Co-occurrence of the foraminifer *Mohlerina basiliensis* with *Bacinella–Lithocodium* oncoids: palaeoenvironmental and palaeoecological implications (Late Oxfordian, Swiss Jura)

STÉPHANIE VÉDRINE

Department of Geosciences – Earth Sciences, University of Fribourg, Pétroles, 1700 Fribourg, Switzerland (Current address: School of Earth and Environment, University of Leeds, Leeds LS2 9JT, UK (e-mail: steph_vedrine@yahoo.fr)

ABSTRACT – The stratigraphical and spatial distribution of the foraminifer *Mohlerina basiliensis* and *Bacinella–Lithocodium* oncoids was studied in the lagoonal deposits of the oncoid-rich Hauptmumienbank Member from the Swiss Jura Mountains (Late Oxfordian, NW Switzerland). *Mohlerina basiliensis* has a double-layered wall structure (thick outer hyaline-radial calcite layer with a lamellar structure and thin inner microgranular calcite layer) and is preferentially found in low-energy facies and associated with normal-marine bioclasts and *Bacinella–Lithocodium* oncoids. The distribution of *Mohlerina basiliensis* is relatively patchy. The ‘distal’ platform facies present a higher abundance and a more extensive stratigraphic occurrence of this foraminifer. The timing of the ecological evolution is given by the sequence- and cyclostratigraphic framework and illustrates the stepwise flooding of the platform. *Bacinella–Lithocodium* oncoids have diameters of a few millimetres to several centimetres and are composed of an alternation of *Bacinella–Lithocodium* meshwork and thin micritic laminae. They are found preferentially in low-energy facies (bioclastic wackestones) of open lagoons. The distribution of *Bacinella–Lithocodium* oncoids through time and space is also patchy; however, they appear more abundantly in ‘distal’ platform facies. This study reveals the co-occurrence of *Mohlerina basiliensis* and *Bacinella–Lithocodium* oncoids and thus suggests similar environmental conditions.


KEYWORDS: benthic foraminifer, *Bacinella–Lithocodium* oncoids, carbonate platform, Late Oxfordian, Swiss Jura Mountains

INTRODUCTION

Benthic foraminifera have a great potential as indicators of depositional environments in the geological past (e.g. Smith, 1955; Martin, 1988; Cannariato et al., 1999). These bottom-dwelling organisms occur in a wide range of marine environments. The foraminifer *Mohlerina basiliensis* ranges from the Middle–Late Bathonian to the Valanginian and is usually found from the internal platform down to the slope (Flügel, 2004). Oncoids are also used as palaeoenvironmental proxies for ancient carbonates (e.g. Peryt, 1983). They are irregularly shaped carbonate grains formed by microbiol activity: trapping of particles by organic filaments and/or calcified filaments forming an anastomosing pattern. Their morphology (sphericity) and surface morphology indicate the rolling intensity on the seafloor and thus the degree of wave or current energy. The biotic composition and the encasing sediment reveal the trophic conditions, water energy and water depth that dominated during their formation (Védrine et al., 2007). This study describes the main characteristics and the distribution of these two components (*Mohlerina basiliensis* and *Bacinella–Lithocodium* oncoids) encountered within a transgressive interval well defined by high-resolution sequence- and cyclostratigraphy.

GEOLOGICAL CONTEXT

The study area is located in the Swiss Jura Mountains of northwestern Switzerland (Fig. 1). In the Late Oxfordian, this region was a shallow-water carbonate platform (Fig. 2). At the beginning of the Bimammatum Ammonite Zone, an important lithological change is observed from the siliciclastic-dominated ‘Röschenz Member’ to the carbonate-dominated ‘Hauptmumienbank Member’ (Gygi & Persoz, 1986; Gygi et al., 1998). The Röschenz Member is composed of marls and limestones, whereas the Hauptmumienbank Member presents...
Massive oncoid-rich limestone beds (e.g., Gygi, 1992, 2000). This study concentrates on the latter member, which lies in the Semimammatum and Berrense Ammonite Subzones (Fig. 3; Gygi & Persoz, 1986). The studied interval corresponds to the transgressive part of the medium-scale Ox6+ sequence (Védrine et al., 2007), which is found at the beginning of a second-order transgressive sea-level evolution and is interpreted as being formed in tune with a 400 ka orbital cycle (Strasser et al., 1999).

