

Intraorganismal Homology, Character Construction, and the Phylogeny of Aetosaurian Archosaurs (Reptilia, Diapsida)

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Abstract.— Character construction, the methods by which characters and character states are produced from observations of variation, is a crucial but poorly understood step in phylogenetic analysis. Alternative approaches are used in practice, but there has been relatively little investigation of their theoretical bases and analytical consequences. We reviewed three published numerical analyses of the phylogenetic relationships within the Triassic Aetosauria. Combined data from these studies were used to explore the impact of alternative approaches to character construction. Some previous aetosaurian characters represent parallel variations in the morphology of osteoderms from different body regions, and their independence is questionable, leading us to propose more composite alternative constructions. Phylogenetic analyses revealed that inferred relationships within the Aetosauria are in general poorly resolved and weakly supported by the available data and are sensitive to alternative approaches to character construction. Thus, the results from this and previous studies should not, for the most part, be accepted as robust hypotheses of aetosaurian interrelationships. The treatment of systems of intraorganismal (e.g. serial, antimeric) homologues, such as osteoderms, in character construction is discussed. Applied to parallel variations in systems of intraorganismal homologues, previous advice on choosing among alternative character constructions and Hennig's auxiliary principle agree in favoring a more composite approach, in accordance with common practice. [Characters; coding; evolution; morphology; osteoderms; Triassic.]

Character construction, the way in which observed variation is partitioned into characters and character states, is a crucial part of any numerical phylogenetic analysis using discrete morphological characters. Together with scoring and weighting, construction determines the numerical results. Phylogeneticists have recognized a number of methodological issues concerning character construction, including the treatment (ordered or unordered) of multistate characters (Hauser and Presch, 1989; Wilkinson, 1992), the interpretation of complex structures as complex characters or character complexes (Pleijel, 1995; Wilkinson, 1995a), the treatment of polymorphism (e.g., Wiens, 1995; Kornet and Turner, 1999), and the representation of inapplicability (e.g., Maddison, 1993; Strong and Lipscomb, 1999). Practicing phylogeneticists necessarily confront issues of character construction, and the approaches they adopt have practical consequences for what they can infer using numerical phylogenetic methods. However, there has been surprisingly little discussion of generalities. In a recent survey, Hawkins (2000) demonstrated the existence of a variety of approaches to character construction but found little discussion of why any particular approach was selected. Similarly, Poe and Wiens (2000) found that few workers provided any explicit justification for their approaches to morphological character selection. The comparison of alternative approaches to character construction, although important, is still in its infancy and deserves more attention (see also Wiens, 2001; Rieppel and Kearney, 2002).

Many phylogeneticists seemingly use their own intuitive approach to character construction rather than make explicit choices among the available alternatives, of which they may be only dimly aware. The practicing phylogeneticist is most likely to be keenly aware of alternative approaches upon discovering that they would (or do) do things differently from other workers. Such a discovery was the stimulus to Wilkinson's (1995a) discussion of reductive and composite coding approaches

to the treatment of complexity. A parallel discovery made during investigations of aetosaurian phylogeny prompts us to highlight and discuss here alternative approaches to the construction of characters from anatomical systems comprising multiple parts that are themselves homologous within organisms.

As noted by Ghiselin (1976:134), "It is a brute fact of nature that lots of organisms are built up of repeated units having similar, if not identical, arrangements of their components." Owen (1843) coined the term serial homology for corresponding anatomical units in different segments within organisms, such as vertebrae or the humerus and femur, in contrast to special homology, which pertains to correspondences among organisms, including those of different species. Ghiselin (1976) took serial homology to apply only to features that occur in a linear spatial arrangement within an organism, and he noted the existence of many other kinds of correspondences within organisms. For example, his antimeric homology pertains to the correspondence between bilaterally paired structures. Whereas the interpretation of special homology appears to have, for the most part, become evolutionary, intraorganismal homology remains a poorly understood but seemingly fundamental aspect of organismal organization (Ghiselin, 1976).

Wilkinson (1995a) distinguished between two approaches that have been used to construct characters from interorganismal variation in complex features, i.e., those made of multiple parts. In the more composite approach, the complex feature is taken as the character and each variant is a different character state. With more reductive coding, separate characters are used to describe variations in the different parts of the complex. In practice there is a continuum of approaches that are more or less composite or reductive. Which approach is adopted can impact both what relationships are taken to be supported by the underlying variation and the weight ascribed to that evidence (Wilkinson, 1995a).

Intraorganismal homologues are a special case of a complex feature, in which complexity is built upon some degree of repetition. Here we investigate relatively composite and reductive alternative approaches to character construction applied to interorganismal variation in systems of intraorganismal morphological homologues and discuss the relative merits of these alternatives in this specific context.

Aetosaurians are extinct Triassic suchian archosaurs, the closest living relatives of which are crocodylians (e.g., Gower and Wilkinson, 1996). Their distinctive morphology includes bony dermal armor composed of discrete osteoderms or scutes (Fig. 1) and a specialized dentition indicating that they may have been the earliest radiation of herbivorous/omnivorous archosaurs (e.g., Walker, 1961; Parrish, 1994; Small, 2002). The systematics of aetosaurians is of special interest for several reasons. Their fossil remains have been used as biochronologic indicators and interest has recently developed in their biogeography and biostratigraphy (e.g., Parrish, 1994; Heckert and Lucas, 1999, 2000). However, there is lack of agreement concerning their relationships to other major clades of suchian archosaurs (Gower and Wilkinson, 1996; Gower and Walker, 2002), and they have recently been suggested as relevant to the controversy over the phylogenetic affinities of turtles (Hedges and Poling, 1999).

Aetosaurian phylogeny has been addressed in three recently published phylogenetic analyses by Parrish

(1994), Heckert et al. (1996), and Heckert and Lucas (1999). We reviewed these studies and developed alternative reductive and composite combined data matrices based on these studies. These alternatives differ only in the treatment of intraorganismal homologues. We then used these data to investigate both aetosaurian phylogeny and the practical impact of alternative approaches to character construction.

MATERIALS AND METHODS

Published data matrices from each of the three previous studies (Parrish, 1994; Heckert et al., 1996; Heckert and Lucas, 1999) and any revisions thereof were investigated with parsimony analysis. Combined data matrices incorporating revised characters from all previous studies were developed with either reductive or composite representations of variation in intraorganismal homologues. These data sets were used to investigate the impact of the alternative approaches to character construction in quantitative phylogenetic analyses. Unless stated otherwise, all analyses were performed using PAUP 4.0b4a (Swofford, 1999). Characters were weighted equally, and searches for most-parsimonious trees (MPTs) were exact (branch and bound). Tree length (L) and consistency index (CI) were recorded for each MPT. Multiple MPTs were summarized with the strict reduced consensus (SRC) method (Wilkinson and Thorley, 2003) as implemented in RadCon (Thorley

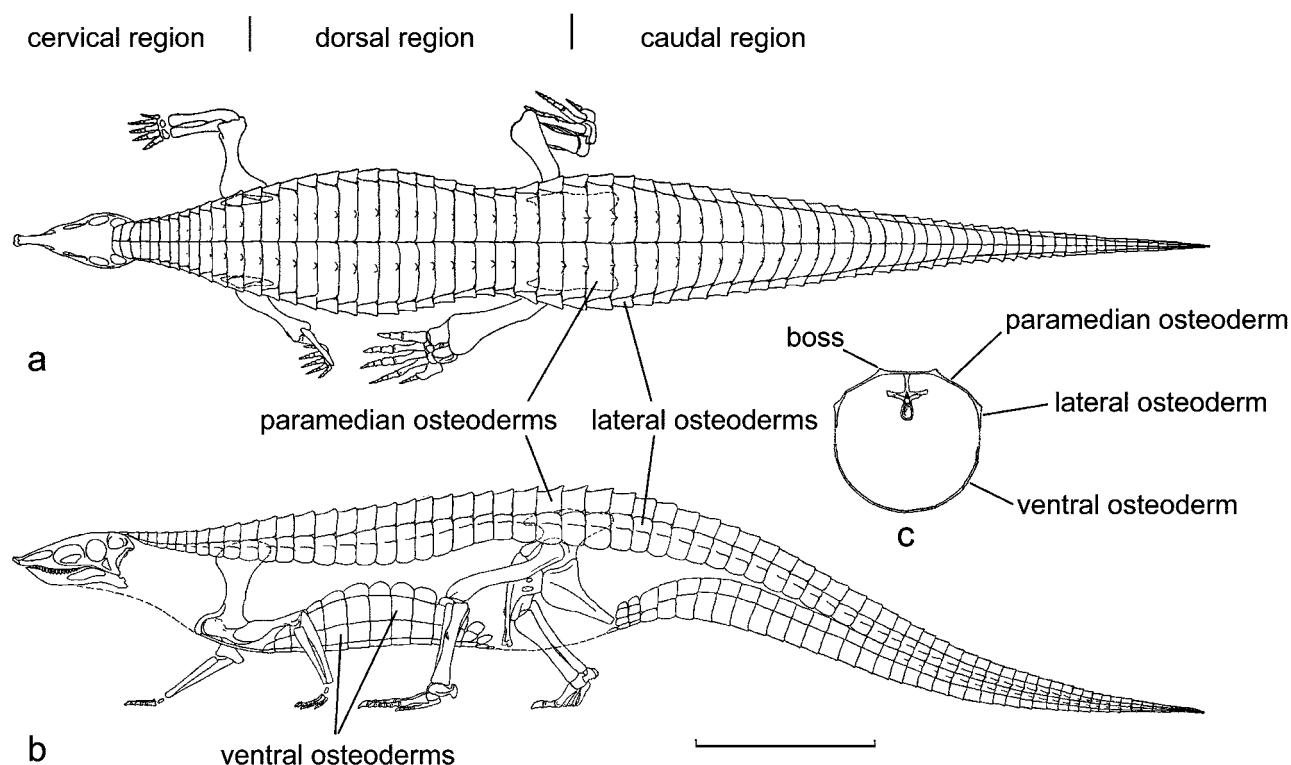


FIGURE 1. Skeletal reconstructions of the Triassic aetosaurian archosaur *Stagonolepis robertsoni* Agassiz, showing the disposition of the dermal ossifications or osteoderms. (a) Dorsal view. (b) Lateral view. (c) Transverse section at midbody. Bar = 0.4 m. Modified from Walker (1961: fig. 23) and reproduced with permission from the Royal Society of London.

and Page, 2000). This method identifies all cladistic relationships that are common to the MPTs and are thus unambiguously supported by the parsimonious interpretation of the data (Wilkinson, 1994). It may produce multiple consensus trees, together termed a profile. If the "strict" consensus (Sokal and Rohlf, 1981), referred to here as strict component consensus (SCC; Wilkinson, 1994; Wilkinson and Thorley, 2001b) is informative it will be a member of the SRC profile. RadCon was used to determine Thorley et al.'s (1998) cladistic information content (CIC) and Wilkinson and Thorley's (2001a) consensus efficiency (CE). As the names suggest, CIC is a measure of the information content of trees (including consensus trees) and CE quantifies how well a consensus represents the set of trees it stands for, scaled between zero (minimal efficiency) and 1 (maximal efficiency).

