extant taxa are in bold type.

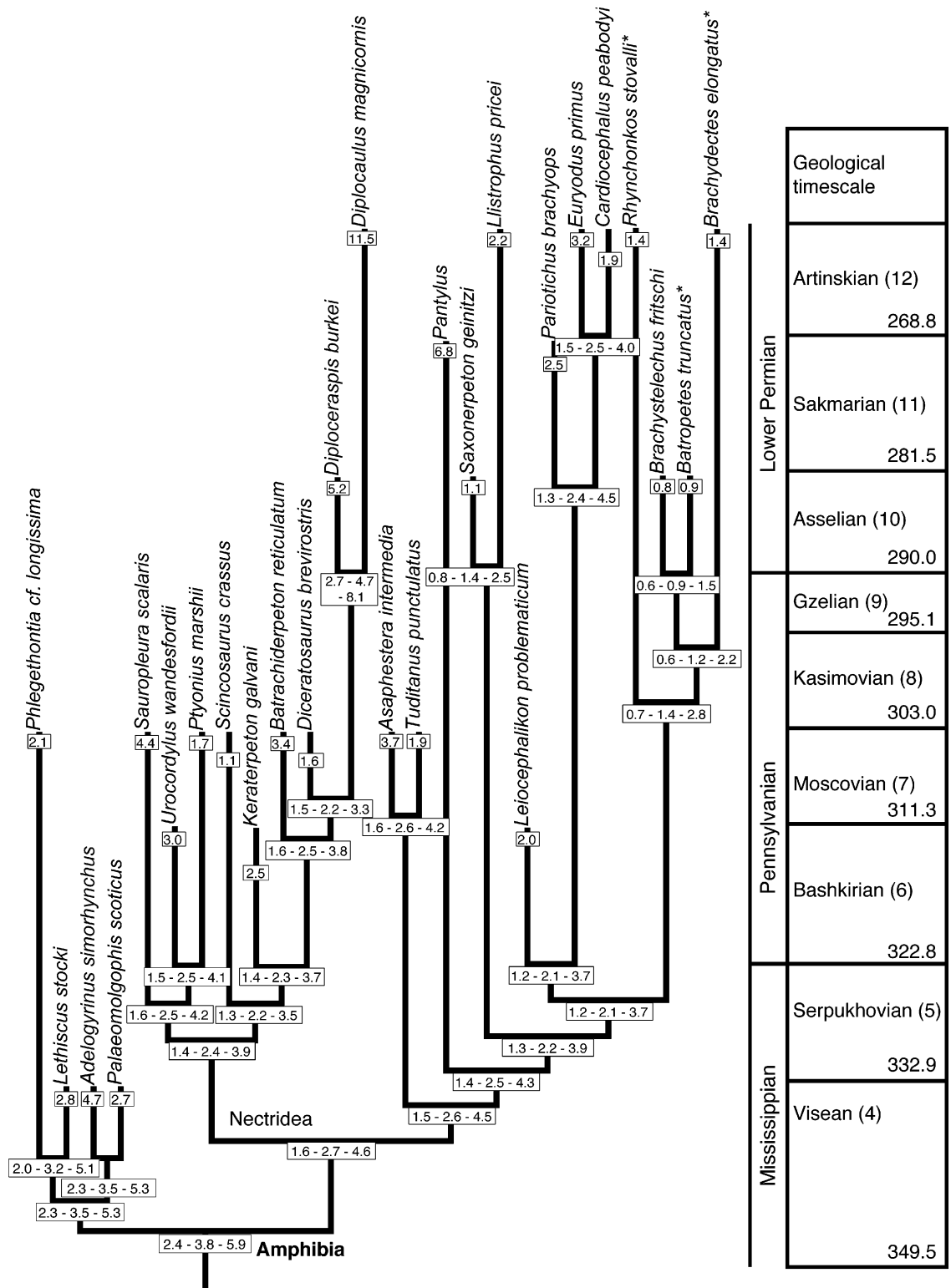


FIGURE 6. Cranial length evolution in early amphibians. The taxa marked by an asterisk (*) have been argued to be closely related to lissamphibians, or to at least one group of lissamphibians. All lengths are expressed in cm, and represent the distance from the anterior tip of the premaxilla to the posterior end of the skull table. Extant taxa are in bold type.

TABLE 7. Impact of branch length and topology on cranial length optimization. All lengths are in cm. In each case, the three values given are (as in Figs. 3 to 10) the lower bound of the 95% confidence interval, the best estimate, and the upper bound of the 95% confidence interval, respectively. The trees are described in Tables 5 and 6 and illustrated in Figures 1 and 2, except for trees 1Wa, 1Wr, 2Wa, 2Wr, which are simply trees 1 and 2 in which *Westlothiana* is placed among amphibians (Wa) or reptiliomorphs (Wr), as shown in Figure 1.

Node	Tree 1	Tree 1Wa	Tree 1Wr	Tree 2	Tree 2Wa	Tree 2Wr	Tree 3
1 (Tetrapoda)	2.8, 4.5, 7.3	3.3, 5.5, 8.9	2.8, 4.4, 7.1	2.8, 4.7, 7.8	3.2, 5.5, 9.4	2.9, 5.1, 8.7	6.8, 12, 20
2	N/A	N/A	2.5, 4.0, 6.5	N/A	N/A	2.8, 4.8, 8.5	3.9, 7.2, 13
3	3.3, 5.9, 11	3.7, 6.6, 12	2.8, 4.7, 7.9	3.1, 5.5, 9.9	3.5, 6.5, 12	3.1, 5.6, 10	4.0, 7.4, 14
4 (Cotylosauria)	3.5, 6.1, 11	3.8, 6.6, 12	3.0, 5.2, 8.8	3.3, 6.0, 9.9	3.6, 6.7, 12	3.3, 6.0, 11	3.9, 7.3, 14
5 (Amniota)	3.5, 6.0, 10	3.7, 4.7, 11	3.1, 5.3, 8.9	3.3, 5.9, 10	3.6, 6.4, 11	3.3, 5.9, 11	3.7, 6.8, 12
6 (Sauropsida)	3.1, 5.4, 9.3	3.3, 5.6, 9.7	2.9, 4.9, 8.5	2.9, 5.3, 9.6	3.1, 5.6, 10	2.9, 5.3, 9.6	3.1, 5.8, 11
7 (Synapsida)	3.9, 6.9, 12	4.0, 7.2, 13	3.6, 6.4, 12	3.9, 7.3, 14	4.1, 7.6, 14	3.9, 7.3, 14	4.1, 7.8, 15

