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Devonian rugose coral '*Amplexus*' and its relation to submarine fluid seepage

Michal Jakubowicz [a,*], Blazej Berkowski [b], Zdzislaw Belka [c]

[a] Institute of Geoecology and Geoinformation, Adam Mickiewicz University, ul. Dzięgielowa 27, 61-680 Poznań, Poland
[b] Institute of Geology, Adam Mickiewicz University, ul. Maków Polnych 16, 61-606 Poznań, Poland
[c] Isotope Laboratory, Adam Mickiewicz University, ul. Dzięgielowa 27, 61-680 Poznań, Poland

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ABSTRACT

The rugose coral '*Amplexus*' occurs frequently in the sedimentary cover of the Devonian submarine volcanic intrusion in the eastern Anti-Atlas, southern Morocco. This study elucidates the palaeoecology of '*Amplexus*', which forms very rich and mostly monospecific, spot assemblages within the Lower and Middle Devonian carbonates. Geological and isotopic evidences show that these associations developed at hydrothermal vents and at a cold seep site. The assemblages are always spatially associated with micritic carbonate bodies, occurring within bedded, hemipelagic deposits. The '*Amplexus*' corals preferred locations in the close proximity of submarine hydrothermal fluid seepage, but they generally avoided places with the most elevated temperatures. The corals colonised also a hydrocarbon seep, probably only in its terminal phase of development, when the fluid flow was still at least periodically active. This was only possible as a result of the corals following a calice-in-calice growth, developed due to the environmental toxicity, which facilitated selective survival of larvae that settled in the shelter of empty calices. The '*Amplexus*' corals appear to have constituted ecological opportunists, thriving in the nutrient-rich, venting- and seepage-affected areas that were hostile for other benthic organisms. It can be suspected that the unusual, extremely simplified morphology of '*Amplexus*' made it particularly well adapted to living in environments typified by harsh and unstable conditions.

1. Introduction

Successive discoveries of rich, cold-water scleractinian coral associations in the past three decades began a broad debate on factors controlling the distribution of corals in the deep sea. The main challenge in these discussions was to reconcile the extraordinary productivity of these ecosystems, variously referred to as deep (or cold)-water reefs, mounds, bioherms or banks, with their occurrence in cold, aphotic waters, previously regarded as hostile for rich coral communities (cf., Newton et al., 1987; Stanley and Cairns, 1988; Freiwald and Roberts, 2005).

It was noted early in these discoveries that some of the deep-water coral reefs appear to be spatially associated with the areas affected by submarine hydrocarbon seepage (Hovland, 1990), which led to formulating the concept of the 'hydraulic theory'. This model, based on an analogy with chemosynthesis-based ecosystems of hydrothermal vents and hydrocarbon seeps, assumed a direct dependence of cold-water corals on locally increased nutrient fluxes associated with methane emissions (Hovland, 1990; Henriet et al., 1998; Hovland et al., 1998). Nevertheless, while in several locations, situated mostly off Norway, increased concentrations of hydrocarbons have been indeed measured (Hovland et al., 1998), the following worldwide researches failed to find any indications of fluid seepage in the majority of the deep-water coral reefs (e.g., De Mol et al., 2002; Duineveld et al., 2004; Etiope et al., 2010). Likewise, the 'hydraulic theory' has been found difficult to reconcile with the scarcity of corals at typical examples of hydrocarbon seeps (Tunnicliffe et al., 2003; Levin, 2005), and, on the other hand, with the usual absence of specialised (symbiont-dependent) vent or seep biota in cold-water coral ecosystems (Cordes et al., 2008; Roberts et al., 2009).