Null hypotheses that data are no more structured than expected by chance were tested by randomization using two distinct measures of data quality: parsimony tree lengths (Archie, 1989; Faith and Cranston, 1991) and the number of pairwise hierarchical nestings of characters (Alroy, 1994). These measures yield matrix parsimony (MP) and matrix nesting (MN) permutation tail probabilities (PTPs), respectively. All randomization tests used 1,000 trials giving minimum possible PTPs of 0.001. The distribution of missing data in data matrices is typically nonrandom and ideally should be held constant during random permutation of the data. This is not possible with PAUP's implementation of the MP PTP but was applied in our determinations of MN PTPs, using PICA 4.0 (Wilkinson, 2001a). Bootstrapping (Felsenstein, 1985) and decay analysis (Bremer, 1988; Donoghue et al., 1992) were used to quantify support for relationships (splits). Bootstrap proportions were based on 1,000 replicates and are reported for clades. Decay indices were determined through constrained analyses and are reported for clades and for less inclusive relationships (partial splits) recovered by the SRC method. The latter were determined using back-

bone constraints (Wilkinson, 1997). Scope for safe taxonomic reduction, the elimination of taxa that have no effect upon inferred phylogeny (Wilkinson, 1995b), was determined using TAXEQ3 (Wilkinson, 2001b).

The process that culminates in the recording of a datum in a matrix is made up of at least two parts, construction and scoring. Scoring is the ascribing of state(s) to a particular terminal. Construction (also formulation) is more complex, involving the partitioning of phenotypes into discrete characters, the partitioning of variants into character states, and hypothesizing the relations among them (i.e., choosing a character type). Scoring, as understood here, is sometimes termed coding by other authors (e.g., Yeates, 1995), but this term has also been used to describe some aspects of character construction, e.g., additive binary coding (Farris et al., 1970), composite, and reductive coding (Wilkinson, 1995a). We consider coding to be part of character construction. The dermal ossifications that form the armor of aetosaurians are variably termed osteoderms and scutes throughout the literature; we use the term osteoderm.

RESULTS

Reviews of the three previous analyses of aetosaurian phylogeny (Parrish, 1994; Heckert et al., 1996; Heckert and Lucas, 1999) are given in Appendix 1. These reviews address a number of character construction and scoring problems. Typographical errors in the published matrices and discrepancies between matrices and character descriptions were resolved, and alternative codings were introduced for some characters. From our reviews, we constructed a combined matrix based primarily on the latest and most extensive study (Heckert and Lucas, 1999). Characters used in the two earlier studies (Parrish, 1994; Heckert et al., 1996) that were not present in the data of Heckert and Lucas (1999) were added to create the combined matrix. The combined matrix (Table 1) comprises all 60 characters for the 14 taxa included in the

TABLE 1. Matrix combining characters and data from the three previously published studies of aetosaurian phylogeny. Characters 1–60 are characters 1–60 of Heckert and Lucas (1999), characters 61–63 are characters 1, 2, and 5 of Parrish (1994), and characters 64–66 are characters 12, 15, and 23 of Heckert et al. (1996). The composite combined matrix was constructed by removing characters 33, 38, 47, 55, and 58. Character 3 for *Paratypothorax* was rescored (see Appendix 1).

Taxon	Characters													
	12345	1	11111	11112	22222	22223	33333	33334	44444	44445	55555	55556	66666	6
Rauisuchia	00000	00000	00000	00000	00000	00000	00000	00000	000?0	?????	?????	0?000	110??	?
<i>Coahomasuchus</i>	?????	?1???	?????	?1???	?1???	??100	0?00?	111??	00???	00000	00?00	01011	?????	?
<i>Aetosaurus</i>	11000	00101	11111	01?0?	1111?	?1100	00000	00000	000?0	00000	00?0?	01011	11100	0
<i>Stagonolepis robertsoni</i>	11111	01101	11111	01100	11111	01100	00001	10000	000?0	00000	00?00	11011	11100	0
<i>S. wellsi</i>	?????	?????	?????	?1110	1????	01100	00001	?0010	000?0	00010	00000	11011	?????	?
<i>Longosuchus</i>	11111	?1101	11111	11?0?	11110	0?100	10001	00000	?00?0	10111	11010	01?11	11100	1
<i>Lucasuchus</i>	?????	?1???	?????	??00?	?????	01100	10000	00010	?00?1	1?111	11000	01???	?????	?
<i>Desmatosuchus</i>	11110	11101	11111	11011	1111?	11110	11100	00010	100?1	11111	01011	11???	11100	1
<i>Acaenosuchus</i>	?????	?????	?????	?????	?????	??110	11100	00001	?00??	01011	?00?1	11???	?????	?
<i>Typothorax</i>	11110	101?1	11111	01110	1111?	01101	0111?	111??	10100	01010	01110	01???	11101	1
<i>Aetosauroides</i>	11111	0?1?1	11???	01100	1111?	01100	00001	00000	000?0	00000	00?00	11011	11100	0
<i>Neoaetosauroides</i>	1111?	0?111	11?11	11??1	1111?	??100	00000	00010	000?0	00000	00?00	0101?	11100	1
<i>Paratypothorax</i>	???1?	?????	???21	??1??	?????	??101	?0001	?0010	100?0	00101	11110	11???	??101	1
<i>Redondasuchus</i>	?????	?????	?????	?????	?????	??100	0111?	111??	11110	?????	?????	0????	???10	1

matrix of Heckert and Lucas (1999) plus characters 1, 2, and 5 of Parrish (1994) and 12, 15, and 23 of Heckert et al. (1996). Taxa were scored as unknown (?) in the combined matrix for those characters that they had not been scored for in any of the three analyses.

Within this combined data matrix (referred to hereinafter as the reductive combined matrix), we identified three sets of covarying characters that describe variation in intraorganismal homologues. There are alternative more composite constructions for these sets of characters whereby each set is replaced by a single character. The more composite constructions for these characters were implemented in a modified version of the combined data matrix (see Table 1) referred to hereinafter as the composite combined matrix.

Heckert and Lucas's (1999) characters 32, 33, 47, and 58 describe variation in the patterning (radiate or random) on the cervical paramedian, dorsal paramedian, lateral, and ventral osteoderms, respectively. Excluding missing data, these characters almost all covary. The single exception is that *Redondasuchus* was scored as having a radiate patterning on its lateral osteoderms (character 47) and random patterning on all other osteoderms. However, *Redondasuchus* is believed to lack lateral osteoderms (Heckert et al., 1996), and we preferred to score this character as unknown for this taxon. In our alternative construction, the four characters were merged into a single character (character 32, Table 1). Until aetosaurian specimens that exhibit radiate and random patterning in the different anatomical regions are documented this alternative is at the very least plausible.

Similarly, Heckert and Lucas's (1999) characters 29 and 55 describe the presence or absence of anterior bars on dorsal paramedian and lateral osteoderms: 29-anterior bars on dorsal paramedian osteoderms: present or not applicable (0), absent (1); 55-anterior bars on lateral osteoderms: present (0), absent, replaced by laminae (1). For character 29, "not applicable" is combined in a single character state along with "present," and this unusual construction was not explained. More importantly, the character state distributions for these two characters are virtually identical among the included taxa (except for *Aetosaurus*, which is scored 0 for character 29 and ? for character 55). In the absence of specimens exhibiting anterior bars on either their dorsal or lateral osteoderms only, we merged characters 29 and 55 into a single character (character 29, Table 1), maintaining a 0 score for *Aetosaurus*.

In Heckert and Lucas's (1999) study, all taxa with bosses on their dorsal paramedian osteoderms (character 37) were scored as also having bosses on their caudal paramedian osteoderms (character 38), whereas taxa that lack bosses on their dorsal osteoderms were scored as also lacking them on their caudal osteoderms. We merged Heckert and Lucas's characters 37 and 38 into a single character in the composite combined matrix (character 37, Table 1).

