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Evolution of orbitolinid foraminifers and anoxic events: A comment on an article by J. Guex, *Eclogae geol. Helv.* 94 (2001) 321–328

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Key words: Black shales, anoxic events, orbitolinid foraminifers, phylogeny, Cretaceous

ABSTRACT

With reference to a study by Hofker (1963) on the evolution of the Cretaceous large foraminifer *Orbitolina*, Guex (1992, 2001) took the view that repeated abrupt size decreases in the deuterocoenoch of the embryo during overall global size and morphological complexity increase of this structural element was generated by anoxic events. However, our present knowledge on systematics, phylogeny and stratigraphical distribution of this foraminiferal group reveals that the conceptions on this matter of Hofker are largely obsolete. There are no evolutionary breaks, which can be correlated with any of the known Mid-Cretaceous anoxic events.

ZUSAMMENFASSUNG

Unter Bezug auf eine Arbeit von Hofker (1963) über die Entwicklung der Kreide-Großforaminifere *Orbitolina* war Guex (1992, 2001) der Auffassung, daß wiederholte plötzliche Verkleinerungen des Deuterocoenoches der Embryonen im Verlauf der global durch Vergrößerung und Komplizierung dieses Strukturelementes gekennzeichneten Gesamtentwicklung auf anoxische Ereignisse zurückzuführen sind. Unser gegenwärtiger Kenntnisstand über Systematik, Phylogenie und stratigraphische Reichweite dieser Foraminiferengruppe zeigt jedoch, daß die diesbezüglichen Vorstellungen von Hofker weitgehend überholt sind. Es lassen sich keine Unterbrechungen in der Entwicklung nachweisen, welche mit irgendeiner der bekannten anoxischen Episoden der Mittelkreide korreliert werden können.

The Cretaceous Period is characterized by some widespread sequences of organic-carbon rich black shales occurring in both deep- and shallow-marine settings and being the subject of intensive stratigraphical, geochemical, and paleoceanographical studies in the last decades (Arthur et al. 1990). The two major episodes of these “Oceanic Anoxic Events” (OAEs) are the late early Aptian Selli Level (= OAE 1a) and the latest Cenomanian Bonarelli Level (= OAE 2).

Numerous studies carried out during the last years have shown that these extreme paleoceanographic environments have led to important biotic changes (modification of the assemblage composition and abundance until the end of the perturbation). For example, Premoli Silva et al. (1999) pointed out that the Selli Level is characterized by temporary disappearance of nannoconids among the calcareous nannofossils and a decrease in diversity among the radiolarians and planktonic foraminifers. In the Bonarelli Level occurred a major turnover within the radiolarians and calcareous nannofossils. At the beginning of this latter event the most specialized planktonic foraminifers (e. g. rotaliporids) became extinct, whereas the less specialized groups (the younger dicarinelids

and whiteinellids) together with the opportunistic hedbergelids and heterohelicids survived.

In two publications, dealing mainly with problems of ammonoid evolution, Guex (1992, 2001) was also concerned with the influence of anoxic events on the phylogenetic evolution of the Cretaceous large foraminifer *Orbitolina*. Based exclusively on the evolutionary conceptions of this group, represented by Hofker (1963: chart X), and without considering the progress on this subject during the last forty years, he took the view that repeated abrupt size decreases in the deuterocoenoch of *Orbitolina* during overall global size and morphological complexity increase of this structural element was generated by three anoxic events (Fig. 1A of this paper). For the stratigraphic position of these events, Guex (1992: 136) referred to a publication of Jenkyns (1980). However, this latter author (p. 178) distinguished within the Mid-Cretaceous only two anoxic episodes: a broadly defined and relatively large time interval ranging from the middle of Barremian up to the Albian-Cenomanian boundary, and a short episode at the Cenomanian-Turonian boundary. Furthermore, the positions of the three anoxic events reported by Guex are contradictory in his two

