

**Inferring evolutionary order and durations using both stratigraphy and cladistics in
a fossil lineage (Bryozoa: *Peronopora*)**

Joseph F. Pachut^{1*} and Robert L. Anstey²

¹*Department of Earth Sciences, Indiana University–Purdue University, Indianapolis, Indiana 46202, USA; and* ²*Department of Geological Sciences, Michigan State University, East Lansing, Michigan 48824, USA*
e-mail: jpachut@iupui.edu

*Corresponding author.

Keywords: biostratigraphy, Ordovician, stratigraphic range, indices, rate, tempo.

ABSTRACT

In the Ordovician bryozoan genus, *Peronopora*, stratigraphic occurrences and cladistic branching order are significantly correlated, indicating sequential development of both patterns in geological time. Five species have stratigraphic first appearances in the exact order predicted by cladistics, but eleven species require downward-range extensions to match cladistic order. Reduced major-axis regression-based corrections and ghost range extensions represent two alternative modifications of first appearance data, with the latter more strongly supported by stratigraphic congruence indices. Tests of the robustness of observed first appearances, based on the density of sampled horizons and magnitudes of stratigraphic gaps, support the probabilistic appearance of descendant species stratigraphically above their putative ancestors in eight of fifteen ancestor-descendant pairs. A 24 m sampling gap occurs below the base of the Brannon Member of the Lexington Limestone, a unit marking the first appearances, or extended ranges, of nine species of *Peronopora*. A test for the presence of a uniform distribution of occurrence probabilities indicates that seven of the nine species could have originated during the time interval represented by the gap. The early branching rate within *Peronopora*, during the time span encompassing all first appearances of species, is 1.05 cladogram nodes per meter of strata. The rate of clade production within that interval is 0.73 (baseline) clades per meter of strata. Extrapolating downward using both rates indicates that the median position of the root of the generic clade is approximately 1.08 myr earlier than sampled. The estimated speciation rate in *Peronopora* is 5.73 species per myr, while the average time between speciation events is 186 kyr. Intraspecific clades, possibly including cryptic species, formed at a rate of 19.35 clades per myr, with an average waiting time per clade of 48.107 kyr. These metrics indicate very short origin times for species within the genus compared to their total stratigraphic ranges, a pattern consistent with punctuated speciation.