Analysis of the reductive combined matrix produced a single MPT (Fig. 2a). This tree has the same topology and essentially the same support as that recovered from

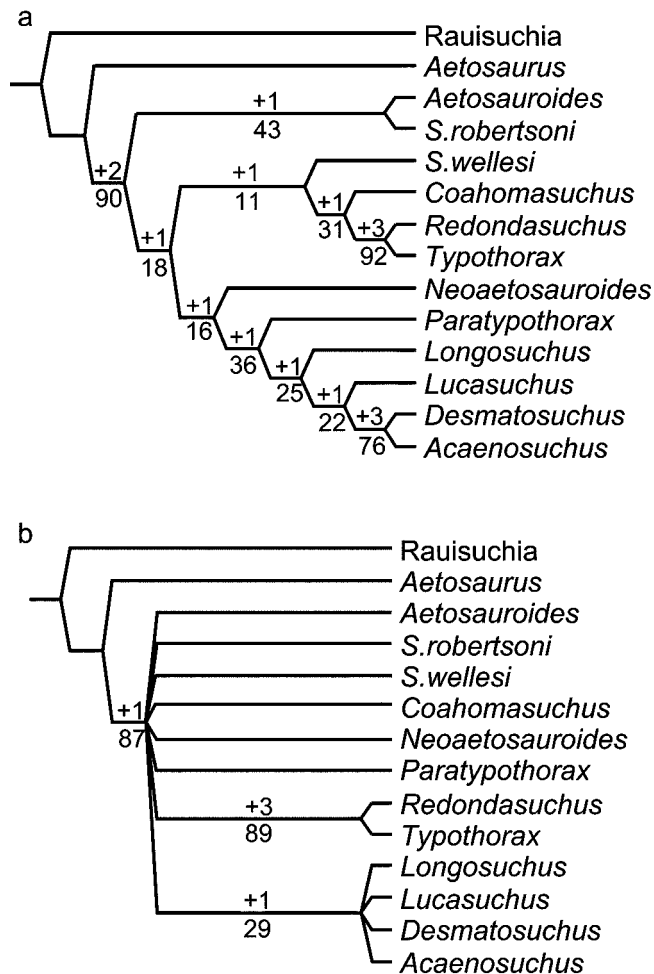


FIGURE 2. (a) Single MPT ($L = 91$, $CI = 0.681$) from analysis of reductive version of combined data from the three previous studies of aetosaurian phylogeny. (b) Strict component consensus of nine MPTs ($L = 86$, $CI = 0.682$) from analysis of modified (more composite) version of combined data ($CIC = 17.251$, $CE = 0.4924$). Numbers above and below branches are decay indices and bootstrap proportions, respectively.

analysis of our altered version of Heckert and Lucas's (1999) data (data set rH99, see Appendix 1). This result is not surprising given that four of the six characters added from Parrish (1994) and Heckert et al. (1996) were parsimony uninformative.

Analysis of the composite combined data (see Table 1) yielded nine MPTs. The SCC (Fig. 2b) of these MPTs is poorly resolved. All nodes supported by a decay value of 1 in the analysis of the reductive combined data were lost except for that grouping *Longosuchus*, *Lucasuchus*, *Desmotosuchus*, and *Acaenosuchus*. The sister group relationship of *Desmotosuchus* and *Acaenosuchus*, which is supported by a decay value of 3 in the analysis of the reductive combined data, also was lost. Support for *Aetosaurus* as the sister group to all other aetosaurians was reduced.

The reduced consensus profile of the nine MPTs from analysis of the composite combined matrix produced a

TABLE 2. Partition table showing relations (full and partial splits) common to the nine MPTs from analysis of the composite combined matrix. The dot and the asterisk indicate the partition of taxa in the corresponding split. A question mark indicates exclusion of taxa from partial splits.

Split	Taxa ^a		
	12345	1 67890	1111 1234
1*	...*
2	****.	...*
3	*..*	*****	****
4	?.*	*...*
5*?.	...*
6	...?.	****?	...?*
7	...?*	????*	...?*
8	...?*	????*	...?*

^a1 = *Rautisuchia*; 2 = *Coahomasuchus*; 3 = *Aetosaurus*; 4 = *Stagonolepis robertsoni*; 5 = *S. welllesi*; 6 = *Longosuchus*; 7 = *Lucasuchus*; 8 = *Desmotosuchus*; 9 = *Acaenosuchus*; 10 = *Typhothorax*; 11 = *Aetosauroides*; 12 = *Neoaetosauroides*; 13 = *Paratyphothorax*; 14 = *Redondasuchus*.

profile of six SRC trees, comprising the SCC (Fig. 2b) and five other trees. Examination of the SRC trees and their summary partition table (Table 2) reveals that the lack of resolution in the SCC is complicated and cannot be attributed to the instability of only one or two taxa. The three reductive sets of intraorganismal homologue characters and their composite alternatives were implemented separately to further explore the cause of loss of resolution. Implementation of the composite versions of only characters 32, 33, 47, and 58 or 29 and 55 did not alter the topology of the single MPT recovered from analysis of the reductive combined matrix, but each composite character lowered support for the *Desmotosuchus* + *Acaenosuchus* clade by 1 in the decay analyses. In contrast, implementation of only the composite version of characters 37 and 38 had a major impact on tree topology, leading to 66 MPTs. The two reductive characters (37 and 38) support the clade comprising *Coahomasuchus*, *Typhothorax*, and *Redondasuchus*, which is present in the MPT recovered from analysis of the reductive combined matrix. Collapse of this clade renders much of the rest of the tree highly unstable, indicating a complex interplay among the remaining data for these taxa.

DISCUSSION

Aetosaurian Phylogeny

All three of the published studies reviewed in the Appendix (Parrish, 1994; Heckert et al., 1996; Heckert and Lucas, 1999) are worthy preliminary investigations into the phylogenetic relationships of a little discussed group. They have provided new morphological data for *Longosuchus*, *Redondasuchus*, and *Coahomasuchus* and identified potentially useful systematic characters. However, all three previous studies and our combined analyses consistently support only three hypotheses of relationships: (1) *Aetosaurus* is the sister group of all other aetosaurians, (2) *Aetosauroides* is the sister group of *Stagonolepis (robertsoni)*, and (3) *Longosuchus* and

Desmotosuchus are more closely related to each other than either is to *Neoaetosauroides*. These hypotheses are the only ones in which we are willing to invest much confidence.

The results of previous studies and our own reanalyses should not, for the most part, be accepted as robust hypotheses of aetosaurian interrelationships. This conclusion follows from (1) lack of agreement among different studies, (2) generally low support values in each of the analyses, and (3) sensitivity to alternative character constructions. Much instability is likely to result from abundant missing entries, and less pessimistic assessments of the robustness of some relationships might be achieved using more sensitive methods such as reduced consensus bootstrapping (Wilkinson, 1996) and double decay analysis (Wilkinson et al., 2000). However, issues of character construction and scoring should be resolved before more extensive investigation of support is merited. Aetosaurian phylogenetics could benefit from better fossils and additional characters from more character systems, but ultimately with fossil data there will be an upper bound, which is why it is important to get the character construction right. Future studies of aetosaurian phylogeny must resolve outstanding issues of scoring and should not exclude taxa without good reason. Such studies will have to address issues of character construction, including the treatment of intraorganismal homologues.

Intraorganismal Homology, Character Independence, and Character Construction

Our review of aetosaurian phylogenies highlights the potential for alternative approaches to constructing characters from variations in osteoderms in particular and from systems of intraorganismal homologues in general. Our results demonstrate that alternative approaches can have a profound impact upon phylogenetic conclusions, both on the relationships that are recovered and on the apparent strength of support for those relationships. Osteoderms comprise a system of more or less similar units that we presume are intraorganismal homologues, meaning that they are instances of a repeated pattern that has some common cause (Ghiselin, 1976) or are instances of a repeated or common developmental pattern (Roth, 1984). Intraorganismal homology is not a minor phenomenon. Repetition is ubiquitous at all levels of organismal organization and is an important component of much complexity. Wilkinson's (1995a) discussion of composite and reductive coding focused on spatially associated complex structures, such as entire organs, and did not consider intraorganismal homologues per se. However, the distinction between reductive and composite coding applies equally to intraorganismal homologues, which are a special case of complexity built upon similar units that may or may not be spatially or temporally associated.

Heckert and Lucas (1999) constructed a number of sets of characters by using similar variations in what they viewed as different osteoderm regions as the bases of

independent characters. Osteoderm morphology does vary within aetosaurians, making it possible to distinguish paramedian from lateral osteoderms and often to identify from which approximate region along the axial skeleton isolated osteoderms may originate (e.g., Walker, 1961; Long and Ballew, 1985). However, there can be uncertainty over the regional identity of isolated osteoderms and similarity among osteoderms from different regions in different taxa (e.g., Hunt and Lucas, 1991:732). Three of Heckert and Lucas's osteoderm character sets covary in the distribution of their character states. We consider these relatively reductive character constructions of Heckert and Lucas (1999) too reductive. Naylor and Adams (2001:450) reacted similarly to several sets of mammalian dental characters used by O'Leary and Geisler (1999), noting that "because the same underlying genetic architecture generates teeth in a particular tooth group, similar structures on different teeth (e.g., the hypocone) are de facto serially homologous. Therefore, measuring the same feature on multiple teeth in a tooth group represents a redundant and non-independent sampling."

Character independence is considered a fundamental assumption of many phylogenetic methods both for choosing among trees and for assessing support (e.g., Farris, 1973; Felsenstein, 1985). Characters are logically dependent if the scoring of one or more characters entails some restriction on the coding of another character, and they are biologically dependent if their evolution is causally linked, as might be expected in highly integrated functional complexes (Wilkinson, 1995a). Logically independent characters may be more or less biologically independent, contingent upon the actual process of evolution. Biological dependence can be viewed probabilistically: If the probability of transformation between the states of one character is conditional upon state changes in one or more other characters, then the characters are dependent (O'Keefe and Wagner, 2001).

Independence is a simplifying assumption that facilitates quantitative evaluation of the weight of evidence and is therefore a desideratum of methods that assume independence. The link between independence and weight of evidence is important because the potential danger in violating the assumption is that too much weight is given to some misleading evidence. For example, the two binary characters "X wider than long or not" and "X shorter than broad or not" are simply different ways of expressing the same notion. Using both characters, the underlying variation is given twice the weight (assuming equal weighting) than if just one of these logically dependent characters is used. Similarly, if parallel variations in aetosaurian osteoderms resulted from global changes to the aetosaurian osteoderm system, reductive coding would violate the assumption of biological character independence and overweight the evidence.

