

## Reconstruction of an ancestral amniote trackmaker based on trackway data, track – trackmaker correlation and phylogeny

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### Abstract:

Trackway measures, such as pace angulation, pace length, stride length, gauge width, manus-pes distance (along track) and imprint orientation vary notably among amphibian, stem-amniote and early amniote tracks from Late Carboniferous to Early Permian deposits. Some of this variability can be attributed to evolutionary changes in trackmaker anatomy and locomotion style close to the origin of amniotes. This variability may be explored through phylogenetic approaches following the assignment of certain track types to distinct producer groups.

Based on trackway averages of various parameters measured for eight tetrapod ichnotaxa from the Early Permian of the Thuringian Forest Basin as well as two additional Late Carboniferous ichnotaxa we infer ancestral states for functionally controlled trackway measures by means of parsimony and maximum likelihood.

We use basal amniote trees from recent literature and consider two alternative trackmaker phylogenies, where: (1) diadectomorphs as probable producers of Late Carboniferous to Early Permian *Ichniotherium* tracks form the sistergroup to all amniotes; (2) they form the sistergroup of more derived synapsids within Amniota.

According to our results, the ancestral amniote trackmaker had a body size higher than the sampled amphibian and reptilian track producers but was smaller than diadectomorph and early synapsid trackmakers. Its tracks were characterized by higher pace angulations, somewhat narrower gauges and lower normalized stride lengths than those of its non-amniote predecessors, whereas neither the normalized distance between consecutive manual and pedal imprints nor the orientation of the pedal imprints appear to have changed much on the amniote stem. The manual imprints were more outward positioned and had a more parallel orientation than those made by earlier stem-amniote producers. Early Permian *Ichniotherium* trackways display certain similarities to contemporaneous synapsid tracks, whereas other measures, most notably the orientation of manual and pedal imprints, differ considerably, demonstrating their limited use as model tracks of basal amniotes.

**Keywords:** ichnotaxa, track-trackmaker correlation, Ancestral State Reconstruction (ASR), Carboniferous