

# Discovery of thermophilic corals in an ancient hydrothermal vent community, Devonian, Morocco

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## ABSTRACT:

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Living corals are remarkably broad in their thermal and bathymetric ranges. But corals that could tolerate abnormally high temperatures (higher than 40°C) are unknown both in the living communities and in the fossil record. Here we report the discovery of small thermophilic rugose corals in the Devonian vent community of southeastern Morocco. These organisms were adapted to conditions prevailing within chimney conduits of a hydrothermal system that developed on the roof of a submarine volcanic high. The coral larvae followed a calice-in-calice settlement and growth strategy to survive the contact with thermal fluids. This adaptation was not related to taxonomy and characteristic of all coral taxa present in the vents. Monospecific coral population was identified in several Emsian vents whereas the coral fauna of the single Givetian vent was more diverse and included four species. The entry of different rugose coral species into the hot vents resulted from a trophic relation to ostracods flourishing in the chimneys.

**Key words:** Vent corals, Hydrothermal vents, Mud mounds, Devonian, Morocco.

## INTRODUCTION

Recent corals occur from the high tide line to depths of 6,200 m and can tolerate temperatures from - 1 to 40°C (e.g. WELLS 1967, FAGERSTROM 1987, VERON 1995). The environmental tolerance of individual coral species, however, is often distinctly limited and principally related to the presence, concentration, or absence of symbiotic zooxanthellae in the coral polyps. Scleractinians containing symbiotic zooxanthellae prefer temperatures between 23 and 28°C, and because of light dependence of symbionts they are confined to the photic zone. The optimum temperatures for non-zooxanthellate forms are significantly lower, mostly between 6 and 10°C. Low temperature stress is a common factor limiting the distribution of shallow-water corals, whereas heat stress is responsible for the breakdown of

coral/zooxanthellae symbiosis (bleaching) and may cause regional mass mortality (GLYNN 1990, GUZMAN & CORTES 1992, GLYNN 2000). All deep-water corals are non-zooxanthellate, widespread, and live at low temperatures (CAIRNS & STANLEY 1981). Some of them form spectacular reef-like structures and seem to be related to hydrocarbon seeps (HOVLAND & *al.* 1998, HOVLAND & RISK 2003). Deep-water scleractinian corals, however, have never been observed in the hydrothermal vent communities associated with mid-ocean ridges and/or back-arc spreading centers (e.g. TUNNICLIFFE 1992, GALKIN 1997, MCARTHUR & TUNNICLIFFE 1998). Until now, corals have neither been reported from biological communities at shallow-water gasohydrothermal vents (e.g. TARASOV & *al.* 1990, KAMENEV & *al.* 1993, DANDO & *al.* 1995) nor from fossil vent communities (LITTLE & *al.* 1998).

Septate corals belonging to the Rugosa lived during almost all of Paleozoic time. They differed markedly from the living scleractinians in skeletal architecture and mineralogy, and therefore it is still a matter of debate whether these coral groups are phylogenetically related or not (e.g. OLIVER 1996, FEDOROWSKI 1997, STANLEY 2003). Rugose corals were most likely non-zooxanthellate. They were common in a broad spectrum of marine Paleozoic environments (SCRUTTON 1999). In contrast to Cenozoic scleractinians, shallow-water rugosans played only a secondary role in the reef and mound construction (FAGERSTROM 1987), being only a subordinate component of buildups dominated by other organisms (e.g., stromatoporoids, sponges). Moreover, rugosans were generally rare in very shallow-water environments, a restriction that may have resulted from their non-zooxanthellate character. Rugosans that are found in sediments deposited in deep-water environments are characterized by mostly small non-dissepimented or poorly dissepimented solitary and horn-shaped forms. There is no evidence for colonial rugosans settling in deeper environments, although tabulates, a group of strictly colonial Paleozoic corals, are known from deep-water sediments.

Mud mounds are the most common type of Paleozoic carbonate buildups (SCHLAGER 2003, KRAUSE & *al.* 2004). Most of them developed in deep-water settings of shelf areas. They display a variety of structures and commonly

a complex origin (for examples, see BOURQUE & BOULVAIN 1993, WENDT & *al.* 1993, MONTY & *al.* 1995, WENDT & *al.* 1997, KAUFMANN 1998, BELKA 1998). Their origin is also enigmatic because the origin of the rare modern counterparts is still a point of debate (HOVLAND & *al.* 1994, HENRIET & *al.* 2001, DE MOL & *al.* 2002). Many mud mounds appear to have a microbial character and several recent studies provided evidence for mound formation in response to episodic hydrocarbon seepage or hydrothermal venting (e.g. BEAUCHAMP & SAVARD 1992, GAILLARD & *al.* 1992, KAUFFMANN & *al.* 1996, HOVLAND & MORTENSEN 1999).