Biological dependence and correlated character evolution are believed to be common in morphology (e.g., Emerson and Hastings, 1998). These processes have been shown through simulation to have the potential to

reduce accuracy of parsimony analyses (Wagner, 1998; Huelsenbeck and Nielsen, 1999) and are expected, as found here, to exaggerate support measures (O'Keefe and Wagner, 2001). Detecting and appropriately weighting correlated character evolution resulting from biological dependence are therefore important issues in phylogenetics (Sneath and Sokal, 1973; O'Keefe and Wagner, 2001). Biological dependence can be complete or partial. For example, if one or more character state transitions entail some other transition (so that the conditional probability of the latter on the former is one), then dependence is complete, whereas if the former merely makes the latter more likely, then the dependence is partial. Several workers have proposed methods for detecting correlated evolution given a phylogenetic tree (e.g., Maddison, 1990, 2000; Pagel, 1994). O'Keefe and Wagner (2001) developed very promising statistical tests of correlated character evolution based on patterns of mutual character compatibility that can be used prior to building trees and that are applicable whether dependence is complete or partial. The reductive codings of aetosaurian osteoderm characters suggest a special case in which complete dependence results from a single underlying change that produces the same kind of variation in different subsets of intraorganismal homologues that have been individuated on some other basis. Hecht and Edwards (1977) suggested that suites of characters resulting from change in a single developmental mechanism should be treated as a single character. In such cases, the reductive characters repeat the same pattern of character state distributions (they covary) and have the same patterns of compatibility. The alternative, more composite approach leads to a single character with the same distribution of character states as the reductive characters. The reductive and composite alternatives produce characters having the same phylogenetic significance (in the sense of supporting the same relationships) but they ascribe different weights to the variation.

Heckert and Lucas's (1999) reductive characters describe the same kind of variation in aetosaurian osteoderms of different regions, which is why we prefer a more composite approach. For example, patterning on the osteoderms of the cervical paramedian, dorsal paramedian, lateral, and ventral osteoderms is either radial or random. Each reductive character represents hypothesized interorganismal homology of and explanation for the similarity of the patterning of the osteoderms of a particular region. Because osteoderms comprise a system of intraorganismal homologues, the covarying interorganismal similarity of patterning in different regions may be explained by homology, and the covariation may be explained by global change to the system rather than by separate local changes. Reductive coding treats the intra- or interorganismal similarity of similar patterning in different regions, such as cervical and dorsal, as coincidental and not homologous. Composite coding, treating variations across the whole osteoderm system as the character, provides a potential explanation for observed similarity of both intra- and interorganismal homologies that is more complete, more parsimonious, and more plausible.

Covariation of characters does not entail any dependence between characters. Conversely, lack of covariation does not guarantee character independence, either complete or partial, and does not eliminate concern over appropriate weight (O'Keefe and Wagner, 2001). However, lack of covariation does indicate that not all inter- or intraorganismal similarities can be homologous. Characters that do not covary provide evidence for different phylogenetic relationships. Separate character-state changes in different parts of the tree must be invoked to explain the observed different distributions, whether these events are causally independent or not. Some degree of independence is a plausible explanation of such separate changes and consequent lack of covariation and homology. Thus, lack of covariation in characters is considered evidence of character independence and is a cause for less concern over potential overweighting by reductive coding. In practice, any overweighting of characters that do not covary is spread across different relationships. With covariation, which is readily identified by inspection of the data, any overweighting is more concentrated. The covariation of reductive characters describing the variation of intraorganismal homologues makes the danger of overweighting particularly severe.

Investigation of character dependence in noncovarying characters requires advanced techniques such as those proposed by O'Keefe and Wagner (2001), whereas the special case we are concerned with here is amenable to simple and routine evaluation. Six sets of dental characters used by O'Leary and Geisler (1999) were identified a priori as potentially dependently linked as serial homologues by Naylor and Adams (2001:450). To test this hypothesis, Naylor and Adams generated a matrix of pairwise differences among all 45 dental characters and performed a principal coordinates analysis. Four of the six characters sets identified a priori formed distinct clusters, supporting their assessment that "the characters within each of these four sets are not independent." Although not stated explicitly, the failure of the other character sets to cluster together was taken as evidence for their independence. Contrary to Naylor and Adams (2001), one of the four sets of characters accepted as non-independent (characters 74–76) does not form an exclusive cluster (see their fig. 3). Naylor and Adams's (2001) approach agrees with ours in proceeding from an a priori assessment of potential dependence founded on hypotheses of intraorganismal homology to a test of the predicted association of candidate sets of characters. It differs in the use of ordination and clustering to test the association of characters.

We examined the distributions of character states in the six sets of characters identified a priori by Naylor and Adams (2001). The two sets considered by Naylor and Adams to comprise independent characters on the basis of their failure to cluster in ordination have very different character-state distributions. In contrast, within all four sets considered to comprise dependent characters by Naylor and Adams, the character-state distributions are very similar. In three sets, the distributions are iden-

tical or identical except for missing entries, and in the fourth (the one that does not form a discrete cluster in the ordination) characters differ in the scoring of a single taxon. Simply on the basis of their covariation (which entails their coclustering), we accept three sets of characters as comprising potentially redundant characters that would be better represented by a single composite character. On the basis of their lack of covariation, we are more accepting of the reductive coding of the three remaining sets (notwithstanding additional insights that may be gained through the application of advanced techniques).

Morphologists routinely construct characters from systems of intraorganismal homologues. The approach to character construction adopted appears to be mostly influenced by the degree to which subsets of intraorganismal homologues can be individuated based on intrinsic features. Evolutionary differentiation of units or groups of units within a system of intraorganismal homologues must result from local (with respect to the system) evolutionary change, making reductive coding a reasonable approach. Although some workers have used relatively reductive codings of parallel variations in extrinsically individuated subsets of intraorganismal homologues (Heckert and Lucas, 1999; O'Leary and Geisler, 1999), there is a clear preference for more composite coding whenever interorganismal variations in intraorganismal homologues could be plausibly explained by a single change. For example, we know of no case where the same variations in the antimeres of bilaterally symmetric organisms have been treated as separate characters. In adopting composite character construction for parallel variations in intraorganismal homologues, common practice is good practice. The remaining discussion is intended to clarify why this is so.

In the more general context of complexity, Wilkinson (1995a:307) argued that neither reductive nor composite coding "has a monopoly of advantages or dangers and the task of constructing characters from character complexes or complex characters requires due consideration of these alternative approaches." The choice between more reductive or composite character constructions turns ultimately on assessments of plausibility and must be made on a case-by-case basis. To guard against overweighting by excessive reductive coding in cases where the reductive characters covary, Wilkinson (1995a:302) suggested asking whether covarying reductive characters can be combined into a composite character representing a real unit of biological organization with parts that are plausibly biologically dependent and that could evolve in concert. He suggested that if the answer is affirmative, then the more composite alternative should be considered. Applied to the reductive coding of aetosaurian osteoderms, the answer is affirmative by virtue of the relation of osteoderms as intraorganismal homologues, suggesting that composite coding is sufficiently plausible to warrant consideration in the special case of covarying intraorganismal homologues.

Further guidance on the choice of character construction comes from Hennig's auxiliary principle. Any

similarity between organisms may be explained as either homologous or convergent (homoplastic). Confronted with this truism, Hennig (1966) proposed that similarities should be explained as homologous unless incongruence entails convergence. This is Hennig's auxiliary methodological principle, and he argued that it is needed to establish a link between similarity and phylogeny. If convergence were our preferred explanation, similarities would not be taken as evidence of relationships.

Hennig's auxiliary principle invokes a common cause in preference to separate causes. It can be readily interpreted in the context of character construction as advising phylogeneticists to represent similarities as a priori hypotheses of homology. Typically, this is achieved through character-state identity, but in the case of multistate characters the principle can also lead to specific ordering of character states (Wilkinson, 1992). The reductive approach to aetosaurian osteoderms treats the evolution of, for example, bosses on the lateral and paramedian osteoderms to be independent events. The similarity that exists between bosses on lateral and paramedian osteoderms is therefore interpreted as coincidental and homoplastic, in violation of Hennig's auxiliary principle. With composite coding, the similarity of the parallel variations in different regions is taken as homologous, in greater conformity with Hennig's auxiliary principle.

We believe that the conformity with Hennig's auxiliary principle of the composite coding of covarying differences among intraorganismal homologues provides a methodological justification for common practice and the seemingly near universal preference for this sort of coding. However, conformity with Hennig's auxiliary principle may be more or less impressive depending on the plausibility of common cause. Many factors may impact this plausibility, and decisions on character construction must be made on a case-by-case basis. The hypothesis of single change implicit in the composite coding of covarying intraorganismal homologues is at least sufficiently plausible to always warrant explicit consideration. More reductive treatments are not ruled out in specific cases, but they might require some additional justification.

This discussion of the role of intraorganismal homology in character construction is a cursory foray into an important but underappreciated topic. We have dealt only with relatively simple cases and expect that biological complexity will confront phylogeneticists with more difficult but also more interesting gray areas. We do not claim to be inventing or advocating any novel principles for phylogeneticists. Rather, we hope to clarify why the practice used by the majority of phylogeneticists of adopting composite character constructions is a good practice and why more reductive codings, although potentially justifiable, seem intuitively problematic.

ACKNOWLEDGMENTS

We thank Michael Parrish and Andrew Heckert for discussion and for supplying corrected versions of their matrices for analysis. We are grateful to Nick Arnold, Barry Clarke, Julia Day, and Bronwen Presswell for discussing aspects of coding variation in intraor-

ganismal homologues, to Dave Williams for helpful pointers to the literature, and to Mike Benton, Chris Brochu, and Robin O'Keefe for helpful critical reviews. S.R.H. was supported by NERC grant NER/S/A/2000/03255. PICA 4.0 and TAXEQ3 may be downloaded from <http://www.nhm.ac.uk/zoology/home/wilkinson.htm>.