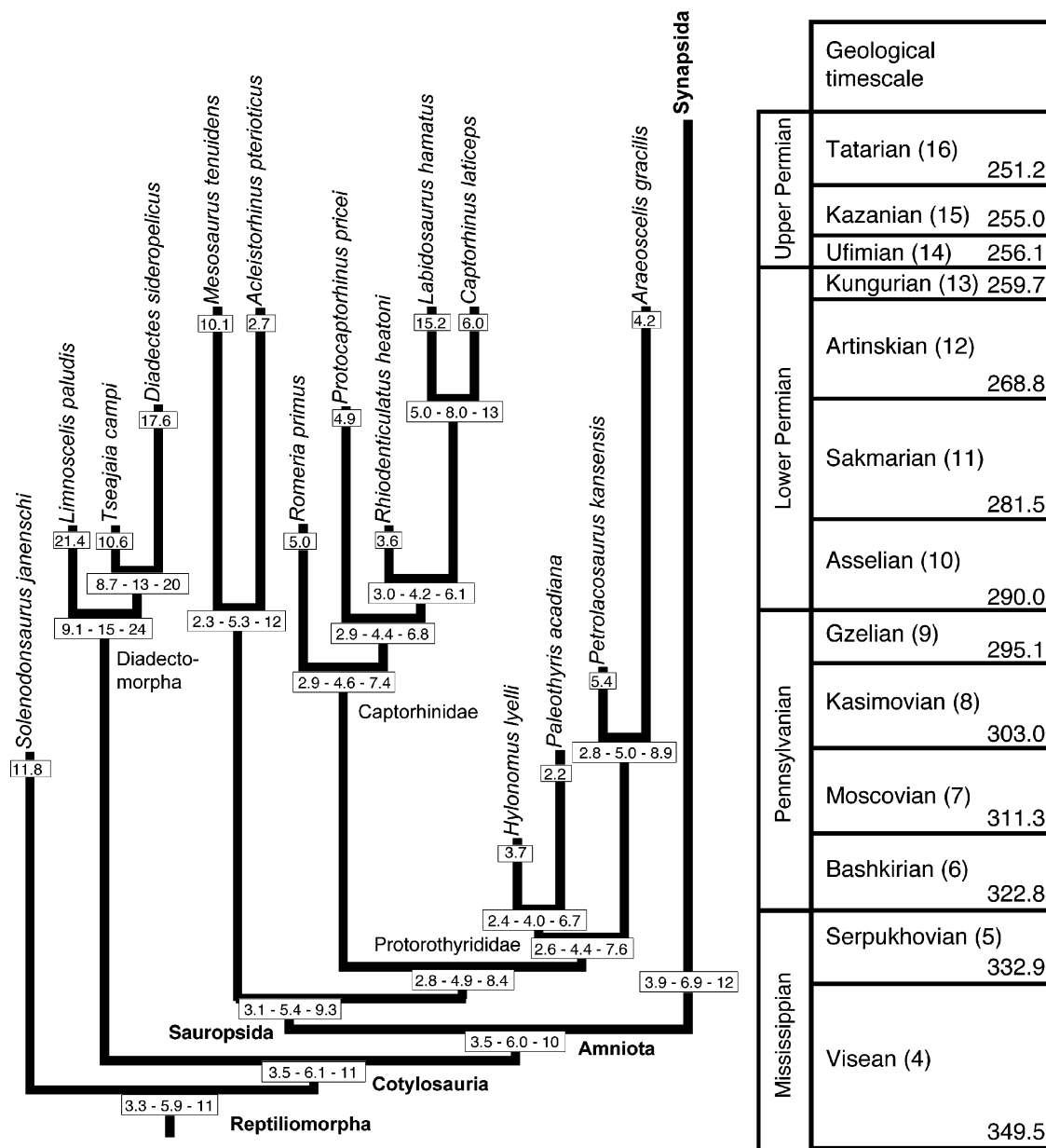


FIGURE 7. Cranial length evolution in reptiliomorphs. All lengths are expressed in cm, and represent the distance from the anterior tip of the premaxilla to the posterior end of the skull table. Abbreviations as in Figure 4. Extant taxa are in bold type.

TABLE 8. Impact of branch length and topology on presacral length optimization. All lengths are in cm. In each case, the three values given are (as in Figs. 3 to 10) the lower bound of the 95% confidence interval, the best estimate, and the upper bound of the 95% confidence interval, respectively. The trees are described in Tables 5 and 6 and illustrated in Figures 1 and 2, except for trees 1Wa, 1Wr, 2Wa, 2Wr, which are simply trees 1 and 2 in which *Westlothiana* is placed among amphibians (Wa) or reptiliomorphs (Wr), as shown in Figure 1. Node 3 cannot be evaluated because the presacral length of *Solenodonsaurus* is unknown.

Node	Tree 1	Tree 1Wa	Tree 1Wr	Tree 2	Tree 2Wa	Tree 2Wr	Tree 3
1 (Tetrapoda)	12, 19, 31	13, 21, 34	12, 19, 20	11, 19, 31	12, 20, 36	11, 18, 30	20, 33, 57
2	N/A	N/A	9.5, 15, 24	N/A	N/A	10, 17, 30	13, 24, 45
4 (Cotylosauria)	12, 22, 39	13, 23, 41	10, 17, 28	12, 22, 40	12, 23, 44	11, 19, 35	13, 25, 48
5 (Amniota)	13, 22, 37	13, 22, 39	11, 18, 30	12, 22, 39	13, 23, 42	11, 20, 36	13, 24, 44
6 (Sauropsida)	11, 19, 33	11, 20, 34	10, 17, 29	10, 19, 35	11, 20, 36	9.9, 18, 33	11, 20, 38
7 (Synapsida)	15, 27, 49	15, 27, 50	13, 24, 43	15, 29, 55	16, 30, 56	15, 28, 52	16, 31, 59

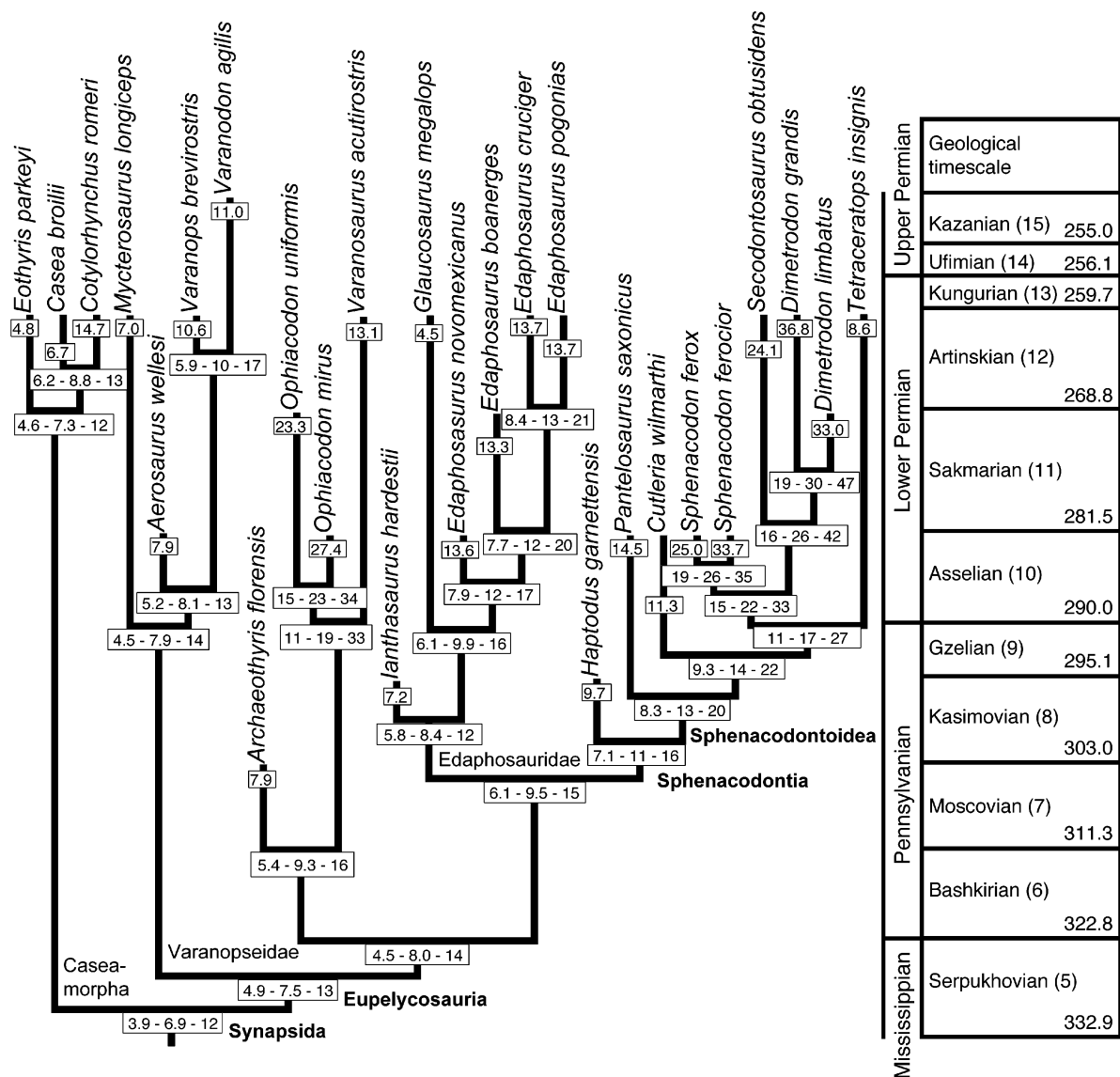


FIGURE 8. Cranial length evolution in synapsids. All lengths are expressed in cm, and represent the distance from the anterior tip of the premaxilla to the posterior end of the skull table. Extant taxa are in bold type.