An unusual submarine hydrothermal system has been recognized in the Devonian of the eastern Anti-Atlas, Morocco (BELKA 1998, MOUNJI & *al.* 1998). It developed on the passive continental margin of Gondwana, and hence is not a counterpart to hydrothermal vents widespread in the modern deep sea. More than 40 spectacular mud mounds were formed in places where hydrothermal fluids from an underlying intrusive laccolithic body reached the sea floor. The mud mounds are exposed about 16 km southeast of Erfoud (Text-fig. 1) where they are concentrated in a relatively small area on the Hamar Laghdad elevation. The peculiarity of the Hamar Laghdad vent system is that episodically hot fluids contained thermogenic methane. Thus, the Hamar Laghdad vents represent an example of an ancient gasohydrothermal system that exhibits links both to recent shallow-water and deep-sea vents. The present paper reports the discovery of thermophilic corals in the Hamar Laghdad vent community.

## GEOLOGICAL BACKGROUND

During much of the Paleozoic, the eastern Anti-Atlas constituted a fragment of a broad shelf area expanding over the northern continental margin of the West African Craton. Its depositional and tectonic evolution were controlled by regional, east-west trending strike-slip faults (BELKA & *al.* 1997). They acted as overstepping fault systems and thus influenced the subsidence pattern and occasionally were sites of volcanic activity. During the Early Devonian, a submarine volcanic eruption created an elevation on the sea floor (exhumed as a topographic ramp – Hamar Laghdad in the present-day landscape), which subsequently became a site of extensive crinoid and brachiopod colonization. As a result, up to 140-m-thick crinoidal packstones accumulated on the peperites and volcanoclastic deposits (AITKEN & *al.* 2002). During the late Emsian, reactivation of magmatic processes caused doming of the laccolithic complex and the overlying sedimentary strata. In consequence, a network composed of

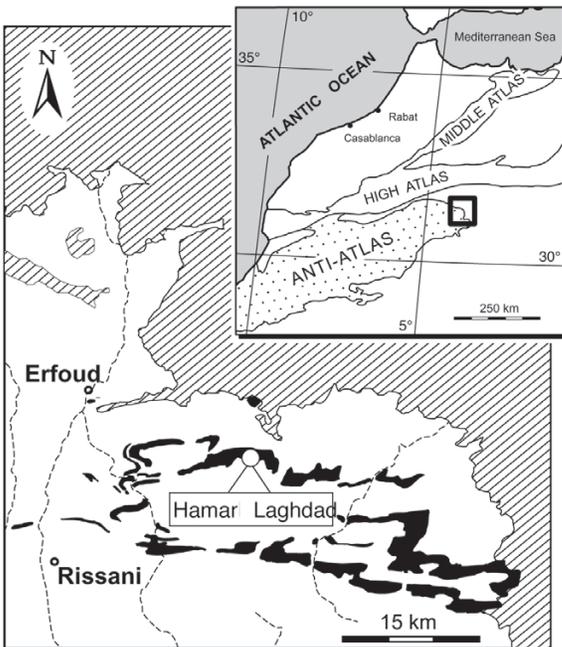


Fig. 1. Simplified geologic map of the northeastern Anti-Atlas showing distribution of Devonian rocks and location of the Hamar Laghdad hydrothermal vents; hatched area is the Cretaceous-Tertiary cover of the Hamada. Inset shows regional geology and location of the study area

radial and tangential faults originated (BELKA 1998). Subsequently, these faults served as conduits for migration of hydrothermal fluids to the sea floor and conical mud mounds, up to 55 m high, started to grow at vent sites (Text-fig. 2). Hot fluids migrated through the buildups via a complex system of chimneys and fissures. Geochemical data suggest that mud mound carbonates precipitated from brines comprising a mixture of hydrothermal fluids and seawater (BELKA 1998, MOUNJI & *al.* 1998). Fluid inclusion measurements indicate low temperatures (with most between 75 and 135°C) of hydrothermal fluids (Ph. Eisenmann, personal commun., 2003). Metalliferous and sulphide phases are absent but vent carbonates exhibit locally high Ba (up to 3950 ppm), Zn (up to 260 ppm), and Cu (up to 420 ppm) content. Vents were episodically active during a time of approximately 30 Ma (from the late Pragian until the early Frasnian). Large mud mounds, however, developed only during the Emsian. During the Eifelian phase of hydrothermal activity hot fluids locally contained thermogenic methane derived presumably from the underlying basaltic intrusives. Hydrocarbons contributed to a rapid insitu cementation of the carbonate mud and led to development of a community dominated by bivalves (PECKMANN & *al.* 1999, AITKEN & *al.* 2002). By itself, the rich mound biota does not provide any precise indication for the water depth, but lack of calcareous algae, microborings, and micritic envelopes suggests that the Hamar Laghdad mud mounds grew within an aphotic environment (BELKA 1998).



