

Ber. Inst. Erdwiss. K.-F.-Univ. Graz	ISSN 1608-8166	Band 16	Graz 2011
<i>IGCP 596 Opening Meeting</i>		Graz, 19-24 th September 2011	

Echinoderm Community Evolution in the Devonian and Mississippian

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Crinoids and blastoids reached their zenith in generic richness and abundance during the Mississippian, leading many paleontologists to refer to the interval as the “Age of Crinoids” (KAMMER & AUSICH 2006). Crinoids and blastoids were so abundant that encrinites, grainstones and packstones with >50% echinodermal debris, contributed 1000s of km³ of carbonate deposition globally.

Explanations for the increased diversity and superabundance of crinoids and blastoids in the Mississippian include the following: 1. Rising biodiversity of advanced cladids during the transition from the Middle Paleozoic to the Late Paleozoic Crinoid Macroevolutionary Fauna (KAMMER & AUSICH 2006), 2. The establishment of widespread carbonate ramps after the demise of Late Devonian reef communities (KAMMER & AUSICH 2006), and 3. Response to declining predation pressure caused by extinctions of major groups preying on crinoids at the Hangenberg extinction event (SALLAN *et al.* 2011).

Although the causes of the Mississippian crinoid explosion are probably multifaceted, climatic events in the Devonian likely played a major role. KAMMER & AUSICH (2006) recognized a peak in crinoid generic richness in the Early Devonian. The Emsian peak reflects the success of the camerate-dominated Middle Paleozoic Crinoid Macroevolutionary Fauna (MPCMF) during an interval of widespread reefal facies. Emsian blastoids also are diverse and locally abundant for the first time in the history of the clade, although the most abundant faunas were associated with deeper water microbial mud mounds not shallow water reefal facies. Throughout most of the Devonian, crinoid diversity paralleled the diversity found in reefal ecosystems, which paralleled patterns of low latitude sea surface temperature (JOACHIMSKI *et al.* 2009). This pattern changed after the Givetian / Frasnian and Frasnian / Famennian extinction events, which significantly reduced crinoid diversity and decimated reefal faunas respectively.

Historically Famennian crinoid and blastoid diversity was thought to be quite low suggesting that these faunas did not recover from the G/F and F/F extinctions until well into the Mississippian. Over the past decade, however, discovery of new Famennian echinoderm faunas and re-evaluation of existing faunas have resulted in a 500% increase in generic diversity from that reported in SEPKOSKI (2002). In terms of crinoid generic diversity, global Famennian echinoderm communities are dominated by cladid crinoids (WATERS & WEBSTER 2009) and more closely resemble Late Paleozoic rather than Middle Paleozoic Crinoid Macroevolutionary Faunas. The demise of reef communities in the Late Devonian led to the development of widespread carbonate ramps in the Mississippian and for a time the resurgence of the camerate-dominated MPCMF. The ultimate success of the Late Paleozoic Crinoid Macroevolutionary Fauna reflects the climate-controlled transition from carbonate-dominated sedimentation in the Lower and Middle Mississippian to clastic-dominated sedimentation in the Late Mississippian and Pennsylvanian. The long-term iterative nature of the transition between the two crinoid faunas suggests that the driving force was climatic and not changes in predation pressure.

In a novel paper, RIDING (2009) suggested that significant changes in Devonian atmospheric chemistry in the Devonian led to changes in phytoplankton communities which led to significant increases in abundance of suspension-feeding echinoderms beginning in the Late Devonian and accelerating into the Mississippian. Riding’s analysis provides an explanation for the “phytoplankton blackout” in the Late Devonian as a taphonomic artefact reflecting the shift from acritarch-sized plankton to smaller picophytoplankton.

Testing Riding’s hypothesis on the relationship between changes in phytoplankton composition and crinoid and blastoid abundance involves a more detailed understanding of feeding preferences of different clades of Paleozoic crinoids and blastoids than is currently available. However, it does present an intriguing possible explanation for the occurrences of abundant blastoids in deep-water environments in the Lower Devonian of Spain. It also provides support for the apparent divergence of

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patterns of diversity reefal ecosystems and crinoid diversity in the Famennian, and the halos of crinoids and blastoids that occur around deep water Waulsortian mud mounds that are common in the Early Mississippian.

Although much work remains to understand the dynamics of echinoderm community evolution in the Devonian and Mississippian, climate mediation rather than changing predation pressures seems a more plausible process. The relationship between the Middle and Late Paleozoic Crinoid Macroevolutionary Faunas and large-scale sedimentological regime has been understood for many years. That the patterns in sedimentation are more climatically controlled rather than tectonically controlled now seems clear. Crinoid communities were able to be successful both in the Lower Devonian greenhouse world and in the Mississippian icehouse world because different clades were able to adapt to changing climates and the demise of reef ecosystems and flourish. Whether this success was the result of adaptation to changing sedimentological regime or changing patterns of plankton diversity is unclear at the present time.

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