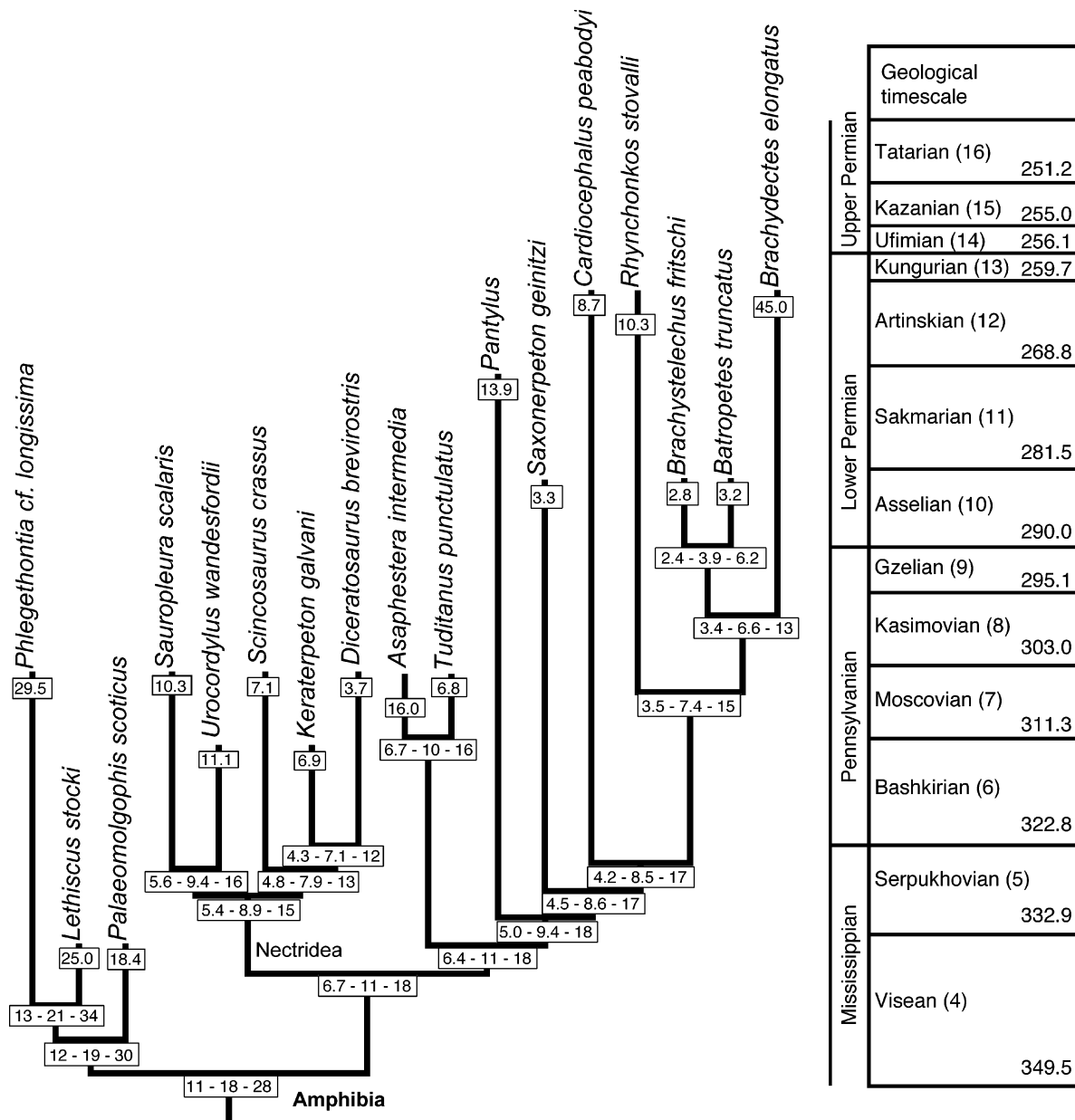


FIGURE 9. Presacral length evolution in early amphibians. The taxa marked by an asterisk (*) have been argued to be closely related to lissamphibians, or to at least one group of lissamphibians. All lengths are expressed in cm, and represent the distance from the anterior tip of the atlantal centrum to the anterior tip of the sacral centrum. Extant taxa are in bold type.

(lower limit of the 95% confidence interval), and when added to the corresponding cranial length (about 2.5 cm), this results in a snout-vent length of at least 12 cm.

Statistical Assessment of Body Size Evolution

The multiple regression analysis performed using Permute 3.4 alpha 9 on cranial length (log-transformed) versus geological time and controlling for phylogenetic distance suggests that there was no global trend toward cranial size increase (or decrease) with geological time in stegocephalians (Table 9). A simple plot of average cra-

nial length (log-transformed) over time strengthens this conclusion (Fig. 11a). Thus, prediction 1 is not supported. If the analysis was restricted to reptiliomorphs (to test Carroll's hypothesis that early amniotes increased in size after the amniotic egg appeared), their apparent size increase (Fig. 11c) was not statistically significant (Table 9). Analyses within synapsids and sauropsids failed to yield significant results. Only including *Westlothiana* with reptiliomorphs yielded a significant trend towards size increase, consistent with prediction 4 (Table 1). This is not surprising because *Westlothiana* is much older than all undisputed reptiliomorphs, and it is smaller than all of

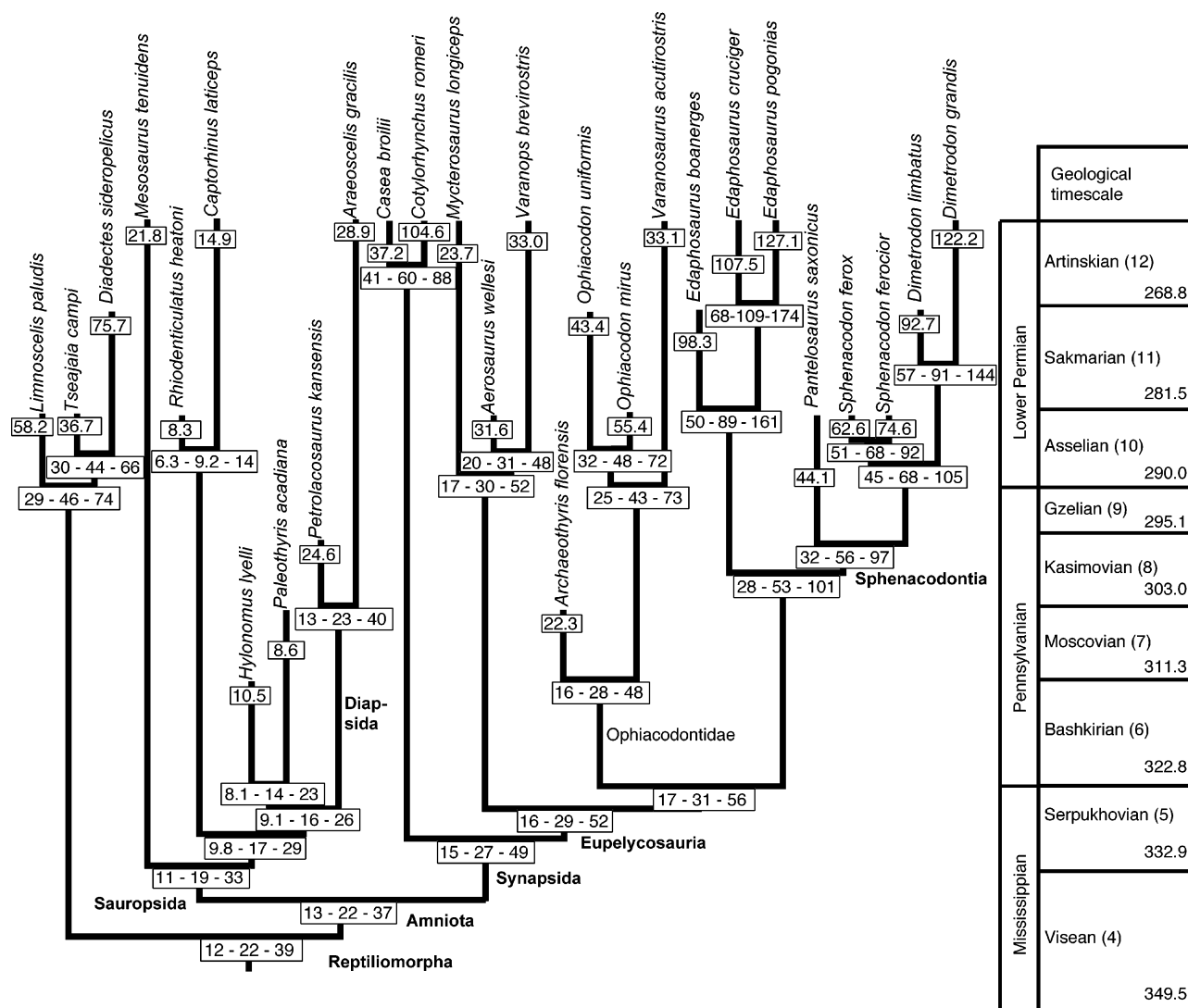


FIGURE 10. Presacral length evolution in early reptiliomorphs. All lengths are expressed in cm, and represent the distance from the anterior tip of the atlantal centrum to the anterior tip of the first sacral centrum. Extant taxa are in bold type.

them in cranial length (Appendix 2). However, as mentioned above, the position of *Westlothiana* is uncertain, and its most parsimonious placement is on the tetrapod stem (Laurin and Reisz, 1999) or on what is here interpreted as the amphibian stem (Ruta et al., 2003). Under the most parsimonious hypotheses, there seems to be no trend towards increase of cranial lengths in our dataset.

These analyses also show that geological time and phylogenetic distance explain a very small proportion of the observed variation in cranial length ($r^2 = 0.053$ or less), although the effect of phylogenetic distance is probably underestimated by this method because the relationship between this distance and the size difference is probably not linear. The results obtained by random tree length distribution support this hypothesis because the phylogenetic signal is fairly strong (Table 5).

Independent contrast analyses yield congruent results; there appears not to be an increase in cranial length in

stegocephalians, reptiliomorphs, synapsids, or sauropsids (Table 9). The single exception is a marginally significant size increase in reptiliomorphs if *Westlothiana* is placed at the base of reptiliomorphs, but if corrections are made for the fact that the hypothesis of size increase is tested multiple times in reptiliomorphs (Scherrer, 1984: 438–440; Zar, 1984: 162–163), this result becomes non-significant.

