



FORAMS 2006

Taxonomic revision of coarsely ornamented Upper Cretaceous trochospiral planktonic foraminifera

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Taxonomic revision of coarsely ornamented Upper Cretaceous trochospiral planktonic foraminifera is proposed based on extensive SEM observation of test ultrastructure, ornamentation, and porosity. This study was carried out on very well preserved material from the Cenomanian-Maastrichtian of a number of DSDP/ODP holes. Our observations reveal considerable variability of test morphology that nonetheless defines an evolutionary continuum within the Superfamily Alethogerinacea nov. sup., which is proposed herein to accommodate tests with strong ornamentation of the Upper Cretaceous (Cenomanian-Maastrichtian). Iterative and parallel evolution commonly occurs in the group's evolutionary history.

The coarsely ornamented trochospiral planktonic foraminifera commenced their evolutionary history in the middle Cenomanian with the evolutionary appearance of the genus *Whiteinella*, characterized by prominent pustulose test ornamentation, lack of peripheral structures, and a primary aperture bordered by a poorly developed porticus (flap). A new genus, *Alethogerina* nov. gen. (type species: *Archaeoglobigerina australis* HUBER), is proposed to accommodate non-keeled tests with strongly pustulose test ornamentation. It is the directly descendant from *a:Whiteinella*. This newly emerged group morphologically diversified with development of plano-convex, single keeled genera (e.g., *Helvetoglobotruncana*, *Bucherina*), high-trochospired tests with papillose ornamentation (e.g., *Kuglerina*), and tests with meridional ornamentation on both sides (e.g., *Costellagerina*). Peripheral structures, when present, are key features for the most specialized taxa (e.g., *Helvetoglobotruncana*, *Bucherina*). This group is now formalized in the Family Alethogerinidae nov. fam. (Cenomanian-Maastrichtian).

The first major adaptive radiation of the Alethogerinacea occurred in the Coniacian and resulted in the development of tests with peripheral structures that persisted throughout the evolutionary history of the Family

Archaeoglobigerinidae (Coniacian-Maastrichtian). *Archaeoglobigerina* is the oldest genus, presenting an imperforate peripheral band bordered by two rows of pustules. Two lineages descended from *Archaeoglobigerina* in the latest Campanian-Maastrichtian, with development of tests having robust peripheral structures (e.g., *Gansserina*, and *Globotruncanella-Abathomphalus* lineage). Notably, complex, asymmetrical test ornamentation that is meridional on the umbilical side and parallel to the periphery on the spiral side may be present in this group (e.g., *Abathomphalus mayaroensis*).

The second adaptive radiation led to the evolutionary appearance of tests with meridional ornamentation on the dorsal and ventral sides and the primary aperture bordered by a tegillum. The genus *Rugoglobigerina* is the oldest member of the Family Rugoglobigerinidae, its first evolutionary occurrence being dated as middle Campanian. This group underwent morphological diversification, resulting in development of tests with a spinose periphery (e.g., *Plummerita*), a truncated single keeled periphery (e.g., *Trinitella*), and a double-keeled test periphery with asymmetrical test ornamentation (e.g., *Rugotruncana*).

The Superfamily Alethogerinacea nov. sup. is the sixth Mesozoic planktonic foraminiferal superfamily, and the first one described according to the principles of phylogenetic classification. The other five superfamilies include: Heterohelicacea (serial taxa), Planomalinaea (planispiral taxa), Favusellacea (primitive, globular-chambered trochospirals, probably with aragonite test), Rotaliporacea (trochospirals with supplementary apertures on the umbilical side), and Globotruncanacea (lightly ornamented trochospirals, with truncated and single- or double-keeled periphery).