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Phylogeny and evolutionary modularity of a trilobite family over the Ordovician Radiation

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ABSTRACT

Trilobites are organized in packages; the adult trilobite body plan is composed of a cephalon (head), thorax (midsection), and pygidium (tail). These packages, or modules, are composed of traits that evolve semi-independently such that change in one module does not necessarily beget change in another module. At the macroevolutionary level, this decoupling and relaxation of evolutionary constraints is thought to promote evolvability. Thus, it is thought that modularity facilitates rapid diversification in diverse evolutionary directions, the hallmark of an adaptive radiation, as evolutionary rates among modules can vary along phylogenetic branches. Trilobites provide an unmatched fossil record, due to their biomineralized exoskeleton, to examine the long-term relationship between macroevolutionary diversification and modularity.

However, the lack of a phylogenetic framework for major trilobite groups hampers the study of macroevolutionary questions. For instance, the trilobite family Pterygometopidae diversified during the Middle and Late Ordovician in Baltica, Avalonia, Laurentia, and Siberia. This group traditionally comprises four subfamilies with strong biogeographic signal including Pterygometopinae, Chasmopinae, Eomonorachinae, and Monokainae. However, relationships between and within subfamilies remain unresolved. Further, relationships with other families in the suborder Phacopina, especially with Phacopidae, remain unclear.

To even begin tackling the relationship between macroevolution and modularity, phylogenetic relationships must be resolved in this trilobite group. To do so, we constructed a comprehensive character matrix comprising >240 characters including discrete, meristic, and continuous characters. Analyses include taxa from all 36 genera assigned to Pterygometopidae and include Ordovician exemplars from the trilobite families Diaphanometopidae, Phacopidae, Dalmanitidae, and Acastidae. We ran Bayesian phylogenetic analyses to produce trees that would co-estimate topology and evolutionary rates using the birth-death model.

Further, we quantified the 3D morphology of the trilobite head using high-density geometric morphometrics for exemplar taxa within Pterygometopidae to identify the structure and degree of modularity of the trilobite head in this group. Future work will assess evolutionary rates for the trilobite head and, importantly, evolutionary rates of individual modules over the Ordovician Radiation to determine an increase or decrease in modularity over this diversification event.

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