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First submitted 24 September 2001; reviews returned 11 March 2002;
final acceptance 14 December 2002
Associate Editor: Mike Steel

APPENDIX 1

REVIEW OF AETOSAURIAN PHYLOGENETICS

Here, we present reviews of the three previous numerical phylogenetic analyses of aetosaurians, by Parrish (1994), Heckert et al. (1996), and Heckert and Lucas (1999). These analyses are treated in chronological order. For each, a summary is given of the published analysis, followed by reports of reanalyses of the data (including any modifications), assessments of support, and discussion of any character construction issues that were identified. Summary statistics for our reanalyses are given in Appendix 2. These reviews form the basis of a combined matrix, the analysis of which is presented in the main text.

Parrish (1994)

Review.—Parrish (1994: table 2) presented a data matrix of eight aetosaurian genera and two outgroups (Prestosuchia and Rauisuchia) scored for 15 binary characters. He reported that parsimony analysis of these data produced three MPTs of $L = 16$ and $CI = 0.938$ and presented the strict component consensus of these (Fig. 3).

Consideration of the published matrix (Appendix 3), consensus tree (Fig. 3a), and descriptive statistics of the MPTs reveals that the data presented could not be those analyzed. There is no incongruence in the published data (Appendix 3). Consequently, the CI of the MPTs must be 1, and the tree length must be equal to the number of (binary) characters (i.e., 15 rather than 16). Additionally, *Stagonolepis* and *Longosuchus* are scored identically for all characters in the published matrix and must therefore be subtended by the same node in any MPT for these data. This is not true of Parrish's published consensus tree.

Reanalysis.—Reanalysis of the published matrix confirmed its disagreement with the published results, yielding three MPTs of expected length 15 and a CI of 1. The strict component consensus (and unique SRC) of these trees (not shown) also differs from that published by

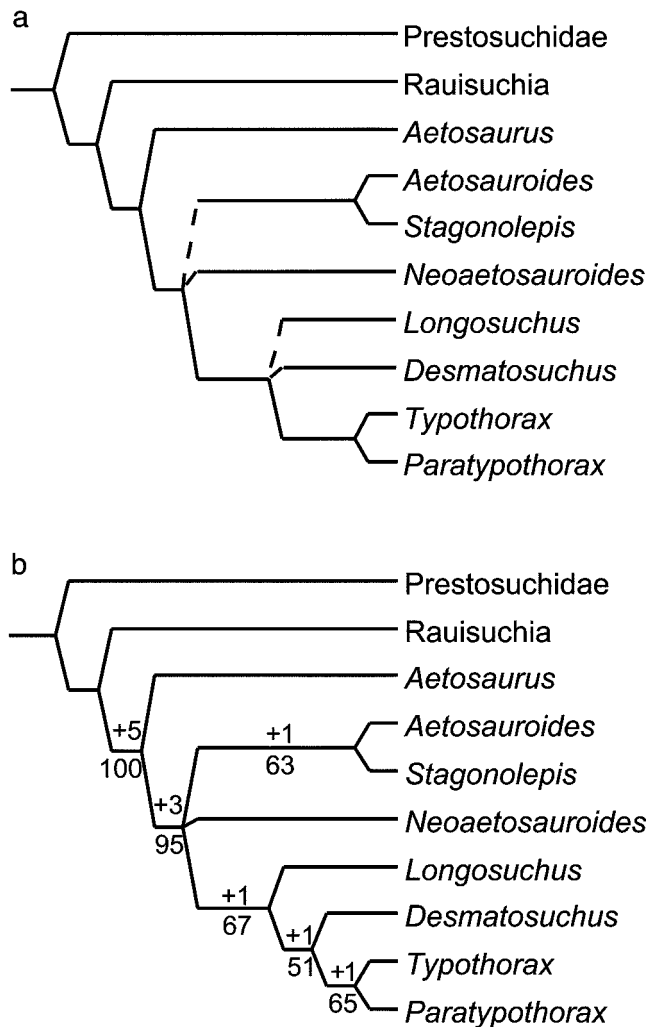


FIGURE 3. Strict component consensus trees for data from Parrish (1994). (a) SCC of three MPTs ($L = 16$, $CI = 0.938$) published by Parrish (1994). Dashed lines were unexplained. The same MPTs and consensus were also recovered from analysis of data matrix P94 ($CIC = 17.781$ bits, $CE = 0.968$). (b) SCC of the three binary MPTs ($L = 15$, $CI = 1.000$) recovered from analysis of rP94 (Appendix 2) ($CIC = 19.366$ bits, $CE = 1.000$). Numbers above and below branches are decay indices and bootstrap proportions, respectively.

Parrish, suggesting that the published matrix is not that used in Parrish's analyses. Parrish (pers. comm., 1996) confirmed this and explained that the entire row of data for *Stagonolepis* was inadvertently reentered for *Longosuchus* and that *Paratypothorax* was misscored (0 instead of 1) for character 15. The matrix that was originally analyzed and should have been published (Parrish, pers. comm., 1996) is given in Appendix 3 and is referred to here as P94. Analysis of P94 recovered the trees and descriptive statistics reported by Parrish (1994).

There are some discrepancies between P94 and Parrish's (1994) text. *Longosuchus* is scored as having an edentulous anterior premaxilla (character 3), but the description (1994:196) states that the anterior of the premaxilla is missing, implying that character 3 should be scored as unknown (?) for this taxon. Character 12 concerns the presence or absence of posterior premaxillary teeth. In the matrix, *Longosuchus* is also scored as possessing posterior premaxillary teeth (character 12) and the description of *Longosuchus* supports this scoring, drawing attention to (1994:196) "what seems to be a single premaxillary tooth." However, absence of premaxillary teeth (1994:207) is described as a synapomorphy of the unnamed clade containing *Longosuchus*, *Desmatosuchus*, *Typotho-*

rax, and *Paratypothorax*. *Aetosaurus* and *Typothorax* are scored as lacking a deep hemispherical fontanelle (state 0, character 14), yet in a list of the synapomorphies (1994:207) for the unnamed clade comprising *Longosuchus*, *Desmatosuchus*, *Typothorax*, and *Paratypothorax*, this character is described as "indeterminate in *Paratypothorax*, *Typothorax*, *Aetosaurus*, *Aetosauroides* and *Neoaetosauroides*."

A revised matrix (rP94) that resolves these discrepancies was prepared (see Appendix 3) in which *Longosuchus* was rescored as unknown for character 3 and *Aetosaurus* and *Typothorax* were rescored as unknown for character 14. We accepted Parrish's scoring of *Longosuchus* for character 12. Analysis of rP94 recovered two (three binary) MPTs. The rescored *Typothorax* removes all conflict from the matrix, and therefore the two trees have a length of 15 and CI of 1. The unique SRC (and SCC) (Fig. 3) of the two MPTs is slightly more resolved than Parrish's published tree (Fig. 3a).

Support.—Although P94 and rP94 yield similar phylogenies, they cannot be considered a compelling hypothesis for a number of reasons. Of the 15 characters in the matrix, two (1 and 2) are parsimony uninformative, and five (3–7) provide evidence that only serves to support a split between the outgroup and ingroup taxa. This leaves just eight characters to provide evidence for relationships among the eight included aetosaurians. Of these characters, three (8–10) support the ingroup split between *Aetosaurus* and all other aetosaurians, so that just five characters provide evidence for the relationships among the remaining seven genera.

Matrix randomization tests of the full data sets allow rejection of the null hypotheses that P94 and rP94 are no better than comparable random, phylogenetically uninformative data ($PTPs < 0.05$; Appendix 2), a minimum requirement for phylogenetic data. However, this rejection does not indicate that significant structure is distributed throughout the data (Faith and Cranston, 1991). When the two outgroup taxa are removed and the tests are applied to the ingroup-only data (eight taxa and eight characters), only the nesting-based test yields significant PTPs. Alroy (1994) advocated this test for its sensitivity, and our results provide empirical support for its use. However, although these data appear to be nonrandomly structured, the fact that the ingroup-only data fail the parsimony randomization tests suggests that ingroup trees based on parsimony analysis of these data should be viewed cautiously. With *Aetosaurus* also excluded, matrix randomization tests of the remaining data (seven taxa, five characters), including Alroy's (1994) highly sensitive nesting test, give nonsignificant results ($PTPs > 0.05$) despite the complete absence of conflict in rP94. Parrish (1994) did not measure support. With the single exception of the clade comprising all aetosaurians except *Aetosaurus*, all clades within Aetosauria that are supported by the parsimonious interpretation of rP94 (Fig. 3) have minimum decay indices (+1) and low (51–69%) bootstrap proportions. The matrix rP94 includes too few characters to provide a well-supported hypothesis of the relationships of the included aetosaurians.

Heckert et al. (1996)

Review.—Heckert et al. (1996) scored 23 characters for nine aetosaurian genera, including all genera used by Parrish (1994) plus *Redondasuchus*. Nonaetosaurian outgroups were not included, and trees were rooted on *Aetosaurus*. Exclusion of a nonaetosaurian outgroup meant that Parrish's (1994) characters 1–7 were also excluded. Heckert et al.'s character 23, describing variation in the gross morphology of the tail region, was not used in all of the analyses they reported. Parsimony analysis of Heckert et al.'s restricted data (minus tail character 23) was reported as producing five MPTs, the SCC of which is shown in Figure 4. Analysis of the full data set (including character 23) was reported as yielding a single MPT (Fig. 4).

