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Growth strategies of the tabulate coral *Favosites bohemicus* on unstable, soft substrates: An example from the Hamar Laghdad (Lower Devonian, Anti-Atlas, Morocco)

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ABSTRACT

Coralla of the tabulate coral *Favosites bohemicus* coming from the famous Kess-Kess mud mound locality of the Hamar Laghdad (SE Morocco) area have been studied with respect to their growth patterns and colony development. The Emsian Kess-Kess mounds developed in a relatively deep-water, low-energy environment, below fair-weather wave-base. After the mound growth ceased, the slopes of the mounds were covered by soft, muddy sediment and colonised by tabulate corals. The morphological characteristics of *F. bohemicus* coralla analysed in the present study document various responses of the coral colonies to sediment creeping on the steeply inclined slopes. The coralla are massive and display a strong variability in shape and size; most of the specimens are, however, of spherical and sub-spherical shape. The striking feature of the majority of the colonies is that they are either deflected and tilted in one direction, or display indications of being continuously overturned, both features reflecting changes in growth direction of the corals. The tilted and curved direction of growth was likely caused by the slow creeping of the sediment, along with which the colonies were being slowly moved down the slope. The most important factor that controlled the intensity of the mass movements was presumably the slope inclination, which varied among both different mounds and different slopes of individual mounds. Since corals affected differently by mass movements of variable strength attained various sizes and shapes, morphological analyses of *F. bohemicus* provide clues on the sediment characteristics, as well as type and frequency of mass movements in the cover of the Kess-Kess mud mounds, enabling valuable insights into the initial stages of their burial.

1. Introduction

The Devonian is widely known as a period of widespread development of reefs on a global scale, with tabulate corals being some of the most important contributors to reefal assemblages (Wood, 1998; Copper, 2002). However, there were also other coral assemblages that thrived during that time. The association of tabulate and rugose corals of the Lower Devonian (Emsian) Kess-Kess mud mounds in the Hamar Laghdad area of Morocco is one such example. Settled in a relatively deep-water environment, on the steep, unstable, soft sediment-covered slopes of the mounds, the corals developed various strategies for survival (Berkowski, 2008, 2012). Although life strategies of favositid corals inhabiting soft bottoms have been studied before (e.g. Gibson and Broadhead, 1989; Seilacher and Thomas, 2012), it has not yet been analysed how they could have survived on steeply inclined surfaces, where mass movements resulted in a large degree of substrate and habitat heterogeneity and instability.

Symbiosis with algae (*Symbiodinium*) provides modern scleractinian corals with both great benefits and limitations with respect to their environmental tolerance. The question of when the corals developed photosymbiosis with algae has been a matter of some controversy (e.g. Scrutton, 1998; Wood, 1998; Copper, 2002; Zapalski, 2014; Jakubowicz et al., 2015). The tabulate coral *Favosites bohemicus* colonised the Kess-Kess mounds in a relatively deep-water environment, commonly accepted to represent a depth below the euphotic or even in the aphotic zone (Brachert et al., 1992; Belka, 1998; Berkowski, 2008; Jakubowicz et al., 2014, 2015). Furthermore, the *F. bohemicus* coralla lack any internal structures (e.g. septal spines, squamulae) suggestive of the presence of algal symbionts. Therefore, the possibility of a photosymbiotic lifestyle of *F. bohemicus* can be considered very unlikely. Under that assumption, the present study attempts to decipher other factors that could control the development and life strategies of *F. bohemicus* from the Hamar Laghdad area.

Tabulate corals of the Hamar Laghdad ridge were previously studied from the taxonomical standpoint by Termier and Termier (1950, 1980),

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LeMaitre (1952, 1956), Potthast and Oekentorp (1987), Tourneur (1991), as well as Tourner in Brachert et al. (1992) and Plusquellec et al. (2004). A case study of tabulate-crinoid biocoenosis from Hamar Laghdad was presented by Berkowski and Zapalski (2014). In addition to the tabulate studies, some solitary rugose corals affected during life by mass movements on the slopes of the Kess-Kess mounds were investigated by Berkowski (2008, 2012). The present approach aims to investigate the development and life strategies of tabulates of the genus *Favosites*, represented by *F. bohemicus*, which lived on soft, mound-covering sediment undergoing mass movements. The study provides new clues on both environmental controls on tabulate growth, as well as the late sedimentary history of the Kess-Kess mud mounds, which, given the scarcity of exposures of mound-covering strata, to date, remain poorly understood.

2. Geological setting

Hamar Laghdad ridge is located 16 km southeast of the city of Erfoud in the eastern Anti-Atlas of South-Eastern Morocco (Fig. 1A). The area is famous because of the conical, partly exhumed Kess-Kess mud mounds (Fig. 1B, C), which represent an unusual type of carbonate build-up, in which baffling and binding of fine-grained material presumably did not play an important role in their formation (see Brachert et al., 1992 and the references therein).

