

ORDER TRIMERELLIDA (BRACHIOPODA, CRANIFORMEA): ORIGIN,  
RADIATION, AND EXTINCTION

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In addition to their probable aragonitic shells, the Trimerellida comprise some of the morphologically most distinctive brachiopods among the low latitude, warm water faunas from the mid to late Ordovician and the early to early-late Silurian. Until comparatively recently they were known mostly from the Silurian, but discoveries of diverse trimerellide stocks from the mid and late Ordovician of Australia, South China and Kazakhstan now demonstrate that these enigmatic, often gigantic brachiopods evolved rapidly and underwent considerable morphological differentiation mostly during the Caradoc and early Ashgill. The oldest known assemblages are from Kazakhstanian terranes, where they occur just below the first appearance of *Nemagraptus gracilis* Biozone graptolites, suggesting an early to mid Llandeilo age; this fauna includes *Ussunia*, which appears to retain many characters reminiscent of the Order Craniopsida, regarded here as the most probable ancestral group.

By contrast with faunas from Kazakhstan, South China and Australia, Ordovician trimerellides from other regions are represented usually by only one, or rarely two genera. In South China, the Ordovician assemblages are unique in containing taxa with excavated and vaulted visceral platforms (e.g. *Trimerella*), which are features unknown elsewhere in Ordovician trimerellides, but which became widespread in the Silurian. Almost all local lineages outside South China, and possibly Australia, became extinct just before the Hirnantian, and there is no record of trimerellides in those local Hirnantian and Rhuddanian brachiopod faunas; they re-appeared in the mid to late Llandovery (mostly *Dinobolus*). During the Wenlock, trimerellide faunas with a near-cosmopolitan distribution were dominated by *Monomerella*, *Trimerella* and *Dinobolus*. Only *Gasconsia*, known from eastern North America, Bohemia and Scandinavia, survived into the early Ludlow, after which the Order became extinct.

Two major episodes of migration from the Kazakhstanian terranes can be invoked to explain observed patterns of Ordovician trimerellide distribution: (1) in the early Caradoc, to Gondwanaland and Laurentia; (2) in the late Caradoc, to Baltica and Angaria. Ordovician trimerellide biogeography suggests that the microplates and island arcs making up the Kazakhstanian terranes were situated most probably between the Baltic plate and the Australian segment of Gondwanaland; these crustal fragments may have drifted westwards sometime during the mid to late Ordovician as part of the hypothetical Kypchak Arc. The appearance in North America of early Caradoc trimerellides with strong Australian affinities lends some support to palaeomagnetic data suggesting that Laurentia may have had a conjugate margin with the South American area of Gondwanaland during the early to mid Ordovician.