Reanalysis.—Heckert et al. justified the removal of character 23 from some analyses because "it is not at all clear that reduction of the tail has a single, uniform cause" (1996:629), but we have included it in all our reanalyses. Reanalysis of the published matrix yielded Heckert et al.'s MPT (Fig. 4) but with different tree statistics. Heckert et al.'s data matrix was based in part on that presented by Parrish (1994), but several changes in scoring were incorporated. Two of these (from ? to 0 for *Aetosauroides* for character 13 and for *Typothorax* for character 20) were intentional corrections of assumed mistakes in Parrish's scoring (Heckert, pers. comm., 2000). However, three changes (from 0 to 1 for *Aetosaurus* and from ? to 1 for *Paratypothorax* for character 18 and from

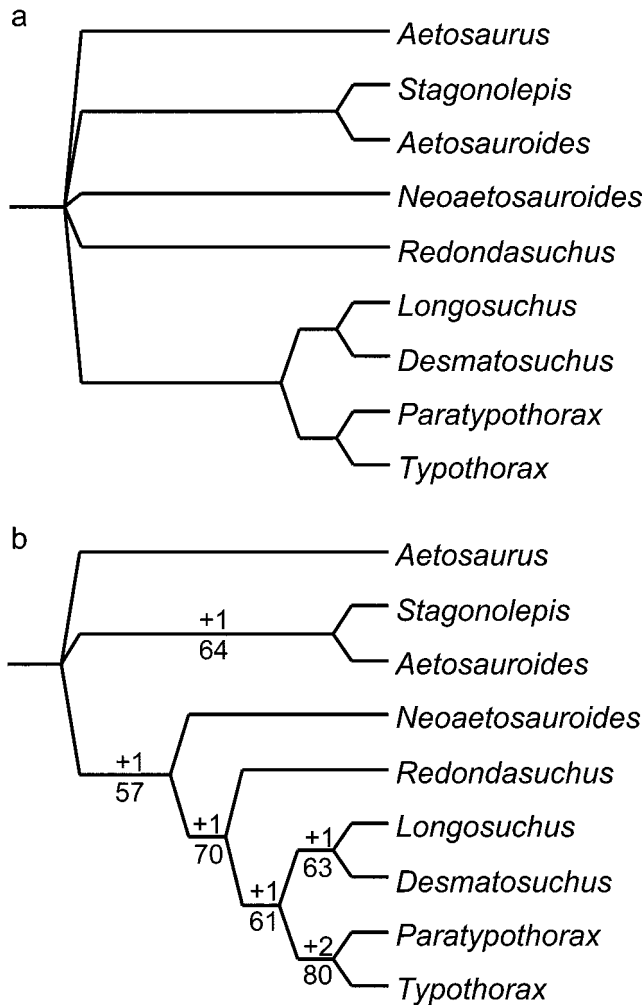


FIGURE 4. Trees for data from Heckert et al. (1996) (a) SCC of five MPTs ($L = 26$, $CI = 0.850$) from analyses excluding their character 23. (b) Single MPT (reported as $L = 29$, $CI = 0.793$) from their analysis of their full data. This tree was recovered in our reanalysis but with $L = 27$ and $CI = 0.815$. Numbers above and below branches are decay indices and bootstrap proportions, respectively.

0 to 1 for *Longosuchus* for character 21) were accidental (Heckert, pers. comm. 2000). A version of the matrix with these accidental changes rectified was prepared and is referred to as H96 (Appendix 4). Parsimony analysis of H96 recovered two MPTs, the unique SRC (and SCC) tree of which (Fig. 5) differs from the published tree (Fig. 4b) in leaving the relationships of *Longosuchus*, *Desmatosuchus*, and *Paratypothorax* + *Typothorax* unresolved.

Support.—Randomization tests of H96 yielded significant PTPs (Appendix 2), allowing rejection of the null hypothesis that these data are no more structured than would be expected from chance alone. However, decay indices are minimal (+1) for four of the five clades in the SCC tree (Fig. 5). The fifth (*Paratypothorax* + *Typothorax*) has a decay index of +2. Bootstrap proportions show only moderate support values (66–79%) for all of the clades. Such low support coupled with the impact of a few small corrections indicate that most relationships inferred from H96 cannot be considered robust.

Characters.—Some aspects of H96 relating either to Heckert et al.'s approach to character construction or to their scoring of inapplicable characters are problematic. Specifically, the independence of one pair of covarying characters is questionable. In addition, taxa for which particular osteoderms are unknown were nonetheless sometimes scored for characters based on features of those osteoderms.

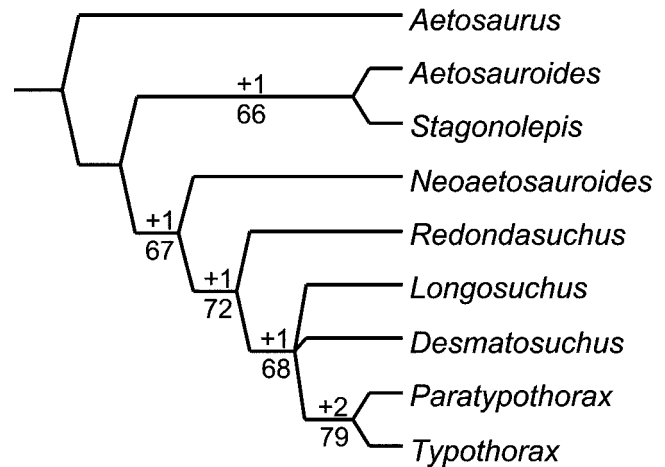


FIGURE 5. SCC ($CIC = 15.460$ bits, $CE = 0.964$) of the two MPTs ($L = 29$, $CI = 0.793$) from analysis of data set H96. Numbers above and below branches are decay indices and bootstrap proportions, respectively.

Characters 4 and 16 describe variation in the shape of the dorsal paramedian osteoderms and the gross morphology of the “carapace” to which they contribute. Character 4 distinguishes width: length ratios of the dorsal paramedian osteoderms of less than 4:1 from higher ratios. Character 16 describes the presence or absence of a discoidal carapace. Those taxa with discoidal carapaces also have wide dorsal paramedian osteoderms and vice versa (Appendix 4). Given that broad paramedian osteoderms contribute to a discoidal carapace, the two characters might reasonably be considered to be logically dependent. Heckert et al. acknowledged this linkage (1996:628) but argued that the two characters are independent “because: (1) it [discoidal carapace] represents a dramatically different body plan amongst the aetosaurs, and (2) it is possible to imagine aetosaurs with narrower paramedians still obtaining a discoidal carapace, or aetosaurs with wide paramedians retaining a more primitive body plan.” The latter would seem to require some compensatory reduction in the width of other osteoderms. We also suggest that if similar discoidal carapace shapes reflected dissimilar underlying patterns of osteoderms, then this might reasonably be taken as an indication that the similar carapace shapes were not homologous. Given the absence of aetosaurians with both discoidal carapaces and paramedian osteoderms less than four times as wide as long or with osteoderms more than four times wider than long and without discoidal carapaces, we consider the hypothesis that the two characters are not independent sufficiently plausible to adopt a more composite character construction. We prepared a revised matrix, referred to here as rH96 (Appendix 5) in which this pair of reductively coded characters was represented by a single more composite character.

Phylogenetic data matrices often include characters that describe variation with respect to the form of some features that are entirely absent in some of the taxa (e.g., variations in tooth crown morphology in edentulous mammals). Such characters are termed inapplicable. Although the scoring of inapplicable characters and their analytical treatment is controversial (Platnick et al., 1991; Maddison, 1993), most workers advocate that where characters are inapplicable, taxa should be scored as unknown, i.e., with missing entries (e.g., Hawkins et al., 1997; Lee and Bryant, 1999; Strong and Lipscomb, 1999). Heckert et al. did not adopt any particular convention for the treatment of inapplicable characters. Their data set included a number of such characters in which the taxon lacking the feature was scored for one of the character states seen in other taxa. In no case was the scoring justified, and the choice of character state therefore appears arbitrary. For example, *Redondasuchus* has been described as lacking lateral osteoderms (Heckert et al., 1996) and conventionally would be scored as unknown for characters relating to aspects of the morphology of lateral osteoderms. However, Heckert et al. (1996) score *Redondasuchus* as exhibiting state 0 for characters 13, 14, and 15 (Appendix 4), all of which describe variation

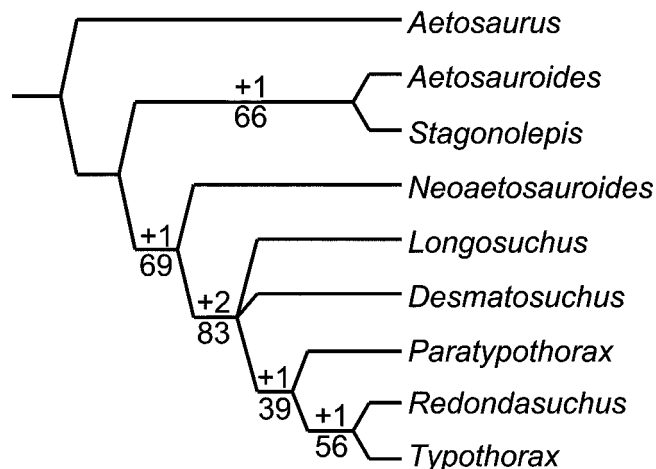


FIGURE 6. SCC (CIC = 15.459, CE = 0.964) of the two MPTs (L = 26, CI = 0.846) from analysis of data set rH96. Numbers above and below branches are decay indices and bootstrap proportions, respectively.

in lateral osteoderm morphology. This approach effectively assumes a conditional model of evolution in which state 0 is considered relatively primitive and state 1 is derived if lateral osteoderms are themselves derived or the opposite if it is the absence of lateral osteoderms that is derived. Although either model of evolution might be correct, no evidence has been presented to support them; therefore, we rescored these three characters in rH96 as unknown (?) for *Redondasuchus* (Appendix 5). A similar treatment of inapplicable character scoring occurs with characters 7 and 8 (Appendix 4), relating to the presence of bosses on the paramedian osteoderms and the position of such bosses, respectively. In Heckert et al.'s matrix (Appendix 4), the position of bosses on osteoderms in taxa which lack bosses (*Aetosaurus* and *Redondasuchus*) was scored as "on posterior margin." We rescored these taxa as unknown (?) for character 8 in the data matrix rH96.