Fig. 2. Early Devonian Kess-Kess mud mounds exposed at Hamar Laghdad, eastern Anti-Atlas, Morocco. The mounds developed at sites of submarine hydrothermal venting. Each mound has several chimney conduits inhabited by vent rugose corals. Mound in foreground is about 40 m high

## VENT COMMUNITY

The carbonates of the Hamar Laghdad mounds are very fossiliferous (ALBERTI 1982, BRACHERT & *al.* 1992, BELKA 1998, AITKEN & *al.* 2002). It appears from new investigations, however, that some spectacular fossil assemblages, such as trilobite lumachelles and rich cephalopod limestones, constitute an infilling of neptunian dikes that originated during the time when hydrothermal vents were not active (BELKA & *al.* 2003). The most frequent biotic elements in the mound facies are small tabulates (predominantly auloporoids) which are associated with subordinate crinoids, dacroconarids, rugose corals, brachiopods, and trilobites. The vent fauna is restricted to chimneys and zones surrounding the vent outlets (Text-fig. 3). It includes rugose corals (Text-fig. 4), bizarre trilobites of the genus *Andegavia*, gastropods, sponges, monoplacophorans, and locally, extremely numerous ostracods (Text-fig. 5E). Most of the taxa are new to science and are characteristically small-sized. Only ostracods are represented by relatively large forms (usually up to 5 mm long). The hydrothermal vent fauna changed taxonomically with time. Moreover, it differs significantly in its composition from the fossil community that developed at gas venting sites in the eastern part of the Hamar Laghdad area during the Eifelian.



Fig. 3. Outlet of vent chimney conduit exposed at the top of the Emsian mound. Zone A is a later sediment infilling inside the hollow conduit partly lined by thick hydrothermal calcite cements (arrow); Zone B represents the wall of the chimney and is dominated by densely packed, vent rugose corals (the contact of this coral-rich rim with hydrothermal cements is enlarged in Fig. 4); Zone C, the outermost zone, is dominated by tabulate corals