Today, there seems to be a widely accepted consensus that the known species of deep-water corals do not depend directly on seeping fluids, and that their distribution is controlled primarily by factors such as availability of hardgrounds and local seafloor elevations, activity of internal waves and bottom currents, as well as the location of upwelling and downwelling zones, flushing the corals with nutrient- and/or oxygen-rich waters (Frederiksen et al., 1992; White et al., 2005; Roberts et al., 2009). Likewise, where found in the proximity of hydrocarbon seeps or hydrothermal vents, the modern deep-water corals appear to have been attracted primarily by the presence of hard, elevated seafloor, formed by authigenic carbonates, precipitating as a result of microbial oxidation of methane or abiotic hydrothermal processes. Sure enough, while it can be suspected that the increased biomass production at hydrocarbon seeps and hydrothermal vents is of some importance in stimulating the coral colonisation, the cold-water corals seem to inhabit more readily inactive seeps and vents, and, if present near active fluid expulsions, occupy preferentially the areas somewhat remote to the main fluid outlets (Fruh-Green

* Corresponding author. Tel.: +48 618296044; fax: +48 618296349.
E-mail addresses: mjakub@amu.edu.pl (M. Jakubowicz), bbrk@amu.edu.pl (B. Berkowski), zbelka@amu.edu.pl (Z. Belka).

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et al., 2003; Cordes et al., 2008; Le Guilloux et al., 2009; Liebetrau et al., 2010).

Although it is beyond doubt that many similarities exist between modern, mostly scleractinian corals and their Palaeozoic, rugose relatives, it is also commonly accepted that both groups cannot be treated as direct ecological counterparts (Hill, 1981; Fedorowski, 1997; Scrutton, 1998). Many studies have brought evidences of unusual environmental tolerance of some solitary deep-water rugose corals, often together termed as '*Cyathaxonia*' or 'Laccophyllid' fauna (Hill, 1938; Różkowska, 1969; Oliver, 1992), best emphasised by their common occurrence in dark, anoxic, pelagic sediments, not uncommonly devoid of any other macrobenthos (Kullmann, 1997; Scrutton, 1998). Hence, it might be speculated that some Palaeozoic corals could have been able to colonise the seepage-affected areas, or even to benefit directly from fluid emissions. Still, to date, no unequivocal evidence has been found for Palaeozoic corals inhabiting hydrocarbon seep-related environments, and only one example of rugose coral assemblages apparently related to hydrothermal venting has been reported (Berkowski, 2004; Belka and Berkowski, 2005). Here, we describe several rich, monospecific associations of deep-water '*Amplexus*' corals from the Devonian of the Hamar Laghdad area in southern Morocco (Fig. 1). The '*Amplexus*' (and *Amplexus*-like) corals are morphologically simple, non-dissepimented forms known from deep-water sediments, and often regarded as typical members of the '*Cyathaxonia*' fauna. In the present paper we present evidences that these corals developed at active hydrocarbon seeps or at hydrothermal vents. We discuss further the mechanisms that enabled colonisation of these stressful environments, with special attention paid to the unusual morphology of '*Amplexus*', as well as to the peculiar 'calice-in-calice' settlement and growth pattern (Berkowski, 2004; Belka and Berkowski, 2005; Berkowski, 2006), which origin remains, until now, not fully understood.

2. Geological setting

The study focuses on Devonian carbonate rocks exposed at Hamar Laghdad in the eastern Anti-Atlas, southern Morocco (Fig. 1). Structurally, the Anti-Atlas is a NE–SW trending anticlinorium which comprises a Precambrian crystalline basement overlain by a very thick sedimentary cover, Late Proterozoic to Late Carboniferous in age (see for review Michard et al., 2008). The sequence is strongly differentiated with respect to facies and thickness. Its depositional history reflects both the progressive disintegration of the northern, passive margin of Gondwana (Wendt, 1985) and climatic changes related to the northward drift of this palaeocontinent during the Palaeozoic. During the Devonian, the eastern Anti-Atlas was the site of mixed siliciclastic and carbonate depositions (Wendt, 1988). E–W trending strike-slip faults controlled the sedimentary development and episodically were the places of volcanic eruptions (Belka et al., 1997).