Similar analyses performed on presacral vertebral column length yield slightly different results. Multiple linear regression analyses reveal an increase in presacral vertebral column length in reptiliomorphs under all phylogenies (Table 10; Fig. 11d), whether or not *Westlothiana* is included, and this supports prediction 4 (correction for multiple tests still indicate a statistically significant result). The proportion of the variance explained by the geological time and phylogeny reaches nearly 0.16, when *Westlothiana* is included (Table 10). Presacral length also

TABLE 9. Evolution of the skull length (log-transformed) through time. This analysis is based on a permutational multiple linear regression analysis and independent contrast analysis (using least squares regression). The effect of phylogenetic relationships and of geological age on size variations is assessed by the probability that the value of their b coefficients (slope of regression of size versus geological time) are 0. For the permutational regression analysis, statistical significance was based on 999 replicates. The differences between the trees are explained in the legend of Tables 5 and 6.

Tree	Taxon	N	Permutational multiple regression analysis					Independent contrast analysis		
			B coefficient geological age	Probability geological age	B coefficient phylogenetic	Probability phylogenetic	R^2 (total)	Slope	Probability (2-tailed)	R^2
1	All	107	-0.0397	0.161	0.0808	0.034*	0.0090	0.0041	0.287	0.0108
1	Reptiliomorpha (with <i>Westlothiana</i>)	42	0.2074	0.009**	0.1007	0.082	0.0471	0.01280	0.038*	0.1028
1	Reptiliomorpha (without <i>Westlothiana</i>)	41	0.0510	0.196	0.0929	0.105	0.0095	0.0077	0.247	0.0342
1	Synapsida	26	-0.0482	0.317	0.0803	0.234	0.0102	0.0039	0.631	0.0097
1	Sauropsida	11	0.0244	0.363	0.0973	0.290	0.0096	0.0127	0.319	0.1100
2	All	107	-0.0488	0.109	0.0911	0.012*	0.0109	0.0043	0.262	0.0120
2	Reptiliomorpha (with <i>Westlothiana</i>)	42	0.2062	0.011*	0.1269	0.048*	0.0531	0.0105	0.092	0.0694
2	Reptiliomorpha (without <i>Westlothiana</i>)	41	0.0527	0.190	0.1164	0.057	0.0144	0.0068	0.297	0.0278
2	Synapsida	26	-0.0378	0.372	0.1222	0.102	0.0183	0.0033	0.677	0.0073
2	Sauropsida	11	0.0234	0.364	0.0909	0.293	0.0084	0.0117	0.3745	0.0884
3	All	107	-0.0340	0.218	0.1297	0.001***	0.0192	0.0013	0.733	0.0011
3	Reptiliomorpha	55	0.0983	0.054	0.0100	0.436	0.0099	0.0083	0.114	0.0466

*Statistically significant at a 0.05 threshold; **statistically significant at a 0.01 threshold. N refers to the number of terminal taxa included in each analysis. For the independent contrast analysis, the P -value is from a standard least square regression analysis (sign tests usually yield higher probabilities).

appears to increase in synapsids. However, for the other groups tested (all stegocephalians, sauropsids), no significant trend was detected.

Independent contrast analyses yield similar results (no presacral length increase in stegocephalians, but an increase in reptiliomorphs, especially if *Westlothiana* is included), although the probabilities are generally higher (the marginally significant result for presacral length increase in stegocephalians found in tree 2 becomes non-significant if a correction for multiple tests is done). Thus, the size increase in reptiliomorphs is clearly significant if *Westlothiana* is included, but if this genus is excluded, the results are only marginally significant (Table 10). Again, the position of *Westlothiana* has a significant impact, and this is consistent with its geolog-

ical age (it predates all undisputed reptiliomorphs by more than 20 My) and its small size (the only undisputed reptiliomorph that has a slightly shorter presacral length is the sauropsid *Paleothyris*). Independent contrast analysis fails to reveal a significant presacral length increase in synapsids (this is consistent with the generally higher probabilities than using permuted multiple linear regressions).

The contradiction between the size increase in presacral length and the absence of increase in cranial size may be explained by a change in body proportions. However, regression of the skull length/presacral length ratio on geological time failed to show a statistically significant trend in reptiliomorphs or in stegocephalians (Table 11).

TABLE 10. Evolution of presacral vertebral column length (log-transformed) through time. This analysis is based on a permutational multiple linear regression analysis and independent contrast analysis (using least squares regression). The effect of phylogenetic relationships and of geological age on size variations is assessed by the probability that the value of their b coefficients (slope of regression of size versus geological time) are 0. For the permutational regression analysis, statistical significance was based on 999 replicates. The differences between the trees are explained in the legend of Tables 5 and 6.

Tree	Taxon	N	Permutational multiple regression analysis					Independent contrast analysis		
			B coefficient geological age	Probability geological age	B coefficient phylogenetic	Probability phylogenetic	r^2	Slope	Probability (2-tailed)	r^2
1	All	63	-0.0521	0.130	0.1194	0.049*	0.01778	0.0074	0.106	0.0422
1	Reptiliomorpha (with <i>Westlothiana</i>)	28	0.3795	0.001***	0.2052	0.004**	0.1582	0.0181	0.004**	0.2812
1	Reptiliomorpha (without <i>Westlothiana</i>)	27	0.3053	0.006**	0.2125	0.007**	0.1086	0.0169	0.027*	0.1806
1	Synapsida	17	0.2065	0.032*	0.3251	0.004**	0.1184	0.0125	0.248	0.0880
1	Sauropsida	7	0.131	0.221	0.1016	0.309	0.0195	0.0137	0.688	0.3519
2	All	63	-0.0665	0.065	0.0905	0.094	0.0117	0.0092	0.050*	0.0615
2	Reptiliomorpha (with <i>Westlothiana</i>)	28	0.3677	0.001***	0.2031	0.005**	0.1580	0.0177	0.008**	0.2402
2	Reptiliomorpha (without <i>Westlothiana</i>)	27	0.2992	0.006**	0.2125	0.006**	0.1092	0.0164	0.032*	0.1713
2	Synapsida	17	0.2010	0.035*	0.2763	0.007**	0.0899	0.0131	0.235	0.0926
2	Sauropsida	7	0.1102	0.220	0.0909	0.325	0.0175	0.0132	0.174	0.3348
3	All	63	-0.0356	0.284	0.2225	0.001***	0.0523	0.0049	0.281	0.0190
3	Reptiliomorpha	35	0.1567	0.044*	0.0165	0.441	0.0246	0.0116	0.057	0.1053

*Statistically significant at a 0.05 threshold; **statistically significant at a 0.01 threshold; ***statistically significant at a 0.001 threshold. N refers to the number of terminal taxa included in each analysis. For the independent contrast analysis, the P -value is from a standard least square regression analysis (sign tests usually yield higher probabilities).

