## Wetzeliella and its allies - the "hole" story: a new look at the Paleogene dinoflagellate subfamily Wetzelielloideae

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Dinoflagellate cysts are found as organic-walled microfossils in Mesozoic-Cenozoic strata. They have distinctive and variable morphology and evolved rapidly; hence they have become invaluable for providing biostratigraphic control in shelfal marine sediments. Many living dinoflagellates have a distinctive cellulosic "armour" of plates, the pattern of which tends to be reflected in various ways on the resistant organic walls of fossilizable cysts. For example, the excystment aperture (archeopyle) of cysts tends to consistently occur within a genus or species at the site of one or more specific reflected plates. Members of the Paleogene (now extinct) subfamily Wetzelielloideae have a stable reflected tabulation pattern distinguished by a four-sided (quadra) rather than a sixsided (hexa) mid-dorsal 2a plate. Aside from tabulation, wetzelielloideans show great morphological variability, especially in ornamentation and horn development, but also in wall structure. This variation shows no clear trends through time, but has dominated criteria for the definitions of genera and species, leading to frustrations in attempts to use wetzelielloideans as stratigraphic index fossils. Diversity in shape, wall structure and ornamentation has also distracted attention from the morphological variation of the archeopyle, which, although always formed through loss of the 2a plate only, shows variations that we consider critical in unravelling the group's phylogeny, and hence stratigraphic utility. Important factors are the shape and relative dimensions of the archeopyle and whether the operculum is attached or detached. These parameters allow us to define five archeopyle types: equiepeliform, hyperepeliform, hypersoleiform, latiepeliform and soleiform. Based primarily on archeopyle type and secondarily on wall and morphology and ornamentation, we recognise six genera with an equiepeliform archeopyle, four with a hyperepeliform archeopyle, five with a latiepeliform archeopyle, five with a soleiform archeopyle, and one with a hypersoleiform archeopyle. The earliest-known wetzelielloideans, which occur around the Paleocene- Eocene boundary, have an equiepeliform archeopyle. Other archeopyle types evolved rapidly: taxa with hyperepeliform, latiepeliform and hypersoleiform types are known from the Ypresian. Latiepeliform and hyperepeliform types are restricted to the Ypresian and Lutetian. Forms with the soleiform archeopyle appeared in the late Lutetian, but were rare until the Bartonian, when they became the dominant type, and they were the only type in Priabonian and younger strata. Wetzelielloideans became extinct in the middle Oligocene. Applying our criteria increases the usefulness of wetzelielloideans in determining the ages of Paleogene strata, as well as providing a better understanding of evolutionary trends within the group.