MATERIAL AND METHODS

Four shallow-water carbonate platform sections (Voyeboeuf, Vorbourg, Savagnières, and Pertuis) were logged at a centimetre scale and densely sampled. Stacking pattern of beds, bed surfaces, facies and microfacies were examined in detail. Depositional environments were identified from the microfacies and from the semi-quantitative analysis of organic and inorganic components. These sedimentological observations were then interpreted in terms of sequence- and cyclostratigraphy. Small-scale and elementary depositional sequences were identified following the methodology of Strasser et al. (1999) and interpreted as 100 ka and 20 ka orbital cycles, respectively. Sequence boundaries (sensu Vail et al., 1991) were placed at the shallowest facies, transgressive surfaces at a rapid facies change to deeper and/or more open-marine facies, and maximum floodings at the deepest or more open-marine facies.

Benthic foraminifera and oncoids are relatively common in the studied sections. The main suborders of benthic foraminifera found in these lagoonal facies are Textulariina, Lagenina and Miliolina. However, this study concentrates only on Mohlerina basiliensis. This foraminifer occurs in small numbers and is distributed sparsely. Mohlerina basiliensis was found in only

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<td>Blur-catus</td>
<td>155.68 Ma</td>
<td>Grossouvrei</td>
<td>SB Ox 6+</td>
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Fig. 3. Lithostratigraphical, biostratigraphical, and sequence-stratigraphical position of the Hauptmumienbank Member on the Swiss Jura platform (after Gygi & Persoz, 1986; Gygi, 1995, 2000; Hardenbol et al., 1998). The studied interval corresponds to one and a half small-scale (100 ka) sequences between the sequence boundary of medium-scale (400 ka) sequence Ox6+ at the base of the Hauptmumienbank Member and the maximum flooding of the medium-scale sequence Ox6+. SB, sequence boundary; MF, maximum flooding; R, second-order regressive trend; T, second-order transgressive trend. Ages of ammonite subzone boundaries and of sequence boundaries according to Hardenbol et al. (1998).
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40 of the 265 analysed thin sections. Its distribution thus appears to be linked to specific environmental factors. The absolute abundance of Mohlerina basiliensis was estimated by counting specimens per surface area in thin section. In the oncoid-rich Hauptmumienbank Member, two groups of oncoids are defined from thin section: micrite-dominated and Bacinella–Lithocodium oncoids (Fig. 4; Védrine et al., 2007). Differences in size, shape, surface morphology and cortex configuration and composition were distinguished. Micrite-dominated oncoids are small (a few millimetres to 1 cm) with a smooth surface; they have a micritic cortex with regular or irregular laminations and are associated with a low-diversity fauna. Bacinella–Lithocodium oncoids are larger (a few millimetres to 5 cm) with a lobate surface and a cortex composed of micritic laminae and Bacinella–Lithocodium meshwork. This study focuses on the relative abundance of Bacinella–Lithocodium oncoids estimated in thin sections.

**TAXONOMY**

**The benthic foraminifer Mohlerina basiliensis**

Suborder Rotalina Delage & Hérouard, 1896

Family Discorbidae Ehrenberg, 1838

Genus Mohlerina Bucur et al., 1996

*Mohlerina basiliensis* (Mohler, 1938) (Pl. 1, figs 1–13)

1938 *Conicospirillina basiliensis* Mohler n. sp.: Mohler; 27, pl. 4, fig. 5.

1991 *Conicospirillina basiliensis* Mohler: Darga & Schlagintweit; 214, pl. 2, fig. 5.

1993 *Archaeosepta basiliensis* (Mohler) nov. comb.: Tasli; 60, pl. 3, figs 6–7.

1996 *Mohlerina basiliensis* (Mohler) nov. comb.: Bucur et al.; 70, pl. 3, figs 3–6; pl. 4, figs 2–3, 5–9.

1999 *Mohlerina basiliensis* (Mohler): Schlagintweit & Ebli; 400, pl. 6, figs 1–2; ?pl. 4, fig. 10.

2000 *Mohlerina basiliensis* (Mohler): Dieni & Radoicic; figs 6a–d.


2004 *Conicospirillina basiliensis* Mohler: Flügel; pl. 69, fig. 6.


**Description.** *Mohlerina basiliensis* is characterized by a plurilocular test, trochospirally enrolled, with a convex spiral side, a concave umbilical side and a secondarily thickened umbilical zone. Chambers have variable forms from oval-rounded to arched (semi-circular in thin section). *Mohlerina basiliensis* is composed of a double-layered wall with a thick outer hyaline-radial calcite layer with a lamellar structure and a thin inner microgranular calcite layer (Pl. 1, figs 1–13).