The Hamar Laghdad ridge (Figs. 1 and 2) constitutes one of three places in the eastern Anti-Atlas where submarine volcanic activity took place during the Early Devonian. This led to the formation of an elevation on the sea floor, composed of peperites and their tuffs, which display geochemical characteristics of typical intra-plate basalts. These volcanics interfinger with shales containing trilobite and tentaculite fauna, Lochkovian and early Pragian in age (Alberti, 1982). After the eruption the elevation became a site of extensive crinoid colonisation and carbonate production. As a result, up to 140 m of crinoidal packstones accumulated (Aitken et al., 2002). During late Emsian time, reactivation of magmatic processes caused doming of the volcanic complex and the overlying sedimentary strata, and in consequence, a network composed of radial and tangential faults originated (Belka, 1998). The faults served subsequently as conduits for hot fluids migrating to the sea floor (Cavalazzi et al., 2007). The most spectacular parts of the carbonate cover constitute large conical

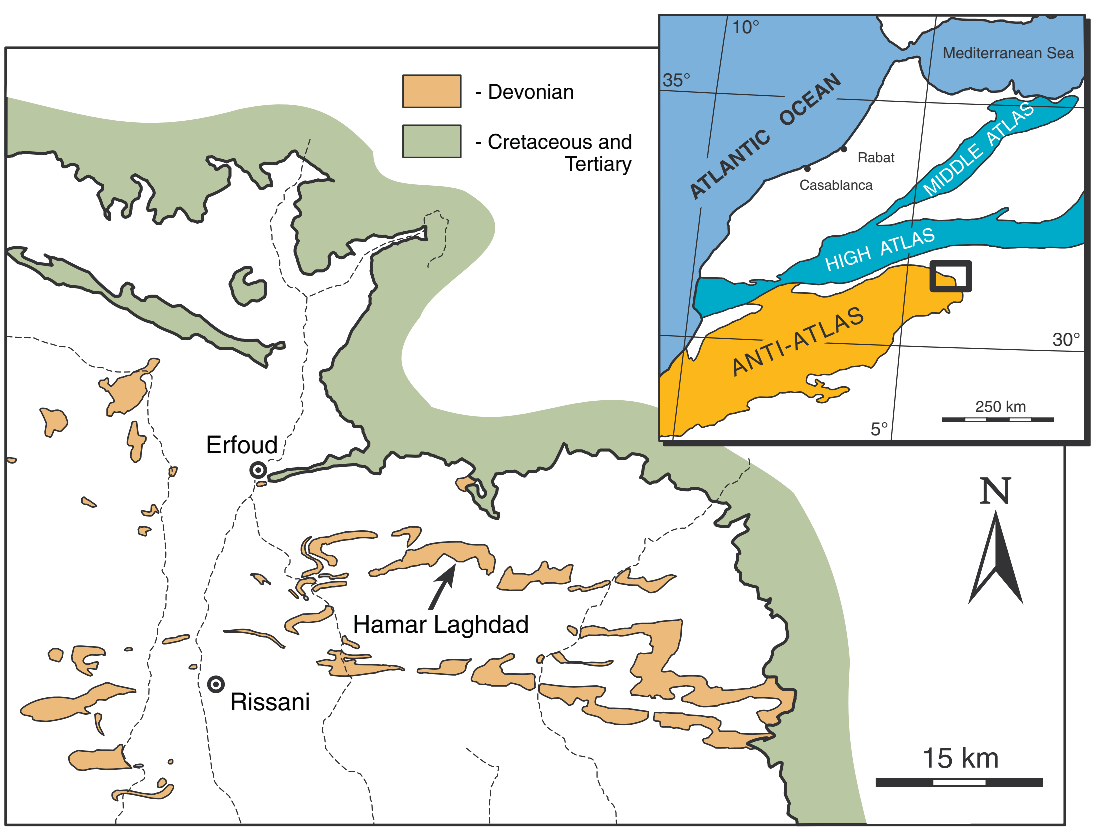

Fig. 1. Simplified geological map of the eastern Anti-Atlas. Devonian rocks and location of Hamar Laghdad are indicated (from Belka, 1998). Inset shows regional geology and location of the study area.