Trilobite expansion into estuarine environments during the Ordovician radiation

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Trilobites have traditionally been considered fully marine. Through the integration of ichnological, palaeobiological and sedimentological datasets within a sequence-stratigraphic and stratigraphic palaeobiology framework, we challenge this assumption. This analysis is based on the study of incised fluvio-estuarine valley deposits from the Furongian Tilcara Member (TM) and the latest Furongian Pico de Halcón Member (PHM) of the Santa Rosita Formation, the early late Tremadocian Cardonal Formation (CF), and the Dapingian–Darriwilian Alto del Cóndor Formation (ACF), from Cordillera Oriental of northwest Argentina. These valleys were incised into wave-dominated shallow-marine strata and filled with transgressive deposits that accumulated in tide-dominated estuaries. Whereas the TM lacks any body or trace fossil evidence of the presence of trilobites in estuarine settings, the other three units reveal that trilobites were able to inhabit these settings. The PHM and CF are host to trilobite trace fossils in outer estuarine facies, both containing various ichnospecies of \textit{Cruziana} (e.g., \textit{C. omanica} and \textit{C. semiplicata} in the TM) and \textit{Rusophycus} (e.g., \textit{R. latus} in both units). In addition, the PHM also contains body fossils of the olenid trilobite \textit{Neoparabolina frequens argentina} in the same deposits in which the trace fossils are preserved, as well as from middle estuarine facies. The ACF displays trilobite trace fossils of the \textit{C. rugosa} group in inner, middle, and outer estuarine deposits, illustrating further landward incursions. This unit also contains body fossils of the asaphid trilobite \textit{Ogyginus} sp. Accordingly, our data indicate two attempts of landward exploration via brackish water: phase 1 in which the outer to middle portion of estuaries were colonized by olenids (Furongian–early late Tremadocian) and phase 2 involving exploration of the inner, middle, and outer estuarine zones by asaphids (Dapingian–Darriwilian). Our study indicates that these trilobites were tolerant to salinity stress and able to make use of the ecological advantages offered by marginal-marine environments migrating up-estuary, following salt wedges either reflecting amphidromy or as euryhaline marine wanderers. It is suggested that tolerance to salinity stress arose independently among different trilobite groups as a result of the broad array of behaviors and adaptations of trilobites during the Ordovician radiation. We speculate that the assumption that all trilobites were stenohaline may have resulted in the misinterpretation of some tide-dominated estuarine deposits as fully marine.