**Remarks.** All the observed specimens of *Mohlerina basiliensis* come from the Hauptmumienbank Member (Vellerat Formation, Semimammatum and Berrense Ammonite Subzones, Late Oxfordian) from the Swiss Jura Mountains (NW Switzerland). *Mohlerina basiliensis* is found from the Middle–Late Bathonian to the Valanginian. The taxonomic position of this species is still in discussion. It was attributed previously to the Suborder Spirillina (e.g. Darga & Schlagintweit, 1991), then to the Suborder Involutinina, Family Ventrolaminidae and Genus *Archaeosepta* (Tasli, 1993) and, more recently, to the Suborder Rotalina and the Family Discorbidae (e.g. Bernier, 1984; Bucur et al., 1996). Based on its double-layered microstructure, Septfontaine (1981) attributed *Mohlerina basiliensis* to the Suborder Fusulinina. Since the Suborder Fusulinina became extinct during the Late Palaeozoic, Septfontaine (1981) named *Mohlerina* ‘Mesozoic Fusulinina’.

In the Hauptmumienbank Member, *Mohlerina basiliensis* is found mostly in oncoid-rich and bioclastic (brachiopods, echinoderms) wackestones, characterizing low-energy conditions and normal-marine conditions (Pl. 1, figs 12, 13). Sporadically, *Mohlerina basiliensis* appears in higher energy deposits such as ooid- and peloid-rich packstones (Pl. 1, fig. 11). Several authors found this foraminifer preferentially in high-energy facies from the internal platform to the slope, commonly associated with *Protopeneroplis* sp., *Trocholina* sp., *Pseudocyclammina* sp., *Andersnolmina* sp., *Nautiloculina* sp., *Lenticulina* sp., *Valvulina* sp. and miliolids (Darga & Schlagintweit, 1991; Sasaran et al., 2000; Schlagintweit & Ebli, 1999; Velic et al., 2002; Gawlick et al., 2003). Recently, Flügel (2004) and Velic et al. (2002) described *Mohlerina basiliensis* as characteristic of upper slope facies.

**Bacinella–Lithocodium oncoids**

These oncoids have diameters of a few millimetres up to 5 cm and display sub-elliptical shapes with lobate contours. The cortex is made of alternating organism-bearing and thin micritic laminations (Pl. 1, figs 12–14; Védrine et al., 2007). The organism-bearing laminations are formed by two microencrusters: *Bacinella irregularis* (Radoicic, 1959; Fig. 5A) and *Lithocodium aggregatum* (Elliott, 1956; Fig. 5B). *Bacinella irregularis* is an enigmatic microencruster with an irregular micritic meshwork and interspaces filled with calcite spar (Fig. 5A). This structure is assumed to represent a cyanobacterial structure (Schmid, 1996; Shiraishi & Kano, 2004). *Lithocodium*, originally interpreted as a codiacean alga by Elliott (1956), is characterized by inner cavities and an aggregated outer wall with numerous alveoli probably containing symbiotic and photosynthetic algae (Schmid & Leinfelder, 1996). These authors thus attributed it to a loftusiacean foraminifer with an encrusting life habit. Recently, Cherchi & Schroeder (2006) interpreted *Lithocodium* as colonies of calcified cyanobacteria because of the absence of apertures connecting neighbouring cavities, and because of the very irregular form and arrangement of these hollows. The *Bacinella–Lithocodium* association characterizes lagoonal environments with oligotrophic conditions, low sediment accumulation rate, clear, oxygenated, shallow and normal-marine waters (Leinfelder et al., 1993; Dupraz & Strasser, 1999; Immenhauser et al., 2005).

