for the transition:transversion ratio because this value is unlikely to be 2.0.

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Phylogenetic Methods and Aetosaur Interrelationships: A Rejoinder

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In a previous paper (Harris et al., 2003), we discussed the treatment of intraorganismal homology in character construction. Our aims were to highlight alternative approaches and to investigate their theoretical foundations and analytical consequences, and we used the phylogeny of aetosaurian reptiles as an example. In a previous study, Heckert and Lucas (1999) employed several characters describing variation in aetosaur osteoderms. Harris et al. (2003) noted that parallel variations (e.g., presence of either radial or random patterning) in the osteoderms of different body regions were represented as separate but covarying characters, implying independent evolutionary changes in different regions. We suggested that osteoderms are intraorganismal homologues and that a single change affecting multiple osteoderm regions, represented by a single composite character, was a plausible alternative to the previous more reductive interpretation. We demonstrated that alternative reductive and composite approaches to constructing characters from variation in osteoderms impacts inferred relationships and their apparent levels of support.

In response, Heckert and Lucas (2003:253) dismissed our interpretation of osteoderms as intraorganismal homologues, arguing that we made "an unverifiable assumption about underlying genetic control" and that we ignored known intraorganismal variation in osteoderms. In fact, we explicitly discussed (2003:244) such variation. Importantly, we argued that osteoderms are intraorganismally homologous, not that they are intraorganismally homogenous. Heckert and Lucas's (2003) preferred, more reductive, coding also entails assumptions that they did not discuss. For example, their use of separate characters to represent parallel variation in cervical and dorsal osteoderms assumes homology within, but nonhomology between, these regions. The latter entails that any changes occurring in both regions are coincidental and homoplastic. As we pointed out, this assumption contravenes Hennig's auxiliary principle (Hennig, 1966). Heckert and Lucas (2003) did not discuss the theoretical issues we raised and dismissed our work as teaching us "not much" about aetosaur phylogeny.

Heckert and Lucas (2003) argued that the alternative character constructions make no difference to inferred relationships, yielding trees that are "remarkably similar," and claimed (2003:253) that the tree obtained with our more composite characters "is still the same as that published by us (compare Harris et al., 2003: fig. 2a with Heckert and Lucas, 1999: fig. 9)." This assertion is incorrect. The cited trees are not the same—they differ in the placement of three of eight ingroup taxa (Fig. 1). Furthermore, the cited tree (Harris et al., 2003: fig. 2a) was based on a reductive, not a composite coding. In fact, composite and reductive approaches yielded substantially

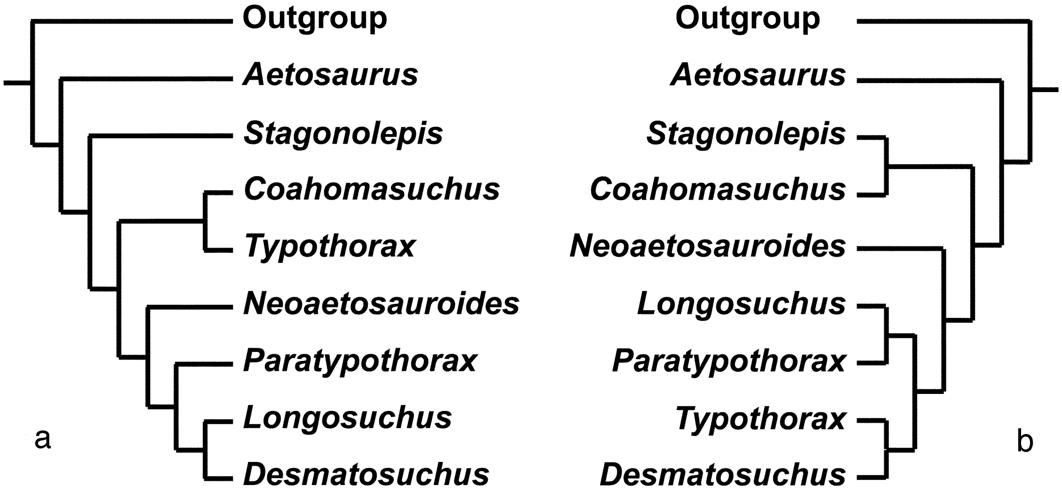

FIGURE 1. Comparison of aetosaur phylogenies produced from our reductive coding approach (a) and Heckert and Lucas's (1999: Fig. 9) analysis (b). Five aetosaur taxa arbitrarily excluded by Heckert and Lucas (1999) have been pruned from our tree (Harris et al., 2003: Fig. 2a) to aid comparison. Transforming either tree into the other requires repositioning of at least three taxa (*Longosuchus, Typothorax*, and *Coahomoasuchus* or *Stagonolepis*).

dissimilar trees that share only three of a possible 11 clades (Harris et al., 2003: fig. 2).

We also identified discrepancies in the literature, resolved these as far as we could, and highlighted problems that remained for future workers. We pointed out inconsistencies and irregularities in the previous treatment of inapplicable characters. We performed more comprehensive analyses including taxa that Heckert and Lucas (1999) had needlessly excluded, and we presented the first quantitative assessments of support for hypothesised relationships. These assessments are particularly important because previous researchers (Parrish, 1994; Heckert et al., 1996; Heckert and Lucas, 1999) provided no caveats whatsoever regarding the inferred relationships, which have been used to underpin revised phylogenetic taxonomy and interpretations of evolutionary patterns (Parrish, 1994; Heckert and Lucas, 2000).

We concluded (2003:243) that our and previous results "should not, for the most part, be accepted as robust hypotheses of aetosaurian interrelationships." This statement reflected the lack of agreement among different studies, generally low support values, and sensitivity to alternative character constructions. Heckert and Lucas (2003:253) accepted the conclusion that aetosaur phylogeny is weakly supported but considered that this has "little to do with analytical tools and much to do with the especially fragmentary nature of the aetosaurian fossil record." We doubt that the problem of missing data is the whole story but are pleased that, for the first time, these aetosaur workers have explicitly acknowledged that support for their phylogenetic hypotheses is weak.

Heckert and Lucas (2003:254) complained that we provided no new data for understanding aetosaur phylogeny (but see Gower and Walker, 2002) and extended an invitation to "push back from their computer terminals and join us in our ongoing search for new aetosaur fossils and thus additional data on aetosaur morphology, from which we will most assuredly learn more about the phylogeny and evolution of these animals." Clearly phylogenetic analyses depend upon generating data. However, thoughtful character construction and careful analyses must also play their part. We attempted to provide the latter. Readers of *Systematic Biology* can judge whether our attempt "contributes nothing toward a better understanding of aetosaur phylogeny" (Heckert and Lucas, 2003:254).

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