

STRATOCCLADISTIC ANALYSIS OF PHYLOGENY IN CALCEOCCRINID CRINOIDS
(PALEOZOIC: ECHINODERMATA): MOSAIC EVOLUTION AND BIOGEOGRAPHY

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Problems arising from mosaic evolution within the Calceocrinidae can be overcome through the application of stratocladistic methodologies. Morphology-based cladistic analyses performed on all genera of calceocrinid crinoids resulted in a large number of equally parsimonious phylogenies. The resolution of phylogenetic relationships within the Calceocrinidae is greatly enhanced with the addition of stratigraphic data. A strong biogeographic component to the evolution of this group is revealed with separate lineages evolving in North America and Europe in the Mid-Late Paleozoic. This is the first comprehensive phylogeny of this highly specialized family.

Calceocrinids are a unique group of Paleozoic crinoids, easily identified by the presence of a hinge between the basal and radial circlets. They are also unusual in their life habit as the stalk in calceocrinids is recumbent on the seafloor. With this posture, flexure of the hinge allowed calceocrinids to raise the filtration fan into the water column for feeding or to collapse the fan along the stem for protection. The distinctive morphology of calceocrinids makes them ideally suited for phylogenetic analyses because there can be little doubt that this collection of crinoids represents a monophyletic clade.

Cladistic analyses based solely on morphological characteristics produced a total of 17,000 equally parsimonious trees. Among these trees only a small number of phylogenetic relationships were resolved. The addition of stratigraphic data using stratocladistic methodologies, resulted in a total of only 16 equally parsimonious trees; a substantial improvement in resolution. One reason for the poor resolution using traditional cladistic methods is the mosaic character of evolution within the Calceocrinidae. Characters in this group display independence in evolution both in rate and direction. This results in multiple reversions and convergences. Stratigraphic data provides an independent character that overcomes this problem.

The phylogeny suggested by this stratocladistic analysis reveals a strong biogeographic component to calceocrinid evolution. Evolution within this group proceeds as radiations of short-lived, biogeographically restricted taxa from longer-lived cosmopolitan genera. Three major radiations are identified; 1) in the Ordovician of North America from the genus Cremacrinus; 2) in the Silurian of North America and Europe from Calceocrinus; and 3) in the Devonian of North America and Europe from Synchirocrinus.