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A reappraisal of the phylogeny of early dinosaurs

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The origin and initial diversification of the dinosaurs are still poorly understood despite the immense focus on dinosaur palaeobiology during the last 30 years. New discoveries of relatively complete material over the past 20 years (*e.g.*, Sereno *et al.* 1993) have added much to our knowledge of basal dinosaurs, yet there is still considerable debate about how these forms fit into the phylogeny of dinosaurs and their closest relatives. Because of this uncertainty of relationships, there are precious little data available to test hypotheses about the initial divergences and diversifications of the main dinosaur clades of Ornithischia, Sauropodomorpha, and Theropoda.

Although additional data in the form of new specimens and taxa are always welcome, it appears that a large part of the chaos surrounding basal dinosaur relationships is methodological. There has been no shortage of phylogenetic analyses of basal dinosaurs over the past 15 years, and many share common weaknesses that may in part prevent the academic community from reaching a consensus. Most published basal dinosaur analyses have only utilized one or two closely related outgroups to polarize their characters, whereas a much deeper sampling of Archosauria is needed to understand the distribution of character-states throughout the clade, especially because many of these non-dinosaurian archosaurs were contemporaries of basal dinosaurs, and fragmentary specimens could be confused with basal dinosaur material. Additionally, nearly all analyses have excluded more fragmentary taxa of basal dinosaurs, even though it is clear that even highly-incomplete fossils can impact the topology of a phylogenetic tree.

New discoveries in the last several years have also necessitated a re-evaluation of basal dinosaurs. Dzik (2003) described the peculiar basal dinosauriform *Silesaurus opolensis* from the Upper Triassic of Poland. The discovery that many alleged Triassic ornithischian taxa cannot actually be considered ornithischians or dinosaurs (Irmis *et al.* 2006a) has led my colleagues and me to re-evaluate all proposed Triassic dinosaur records in North America (Nesbitt *et al.* in press). This comprehensive study has resulted in several important conclusions. First, several character-states previously used to diagnose the Dinosauria or clades within it were found to have a wider distribution among the Archosauria. Using a revised group of robust synapomorphies for identifying Triassic dinosaur taxa, we have determined that many of the purported Triassic dinosaur specimens are not diagnostic, or are chimaeras of dinosaur and non-dinosaur material. The revised record suggests that there are no confirmed occurrences of sauropodomorphs or ornithischians in the Triassic of North America.

My colleagues and I are also studying new material from the Hayden Quarry, a new locality that is near both the Ghost Ranch *Ceolophysis* Quarry and the Snyder Quarry in northern New Mexico (U.S.A.). Preliminary excavations have already yielded associated remains of a basal dinosauriform, several basal dinosaurs, and coelophysoid theropods. The Hayden Quarry is the only site in the world where basal dinosauriforms, basal dinosaurs, and theropods are found in direct association (Irmis *et al.* 2006b).

The author (left) and Sterling Nesbitt (right) excavate early dinosaurs at the Hayden Quarry in northern New Mexico (photo by A. Turner).

To incorporate the new discoveries outlined above and to address the weaknesses of previous phylogenetic hypotheses, I am working on a new phylogenetic framework based on a specimen-level analysis of early dinosaurs and related taxa as part of my PhD dissertation. With this phylogeny, I will be able to evaluate questions about biostratigraphy, evolutionary timing, biogeography and adaptation. For example, did a key adaptation or set of adaptations contribute to the success of the Dinosauria as a clade? What is the tempo and mode of early

dinosaur diversification? What hypotheses might explain the heterogeneous distribution of the major clades of dinosaurs (*i.e.*, ornithischians, sauropodomorphs, and theropods) during the Late Triassic, and can a particular geographic origin be postulated for the group?

The Sylvester-Bradley award allowed me to travel to various European collections to collect data for my phylogenetic analysis, as well as to compare the anatomy of known basal dinosaurs and relatives with the new discoveries from the Hayden Quarry. During my four week research trip, I visited the Natural History Museum (London), Humboldt Museum für Naturkunde (Berlin), Staatliches Museum für Naturkunde (Stuttgart), Institut für Geologie und Paläontologie (Tübingen), and Instytut Paleobiologii PAN (Warsaw). This visit complemented other visits to South America; I have now examined most of the basal dinosaur material in museum collections worldwide.

Although data analysis is still ongoing, preliminary results suggest that the new taxa from the Hayden Quarry do not belong to endemic North American clades. Rather, their closest relatives may be taxa that were previously known only from Argentina. Some material from the Hayden Quarry appears to be most closely related to the dinosauriform *Silesaurus* from Poland. These geographic connections suggest that the early biogeography of dinosaurs is not nearly as simple as the fossil record would lead us to believe. Publications of these results are currently in preparation, and will include a preliminary phylogenetic analysis that utilizes important data from my Sylvester-Bradley funded research trip.

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