Matrix rH96 (Appendix 5) has significant PTPs (Appendix 2), and parsimony analysis yielded two MPTs differing only in their resolution of the positions of *Longosuchus* and *Desmatosuchus*. The relationships in the SCC (Fig. 6) differ from those recovered from analysis of H96 (Fig. 5) in that *Redondasuchus* was recovered as sister taxon to *Typothorax*. Although the clades *Paratypothorax* + *Typothorax* and *Paratypothorax* + *Typothorax* + *Desmatosuchus* + *Longosuchus* were lost when the changes in rH96 were implemented, support for the clade *Paratypothorax* + *Typothorax* + *Desmatosuchus* + *Longosuchus* + *Redondasuchus* increased. The position of *Redondasuchus* was affected by our revisions because this taxon was most affected by inapplicable characters because of its apparent lack of lateral osteoderms. The position of *Redondasuchus* proposed by Heckert et al. (1996) thus appears to be attributable, in part, to inadvertent errors in the original data set.

Heckert and Lucas (1999)

Review.—Heckert and Lucas (1999) scored 60 characters for 14 taxa, including 11 aetosaurian genera, 2 species of a 12th genus, *Stagonolepis*, and an outgroup, Rauisuchia. Incorporated among the 60 characters were all but characters 1, 2, and 5 of Parrish's (1994) study and characters 12, 15, and 23 of Heckert et al.'s (1996) study. Heckert and Lucas (1999:62) reported analyzing "60 characters for *Coahomasuchus* and the 11 taxa listed above." This statement is confusing, because the listed taxa included *Coahomasuchus* and 12 other taxa, and although Heckert and Lucas reported recovering 16 MPTs they did not report tree lengths or other descriptive statistics for any of the 16 trees or their consensus. No reason was given for excluding any taxa at this stage in the analysis. Heckert and Lucas interpreted the consensus tree of their 16 MPTs as confirming their "initial suspicions that *Stagonolepis robertsoni* and *Aetosauroides scagliai* are congeneric, as are *Desmatosuchus* and *Acaenosuchus*, and *Longosuchus* and *Lucasuchus*" (1999:62). On this basis,

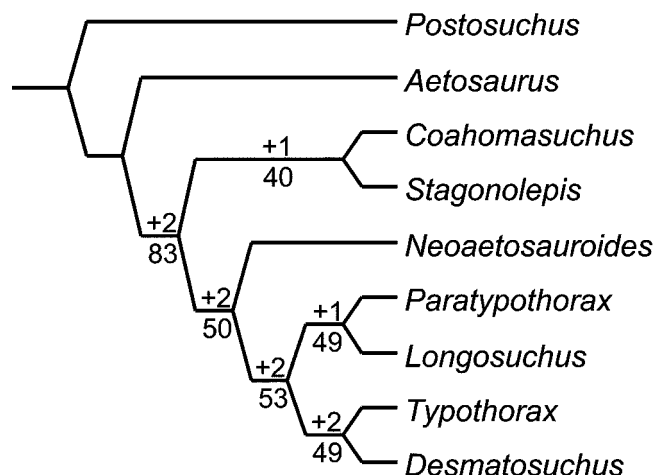


FIGURE 7. Single MPT (L = 76, CI = 0.747) from analysis of Heckert and Lucas's (1999) data with five taxa removed a priori. *Stagonolepis* is represented by *S. robertsoni*, and *Postosuchus* represents the rauisuchian outgroup. Numbers above and below branches are decay indices and bootstrap proportions, respectively.

they removed *Aetosauroides*, *Acaenosuchus*, and *Lucasuchus* from subsequent analyses. They also removed *Stagonolepis wellesi* because they were skeptical of its distinctiveness from *S. robertsoni* and removed *Redondasuchus* because it is too incompletely known. A second analysis carried out on the reduced data set of nine taxa was reported as yielding a single MPT (Fig. 7).

Reanalysis.—Our reanalysis of the reduced data set yielded the reported MPT. Analysis of the full published data set recovered 10 MPTs, for which two of three SRC trees are shown in Figure 8. Relationships supported by the full data set (Fig. 8) conflict with those from the reduced data set (Fig. 7) in several ways. There is a major shift in the position of *Typothorax* and smaller differences in the relationships of *Longosuchus* and *Paratypothorax* and of *Stagonolepis* and *Coahomasuchus*. The lack of resolution in the SCC (Fig. 8) is revealed by the second SRC tree (Fig. 8) to be attributable to the instability of *S. wellesi*. Our analysis of the full data set does not support the view that *Longosuchus* and *Lucasuchus* are congeneric; *Lucasuchus* was recovered as more closely related to a pairing of *Desmatosuchus* and *Acaenosuchus*. The data matrix also shows that there are character state differences between all of the supposedly synonymous taxa. In the most extreme case, there are five differences (characters 39, 40, 46, 48, and 52) between *Desmatosuchus* and *Acaenosuchus*, accounting for nearly 25% of those characters that are scored without missing data for both taxa.

As this example shows, excluding taxa can impact upon the relationships inferred for the remaining taxa. Such exclusion requires justification unless it has no impact. In this case, there is no scope for safe taxonomic reduction (Wilkinson, 1995b; Kearney, 2002), and thus we prefer analysis of the full data set. There are further reasons in this instance for preferring an analysis of the full data set. The 10 MPTs it yields are not unmanageable. Two of the three SRC trees for the full data set (Fig. 8) are more informative than the single MPT for the reduced nine-taxon matrix (CIC = 31.488 and 32.094 versus 17.044 bits), and their efficiency is high.

After consultation (Heckert, pers. comm., 2000), character 3 (teeth recovered-0; teeth conical-1) was rescored for *Paratypothorax* from 1 to ? (Table 1) to again resolve the inadvertent change from the scoring of this character by Parrish (1994). We refer to this modified data matrix as H99. The alteration had no effect on the relationships recovered in our reanalyses. Some conflict exists between the matrix and Heckert and Lucas's text that we were unable to resolve. A maxillary tooth row that does not extend anterior to the posterior end of the external naris (character 5) was scored as present in *Neoaetosauroides* but reported as unknown for that taxon in a list of synapomorphies for all aetosaurians except *Aetosaurus* (1999:63). Similarly, *Longosuchus* was scored as

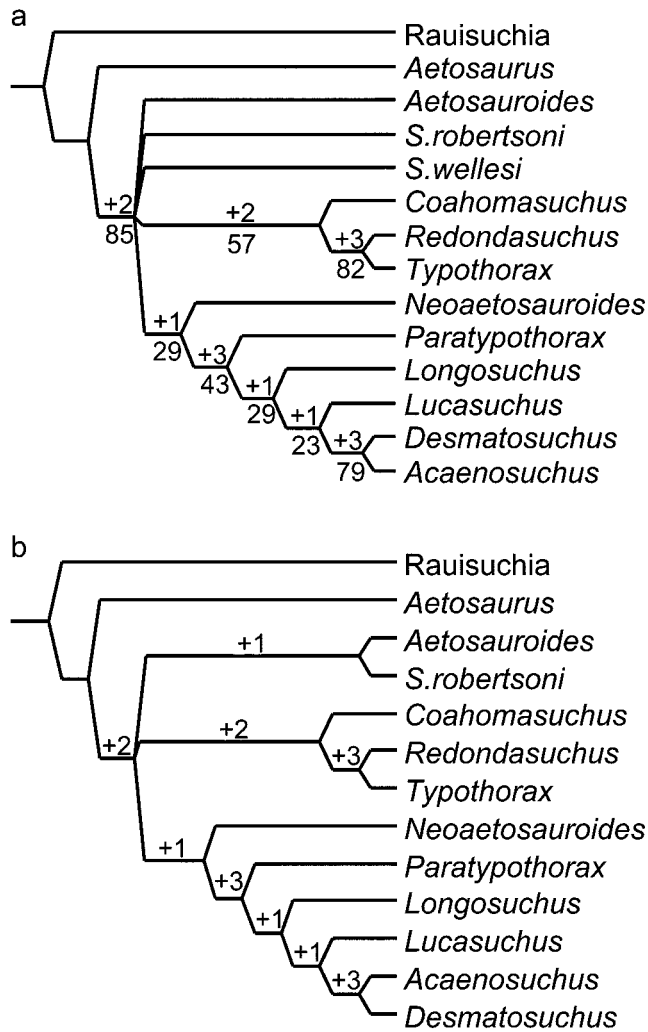


FIGURE 8. SRC profile (in part) of 10 MPTs ($L = 90$, $CI = 0.656$) from analysis of Heckert and Lucas's (1999) full data. (a) SCC tree ($CIC = 31.488$ bits, $CE = 0.903$). (b) Most informative SRC tree ($CIC = 32.094$ bits, $CE = 0.920$) excluding *Stagonolepis wellesi*. A third and less informative SRC tree ($CIC = 11.759$ bits, $CE = 0.337$) completes the profile. Numbers above and below branches are decay indices and bootstrap proportions, respectively.

possessing posterior premaxillary teeth (character 6) but was reported as unknown in a synapomorphy list (1999:64). Heckert and Lucas listed state 1 of their character 9 as weakly supporting the clade comprising *Neoaetosauroides*, *Typothorax*, *Desmotosuchus*, *Longosuchus*, and *Paratypothorax* (1999:64). However, only *Neoaetosauroides* was scored with this state; *Longosuchus* and *Desmotosuchus* were scored with state 0, and *Typothorax* and *Paratypothorax* were scored as unknown. For characters 11 and 12, *Coahomasuchus* was scored as possessing state 1 but was listed (1999:63) as unknown for both characters. In each of these cases, with the exception of character 9, we adopted a conservative approach and scored taxa subject to contradictory reports with missing entries (Wilkinson, 1997). For character 9, the contradiction is less clear, and we employed the scoring in the original matrix. These discrepancies should be addressed in future studies.

