

# **Evolutionary history of the metopid-clevelandellid group (Ciliophora, Armophorea): endosymbionts diversify much more rapidly than free-living lineages**

**P. Vd'ačný<sup>1</sup>, L. Rajter<sup>1</sup>, T. Stoeck<sup>2</sup>, and W. Foissner<sup>3</sup>**

*1. Department of Zoology, Comenius University in Bratislava, Bratislava, Slovakia*

*2. Department of Ecology, University of Kaiserslautern, Kaiserslautern, Germany*

*3. Department of Ecology and Evolution, University of Salzburg, Salzburg, Austria*

Members of the class Armophorea occur in microaerophilic and anaerobic habitats, including digestive tracts of a variety of invertebrates and vertebrates. In spite of their wide distribution and ecological significance in oxygen-depleted environments, phylogenetic kinships within the metopid-clevelandellid group represent a silent part in the ciliate tree of life, conflicting with traditional classifications. To reconcile interrelationships between metopids and clevelandellids and to better understand their morphological evolution and diversification dynamics, we utilized the molecular clock theory as well as information contained in the estimated chronograms and morphology of extant taxa. The radiation of the metopid-clevelandellid group very likely occurred during the Paleozoic/Mesozoic period and the origin of the exclusively endosymbiotic clevelandellids dates back to the Upper Cretaceous. According to diversification analyses, the evolutionary history of the metopid-clevelandellid group was shaped by an explosive radiation that began in the Cretaceous and terminated during the Miocene, and might be mostly attributed to the burst of lineages within the endosymbiotic clevelandellids. Their cladogenic success was very likely associated with sharply isolated ecological niches constituted by their cockroach and amphibian hosts. Conflicts between traditional classifications and molecular phylogenies of the metopid-clevelandellid group very likely come from processes that led to further diversification without extinction of ancestral lineages as well as from morphological plesiomorphies incorrectly used as apomorphies. Our study thus indicates that diversification processes and reconstruction of ancestral morphologies might help to better understand natural sources of paraphyly which occurs in groups of organisms with an apparently long evolutionary history and when speciation prevails over extinction.