

## The enamel microstructure of *Manidens condorensis*: New hypotheses on the ancestral state and evolution of enamel in Ornithischia

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Previous studies on enamel microstructure in Ornithischia have focused on derived lineages of this clade based on species from the northern hemisphere. Here we describe the enamel microstructure of *Manidens condorensis* from the late Early Jurassic of Argentina that belongs to Heterodontosauridae (interpreted as the basal-most clade of Ornithischia). Enamel microstructure in the cheek teeth lacks a basal unit layer, presents incipient divergent crystallite as the dominant enamel type and parallel crystallite enamel type (with or without incrementing lines). Enamel of maxillary and dentary teeth differs from each other in enamel distribution (asymmetric vs. symmetric), structure (presence vs. absence of tubules, and less vs. more abundant parallel crystallite enamel with incrementing lines) and ordering (regular ordering of enamel types vs. in patches). The enamel microstructure of *Manidens* is the simplest of all known Ornithischia, and is more similar to that of the sauropodomorph *Plateosaurus* than to the one reported for the basal theropod *Coelophysis*. Similarities within Ornithischia are present with pachycephalosaurids and, to a lesser extent, with ankylosaurs. Phylogenetic optimization of enamel characters in Ornithischia allows the inference of new ancestral states for the internal nodes of the major lineages and to highlight evolutionary transformations: (i) absence of a basal unit layer and presence of parallel crystallite and incipient divergent columnar enamel as the ancestral state for Ornithischia; (ii) the shared presence of incipient divergent columnar units or poorly developed divergent columnar enamel in Pachycephalosauridae and Thyreophora represents a retention of the plesiomorphic ornithischian condition; (iii) the wavy enamel of Dryomorpha evolved from the ancestral incipient divergent columnar units present in Ornithopoda and; (iv) enamel thickness and asymmetry has independently evolved at least four times in Ornithischia.

**Key words:** Dinosauria, Ornithischia, Heterodontosauridae, *Manidens*, enamel microstructure, evolution, Jurassic, Argentina.

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