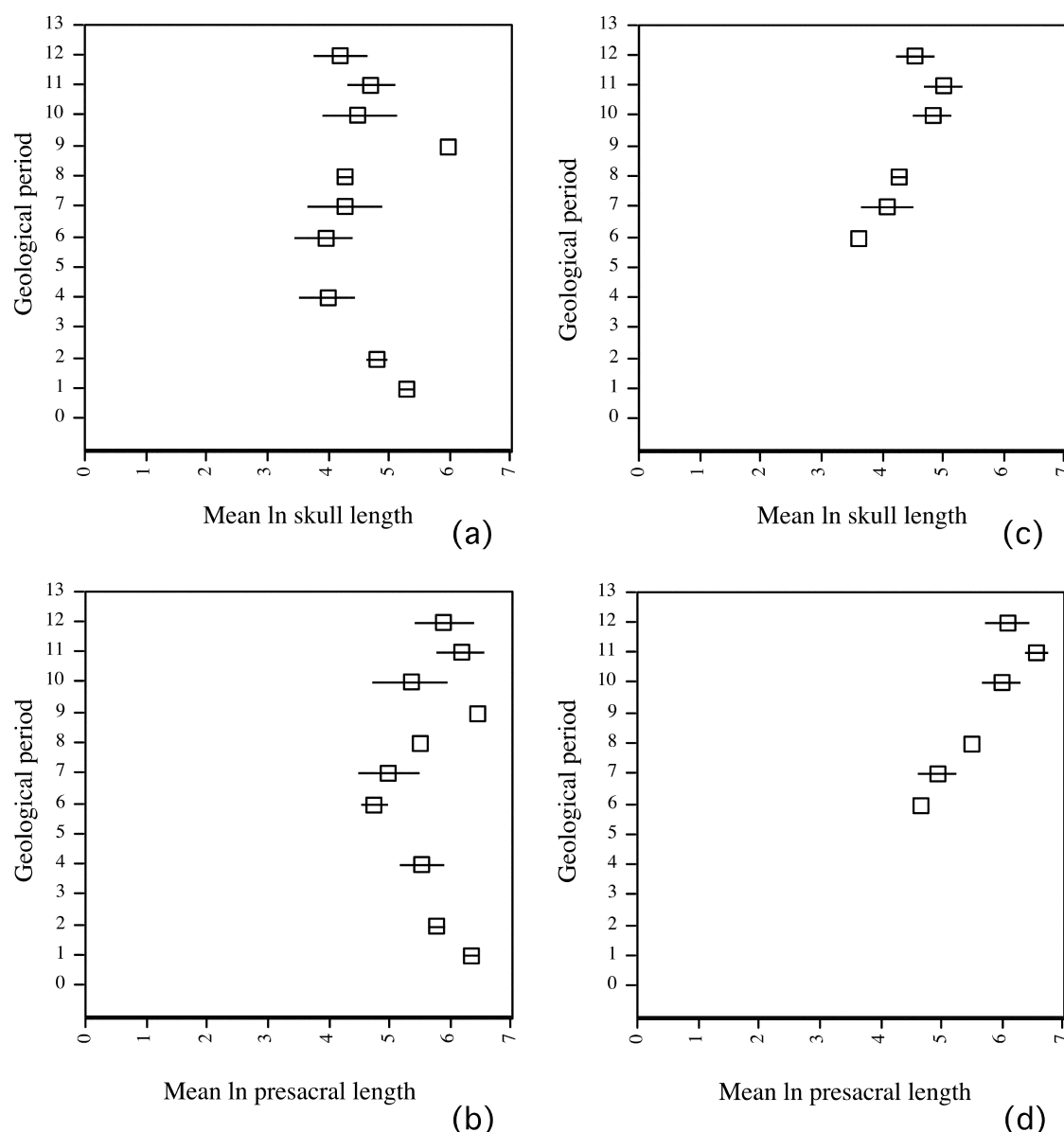


FIGURE 11. Mean body size (x -axis) through time (y -axis). (a) Mean cranial length of stegocephalians. (b) Mean presacral length of stegocephalians. (c) Mean cranial length of reptiliomorphs. (d) Mean presacral length of reptiliomorphs. For reptiliomorphs (c, d), there are no size data before period 6 because reptiliomorphs appear in the fossil record at that time; no size data are available for that group in period 9. In period 1, sampled taxa are finned, primitively aquatic sarcopterygians closely related to stegocephalians; periods 2 to 12 are represented only by stegocephalians. The time periods are defined in Appendix 3. All values have been log-transformed (\ln of the dimensions, in mm). The horizontal bars passing through each point represent the standard deviation. Points without bars represent single values. There are no data for period 3.

DISCUSSION

Character optimization, permutational multiple regressions and independent contrast analyses show that there was no general body size increase in early stegocephalian evolution (between the Devonian and the Lower Permian). Thus, prediction 1 is rejected (Table 1). This is not surprising because in many instances, trends towards body size increase in a taxon result from the small size of the ancestral species of a group. In such cases, the trend towards body size increase simply results

from the diversification of the taxon and the appearance of species of the various body sizes that are compatible with their ecology, morphology, developmental constraints, etc. Arnold et al. (1995: Fig. 4) showed that the Cretaceous-Tertiary event eliminated the large species of planktonic foraminifera, and that the small Danian surviving species diversified and increased progressively in size throughout the tertiary, as they returned more or less to the same average size as their Cretaceous predecessors. Norris (1991: Fig. 7) argued for three successive extinction events that eliminated species or large size

TABLE 11. Evolution of the cranial length/presacral length ratio through time. This analysis is performed using permutational multiple linear regression analysis for (based on 999 replicates).

Tree	Taxon	N	Permutational multiple regression analysis					Independent contrast analysis		
			B coefficient geological age	Probability geological age	B coefficient phylogenetic	Probability phylogenetic	R ²	Slope	Probability (2-tailed)	R ²
1	Stegocephali	63	-0.0249	0.326	0.1413	0.013*	0.0211	0.0002	0.8258	0.0008
1	Reptiliomorpha and <i>Westlothiana</i>	28	-0.0396	0.393	0.1542	0.025*	0.0275	0.0002	0.8505	0.0014
1	Reptiliomorpha (excluding <i>Westlothiana</i>)	27	-0.0366	0.352	0.1591	0.041*	0.0293	-0.0011	0.3383	0.0367
2	Stegocephali	63	-0.0432	0.191	0.1239	0.029*	0.0164	0.0003	0.6930	0.0026
2	Reptiliomorpha and <i>Westlothiana</i>	28	-0.0396	0.393	0.1542	0.025*	0.0275	-0.0001	0.8964	0.0007
2	Reptiliomorpha (excluding <i>Westlothiana</i>)	27	-0.0437	0.318	0.1464	0.050*	0.0259	-0.0010	0.3706	0.0322
3	Stegocephali	63	-0.0405	0.230	0.1217	0.018*	0.0174	-0.0002	0.7777	0.0013
3	Reptiliomorpha	35	-0.0749	0.170	0.0314	0.334	0.0068	-3.4E - 5	0.9656	0.0001

*Statistically significant at a 0.05 threshold; **statistically significant at a 0.01 threshold.

followed by evolutionary radiations that resulted in average size increase in Cretaceous and Tertiary foraminifera. Mesozoic mammals were always rather small, perhaps because most ecological niches in terrestrial ecosystems were occupied by dinosaurs, and with the extinction of most dinosaurs at the end of the Cretaceous, this constraint was lifted and this could explain why tertiary mammals showed a trend towards body size increase. By contrast, the earliest stegocephalians were not particularly small (Fig. 11a, b), so the lack of a trend towards body size increase is not surprising.

Optimization over most phylogenies suggests that there was no decrease in body size in early reptiliomorphs before the amniotic egg appeared. However, this conclusion rests on placement of *Westlothiana* either as a stem-tetrapod (most parsimonious hypothesis) or as a basal stem-amphibian. Placing *Westlothiana* as a stem-reptiliomorph does lead to the conclusion that there was a slight size reduction in early reptiliomorphs. Furthermore, the fossil record of early reptiliomorphs is poor. Thus, prediction 2 (Table 1) is only tentatively rejected.

No matter where *Westlothiana* is placed, optimization suggests that no ancestor of amniotes had a snout-vent length inferior to about 12 cm (a cranial length of 2.5 cm and a presacral length of 9.5 cm). This result takes into consideration the uncertainty of the squared-change parsimony optimization, all plausible topologies and branch lengths. The best estimate of the size of stem-reptiliomorphs on all the phylogenies suggests that stem-reptiliomorphs were not particularly small (at least 19 cm in snout-vent length), even if *Westlothiana* is placed in that group. Thus, prediction 3 (Table 1) is rejected. The only caveat here is that the fossil record of early reptiliomorphs is poor.

There is no general trend towards cranial size increase in reptiliomorphs (unless *Westlothiana* is considered a reptiliomorph), synapsids or sauropsids. However, there is a trend towards presacral length increase in reptiliomorphs. Thus, prediction 4 is confirmed. The trend towards increase in presacral length in reptiliomorphs probably results, as in the other groups that seem to obey Cope's rule, from the small size of the ancestral and oldest species (Fig. 11d).

Of the three predictions derived from Carroll's (1970b, 1991) scenario on the origin of amniotes, one (prediction 3, that some stem-reptiliomorphs measured less than 10 cm in snout-vent length) is refuted, one (prediction 4, that reptiliomorphs increased in size after the origin of the amniotic egg) is confirmed, and one (prediction 2, that stem-reptiliomorphs decreased in size, prior to the appearance of the amniotic egg) can neither be confidently rejected nor confirmed. Thus, the premises that led to the formulation of Carroll's interesting scenario on the origin of amniotes might need to be revised, although part of the scenario may be correct. The idea that stem-reptiliomorphs laid anamniotic eggs on land remains plausible, but the available evidence suggests either that the eggs may have been larger than Carroll (1970b, 1991) inferred, despite their lack of extraembryonic membranes, or that the adult body size of stem-reptiliomorphs was not as tightly constrained by the egg size as Carroll (1991) proposed. Alternatively, if stem-reptiliomorphs did experience a strong size reduction, it is possible that the critical fossils have not yet been found or recognized, and indeed, they may never be discovered.

Remaining Problems

Accuracy of the nodal values.—Character value at nodes can never be known with certainty. Even though squared change parsimony is preferable to linear (Wagner parsimony) to infer character value at a node (Martins, 1999), this does not mean that the nodal value estimates are necessarily reliable. Several recent studies raised doubts about the precision of nodal character value obtained from optimization (Martins, 1999; Oakley and Cunningham, 2000; Webster and Purvis, 2002). These studies assessed the performance of various methods (squared change parsimony, maximum likelihood, and two variants of the generalized least squares method (GLS-linear and GLS-exponential) for inferring nodal values. Accuracy of the estimates was obtained by comparisons with real node values, which were known either because the data had been generated by simulation (using either Brownian motion or other models that include either stabilizing selection or trends), because the

evolution of the lineages had been observed (Oakley and Cunningham, 2000), or because fossils were postulated to represent the ancestors of the taxa investigated (Polly, 2001; Webster and Purvis, 2002).