Support.—Randomization tests of both the complete and reduced (nine taxa) versions of H99 yielded significant PTPs (Appendix 2). With the full data set, decay indices are minimal (+1) for three of the clades in the SCC tree (Fig. 8a), and no clade has a decay index $> +3$. The additional relationship between *Stagonolepis robertsoni* and *Coahoma-*

suchus when *S. wellesi* is ignored (Fig. 8b) has a minimal decay index. Bootstrap proportions are $>50\%$ for only four clades, with strongest support (86%) for *Aetosaurus* lying outside all other aetosaurians. No other clades were recovered in $>77\%$ of bootstrap trees. With the reduced nine taxon data, bootstrap support is again highest (83%) for the clade including all aetosaurians except *Aetosaurus*, but no other clades appear in $>53\%$ of the bootstrap trees, and no clades have decay indices $> +2$. These overall low levels of support for the nine-taxon analysis are not surprising given that over half of the characters (31 of 60) are parsimony uninformative for these restricted data.

Characters.—Of the 60 characters in H99, 33 relate to variation in osteoderm morphology. Some aspects of Heckert and Lucas's (1999) character construction are questionable; thus, we produced a revised matrix, referred to as rH99 (characters 1–60 in Table 1). There are several instances of taxa seemingly arbitrarily scored with states of characters that are inapplicable, and we rescored these as missing. *Redondasuchus* lacks lateral osteoderms (Heckert et al., 1996) but was originally scored as possessing state 0 for the 10 characters (46–53, 55, 57) that relate to variations in the morphology of lateral osteoderms. Character 35 describes the position of bosses on osteoderms. The three taxa (*Coahomasuchus*, *Typothorax*, and *Redondasuchus*) that lack bosses on all osteoderms were originally scored as having bosses not in contact with the posterior margin of the osteoderm. Similarly, these three taxa were scored as having various forms of the (nonexistent) bosses on their dorsal osteoderms (characters 39 and 40). Most of the taxa (*Rauisuchia*, *Aetosaurus*, *Stagonolepis robertsoni*, *S. wellesi*, *Longosuchus*, *Lucasuchus*, *Desmotosuchus*, *Acaenosuchus*, *Aetosauroides*, *Neoaetosauroides*, and *Paratypothorax*) were scored as lacking a ventral keel or strut on dorsal paramedian osteoderms (character 43). However, they were also scored as having ventral keels that are continuous across the width of osteoderms (character 44). We rescored these taxa as unknown for character 44. Characters 49, 50, and 51 describe the presence or absence of lateral spikes on lateral osteoderms, and character 53 describes variation in the angle of spikes on lateral osteoderms. All taxa lacking lateral spikes (*Rauisuchia*, *Coahomasuchus*, *Aetosaurus*, *Stagonolepis robertsoni*, *Aetosauroides*, and *Neoaetosauroides*) were rescored as unknown for character 53.

Randomization tests of rH99, including all taxa, yielded significant PTPs (Appendix 2). Parsimony analysis recovered 1 MPT, shown in Figure 9. Comparison of this tree with the consensus tree in Figure 8a indicates that our alterations had an impact upon what can be inferred from the data. In addition to providing (weak) resolution of the relationships of *Aetosauroides* and the two species of *Stagonolepis*, our alternative character constructions resulted in reduced support for the clades *Redondasuchus* + *Typothorax* + *Coahomasuchus* and *Paratypothorax* + *Longosuchus* + *Lucasuchus* + *Desmotosuchus* + *Acaenosuchus*.

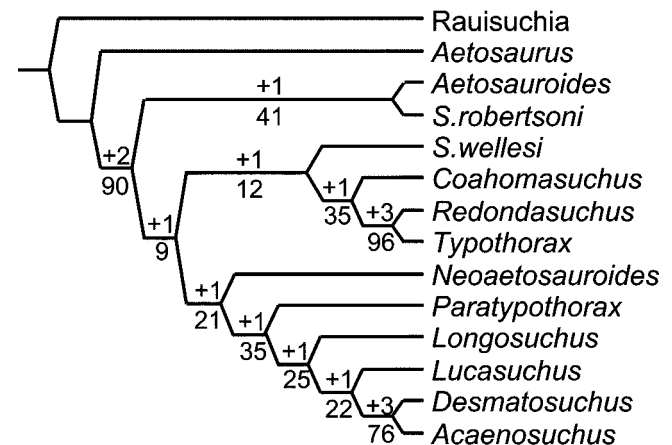


FIGURE 9. Single MPT ($L = 86$, $CI = 0.674$) from analysis of data set rH99. Numbers above and below branches are decay indices and bootstrap proportions, respectively.

APPENDIX 2

Summary statistics for selected analyses. T = number of taxa; C = number of characters; N = number of MPTs; L = tree length; CI = consistency index. Permutation tail probabilities (PTPs) are for matrix randomization tests using parsimony tree length and pairwise character nesting.

Data matrix ^a	T	C	N	L	CI	PTP	
						Parsimony	Nesting
P94 full	10	15	3	16	0.938	0.001 ^b	0.001 ^b
P94 ingroup	8	15	—	—	—	0.277	0.005 ^b
P94 ingroup minus <i>Aetosaurus</i>	7	15	—	—	—	0.473	0.332
rP94 full	10	15	2	15	1.000	0.001 ^b	0.001 ^b
rP94 ingroup	8	15	—	—	—	0.076	0.002 ^b
rP94 ingroup minus <i>Aetosaurus</i>	7	15	—	—	—	0.109	0.118
H96	10	23	2	29	0.793	0.001 ^b	0.001 ^b
rH96	10	22	2	26	0.846	0.001 ^b	0.001 ^b
H99	60	14	10	90	0.656	0.001 ^b	0.001 ^b
rH99	60	14	1	86	0.674	0.001 ^b	0.001 ^b

^aP94 = Parrish, 1994, original (corrected) matrix; H96 = Heckert et al., 1996, original (corrected) matrix; H99 = Heckert and Lucas, 1999, original matrix. The prefix "r" indicates our revision of the original matrices.

^bSignificant (PTP ≤ 0.05).

APPENDIX 3

Data matrix P94, which is a corrected matrix for Parrish's (1994) data. These are the data analyzed but not published by Parrish (pers. comm., 2000). To produce the matrix referred to as rP94, the three underlined character states were changed to ? in order to remove discrepancies between the matrix and Parrish's (1994) text.

Taxon	Characters		
	12345	1 67890	11111 12345
Prestosuchidae	00000	00000	00000
Rauisuchia	11000	00000	00000
<i>Aetosaurus</i>	11111	11000	00000
<i>Stagonolepis</i>	11111	11111	10000
<i>Longosuchus</i> ^a	11111	11111	10000
<i>Longosuchus</i> ^b	11111	11111	00110
<i>Desmotosuchus</i>	11111	11111	01110
<i>Typothorax</i>	11111	11111	?1101
<i>Aetosauroides</i>	11111	111?1	10?20
<i>Neoaetosauroides</i>	11111	11111	000?0
<i>Paratypothorax</i>	????1	11?21	?1?1?1 ^c

^aScoring of *Longosuchus* in Parrish's published matrix.

^bScoring of *Longosuchus* in corrected matrix provided by Parrish (pers. comm.).

^cCharacter 15 for *Paratypothorax* was misscored as state 0 instead of 1 in Parrish's published matrix (Parrish, pers. comm.).

APPENDIX 4

Data matrix H96, which is a corrected matrix of Heckert et al.'s (1996) data.

Taxon	Characters				
	12345	1 67890	111 11 123 45	111 12 678 90	2 22 1 23
<i>Aetosaurus</i>	00000	00000	000 00	000 ^a 00	0 00
<i>Aetosauroides</i>	?2000	01?00	000 ^b 00	001 ?1	0 ?0
<i>Stagonolepis</i>	00000	01000	000 00	001 11	0 00
<i>Neoaetosauroides</i>	???0?	?1?00	000 00	001 10	0 ?1
<i>Redondasuchus</i>	10001	10011	110 00	0?? ??	? ?1
<i>Longosuchus</i>	10000	010?0	001 10	011 10	0 ^a 11
<i>Desmotosuchus</i>	11100	01110	001 10	011 10	1 11
<i>Paratypothorax</i>	?0010	010?0	001 11	11? ^a ??	? ?1
<i>Typothorax</i>	00011	11010	101 11	111 10 ^b	1 01

^aScore as in Parrish (1994) inadvertently changed in original matrix of Heckert et al. (1996).

^bScore as in Heckert et al. (1996) intentionally changed from that of Parrish (1994).

APPENDIX 5

Data matrix rH96, which is modified from the Heckert et al. (1996) matrix from Appendix 4 by incorporating alternative character constructions.

Taxon	Characters				
	12345	11 67890	11111 12345	11122 78901	22 23
<i>Aetosaurus</i>	00000	00?00	00000	00000	00
<i>Aetosauroides</i>	?2000	01?00	00000	01?10	?0
<i>Stagonolepis</i>	00000	01000	00000	01110	00
<i>Neoaetosauroides</i>	???0?	?1?00	00000	01100	?1
<i>Redondasuchus</i>	10001	10?11	11???	?????	?1
<i>Longosuchus</i>	10000	010?0	00110	11100	11
<i>Desmotosuchus</i>	11100	01110	00110	11101	11
<i>Paratypothorax</i>	?0010	010?0	00111	1? ???	?1
<i>Typothorax</i>	00011	11010	10111	11101	01