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MORPHOLOGICAL AND ONTOGENETIC CHANGE IN THE "EARLY" CAMBRIAN TRILOBITE *ZACANTHOPSIS* DURING AN INTERVAL OF ENVIRONMENTAL CHANGE

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High-resolution stratigraphic sampling of silicified nodular limestone beds from Oak Springs Summit in the Delamar Mountains, east-central Nevada, United States, yielded undeformed ontogenetic material documenting a stratigraphic trend in samples of the trilobite *Zacanthopsis*. These limestone beds are interbedded with shales lying in the 10-meter interval immediately below the Dyeran-Delamaran ("Early-Middle" Cambrian) boundary in the Combined Metals Member of the Pioche Formation (Merriam, 1964; Palmer, 1971, 1998; Sundberg and McCollum, 2000). Regional stratigraphy is characterized by karsted calcareous sandstone and oncolitic limestones below the section of interbedded shales and nodular limestone beds and by ribbon limestones above the section (Sundberg and McCollum, 2000), indicating that water depth was increasing as these sediments were deposited (Webster, 2007).

Morphological shape change in the cranidium is documented using principal components analysis of geometric morphometric data (to be presented elsewhere) (Zelditch *et al.*, 2004). Morphologically mature specimens were identified by plotting the Procrustes distance of each specimen from the mean of the smallest three specimens against centroid size: a sharp decrease in the rate of shape change away from the morphology of the smallest specimens indicates the onset of morphological maturity in *Zacanthopsis* cranidia. The primary change in morphologically mature specimens during this stratigraphic interval is a lateral expansion of the cranidium at the palpebral lobes relative to the width of the cranidium at the anterior facial sutures, accompanied by change in the orientation of the lobe (Fig. 1). Similar morphological change associated with increasing water depth has been documented in Ordovician trilobites from the Cincinnati area (Webber and Hunda, 2007) and from central New York State (Cisne *et al.*, 1980).

Principal components analysis including morphologically immature specimens reveals that smaller specimens from all samples overlap in morphospace but that the stratigraphically youngest sample follows a unique trajectory of shape change as specimen size increases (data to be presented elsewhere). This ontogenetic divergence in morphospace is supported by statistical comparison of growth vectors extracted from Procrustes coordinates (methodology discussed in Webster *et al.*, 2001). This sample is thus considered a distinct species and the appearance of the new species was accompanied by allometric repatterning (*sensu* Webster and Zelditch, 2005). The more subtle differences between stratigraphically older samples, however, are not associated with marked ontogenetic modification.

Phylogenetic analysis yielded over 700 most parsimonious trees, all inconsistent with a stratophenetic interpretation of the succession of samples (data to be presented elsewhere). Reconciling this inconsistency requires accepting complex facies tracking of multiple co-existing lineages, each sampled only once and in reverse order of the hypothesized order of phylogenetic branching, as well as long unsampled ghost lineages. However, trees that are consistent with the reading of the stratigraphic series as a phylogenetic trend of a single lineage are only one step longer. It is possible that the inconsistency between the most parsimonious trees and the stratigraphic series is due to uncertainty in choice of outgroup. Because *Zacanthopsis* is one of the oldest genera in the Family Zacanthoididae and the sister group to this family is unknown, outgroups included in the analysis include both derived groups as well as stratigraphically younger species ("Middle" Cambrian). Without appropriate outgroups, character polarity cannot be confidently determined.

We cannot yet determine whether the stratigraphic trend in older samples indicates non-evolutionary clinal variation or anagenesis concurrent with increasing water depth. Nonetheless, the results of the study indicate the usefulness of ontogenetic information in species delimitation. This study also highlights the difficulty in rooting trees where uncertainty in choice of outgroup reduces the confidence with which we can reconstruct ancestral morphologies.

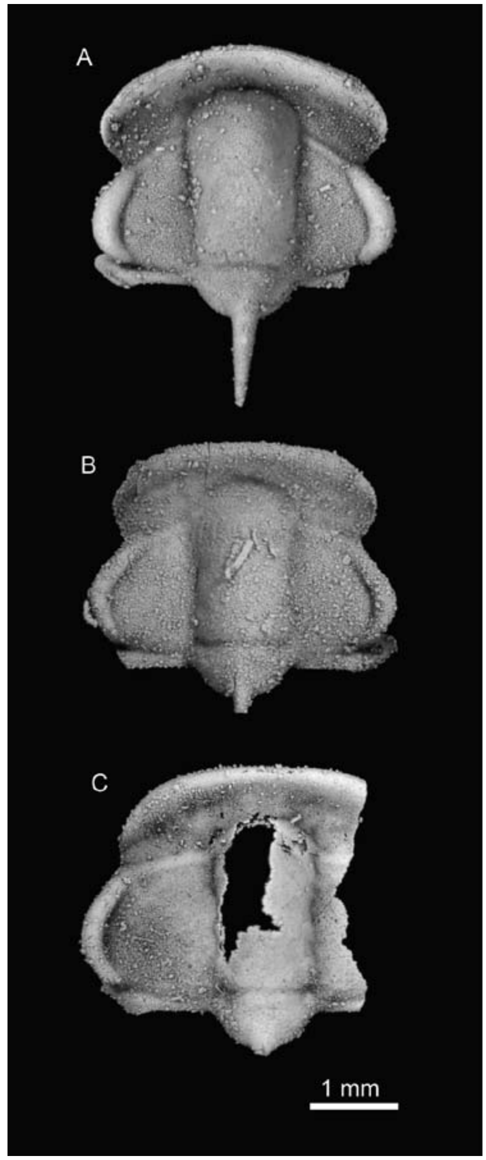

Figure 1. Morphological trend in *Zacanthopsis* cranidia from Oak Springs Summit, Nevada, during the latest Dyeran. Specimens are held at the Institute for Cambrian Studies (ICS). A, Cranidium from the oldest bed, 9.5 meters below the Dyeran-Delamaran boundary, ICS-1152. B, Cranidium from one of the middle beds, 5.5 meters below the Dyeran-Delamaran boundary, ICS-1159. C, Cranidium from the youngest bed, 1.6 meters below the Dyeran-Delamaran boundary, ICS-1287.

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