Most studies found that character value at nodes was poorly estimated. However, simulations show that these methods performed best under Brownian motion, but that even under that assumption, estimates of character value at the root were especially imprecise (Martins, 1999; Oakley and Cunningham, 2000). Accuracy decreased with increasing evolutionary rates (Oakley and Cunningham, 2000). Even methods that attempt to take into consideration stabilizing selection (like the GLS-exponential method) give poor results in the presence of such a selection (Martins, 1999).

Only three original datasets not produced by simulation have been used to assess the accuracy methods of nodal value estimation. Oakley and Cunningham (2000) generated a phylogeny of viruses by subjecting them to radiations. Nodal values were known because the phenotypes were determined at various times during the experiment. Nodal estimates obtained by optimization were relatively imprecise, and this was attributed mostly to evolutionary trends. Webster and Purvis (2002) compared node estimates obtained by optimization of data on Pliocene and Pleistocene foraminifera with observed character value of the hypothesized ancestors (that were older foraminifer species from the Miocene and the Pliocene). They found that the methods that they tested (including squared change parsimony and GLS) yielded fairly inaccurate results, and they attribute this disappointing result to the presence of an evolutionary trends or noise in the characters. Polly (2001) studied molar area in five coeval (Eocene) viverravids (Carnivora), which were used to estimate node values, and four older (Paleocene) viverravids that he considered ancestors and that thus provided an independent assessment of ancestral node value. Polly's (2001) analysis is the only one that suggested that nodal values can be inferred fairly accurately using character optimization. This may be because it is based on the only original dataset (i.e. not generated by simulation) in which evolutionary trends were not pervasive.

In all these attempts to assess the accuracy of methods for inferring nodal character value, the terminal taxa were contemporaneous or nearly so (only the dataset of Webster and Purvis used terminal taxa whose age varied a little, but these variations were minor compared to the tree depth). Thus, these findings may not apply to this study on body size evolution of early stegocephalians because the data set presented here includes terminal taxa from a broad range of geological ages. Therefore, contrary to the above studies, the nodal values near the root in my study are not necessarily less accurate than in other parts of the tree (Fig. 3). None of the extinct species included in this study is considered an ancestor of the others because identifying ancestors is a difficult problem and requires using negative evidence (Nelson, 1989; Smith, 1994: 126-128), and because most of the species included in this study have autapomorphies that indi-

cate that they are not the ancestors of other, later species. Therefore, it is not possible to verify directly the accuracy of the nodal estimates.

None of the previous studies cited above assessed the phylogenetic signal of the data. The finding that random taxon reshuffling on the data of Oakley and Cunningham (2000) and on most of the characters used by Webster and Purvis (2002) did not reveal a phylogenetic signal (Tables 2, 3) is reassuring because it shows that there were no reasons to expect that the optimizations would yield accurate results. Furthermore, of the four characters analyzed by Webster and Purvis (2002), only one (shape, or width/length) has a marginally significant phylogenetic signal ($P = 0.050$), and it is precisely the only character for which they reported (p. 146 and table 2b) that the inferred states did not differ significantly from the real values (i.e., the real value was included within the 95% confidence interval of the inferred nodal value, assuming that they identified the actual ancestors correctly). Conversely, the dataset from Polly (2001), in which optimization yielded fairly accurate results, shows a (marginally significant) phylogenetic signal (Table 4). Thus, it seems that performing a random taxon reshuffling test may reveal whether or not the optimizations will yield reliable results. More work needs to be done to determine the relationship between accuracy of ancestral character value estimates and the presence of a phylogenetic signal (simulations would be especially useful), but the results of the reanalysis of the data of Oakley and Cunningham (2000), Webster and Purvis (2002), and of Polly (2001), along with the presence of a strong phylogenetic signal in the body size data (Tables 5, 6), suggest that the inferences on body size of early stegocephalians (Figs. 3 to 10) are reliable.

Unfortunately, no study has ever been attempted, to my knowledge, to determine whether or not body size evolution follows Brownian motion. This seems a reasonable hypothesis, but it would be interesting to test it. The results (Tables 9, 10) suggest that the trends in body size evolution in early stegocephalians are weaker (when present) than in the viruses studied by Oakley and Cunningham (2000) or the Neogene foraminifera studied by Webster and Purvis (2002). Because trends and other deviations from Brownian motion reduce the accuracy of nodal character value, the inferences of body size reported above are probably more accurate than those obtained by Oakley and Cunningham (2000) or Webster and Purvis (2002).

Independent contrasts vs. permuted multiple linear regressions.—Independent contrasts and permuted multiple linear regressions often gave different probabilities, although the results are broadly comparable in the sense that relationships that were the most statistically significant according to multiple regressions were also statistically significant in the independent contrast analysis. However, the latter technique generally yielded higher probabilities. Because the real relationship between body size, phylogeny, and geological time in the analyzed data set is unknown, it is difficult to determine from the results which technique is the most

accurate in this situation. However, the use of independent contrasts in this study is atypical in that the independent character (geological time) is not completely independent from the branch lengths, and the relationship between independent contrasts of this character and branch lengths is closer still. Thus, I suspect that permutational regressions yield more reliable results, but this would need to be verified using simulations. However, the fact that permutational multiple regressions and independent contrasts yielded broadly congruent results is reassuring because these methods are very different. Permutational multiple regressions are performed using various distance values between terminal taxa, and this does not require assessment of nodal values, whereas independent contrasts assess the magnitude and the direction of change in the dependent character (body size) through estimation of nodal values. The present dataset is in some ways well-suited for independent contrast analysis because of the presence of a strong phylogenetic signal and because taxa are distributed widely through the geological ages. Thus, nodal estimates of the dependent character should not only be fairly accurate, but they should not be more uncertain near the root than near the tips (an assertion supported by the values of the 95% confidence intervals of the nodal values). However, the statistical repercussions of the non-independence between contrasts of the independent character and branch lengths should be investigated (again, simulations appear necessary). This problem is beyond the scope of this study, in which I have simply used analytical methods that could incorporate geological time and phylogenetic position data.

Taphonomic artifacts.—At least part of Carroll's (1970b) scenario rests partly on a literal interpretation of the fossil record: the oldest known amniotes are indeed fairly small. However, these amniotes have been found in fossilized *Sigillaria* (an extinct lycopod) tree trunks that have a diameter of no more than about 60 cm. These tree trunks were initially filled by a loose tissue that decayed before their periphery. Thus, these trunks may have formed small traps, in which small animals were preserved. This type of preservation may create a bias toward preservation of small animals (Laurin and Reisz, 1997). However, despite this, some amniotes found in *Sigillaria* trunks in Joggins (the locality from which the oldest known amniotes are found, located in Nova Scotia, Canada) and Florence (a nearby, and geologically slightly younger locality) are only moderately small, with an estimated snout-vent length of about 30 cm. No attempt has been made to correct for this taphonomic bias because this would have resulted in the exclusion of many of the earliest amniotes, whose inclusion in this analysis was critical. The future discovery early amniotes in fossiliferous localities in which specimens are not found in tree trunks would no doubt yield valuable data to reevaluate Carroll's scenario on the appearance of amniotes and of the amniotic egg.

Taxa of uncertain affinities.—As mentioned above, the enigmatic taxon *Casineria* was excluded, and the

affinities of *Westlothiana* are uncertain. Nevertheless, if both *Casineria* and *Westlothiana* turned out to be stem-reptiliomorphs, and if they did not form a single clade of stem-reptiliomorphs, the conclusion that the origin of the amniotic egg was not associated with an important size reduction might need to be reassessed. However, the conclusion that stegocephalians do not seem to have globally increased in size during the Upper Carboniferous and the Lower Permian is less likely to be affected by future discoveries because the fossil record of that group is much better than that of stem-reptiliomorphs.

Incompleteness of the fossil record.—The greatest remaining problem in evaluating hypotheses on the origin of amniotes is the incompleteness of the fossil record of stem-reptiliomorphs. Under the preferred phylogeny, only two clades of stem-reptiliomorphs are known. Therefore, it is conceivable that if much more data were available on stem-reptiliomorphs and the earliest amniotes, some of the conclusions of this study could be altered. Unfortunately, much energy has been spent looking for such taxa in the last decades, but with little success.

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APPENDIX 1

Sources used to compile the main phylogeny (Fig. 1), classified by taxa.

