The Oldest Horseshoe Crabs (Early Ordovician, Morocco) and the Origins of the Xiphosurid Thoracetron

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A defining apomorphy for the Order Xiphosurida, which contains all modern horseshoe crabs, is the fusion of the opisthosomal tergites into a single shield, the thoracetron. The recently described Lunataspis from the Katian of Manitoba, which until now represented the oldest known horseshoe crab, demonstrates that partial opisthosomal fusion was achieved by the Late Ordovician. At least 150 exceptionally preserved horseshoe crab specimens from six localities within the latest Tremadocian-early Floian (Early Ordovician) of the fully marine Lower and Upper Fezouata Formations of Morocco show that this key innovation originated even earlier. All specimens exhibit a fused preabdomen comprising eight segments, a postabdomen comprising three freely articulating segments and a long styliform telson. The fossils are characterised by a subcircular prosomal carapace that exhibits a weakly expressed cardiac lobe and faint ophthalmic ridges carrying small, anteriorly set eyes. In many specimens the prosomal appendages, including the chelicerae, are preserved in remarkable detail; their morphology is broadly similar to that of most other, younger xiphosuran taxa with known appendages. The abundant material includes various instars of the same new genus, documenting ontogenetic changes in opisthosomal morphology. At three localities, these fossils co-occur with other, more primitive “synziphosurine” horseshoe crabs that retain a fully articulated eleven-segmented opisthosoma. These new finds demonstrate that the xiphosurid fusion of opisthosomal segments occurred earlier in the evolution of Xiphosura than previously thought, and indicate that the acquisition of a fully fused thoracetron was a more complex process than hitherto recognised.