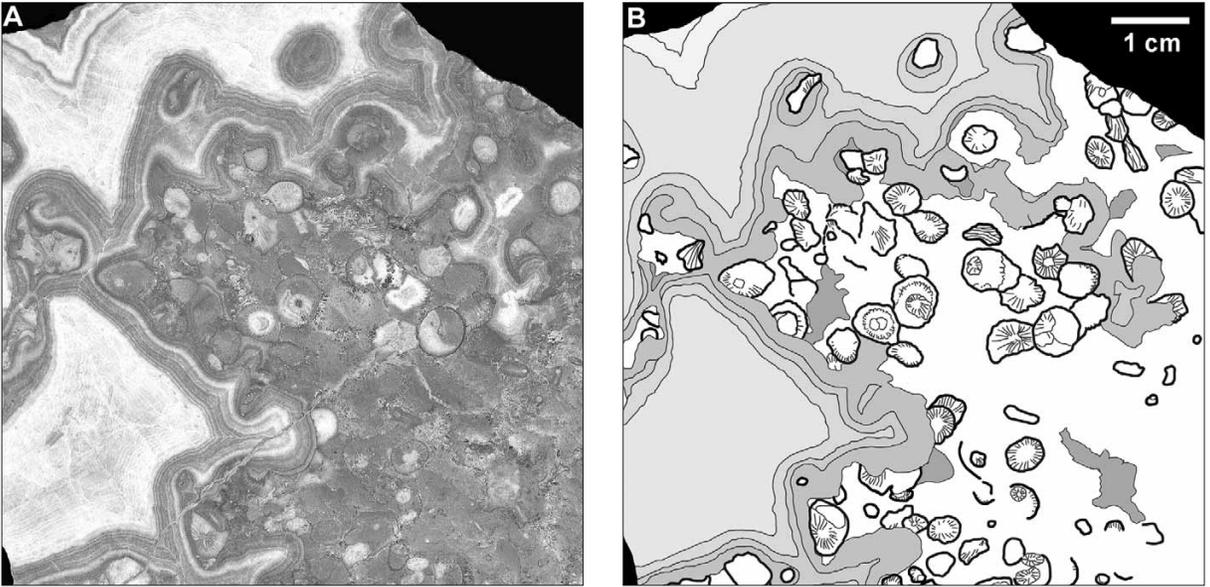


Fig. 4. Horizontally-oriented polished slab (A) and schematic drawing (B) of the inner part of coral-rich rim (Zone B in Fig. 3). Note the densely packed skeletons of *Hamarophyllum belkai* at the contact of carbonate deposit (in white) with hydrothermal calcite cements (in gray shading); coral skeletons are shown schematically (see BERKOWSKI 2004) for detailed description of skeletons and their ontogeny); a large number of coral skeletons (external walls in bold lines) is strongly corroded

## THERMOPHILIC CORALS

The rugose corals, reported here, are associated with hydrothermal vents and do not occur at sites with hydrocarbon seepage. They form dense populations at the edges of fissures (Text-fig. 4) or occur concentrated at the mouths of chimneys, which are usually exposed on the top of mounds. The coral-rich rims are distinct and generally not more than 20-30 cm wide (Text-fig. 3). It is important to note that outside of these rims, rugose corals are very rare in the Hamar Laghdad mud mounds, and if they occur, they represent taxa other than those at the vents.

The vent coral populations consist of small non-dissepimented forms. These rugosans do not differ in their anatomy and skeleton structure from small non-dissepimented corals known from Paleozoic deep-water environments. In several Emsian vents, the population is monospecific and represented by *Hamarophyllum belkai* BERKOWSKI, 2004, a new genus and species of the sub-family Laccophyllinae GRABAU, 1928 (Text-fig. 5C-D). The coral fauna of the single Givetian vent, however, is more diverse and includes four new species: one belonging to the genus *Laccophyllum* SIMPSON, 1900, one belonging probably to the genus *Amplexus* SOWERBY, 1814 (Text-fig. 5A-B), one new genus and species of the family Protozaphrentidae IVANOVSKIY, 1959, and one new species representing a new genus of a new family.

The most distinctive feature of both the Emsian and Givetian coral populations is an identical settlement and growth process. We term it the calice-in-calice strategy. Its name indicates the striking fact that most individuals grew within empty calices of dead skeletons (Text-fig. 5A-D). In the vents investigated in detail, we observed densely packed corallites (10-30 specimens in 100 cm<sup>2</sup>) in life position, with almost all empty calices colonized by larvae (Text-fig. 5D). In some cases, up to five larvae settled in the same calice at the same time (Text-fig. 5B), but finally, only a single individual, or two individuals, won the space competition and survived the juvenile stage (BERKOWSKI 2004). But even these individuals only rarely achieved late adult stages, and consequently their corallites are small. As a result of these processes several generations of individual corals built a kind of frame as the colonial corals do (Text-fig. 5C). This phenomenon, however, represents “false budding” and not a true coloniality or rejuvenescence. It is commonly accepted that after fertilization in the water, larvae of rugose corals (similarly to recent corals) were free-swimming plankton. Most probably only some of them could find places suitable and safe for settlement. The vent habitat does pose problems for colonization because of temperature gradients and also temporal and physical instability of the habitat. It seems that empty calices of dead corals offered places in the vent where larvae could be protected from environmental (venting fluids) and/or