- Sarcopterygii: Zhu and Schultze, 1997; Ahlberg and Johanson, 1998; Zhu et al., 2001.
- Stegocephali: Laurin and Reisz, 1997, 1999; Laurin, 1998a, 1998b.
- Baphetidae: Clack, 1998.
- Temnospondyli: Ingavat and Janvier, 1981; Milner, 1990; Trueb and Cloutier, 1991.
- Cochleosauridae: Milner and Sequeira, 1998.
- Embolomeri: Clack, 1987.
- Seymouriamorpha: Laurin, 1996a.
- Amphibia: as for Stegocephali, and Schultze and Foreman, 1981.
- Nectridea: Milner, 1980.
- Reptiliomorpha: see Stegocephali.
- Diadectomorpha: Sumida et al., 1992.
- Amniota: Laurin and Reisz, 1995; deBraga and Reisz, 1996.
- Synapsida: Reisz, 1986; Reisz et al., 1992; Laurin, 1993.
- Varanopidae: Reisz et al., 1998.
- Ophiacodontidae: Berman et al., 1995.
- Edaphosauridae: Modesto and Reisz, 1992.
- Sphenacodontidae: Reisz et al., 1992.
- Captorhinidae: Ricqlès, 1984; Dodick and Modesto, 1995.

APPENDIX 2. Cranial length, presacral length, and geological age of the studied taxa. Skull length was measured along the midline, from premaxilla to posterior end of skull table. Presacral length was measured from the anterior tip of the atlantal intercentrum to anterior edge of the first sacral centrum. For the legend of the geological stage of appearance, see Appendix 3. Time from origin measures the time elapsed between the beginning of the Givetian (time at which the oldest cladogenetic event between the included taxa must have taken place) and the age of the various taxa. All the Devonian to Lower Permian taxa for which cranial length and presacral column length could be determined and that could be placed in the phylogeny have been included. In addition, a few Upper Permian taxa that belong to higher taxa that were most diverse in Permo-Carboniferous times have been included. Thus, *Kotlassia prima* has been included because it is one of the few seymouriamorphs to have survived beyond the Lower Permian, but Upper Permian therapsids were not included. Abbreviations: ASL, average skull length (cm); APL, average presacral length (cm); GEA, geological epoch of appearance (oldest record only); NSL, number of specimens on which cranial length was measured; TEO, time elapsed since origin of clade. The numbers of specimens (NSL) reported are those from which measurements can be taken, either from illustrations or in tables, and that appear to be adults. For the presacral length (APL), a single specimen could be measured except for *Dimetrodon limbatus*, in which two were measured. When several incomplete specimens were used to produce a reconstruction, the reported number is one. References cited only in this appendix are found below; for those cited in the text and in this appendix, see the main bibliography.

Taxa	ASL	NSL	APL	GEA	TEO	Source of data
Choanates						
<i>Eusthenopteron foordi</i>	16.1	1	48.8	1	13.4	Andrews and Westoll, 1970: fig. 23
<i>Panderichthys rhombolepis</i>	23.3	1	59.1	1	13.4	Vorobyeva and Schultze, 1991: figs. 4, 19
Stegocephalians						
<i>Acanthostega gunnari</i>	8.3	1	25.4	2	17.9	Coates, 1996: figs. 1, 31
<i>Ichthyostega</i>	14.7	4	37.0	2	17.9	Jarvik, 1980: fig. 170; 1996: plates 2, 3, 8, 14
<i>Crassigyrinus scoticus</i>	21.4	1	60.9	4	47.5	Panchen, 1985: fig. 7; Panchen and Smithson, 1990: fig. 9
<i>Megalocephalus pachycephalus</i>	34.3	2		7	77.4	Beaumont, 1977: plates 1, 2
<i>Baphetes kirkbyi</i>	27.6	1		7	77.4	Beaumont, 1977: fig. 21
<i>Loxomma acutirhinus</i>	24.7	1		7	77.4	Beaumont, 1977: fig. 3
<i>Greerpeton burkemorani</i>	14.4	18	47.4	4	47.5	Godfrey, 1989a: fig. 1; Godfrey 1989b: appendix 1
<i>Colosteus scutellatus</i>	8.8	1		7	77.4	Hook, 1983: fig. 1
<i>Adamanterpeton ohioensis</i>	60.1	1		7	77.4	Milner and Sequeira, 1998: fig. 9
<i>Cochleosaurus florensis</i>	12.4	1		7	77.4	Rieppel, 1980: table 1
<i>Chenoprosopus lewisi</i>	8.9	1		10	98.9	Hook, 1993: fig. 1
<i>Edops craigi</i>	54.0	1		10	98.9	Romer and Witter, 1942: fig. 1
<i>Capetus palustris</i>	20.4	2		7	77.4	Sequeira and Milner, 1993: figs. 4, 6
<i>Balanerpeton woodi</i>	4.3	3	10.2	4	47.5	Milner and Sequeira, 1994: figs. 2–4
<i>Dendrerpeton acadianum</i>	8.3	1	17.0	6	69.1	Holmes et al., 1998: figs. 1, 4
<i>Dendrerpeton rugosum</i>	9.5	1		6	69.1	Milner, 1980: 129
<i>Eryops megacephalus</i>	36.7	9	60.0	9	90.4	Sawin, 1941: 410; Moulton, 1974: fig. 1
<i>Zatrachys serratus</i>	11.0	4		12	120.7	Schoch, 1997: figs. 1–4
<i>Acheloma cummingsi</i>	16.6	2		12	120.7	Dilkes and Reisz, 1987: table 1
<i>Dissorophus angustus</i>	13.1	3	24.9	11	111.6	DeMar 1968: table 1; Carroll, 1964b: fig. 14
<i>Tersomius texensis</i>	5.5	3		11	111.6	Carroll, 1964b: table 1; Bolt, 1977: table 1
<i>Amphibamus lyelli</i>	5.7	1	17.2	7	77.4	Carroll, 1964b: figs. 22–25, plate 2
<i>Doleserpeton annectens</i>	1.2	1		12	120.7	Bolt, 1977: table 1
<i>Trimerorachis insignis</i>	15.0	1	38.5	10	98.9	Olson, 1979: 2
<i>Neldasaurus wrightae</i>	15.8	1		10	98.9	Chase, 1965: table 1
<i>Isodectes obtusus</i>	3.8	1		12	120.7	Sequeira, 1998: fig. 4
<i>Sclerocephalus haeuseri</i>	21.0	4		10	98.9	Boy, 1988: fig. 3
<i>Cheliderpeton latirostre</i>	13.7	1		10	98.9	Boy, 1993: fig. 1F
<i>Proterogyrinus scheelei</i>	11.6	2	48.4	4	47.5	Holmes, 1984: fig. 1, table 3
<i>Anthracosaurus russelli</i>	29.5	1		7	77.4	Panchen, 1977: table 1
<i>Archeria crassidens</i>	24.0	1	67.2	11	111.6	Clack, 1987: table 5; Holmes, 1989: fig. 16A
<i>Pholiderpeton scutigerum</i>	27.5	1		6	69.1	Clack, 1987: table 6
<i>Eogyrinus attheyi</i>	34.0	1	156.4	7	77.4	Panchen, 1972: fig. 16; Panchen, 1977: table 1
<i>Gephyrostegus bohemicus</i>	5.7	1	13.6	7	77.4	Carroll, 1970a: figs. 1A, 6A
<i>Kotlassia prima</i>	10.8	1	59.1	16	135.4	Bystrow, 1944: figs. 1, 20
<i>Seymouria sanjuanensis</i>	8.9	6		10	98.9	Berman et al., 1987: table 1
<i>Seymouria baylorensis</i>	11.5	5	31.7	12	120.7	White, 1939: plate 3; Berman et al., 1987: table 1
<i>Westlothiana lizziae</i>	1.9	1	9.3	4	47.5	Smithson et al., 1994: figs. 6, 21
Amphibians						
<i>Palaeomolgophis scoticus</i>	2.7	1	18.4	4	47.5	Andrews and Carroll, 1991: figs. 2, 4
<i>Adelogyrinus simorhynchus</i>	4.7	1		4	47.5	Andrews and Carroll, 1991: fig. 7B
<i>Lethiscus stocki</i>	2.8	1	25.0	4	47.5	Wellstead, 1982: figs. 1A, 6A
<i>Phlegethontia cf. longissimi</i>	2.1	3	29.5	7	77.4	McGinnis, 1967: tables 1, 2
<i>Sauropsis scalaris</i>	4.4	1	10.3*	7	77.4	Bossy, 1976: table 1
<i>Ptyonius marshii</i>	1.7	4		7	77.4	Bossy, 1976: table 3
<i>Urocordylus wandesfordii</i>	3.0*	1	11.1	6	69.1	Bossy, 1976: figs. 72, 74
<i>Scincosaurus crassus</i>	1.1	1	7.1	7	77.4	Milner, 1980: figs. 4C, 5D
<i>Keraterpeton galvani</i>	2.5	1	6.9	6	69.1	Milner, 1980: figs. 4A, 5E
<i>Batrachiderpeton reticulatum</i>	3.4	1		7	77.4	Milner, 1980: figs. 5F

(Continued on next page)

APPENDIX 2. (Continued)

