Genicular structures of retiolitines (Graptolithina) as an indicator of the environmental changes across the lundgreni biotic crisis during the Homerian, Silurian

Anna Kozłowska*[1]

[1]Institute of Paleobiology [Warsaw] – Poland

Abstract

Variable environmental changes during the Silurian are expressed in the adjustment of the graptolite plankton diversity. One of the most dramatic changes was caused by the *lundgreni* environmental crisis which was not survived by most of the monograptids and retiolitines. One of the best adaptations to the varying environmental conditions was shown by the retiolitines, diplograptid graptolites having an additional layer of periderm, built mostly by cortical bandages. The retiolitine *Gothograptus* lineage started to evolve successfully during the *lundgreni* Biozone. Some significant characters of these colonial animals are clearly visible in the *Gothograptus* lineage. The gothograptids were one of the first groups of retiolitids to have developed a genicular list, being a border between the protheca and metatheca. It gives the possibility of growing additional structures, named genicular structures. Short, cylindrical rhabdosomes (tubaria) of *Gothograptus* were ended by the appendix depicting the finite growth of colonies. The appendix probably represented a modified theca of the last zooid. The genicular structures in *Gothograptus* from pre-*lundgreni* event were some kind of apertural covers. One of the most spectacular genicular structures is the reticulated veil of *Gothograptus velo*, growing down covering the orifice and the metathecal part of the previous theca. Some of the veils are connected to the veil of the previous theca, forming an external layer above the thecal orifices and thecae. Thus the entrance to the thecal tube was long and narrow. Differently developed were the thick genicular hoods of the post-*lundgreni* *Gothograptus nassa* in the *nassa* Biozone, the survival time. This type of apertural structure appeared for the first time in *G. kozlowskii*, living during the *lundgreni* Biozone. All these structures were located close to the tubarium wall; they did not extend laterally. The apertural structures developed in the new retiolitine fauna of the recovery period after the *lundgreni* extinction event have a different aspect. They extended laterally from the tubarium and did not cover the thecal orifices. The largest, most developed apertural structures extending horizontally from the ventral wall of the tubarium were developed in *Papiliograptus retimarginatus* from the *praedeubeli/deubeli* Biozone. Their construction was made by two distinct thickened edges forming an obtuse angle with each other. Between the thick edges, the delicate reticulum was spread. The distance between the tips of the genicular processes (2.5 mm) is about twice as wide as the width of the lateral wall of the mature tubarium (1.1 mm). This comparison shows the great size of the extending genicular structures. The two types of colony development, the *Gothograptus* type vs. *Papiliograptus* type, show adaptations to the two extremely different environments occurring in the Homerian. The compact colonies of *Gothograptus* were adapted to highly turbulent water rich in oxygen and food: the surface layer of the oceans. This type of tubarium with the genicular hoods

*Speaker

closely covering thecal orifices allowed hiding the zooids inside and surviving the high-energy environment. The new retiolitine fauna derived from the surviving gothograptids was able to develop new type of colonies during the recovery time, with extensive and delicate genicular structures as in *Papiliograptus.* This indicates calm and nutrient-rich waters. In summary, the development of the genicular list in retiolitines gave the possibility of surviving the big *lundgreni* environmental crisis and gave them an evolutionary advantage over other graptolites. Thus the large retiolitine diversity changes across the Homerian, the *lundgreni* extinction interval, provides some inside into environmental changes.

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