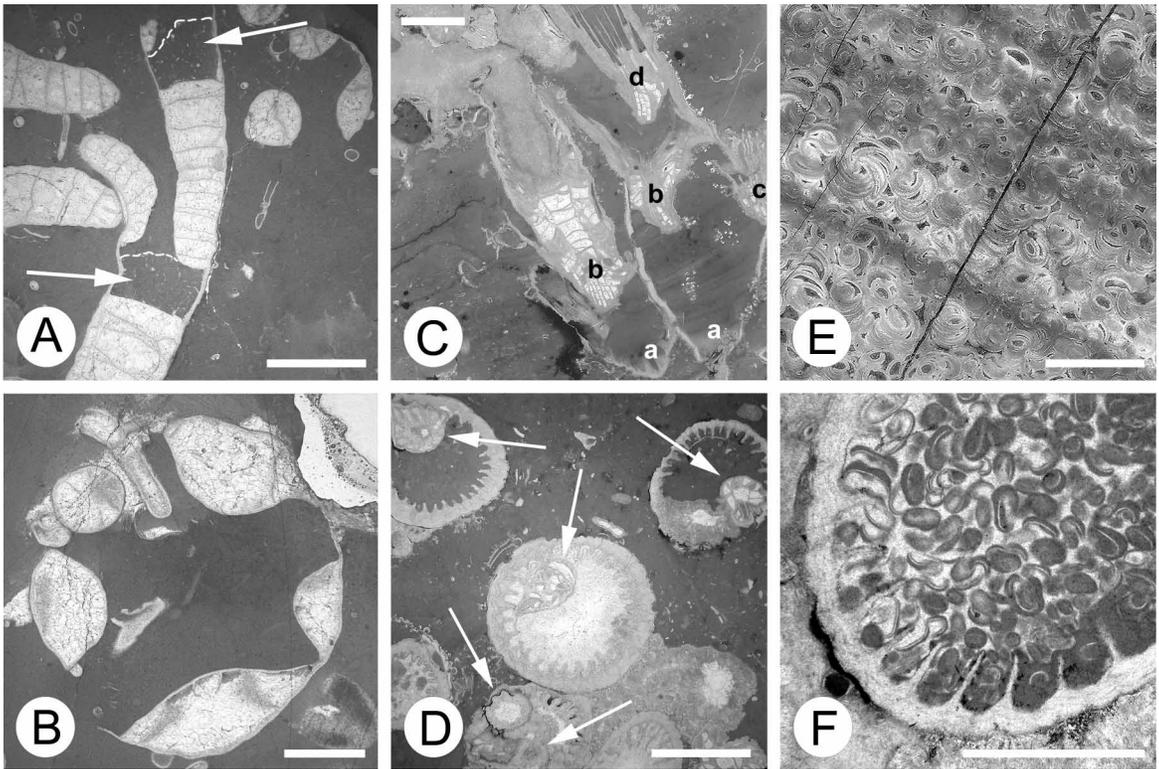


Fig. 5. Thin-section photographs of vent corals and ostracods from the Kess Kess mud mounds. A – “Calice-in-calice” growth of Givetian rugose corals (*Amplexus?* sp.) resulting from settlement of larvae in dead corallites. Note that small sponges (outlined and arrows) frequently grew on the bottom of calices prior to coral larvae colonization; longitudinal section. Scale bar 5 mm. B – Five Givetian juvenile corals (*Amplexus?* sp.) growing on the internal wall of a dead corallite; transverse section. Scale bar 2 mm. C – “Calice-in-calice” growth of the Emsian coral *Hamarophyllum belkai*; the succeeding individuals are indicated – a, b, c, d; longitudinal section. Scale bar 5 mm. D – Juvenile individuals of *Hamarophyllum belkai* (arrows) growing in dead coral skeletons at the margin of chimney conduit; transverse cross section. Scale bar 5 mm. E – Eifelian ostracod lumachelle in the sedimentary infill of chimney conduit. Scale bar 10 mm. F – Calice of Emsian rugose coral filled up with ostracod carapaces; transverse section. Scale bar 4 mm

biological stress (predators). Because the discovered vent taxa are not present outside of the vent sites, it is likely that temperature gradients and/or chemical indicators were used by swimming larvae as a cue when they started to settle down. Detailed statistical evaluation of corals in two selected Emsian and Givetian vents with more than 100 individuals each provided evidence for an advantage of the applied settlement strategy. The number of individuals that grew in the empty calices was 78 percent of fauna in the Emsian vent (BERKOWSKI 2004) and 63 percent in the Givetian one; those growing on the external walls of corallites were 15 percent and 21 percent, respectively. Only 2 percent of individuals started to grow directly on the sediment surface and 5 percent on non-coral skeletal material in the Emsian vent. Within the Givetian vent, which developed along an open fissure on the sea floor, these numbers are 13 percent and 3 percent, respectively.

Because various species of different genera attained a distinctive adaptation at Hamar Laghdad, we believe that

the thermophilic rugose corals were derived from widespread, deep-water relatives and not from long-term in situ evolution. Moreover, the fact that rugose corals could adapt to physical conditions unfavorable for the majority of organisms, points to a strong linkage to nutrient sources. This appears to be evident from features preserved in the corallites. Some of them are completely filled by a dense mass of ostracod carapaces (Text-fig. 5F), although these microfossils are not frequent in sediment between corallites. Ostracod carapaces, however, are extremely frequent in sediments filling the deeper parts of chimneys (Text-fig. 5E). There is no doubt that swarming ostracods flourished in the venting fluids and must have constituted basic food for the corals located at the mouth of chimneys. Corals, however, could not digest ostracod carapaces that together with other mineral and plant material must have episodically escaped from the stomach cavity. This can explain why only a very few corallites are filled up with ostracods. These died... *on a full stomach*.

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