Taxa	ASL	NSL	APL	GEA	TEO	Source of data
<i>Diceratosaurus brevirostris</i>	1.6	1	3.7	7	77.4	Milner, 1980, figs. 4B, 5G
<i>Diploceraspis burkei</i>	5.2	1		10	98.9	Milner, 1980, fig. 2A
<i>Diplocaulus magnicornis</i>	11.5	23		12	120.7	Olson, 1951: table 2
<i>Tuditatus punctatus</i>	1.9	1	6.8	7	77.4	Carroll and Gaskill, 1978: figs. 4, 5
<i>Asaphostera intermedia</i>	3.7	1	16.0	7	77.4	Carroll and Gaskill, 1978: figs. 7, 9
<i>Pantylus cordatus</i>	6.8	1	13.9	11	111.6	Carroll and Gaskill, 1978: figs. 25, 29
<i>Llistrophus pricei</i>	2.2	1		12	120.7	Carroll and Gaskill, 1978: fig. 16
<i>Saxonerpeton geinitzi</i>	1.1	1	3.3	10	98.9	Carroll and Gaskill, 1978: fig. 24
<i>Leiocephalikon problematicum</i>	2.0	1		6	69.1	Carroll and Gaskill, 1978: fig. 63A
<i>Pariotichus brachyops</i>	2.5	1		11	111.6	Carroll and Gaskill, 1978: fig. 45C
<i>Cardiocephalus peabodyi</i>	1.9	2	8.7	12	120.7	Carroll and Gaskill, 1978: figs. 31, 32, 35
<i>Euryodus primus</i>	3.2	1		12	120.7	Carroll and Gaskill, 1978: fig. 36
<i>Rhynchonkos stovalli</i>	1.4	3	10.3	12	120.7	Carroll and Gaskill, 1978: figs. 63A, 64, 67, 72
<i>Batropetes truncatus</i>	0.9	1	3.2	10	98.9	Carroll and Gaskill, 1971: figs. 3, 4
<i>Brachystelechus fritschii</i>	0.8*	1	2.8	10	98.9	Carroll and Gaskill, 1978: figs. 95B, 97A
<i>Brachydictes elongatus</i>	1.4	3	45.0	12	120.7	Wellstead, 1991, figs. 1A, 2A, tables 3, 4
Reptiliomorphs						
<i>Solenodontosaurus janenschii</i>	11.8	1		7	77.4	Laurin and Reisz, 1999: fig. 2
<i>Limnoscelis paludis</i>	21.8	1	58.2	10	98.9	Williston, 1912: fig. 32; Fracasso, 1983: fig. 1A
<i>Tseajia campi</i>	10.6	1	36.7	10	98.9	Moss, 1972: figs. 1, 12
<i>Diadectes sideropelicus</i>	17.6	1	75.7	11	111.6	Case, 1911: plates 4.1, 14A
Synapsids						
<i>Eothyris parkeyi</i>	4.8	1		12	120.7	Reisz, 1986: fig. 6
<i>Casea broilii</i>	6.7		37.2	12	120.7	Romer and Price, 1940: fig. 71, plate 20
<i>Cotylorhynchus romeri</i>	14.7	1	104.6	12	120.7	Romer and Price, 1940: plate 19; Stovall et al., 1966: fig. 17
<i>Aerosaurus wellesi</i>	7.9	1	31.6	10	98.9	Langston and Reisz, 1981: figs. 4, 17A
<i>Varanops brevirostris</i>	10.6	1	33.0	12	120.7	Romer and Price, 1940: plate 5; Langston and Reisz, 1981: fig. 17B
<i>Varanodon agilis</i>	11.0	1		15	129.2	Olson, 1965: fig. 4B
<i>Mycterosaurus longiceps</i>	7.0	1	23.7	12	120.7	Romer and Price, 1940: fig. 71A; Berman and Reisz, 1982: fig. 7
<i>Archaeothyris florensis</i>	7.9	1	22.3	7	77.4	Reisz, 1972: fig. 2
<i>Varanosaurus acutirostris</i>	13.1	1	33.1	12	120.7	Romer and Price, 1940: fig. 42A; Berman et al., 1995: fig. 2B
<i>Ophiacodon mirus</i>	27.4	1	55.4	10	98.9	Romer and Price, 1940: fig. 42B
<i>Ophiacodon uniformis</i>	23.3	1	43.4	11	111.6	Romer and Price, 1940: fig. 43A, plate 3
<i>Ianthasaurus hardestii</i>	7.2	1		8	85.3	Modesto and Reisz, 1990: fig. 4B
<i>Glaucosaurus megalops</i>	4.5*	1		12	120.7	Modesto, 1994: fig. 2
<i>Edaphosaurus novomexicanus</i>	13.6	1		10	98.9	Modesto and Reisz, 1992: fig. 2b
<i>Edaphosaurus pogonias</i>	13.7	1	127.1	12	120.7	Romer and Price, 1940: fig. 68, plate 17
<i>Edaphosaurus cruciger</i>	13.7*	1	107.5	12	120.7	Romer and Price, 1940: fig. 67
<i>Edaphosaurus boanerges</i>	13.3	1	98.3	11	111.6	Romer and Price, 1940: fig. 66; Modesto, 1995: fig. 3
<i>Haptodus garnettensis</i>	9.7	1		8	85.3	Laurin 1993: fig. 1A
<i>Pantelosaurus saxonicus</i>	14.5	3	44.1	10	98.9	Romer and Price, 1940: fig. 58B, table 1; Huene, 1925: fig. 2
<i>Cutleria wilmarthi</i>	11.3	1		10	98.9	Laurin, 1994: fig. 1A
<i>Sphenacodon ferox</i>	25.0	1	62.6	10	98.9	Romer and Price, 1940: fig. 59A, table 1, plate 10
<i>Sphenacodon ferocior</i>	33.7	1	74.6	10	98.9	Romer and Price, 1940: fig. 59B
<i>Secodontosaurus obtusidens</i>	24.1	1		12	120.7	Reisz et al., 1992: fig. 2A
<i>Dimetrodon limbatus</i>	33.0	4	92.7	11	111.6	Romer and Price, 1940: fig. 62, table 1, plate 10
<i>Dimetrodon grandis</i>	36.8	3	122.2	12	120.7	Romer and Price, 1940: fig. 63, table 1, plate 10
<i>Tetraceratops insignis</i>	8.6*	1		12	120.7	Laurin and Reisz, 1996: fig. 3
Sauropsids						
<i>Mesosaurus tenuidens</i>	10.1		21.8	12	120.7	Modesto, 1996
<i>Acleistorhinus pterioticus</i>	2.7			12	120.7	deBraga and Reisz, 1996: fig. 1A
<i>Paleothyris acadiana</i>	2.2	2	8.6	7	77.4	Carroll, 1969: figs. 4B, 12
<i>Hylonomus lyelli</i>	3.7	1	10.5	6	69.1	Carroll, 1964a: figs. 2, 6
<i>Romeria primus</i>	5.0	1		10	98.9	Clark and Carroll, 1973: fig. 9
<i>Protocaptorhinus pricei</i>	4.9	1		11	111.6	Clark and Carroll, 1973: fig. 15
<i>Rhiodenticulatus heatoni</i>	3.6	1	8.3*	10	98.9	Berman and Reisz, 1986: figs. 1B, 3
<i>Captorhinus laticeps</i>	6.0	5	14.9	12	120.7	Seltin, 1959: table 1; Heaton, 1979: table 2; Heaton and Reisz, 1980: 139, fig. 1
<i>Labidosaurus hamatus</i>	15.2	17		12	120.7	Seltin, 1959: table 5; Heaton, 1979: table 2
<i>Petrolacosaurus kansensis</i>	5.4		24.6	8	85.3	Reisz, 1981: figs. 1, 3
<i>Araeoscelis gracilis</i>	4.2	10* ¹	28.9	12	120.7	Reisz et al., 1984: table 1, fig. 4

Asterisks (*) denote estimated (somewhat imprecise) dimensions. (Note. The average length of the skull of *Araeoscelis* is from table 1 of Reisz et al. [1984], who gave the length of an average skull; 14 specimens were available, but not all had good cranial remains, so the estimated number of specimens that may have been used to determine this size must be about 10.)

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APPENDIX 3. Geological time scale used to date the geological time of appearance of the taxa. Based on Harland et al. (1990).

Geological age	Period or subperiod	Absolute age of beginning of stage (Myr before present)	Epoch duration (Myr)	Time from origin of the clade
1, Frasnian	Devonian	377.4	10.4	51.5
2, Famennian		367	4.5	56
3, Tournaisian	Mississippian	362.5	13	69
4, Visean		349.5	16.6	85.6
5, Serpukhovian		332.9	10.1	95.7
6, Bashkirian	Pennsylvanian	322.8	11.5	107.2
7, Moscovian		311.3	8.3	115.5
8, Kasimovian		303	7.9	123.4
9, Gzelian		295.1	5.1	128.5
10, Asselian	Lower Permian	290	8.5	137
11, Sakmarian		281.5	12.7	149.7
12, Artinskian		268.8	9.1	158.8
13, Kungurian		259.7	3.6	162.4
14, Ufimian	Middle Permian	256.1	1.1	163.5
15, Kazanian		255	3.8	167.3
16, Tatarian	Upper Permian	251.2	6.2	173.5