Two types of *Bacinella–Lithocodium* oncoids were identified in the Hauptmumienbank deposits (Types 3 and 4 of Védrine et al., 2007). Type 3 oncoids are composed of an alternation of
Fig. 4. Distribution of *Mohlerina basiliensis* and oncoids along the studied sections. Two orders of depositional sequences (elementary and small-scale sequences) were identified and related to sea-level fluctuations induced by changes of orbital parameters. Elementary and small-scale sequences are interpreted as corresponding to 20 ka and 100 ka orbital (Milankovitch) cycles, respectively.
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*Mohlerina basiliensis* from the Hauptmumienbank Member (Late Oxfordian, Swiss Jura Mountains), fig. 1. Subaxial section of *Mohlerina basiliensis*, sample Vo-20. fig. 2. Enlargement of specimen in figure 1, showing a double-layered wall structure – thin dark microgranular calcite layer (M) and thick hyaline-radial calcite layer with a lamellar structure (R), sample Vo-20. fig. 3. Subaxial section of *Mohlerina basiliensis*, sample Pe-81B. fig. 4. Axial section of *Mohlerina basiliensis*, sample Sa-19A. fig. 5. Enlargement of specimen in figure 3, showing the lamellar structure of the thick outer hyaline radial layer, sample Pe-81B. fig. 6. Subaxial section of *Mohlerina basiliensis*, sample Pe-80B. fig. 7. Equatorial section of *Mohlerina basiliensis*, sample Pe-80B. fig. 8. Equatorial section of *Mohlerina basiliensis*, sample Pe-86B. fig. 10. Oblique section of *Mohlerina basiliensis*, sample Pe-84B. fig. 11. High-energy facies (packstone/grainstone) composed of micritized ooids, peloids, bivalves, *Mohlerina basiliensis* and miliolids, sample Vo-24A. fig. 12. *Bacinella–Lithocodium* (Type 3 of Védrine et al., 2007) oncid wackestone associated with *Mohlerina basiliensis*, sample Vo-22. fig. 13. *Bacinella–Lithocodium* (Type 3) oncid wackestone associated with *Mohlerina basiliensis* and a perforated brachiopod fragment, sample Pe-83A. fig. 14. *Bacinella–Lithocodium* (Type 3) oncid, sample Pe-83A.
Bacinella–Lithocodium meshwork and thin micritic laminae (Pl. 1, figs 12–14), whereas Type 4 oncoids are entirely made of Bacinella–Lithocodium meshwork. These oncoids are preferentially found in wackestones with a well-diversified normal-marine fauna (brachiopods, oysters, foraminifera, echinoderms, bivalves), indicating relatively low-energy conditions.

Fig. 5. (A) Bacinella irregularis meshwork. Pertuis section, Pe-82A. (B) Lithocodium aggregatum with Troglorella incrustans (arrow). Pertuis section, Pe-84A.

Mohlerina basiliensis distribution within elementary and small-scale depositional sequences. The encircled numbers indicate the first occurrence of Mohlerina basiliensis in each section. Superimposed are relative sea-level changes of two different orders leading to the formation of two orders of depositional sequences: small-scale and elementary sequences.

Fig. 6. Mohlerina basiliensis distribution within elementary and small-scale depositional sequences. The encircled numbers indicate the first occurrence of Mohlerina basiliensis in each section. Superimposed are relative sea-level changes of two different orders leading to the formation of two orders of depositional sequences: small-scale and elementary sequences.
and representing an open lagoon. Consequently, the cortex configuration and composition indicate calm periods during which *Bacinella–Lithocodium* could grow and occasional higher energy periods during which the micritic laminae were formed. Consequently, oncoids are generally considered as good proxies for palaeoenvironmental conditions (Dahanayake, 1977; Kuss, 1990; Védrine *et al*., 2007).

**SPATIAL AND STRATIGRAPHIC DISTRIBUTION**

Based on the dominant facies, sections are positioned from ‘proximal’ (Voyeboeuf) to ‘distal’ (Savagnières and Pertuis). However, because platform morphology changed through time, these attributions can only indicate a general ‘proximal–distal’ trend. The *Mohlerina basiliensis* distribution is relatively patchy. The ‘distal’ platform facies present a higher abundance of this foraminifer (Figs 4 & 6). Its minimum abundance (only two specimens per thin section) is found in the relatively ‘proximal’ Voyeboeuf section, and the maximum abundance (up to 12 specimens per thin section) in the relatively ‘distal’ Pertuis section. In the latter, *M. basiliensis* has a more extensive stratigraphic occurrence than in the other sections (Figs 4 & 6).

In addition, the distribution of *Bacinella–Lithocodium* oncoids in time and space is patchy (Fig. 4). However, *Bacinella–Lithocodium* oncoids are more abundant in ‘distal’ platform facies, especially in the Pertuis section (Fig. 4). Micrite-dominated oncoids are present in all the sections but less in the Pertuis section. Occasionally, *Bacinella–Lithocodium* and micrite-dominated oncoids co-exist.

In a time–space diagram (based on the cyclostratigraphic interpretation of the sections; Védrine, 2007; Védrine *et al*., 2007), the *Mohlerina basiliensis* distribution shows a particular evolution (Fig. 6). The first occurrence of the foraminifer differs between sections in time and space but follows the ‘proximal–distal’ evolution. In the most ‘distal’ section (Pertuis), the first occurrence is coeval with the beginning of the second-order marine transgression (‘1’; Fig. 6). In the three other sections, the first occurrence is successively later (Fig. 6). This illustrates the stepwise flooding of the platform during the early *Bimammatum* transgression (Fig. 7). However, *M. basiliensis* distribution does not reveal a clear preferential occurrence within small-scale and elementary sequences or around small-scale and elementary sequence boundaries or maximum floodings.