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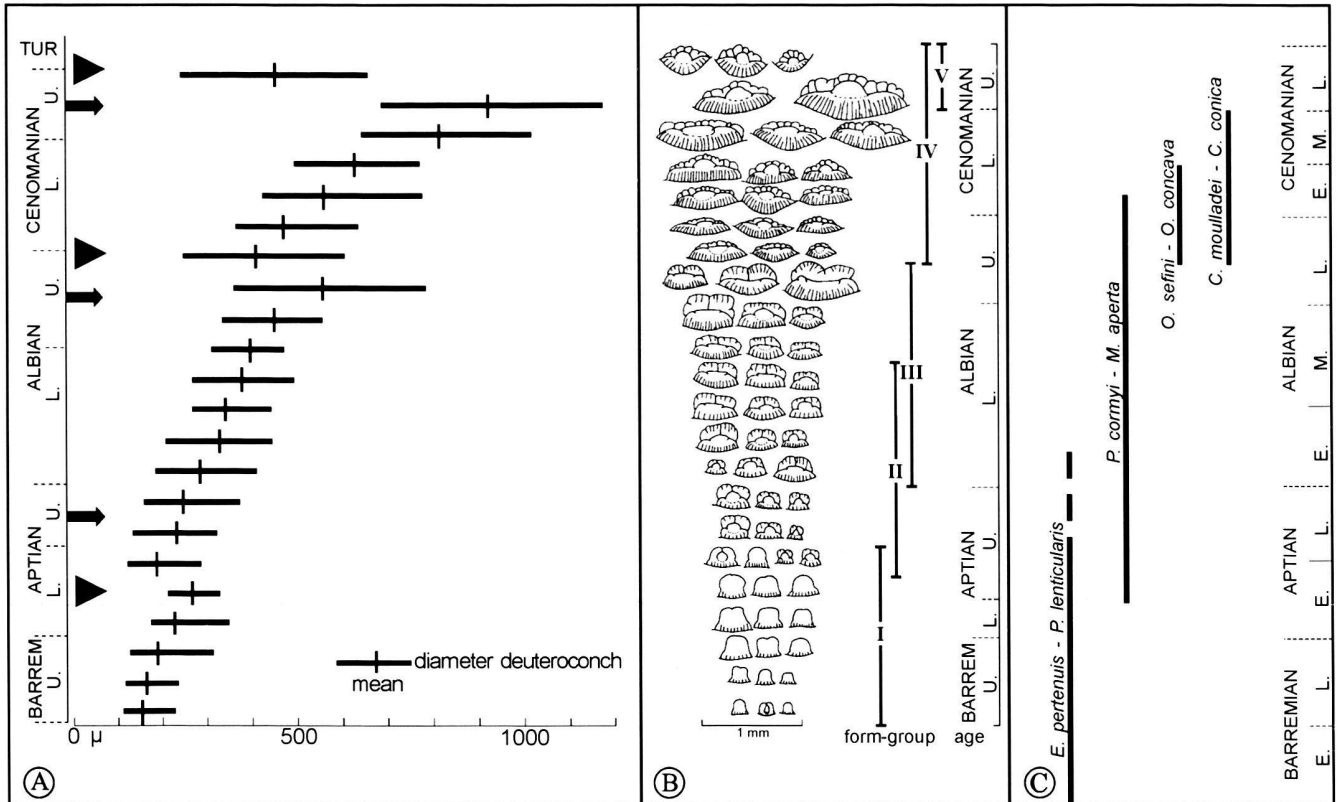


Fig. 1. A: "Abrupt size decrease generated by major Cretaceous anoxic Events" [marked by triangles] "during global size increase in the deuterocoel of *Orbitolina*" (Guex 2001: fig. 1). We have added to this drawing the position of the anoxic events (marked by arrows), indicated in an anterior paper of Guex (1992: fig. 11).

B: Evolution of the megalospheric embryonic apparatus of "*Orbitolina lenticularis*", vertical range of the "form-groups" I-V, and their stratigraphic distribution. From Hofker (1963: chart 10).

C: Stratigraphic distribution of the main Mid-Cretaceous orbitolinid phylogenetic lineages.

publications (Fig. 1A). In the first one (1992: fig. 11) they are placed in the middle of the upper Aptian, and in the middle of the upper Cenomanian (see arrows in Fig. 1A of this paper). In the second one (2001: fig. 1) they are located in the middle of the lower Aptian, at the Albian-Cenomanian boundary, and at the Cenomanian-Turonian boundary (dark triangles in Fig. 1A of this paper). Therefore, the different positions of the three anoxic events in the two figures published by Guex, inevitably lead to the conclusion that these do not refer to any of the known events, but that they are placed at imaginary interruptions within the general increase of the megalospheric embryonic apparatus.

Moreover, Guex apparently did not take notice of the fact that the conception of the evolution of Orbitolinas, proposed by Hofker (1963), has been outdated since decades. Assuming a constant increase of size and complexity of the megalospheric embryonic apparatus, Hofker (1963) concluded that all Mid-Cretaceous "Orbitolinas" belong not only to one phylogenetic lineage ranging from the upper Barremian to the upper Ceno-

manian, but also to a single species named "*Orbitolina lenticularis*" (Hofker 1963: chart X, reproduced in part by Guex 2001: fig. 1; see Fig. 1B of the present paper). "The changes in shape of the megalospheric embryonic apparatus can all be explained as architectonic necessities to cope with the progressive increase in volume; all transitions are gradual and are found to have the usual variation" (Hofker 1963: p. 219). By using the characteristics of the megalospheric embryo, he subdivided the genus "*Orbitolina*" into five "form-groups" (see Fig. 1B). However, it is noteworthy that in this model the different form-groups do not immediately follow one after another (except in the upper Albian), but their vertical ranges considerably overlap.

