

## The features of the evolution of oysters

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The problem of the oysters' evolution and phylogenetic relationships between them were considered in several papers (Cheltsova, 1969; Pugaczewska, 1971; Stenzel, 1971). Taxonomy of oysters in Treatise (Stenzel, 1971) is the closest to the modern taxonomy (Carter et al., 2011), but it has also gone through many changes. New data had allowed revising time boundaries of large oyster's taxa existence. The recent discovery of *Crassostrea tetoriensis* in Callovian deposits in Japan (Komatsu et al., 2002) increases the range of existence of Crassostreinae subfamily from Early Cretaceous to Middle Jurassic. Thus subfamily Crassostreinae is older than subfamily Ostreinae. The study of the genome of modern oysters from genera *Lopha*, *Ostrea* and *Saccostrea* showed affinity of modern members of genera *Ostrea* and *Lopha* and their distance from the genera *Crassostrea* and *Saccostrea* (Foighil, Taylor, 2000). These data prove the validity of the isolation of Mesozoic *Lopha*-like oysters in a single family (Carter et al., 2011) and the lower time boundary shift of the modern Lophinae existence to Miocene (Malchus, 1998).

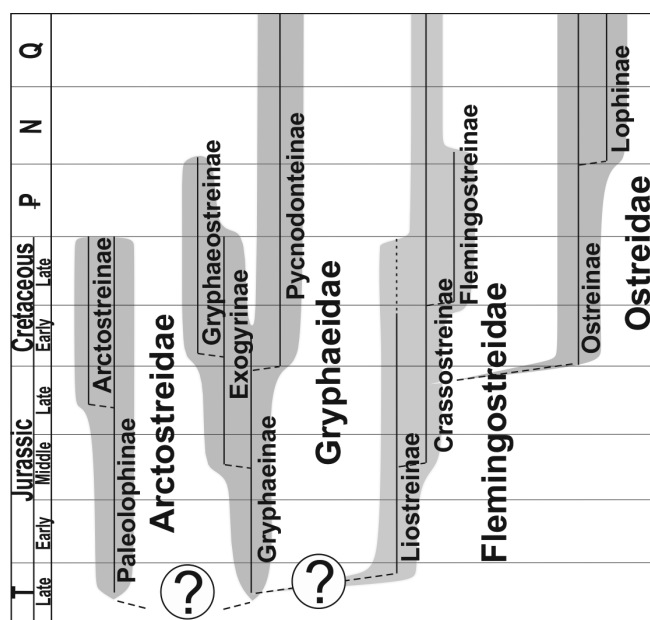


Fig.1.: The model of phylogenetic relationships of superfamily Ostreoidea.  
(based on taxonomy in (Carter et al., 2011))

The model of phylogenetic relationships of large oysters taxa (subfamily and above) based on recent data is presented in figure 1. Based on it, the main stages in the evolution of oysters can be traced. First oysters appeared in Late Triassic. In Carnian *Gryphaea* appeared in the Arctic Basin and Paleolophidae appeared in the Tethys and Paleopacific. During Rhaetian *Liostrea* had settled in the European region. The question about polyphyletic or monophyletic origin of Paleolophidae and Gryphaeidae still remains disputable. The origin of *Liostrea* from *Gryphaea* is also debatable. In Early Jurassic *Gryphaea* migrated from the Arctic Basin and started expansion in Europe. A rapid diversification of oysters began in Middle Jurassic: first Exogyrinae (ubiquitous *Nanogyra*) and

Crassostreinae (in Paleopacific) had appeared. On the Jurassic/Cretaceous boundary dramatic reducing of Gryphaeinae diversity took place, Exogyrinae diversification began and first Pycnodonteinae and Ostreinae appeared. An interesting feature is the independent appearance of chomata in different branches of oysters (Exogyrinae, Pycnodonteinae, Ostreinae). Late Cretaceous is the golden age of oysters, the highest generic diversity is observed. By the end of Cretaceous - beginning of Paleogene, Exogyrinae and Arctostreidae almost all completely extinct. Further flourishing of Crassostreinae and Ostreinae had been occurred during the Cenozoic. Modern Lophinae appeared in Miocene. Pycnodonteinae still continues to exist up to the present day, but their species diversity is not too high.

Oysters in evolutionary terms are conservative group; their morphology has not been radically changed since the moment of their appearance. The main event that led to the diversification of oysters was the transition from an attached lifestyle to living in soft substrate (Seilacher et al., 1985). This transition happened in different groups due to different mechanisms, often leading to the new taxa creation. The change of ethology and morphology had often followed by transformations of shell microstructure. These lifestyle changes have occurred over the evolution of oysters multiple times, leading to the formation of homeomorphic taxa. The "underlying synapomorphies" pattern explains the independent appearance of chomata and chalky chambers in shell microstructure in different branches of oysters (Saether, 1979; Malchus, 1998). This model suggests the existence of a parent species with the genetic code that evolves for a certain character but does not carry the phenotype itself. Thus, only the responsible genes are inherited by descendant species, but not the phenotype. Repeated independent activation of the genetic code, e. g., triggered by environmental factors, then provides the basis for multiple parallel evolution of the phenotype in subsequent lineages. This model also explains the prevalence of oysters homeomorphism.

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