

Thoracospheres: the evolution of calcification in dinoflagellates

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Calcification has evolved multiple times in many different branches of the eukaryotic part of the tree of life, and also one small sprig within the dinoflagellates has acquired this character during its evolution. The timing of this event has long been unclear, as some isolated records of microfossils with morphological characters attributed to the calcareous dinoflagellates, so-called calcispheres, are known from the Upper Triassic, whereas an uninterrupted record of undoubted calcareous dinoflagellates exists only since the Upper Jurassic. Molecular clock calculations with alternative calibration points for the origin of calcareous dinoflagellates indicate that a Jurassic origin is more likely than a Triassic one (Gottschling *et al.*, 2008). This is in good agreement with traditional morphological dinoflagellate taxonomy, as the Triassic calcispheres show no indication of tabulation, whereas the true calcdino tabulation is remarkably stable over their evolutionary history.

A major discrepancy between molecular and morphological classifications lies in the current concept of classifying calcareous dinoflagellates by the crystallographic orientation of the crystals within the wall. Calcification in calcdinos has evolved first in the diploid life-cycle phase, and the majority of species investigated today forms diploid calcareous cysts. Diploid calcification was lost in a subclade of the calcareous dinoflagellates in which the haploid life-cycle phase has diversified. Calcification was regained secondarily in two genera of this clade, and the vegetative calcareous coccoid cells are the dominant life-cycle phase. Therefore, one part of the taxonomic confusion in calcareous dinoflagellates seems to result from comparing non-homologous calcareous structures, *i.e.* diploid resting cysts and vegetative coccoid cells (Meier *et al.*, 2007).

Reinvestigating the ultrastructure of the calcareous walls in calcdinos is therefore urgently needed for a better understanding of unifying molecular, morphological and fossil phylogenies. First results show that the three major clades in calcareous dinoflagellates may be represented also by three different biomineralisation modes. Unfortunately, the underlying biogeochemical processes are largely unknown. There are now first studies on the isotope chemistry of the calcareous wall of dinoflagellates representing different proposed biomineralisation modes, and all of them show a characteristic strong depletion in $\delta^{13}\text{C}$ against equilibrium conditions in modern and fossil species (Friedrich & Meier, 2003; Minoletti *et al.*, 2004; Zonneveld *et al.*, 2007), indicating highly specialized biomineralisation pathways in calcareous dinoflagellates that are maintained despite the evolution of different modes of biomineralisation.

References

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