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Ontogeny and phylogeny of Upper Cenomanian rotaliporids (Foraminifera)

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ABSTRACT

The fossil record of planktonic foraminifera is a key source of data on the evolution of marine plankton. One of the most distinctive groups of Cretaceous foraminifera, the rotaliporids, widely used as a stratigraphic index, has always been considered to be a monophyletic clade. New data on the coiling direction and persistent morphological features of the late rotaliporids from the Upper Cenomanian of the Western Interior Seaway, USA, and the Vocontian Basin of southeast France is used as a phylogenetic proxy. Dealing with key morphological features, the coiling pattern of these keeled morphotypes proves that the rotaliporids group is polyphyletic and composed of *Thalmanninella*, that displays a dextral-coiling preference, and *Rotalipora* s.s., that have a proportionate-coiling mode. The stratigraphically youngest rotaliporids with keels co-occur with globular forms; and all morphologies transitional between these morphotypes are observed. The ontogenetic relationships between them are investigated, indicating that loss of the keel was a selective advantage that enabled those rotaliporids to remain in the surface water, thereby avoiding the expansion of the oxygen minimum zone. Two species are observed: *Thalmanninella multiloculata* and *Rotalipora planoconvexa*. These species are interpreted as having arisen by neoteny from *Thalmanninella greenhornensis* and *Rotalipora cushmani* respectively.

1. Introduction

Most Cenomanian planktonic foraminifera lineages emerged during the late Albian. Among these lineages, the subfamily of Rotaliporinae Sigal (1958) is divided in six genera which are globular and/or keeled morphotypes: *Rotalipora* Brotzen (1942), *Thalmanninella* Sigal (1948), *Anaticinella* Eicher (1972), *Pseudoticinella* Longaria (1973), *Pseudothalmanninella* Wonders (1978) and *Pseudorotalipora* Ion, 1983. Rotaliporinae flourished both in the deep oceans and the adjacent shelf areas before disappearing during the Cenomanian–Turonian anoxic event. Reconstructing the evolution of this single-keeled lineage has been a subject of wide interest, both in establishing a late Albian–Cenomanian biozonation (Caron, 1985; Robaszynski and Caron, 1995) and interpreting major changes in Upper Cretaceous palaeoceanography.

However, some problems still remain with the classification of these genera. Although most micropalaeontologists only retain the genus *Rotalipora* s.l., other authors (Sigal, 1948; Brönnimann and Brown, 1955; Wonders, 1978; Gonzalez-Donoso et al., 2007) use the genera *Rotalipora* s.s., *Thalmanninella* and *Pseudothalmanninella*. This subdivision is based on morphological criteria: *Rotalipora* s.s. has sutural secondary apertures and symmetrical inflated chambers whereas *Thalmanninella* has umbilical secondary apertures and non inflated chambers on the umbilical side. *Pseudothalmanninella* has umbilical supplementary apertures and chambers with a flattened surface, except in the first species.

In contrast, other authors (e.g. Robaszynski et al., 1993) have concluded that these criteria, sometimes ambiguous, are

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insufficient to place all specimens in one of these three genera. Thus, following the suggestions of Robaszynski et al. (1979), Robaszynski et al (1993) recommended using only one morphologic and polyphyletic genus: *Rotalipora* s.l. However, if morphologic criteria are obvious, the same authors advised using the three polyphyletic sub-genera (*Rotalipora* s.s., *Thalmanninella* and *Pseudothalmanninella*), the last of which disappears close to the Albian–Cenomanian boundary.

Consequently to these ambiguities, Gonzalez-Donoso et al. (2007) do not retain the formal name of the subfamily Rotaliporinae and use the informal name of rotaliporids.

One of the main morphological characters used to classify Mesozoic foraminifera is the presence or absence of a keel. During the Upper Cenomanian, *Rotalipora* s.l. gave rise to *Anaticinella*, a genus with an indistinctly marked keel or without a keel, which is the final member of the rotaliporids lineage. However, this example of sympatric speciation leads to more general questions about the genus concept. By comparison, micropalaeontologists currently group different morphotypes in the same genus for the Paleogene and Neogene taxa *Globorotalia crassaformis* and *Globorotalia ronda*.

The main objective of this study is to re-examine the ontogenetic and phylogenetic relationships of all late Cenomanian *Rotalipora* s.l. and *Anaticinella*. Thus, a taxonomic revision of the genera belonging to the rotaliporids is proposed; the need for such revision having been noted by Gonzalez-Donoso et al. (2007).