The distribution of the oncoid types shows a clear correlation with sequence stratigraphy. Micrite-dominated oncoids are found preferentially around 100 ka and 20 ka sequence boundaries and in transgressive deposits, while *Bacinella–Lithocodium*
oncoids occur preferentially around 100 ka and 20 ka maximum floodings and in highstand deposits (Védrine et al., 2007).

The distributions of Mohlerina basiliensis and Bacinella-Lithocodium oncoids show a strong correlation (Fig. 4). M. basiliensis always occurs when Bacinella-Lithocodium oncoids are present (Figs 4 & 6). On the other hand, the presence of Bacinella-Lithocodium oncoids does not imply the occurrence of M. basiliensis. For example, the base of the Voyeboeuf section contains Bacinella-Lithocodium oncoids in three intervals but no M. basiliensis (in the 1.2 and 1.3 elementary sequences; Fig. 4).

PALAEOENVIRONMENTS AND PALAEOECOLOGY

Water depth and water turbidity are important parameters because they control the amount of light received by benthic foraminifera. The substrate on, or in which they live influence the test morphology (Murray, 1991). Other important factors are the oxygen content and food availability, which act on the foraminifer type and diversity (e.g. Jorissen et al., 1995; Fugagnoli, 2004). Temperature and salinity also play a role in foraminifer distribution by modifying the CaCO3 solubility in seawater, which acts on the nature of the test (Greiner, 1969). The palaeoenvironmental and palaeoecological requirements of Mohlerina basiliensis are not well known. The successively later occurrence of M. basiliensis from ‘distal’ to ‘proximal’ platform sections illustrates the stepwise flooding of the platform (Fig. 7) and thus implies a dependence on normal-marine conditions. Its occurrence in high-energy as well as in low-energy facies probably suggests a reworking by waves and currents. Oncoids and their associated microencrusters grow on the sediment surface and thus monitor water transparency and trophic level, which are both controlled by terrigenous influx (clays and nutrients) onto the shallow carbonate platform. The Bacinella–Lithocodium association, included in the oncoid cortex, indicates oligotrophic, clear, oxygenated and normal-marine waters (e.g. Dupraz & Strasser, 1999). In the Hauptmumienbank deposits, Mohlerina basiliensis is always found when Bacinella-Lithocodium oncoids are present (Fig. 4). Hence, the co-occurrence of Bacinella-Lithocodium oncoids and M. basiliensis suggests that this foraminifer required similar ecological conditions. Figure 8 synthesizes the oncoid and foraminifer distribution from protected lagoon to basin. Type 1 and 2 oncoids (micrite-dominated oncoids) are found in protected and semi-open lagoons, respectively, whereas Bacinella-Lithocodium oncoids (Type 3 and 4 oncoids) are found mostly in open lagoons. M. basiliensis has a large distribution from the internal platform to the slope but is more abundant in open lagoons. Finally, the early Bimammatum transgression appears to have created ideal environmental conditions for the co-occurrence of Bacinella-Lithocodium oncoids and Mohlerina basiliensis. Consequently, the spatial and stratigraphical distribution of both Bacinella-Lithocodium oncoids and Mohlerina basiliensis can be used for palaeoenvironmental and palaeoecological reconstructions.

CONCLUSIONS

Mohlerina basiliensis distribution reveals lateral and temporal changes related to a marine transgression. Specimens are more abundant in the ‘distal’ sections than in ‘proximal’ ones and the first occurrence of this foraminifer is in the most ‘distal’ section (Pertuis). The successively later occurrence of Mohlerina basiliensis from ‘distal’ to ‘proximal’ platform sections illustrates the stepwise flooding of the platform during the early
Bimammatum transgression and thus implies a dependence on normal-marine conditions. *Bacinella–Lithocodium* oncoid distribution is relatively patchy through time and space. However, a ‘proximal–distal’ evolution exists with more abundant *Bacinella–Lithocodium* oncoids in the ‘distal’ platform facies. These oncoids are found preferentially around maximum floodings and in highstand deposits (Védrine et al., 2007), indicating a link with relative sea-level fluctuations. The comparison of the distributions of these two components shows that *Mohlerina basiliensis* occurs preferentially when *Bacinella–Lithocodium* oncoids are present. The co-occurrence of these two components thus suggests common environmental factors.

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