The origin of the Kess-Kess mounds has been discussed by many authors since the early 20th century. Menchikoff (in: Roch, 1934) regarded them as reefs, but Gendrot (1973) identified them as mud-mounds and since that time the mounds and surrounding sediments became the subject of numerous sedimentological and palaeontological investigations (e.g. Brachert et al., 1992; Belka, 1998; Mounji et al., 1998; Aitken et al., 2002; Berkowski, 2004, 2008, 2012; Belka and Berkowski, 2005; Cavalazzi et al., 2007; Klug et al., 2009, 2014; Berkowski and Klug, 2012; Franchi et al., 2014; Belka et al., 2015). Belka (1998) and Mounji et al. (1998) linked the formation of the mud mounds with hydrothermal activity. The mud mounds were formed on a Lochkovian volcanic rise, cut by a system of faults, to which the mud mounds are spatially related (Belka, 1998). The faults could have provided a system of conduits for hydrothermal fluids, which probably stimulated the precipitation of carbonate mud (Belka, 1998; Berkowski, 2004; Belka and Berkowski, 2005).

Although the shapes of the Kess-Kess mounds show some variability, in general they are all more or less conical, with their height varying from 1 to over 50 m. The original inclination of their slopes was commonly about 50° (Fig. 1B) (Brachert et al., 1992). After their formation in the Emsian, by the end of the *inversus* conodont zone, the mounds were being gradually covered by fine-grained material throughout the late Emsian (*serotinus* and *patulus* conodont zones), comprising the geological unit known as the Amerboh Group (Fig. 2). During that time, numerous *F. bohemicus* tabulates settled on and in the vicinity of the Kess-Kess mud mounds (Fig. 2). The sediments covering the mounds were mostly marly shales, interbedding with nodular and marly limestones. Together they comprise the mound-covering unit. As a result of their deposition on the steeply sloping flanks of the mounds, they often became unstable and lost their cohesion, temporarily flowing down the slopes together with dead or live coralla of *F. bohemicus*.

3. Material and methods

F. bohemicus is a tabulate species known from the Emsian and Eifelian stages. Outside of Hamar Laghdad, it occurs in Bohemia,

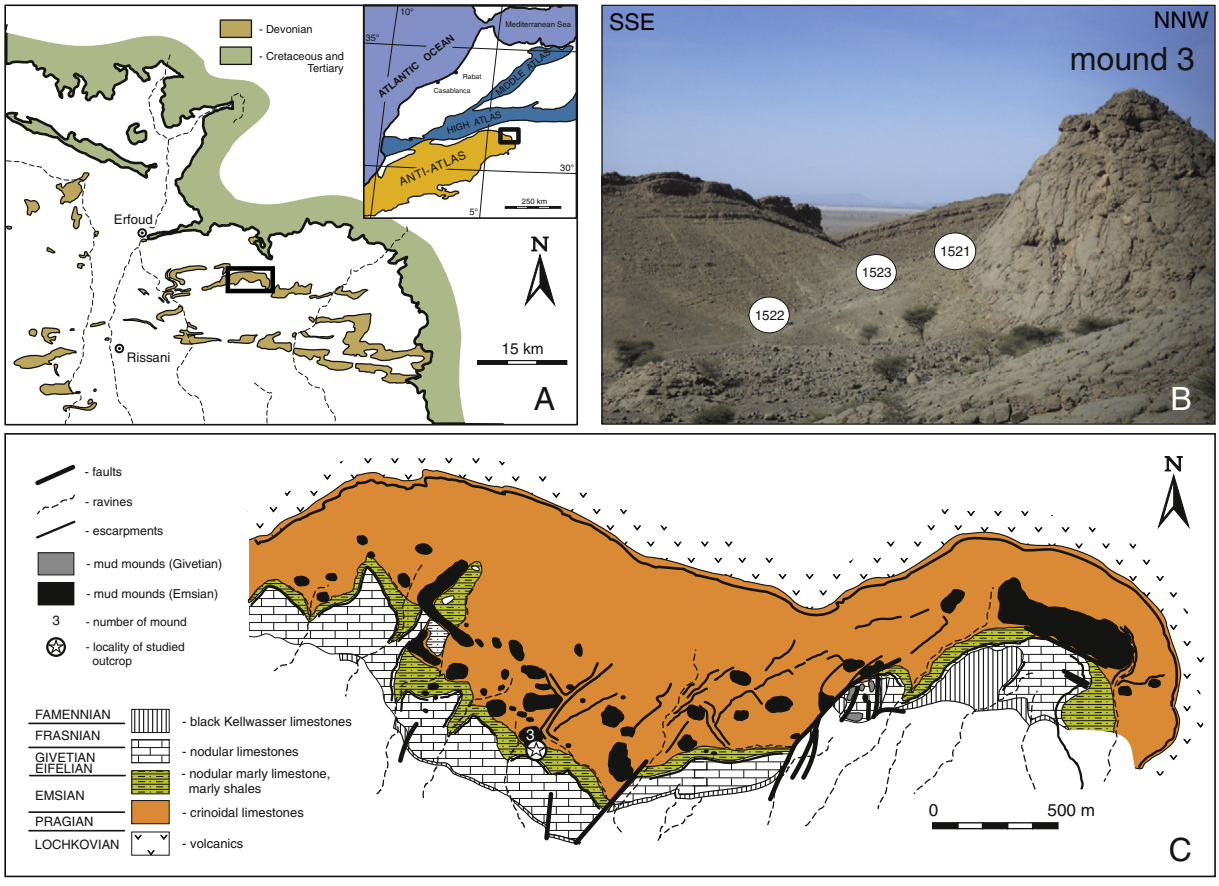

Fig. 1. (A) Index map (study area outlined) and simplified geological map of the north-eastern Anti-Atlas. (B) Mound number 3 with indicated sampling localities. Mound 3 is 46 m high. (C) Detailed geological map of the Hamar Laghdad ridge (after Belka, 1998).