In contrast to the opinion of Hofker (1963) that all hitherto known Orbitolinas belong to a single phylogenetic lineage, represented by a single species, Schroeder (1962, 1963, 1964a, 1964b, 1965, 1973, 1975) took the view that the forms united under this generic name belong in reality to different lineages represented by several genera, which mainly differ by the

structures of their megalospheric apparatuses. In this sense he separated from *Orbitolina* D'ORBIGNY successively in 1962, 1963, and 1973 the new taxa *Mesorbitolina*, *Palorbitolina*, and *Conicorbitolina* (all at first introduced as subgenera). *Mesorbitolina* SCHROEDER originated from *Praeorbitolina* SCHROEDER 1964a, and *Palorbitolina* SCHROEDER developed from *Eopalorbitolina* SCHROEDER & CONRAD 1968; both ancestral genera are characterized by their eccentric megalospheric embryonic apparatus.

While the generic status of all these taxa is now generally accepted, it has not been possible to reconstruct the phylogenetic relations between *Palorbitolina* (including *Eopalorbitolina*), *Mesorbitolina* (including *Praeorbitolina*), *Conicorbitolina*, and *Orbitolina*. Actually we can differentiate between at least four independent main phylogenetic lineages (Schroeder 1975, Schroeder et al. 2002; see Fig. 1C) comprising most of the hitherto known taxa (the species cited in the following are the first, resp. the last representatives of each lineage):

1. *Eopalorbitolina pertenuis* – *Palorbitolina lenticularis* lineage (early Barremian – basal late Aptian; Schroeder et al. 2002~ Schroeder & Cherchi 2002). In the Himalayan – Tibetan domain the latter genus extends up to the latest Aptian (Marcoux et al. 1987) grading into the early Albian *Palorbitolinoides hedini* CHERCHI & SCHROEDER 1980. To this lineage belong all the forms described by Hofker (1963) under the name “*Orbitolina lenticularis* form-group I”.
2. *Praeorbitolina cormyi* – *Mesorbitolina aperta* lineage (early Aptian – early Cenomanian; Schroeder 1975). The majority of the forms comprised by Hofker (1963) as “form-groups II and III” belongs to this lineage.
3. *Orbitolina sefini* – *O. concava* lineage (late Albian – early Cenomanian; Schroeder 1975) including the specimens described by Hofker (1963) as “form-group IV”.
4. *Conicorbitolina moulladei* – *C. conica* lineage (late Albian – middle Cenomanian; Schroeder 1975, Schroeder, in Schroeder & Neumann 1985). The specimens comprising “form-group V” of Hofker (1963) belong to this lineage.

Fig. 1C clearly shows that the ranges of the four lineages considerably overlap. There is no evolutionary break which can be correlated with any of the known Early Cretaceous anoxic events.

At the Cenomanian-Turonian boundary, the sketch of Guex (2001; see Fig. 1A) points to an important size decrease in the embryonic apparatus of Orbitolinas, which was interpreted by that author as due to the actually well known Bonarelli anoxic event (OAE 2). However, this interpretation is based on two errors.

1. The two uppermost horizontal lines in the sketch of Guex (2001) suggest two successive populations of different age; however, it refers to a single population (sample 115024 of Hofker). According to Hofker (1963: chart IX), the “flat”

specimens of this population showing a large embryo („form-group IV“) correspond to the A₂-generation, whereas the “conical” forms with a small embryo („form-group V“) are regarded as specimens of the A₁-generation. In reality, the first group represents a species of the genus *Orbitolina*, whereas the second group has to be assigned to the genus *Conicorbitolina* SCHROEDER (probably *C. conica*). Thus, sample 115024 of Hofker contains representatives belonging to two different phylogenetic lineages.

2. Sample 115024 of Hofker comes from the Sierra de Aulet section (Prov. Huesca, South Central Pyrenees) and was taken in a succession of marls alternating with limestones, which corresponds to the basal part of the Sopeira Formation (Mey et al. 1968; = Sopeira Marls in Caus et al. 1993). This succession concordantly overlies the argillaceous limestones and calcarenites of the Aulet Formation being rich in orbitolinids (Schroeder 1973). Already Hofker (1963: 194) reported 200 m above his sample 115024 “a fauna typical of the uppermost Cenomanian” (including *Rotalipora greenhornensis*). Caus et al. (1993: p. 536) cited “*Orbitolina* (*C.*) *conica*” from two horizons situated 6.2 m resp. 29.3 m above the base of the Sopeira Formation. According to these authors, the lower 130 m of this formation yielded planktonic foraminiferal assemblages of the early Cenomanian *Rotalipora brotzeni* Zone. On the basis of these data it becomes clear that Hofker’s sample 115024 cannot be placed at the Cenomanian-Turonian boundary, but is of early Cenomanian age. The genus *Orbitolina* became extinct at the early/middle Cenomanian boundary, whereas *Conicorbitolina* ranges up to the end of middle Cenomanian (Schroeder & Neumann 1985: tab. 1). Hence, it follows that already for stratigraphical reasons a further discussion on possible effects of the Bonarelli anoxic event on the evolution of orbitolinid foraminifers is superfluous.

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