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Howellella – the root of delthyridoid Spiriferids (Brachiopoda, Silurian to Devonian)

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The cosmopolitan genus *Howellella* is regarded as the root of delthyridoid spiriferids, a group of mainly coarsely plicated and mostly alate brachiopods. During the Silurian and Early Devonian taxa of *Howellella* were globally distributed and closely related to each other. Within the Early Devonian, faunal isolation began resulting in endemic brachiopod provinces and realms each with its own phylogenetic developments in brachiopods. Extinction events followed by the re-settlements of brachiopod communities characterizing each region. At the end of the Emsian, a step-by-step faunal exchange starts resulting in a global distribution of brachiopod genera in the Late Devonian.

The type species of Howellella, H. elegans, occurs in Wenlock strata of Gotland, Sweden, and is characterized by very small specimens with two to three broad, low, and simple ribs on each flank that are rounded in cross-section and a fimbriate micro-ornamentation consisting of single rows of micro-spines at the edge of each growth lamella. Geologically younger species show an increase in size and amount of ribs which are increasingly angular in cross-section and development of other types of micro-ornamentation, e.g., capillate with and without micro-spines, fimbriate with more than one row of micro-spines, or lacrimate with teardrop-like pustules arranged in radial lines at the edge of each growth lamella. Even though all taxa of Howellella seem very similar at first sight, several phylogenetic lineages are recognizable evolving out of Howellella during Early Devonian time, e.g., the vanuxemicycloptera-murchisoni lineage in eastern North America or the cortazari-salicamensisarduennensis-mosellanus lineage in Western and Central Europe. Recent studies show further lineages based on early forms of Howellella, e.g., the phylogenetic development of spiriferids in South China and their geographical dispersion since the Late Emsian. Furthermore, it has turned out that the European/North African genus *Intermedites* has not evolved out of the genus Arduspirifer as hitherto assumed, instead, its origin is somewhere in the Asian branch of delthyridoid spiriferids.

All lineages under consideration are characterized by an increase in shell size of specimens, one of the most spectacular example is the ratio of size between *Howellella* and *Euryspirifer*. It is remarkable that in *Quiringites*, we see a small *Howellella*-like morphotype, small specimens with subcircular outline and few ribs, occurring for a short time again at the beginning of the Eifelian (early Middle Devonian). However, the phylogenetic origin of *Quiringites* is still a matter of debate.

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