

peak of calcareous ooid formation giving rise to a few metres thin but globally recognizable 'oolite disaster-bed', marking the extreme loss of shell-bearing taxa, ecosystem collapse and thus reduced carbonate production in shallow seas. We use own and published records of the Hirnantian Isotope Carbon Excursion (HICE) as a stratigraphic ruler to study the degree of synchronicity of oolite formation across the American Midwest (Oklahoma, Arkansas, Missouri, Illinois), through multiple localities in Norway, Sweden and the East Baltic area, and further on to South China (the Kuanyinchiao Bed in the Hirnantian Global Stratotype Section and Point at Wangjiawan section corresponds to this oolite disaster bed), together representing three continents in the contemporaneous tropical zone. The combined effect of a strongly reduced biological sink for carbonate ions due to mass extinction of shell-bearing organisms, widespread anoxia and CO₂ release during post-glacial transgression across shallow platforms was the likely trigger for the anomalous carbonate production, which represents a short-lived but significant change in sea-floor substrate composition in the early aftermath of the event. Similar unusual environmental conditions and carbonate production turnovers, with seemingly strong ecological impact in carbonate platforms, developed also during mid and late Silurian biocrises that were related to global climate change but that was far less significant in terms of taxonomic loss.

THE ROLE OF ONTOGENETIC TRANSFORMATIONS OF THE LOOP IN THE CLASSIFICATION AND PHYLOGENY OF TEREBRATELLIDINA (BRACHIOPODA)

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The long mineralized loop in terebratellid brachiopods is a geometrically and ontogenetically complex structure; it has played a significant role in constructing terebratulide classification and hypotheses of phylogeny. For over a century, long loops present in all Paleozoic and post-Paleozoic terebratulids have been considered to be homologous, originating from Middle Devonian mutationellids, from which all subsequent terebratellidines evolved. In the 2006 *Treatise on Invertebrate Paleontology*, the classification

of terebratulide brachiopods was thoroughly revised, largely on the basis of patterns of loop ontogeny via resorption and mineralization, as documented in extant terebratellidines. Extant long loop geometry transforms through a series of identifiable ontogenetic stages, resulting in a variety of extant adult loop geometries. As a result of these more recent studies of loop ontogeny: (1) nine superfamilies are recognized, each with at least one extant representative, replacing three superfamilies previously recognized, only one of which included extant taxa; (2) the evolutionary origin of the long loop crown clade is placed in the Triassic, not the Devonian. This suggests that Paleozoic long loops could be analogues, not homologues, to extant long loops. Moreover, this interpretation is in conflict with molecular clock analyses that place the divergence of crown short loop and crown long loop clades in the Devonian. Did the long loop evolve once or twice within Terebratulida, through which morphological transformations, and by what combination of ontogenetic and evolutionary mechanisms?

Extant terebratellidines develop long loops from both the cardinalia and a septal pillar emerging from the center interior of the dorsal valve. Long loops in Paleozoic terebratellidines appear to develop only from the cardinalia; a septal pillar appears to be absent throughout ontogeny. In some extant adult long loop geometries, the septal pillar resorbs completely later in ontogeny, resulting in an adult geometry that is indistinguishable from Paleozoic adult long loops. Finding evidence for stages of ontogenetic development in extinct terebratellidines is a challenge; it is thus difficult to test hypotheses of the existence of a septal pillar in extinct terminal geometries in which it may have resorbed and vanished completely in adults.

Two ontogenetic pathways appear to have evolved in this clade: one lacking a septal pillar throughout, and one with a septal pillar. The septal pillar may represent an evolutionary innovation, as an addition to the Devonian terebratellid developmental trajectory. We argue that these two ontogenetic pathways are homologous, but at a deeper level of homology. As wings of birds and bats are homologous as forearms but evolve independently as wings, long loops of Paleozoic and post-Paleozoic terebratulids appear to be homologous as elongated crural extensions but evolve independently as long loops.

A TRIGGER MECHANISM FOR THE LATE DEVONIAN HANGENBERG CRISIS, AS RECORDED BY MER-