2. Geological setting

In this study, latest Cenomanian sections (Fig. 1) are described across two major palaeogeographic areas, the Western Interior Seaway of the United States and the Vocontian Basin of southeast France. The late Cenomanian corresponds to the beginning of the anoxic event OAE2 which led to the disappearance of rotaliporids. (Hart and Bailey, 1979). During this period of decline, *Rotalipora* s.l. evolved into *Anaticinella* by losing their keel (Eicher, 1972; Longoria, 1973; Leckie, 1985; Desmares et al., 2003), a selective advantage that enabled them to remain in shallower habitats, escaping thus an expanding oxygen-minimum zone.

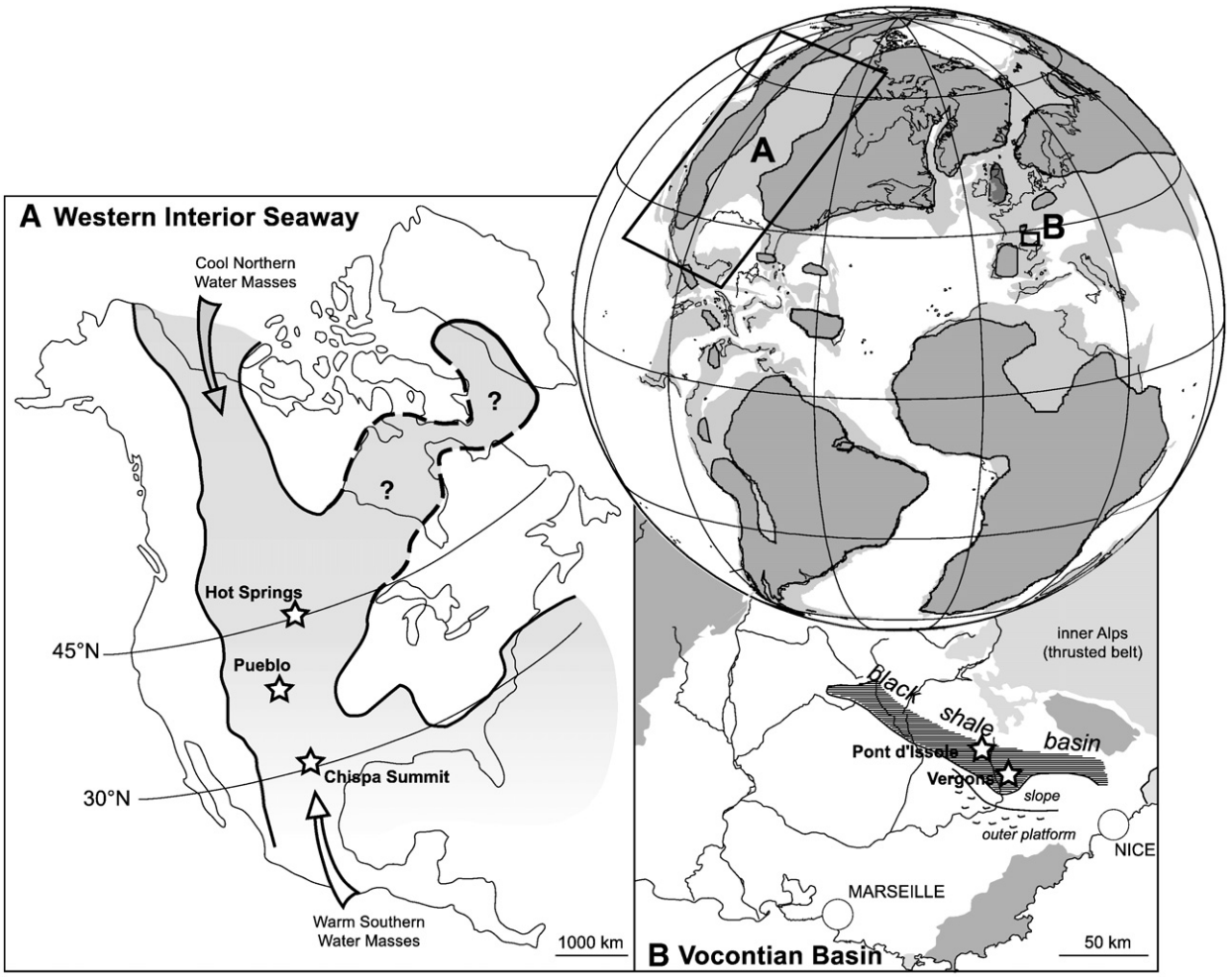

Fig. 1. Location of study areas. (A) Western Interior Seaway sections superimposed onto palaeoceanographic map (after Hattin, 1971; Kauffman, 1984; Eaton and Nations, 1991). (B) Location of sections from Vocontian Basin in southern subalpine ranges (after Grosheny et al., 2006).