

Monospecific rugosan assemblage from the Emsian hydrothermal vents of Morocco

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Unique monospecific assemblages of small, solitary, nondisseminated rugose corals from the Devonian deep-sea hydrothermal venting systems of the Hamar Laghdad (Anti-Atlas, Morocco) are described. Assemblages of numerous rugosans (coral meadows) have been found around the outlets of venting channels irregularly forked within the Emsian mud mound sediments. The majority of rugose corals, which settled around vents, reveal a bizarre pattern of growth called here “calice-in-calice”. The phenomenon of “calice-in-calice” growth is related to selective survival of coral larvae i.e. it is postulated that the larvae, which settled within the calices of dead individuals were more successful in their development than those that settled elsewhere. They probably use empty calices as shelters against the physical (hot or poisoning fluids) or biological (predators) factors. The empty calices also provided a hard surface for attachment. The presence of numerous carapaces of ostracods within the calices of dead rugosans suggests a strong trophic relation between corals and ostracods, which lived around hydrothermal vents. The new genus and species *Hamarophyllum belkai* is proposed.

Key words: Rugosa, hydrothermal venting systems, mud mounds, Emsian, Hamar Laghdad, Anti-Atlas, Morocco.

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Introduction

Hot springs are known as a typical phenomenon commonly related to the latest stages of volcanic activity. During the past decades numerous venting fields were discovered in recent deep marine environments and became a subject of extensive study for marine scientists. These studies demonstrate that life can exist around venting chimneys hundreds and thousands meters below water surface basing on chemosynthesis instead of photosynthesis. The occurrence of these chemosynthetic biocenoses composed of bacteria and unusual invertebrates is restricted to deep-water hydrothermal vents or cold seeps, which are present within active zones of oceanic crust.

In contrast to present-day observations the fossil record of such “vent” communities is very sparse especially in the Paleozoic (Little et al. 1998; Little 2002). This is not surprising given poor preservability of the ancient oceanic crust, especially in the older fossil record.

Hamar Laghdad mud mounds in the eastern Anti-Atlas represent one among few areas described to date, where such communities occur in the Paleozoic rocks. However, they flourished around hydrothermal vents formed within continental crust and hence they are not directly comparable to recent deep-water venting systems.

Also, the Hamar Laghdad mud mound fauna does not resemble recent deep-water, hot vent communities apart from

chemosynthetic clams described from the Givetian “Hollard Mound” (Peckmann et al. 1999). The abundance of different taxa of colonial tabulates and one species of solitary rugosan i.e. corals possessing the stony skeletons well-developed is one of the characters distinguishing the Hamar Laghdad vent assemblage. Scleractinian corals (mostly caryophylliids) are known from recent cold seeps, but they never constitute the main component of the chemosynthetic communities.

This study documents a monospecific assemblage of small solitary rugosans from the Devonian hot vent systems of the eastern Anti-Atlas. Corals living in those unusual environments resemble other Rugosa in morphology, but their larvae displayed a unique pattern of settlement called here “calice-in-calice” growth with important implications for identifying vent coral communities in the fossil record.

Geology and biota

The area of Hamar Laghdad is located on the eastern flank of the Anti-Atlas about 20 km southeast of Erfoud (Fig. 1A). The Devonian strata in this area dip to the south, forming an elevated ramp, where more than fifty conical buildups of various sizes, not exceeding 55m in height are well exhumed (Fig. 1B). These buildups were reported for the first time by Menchikoff (in Roch 1934) who regarded them as coral

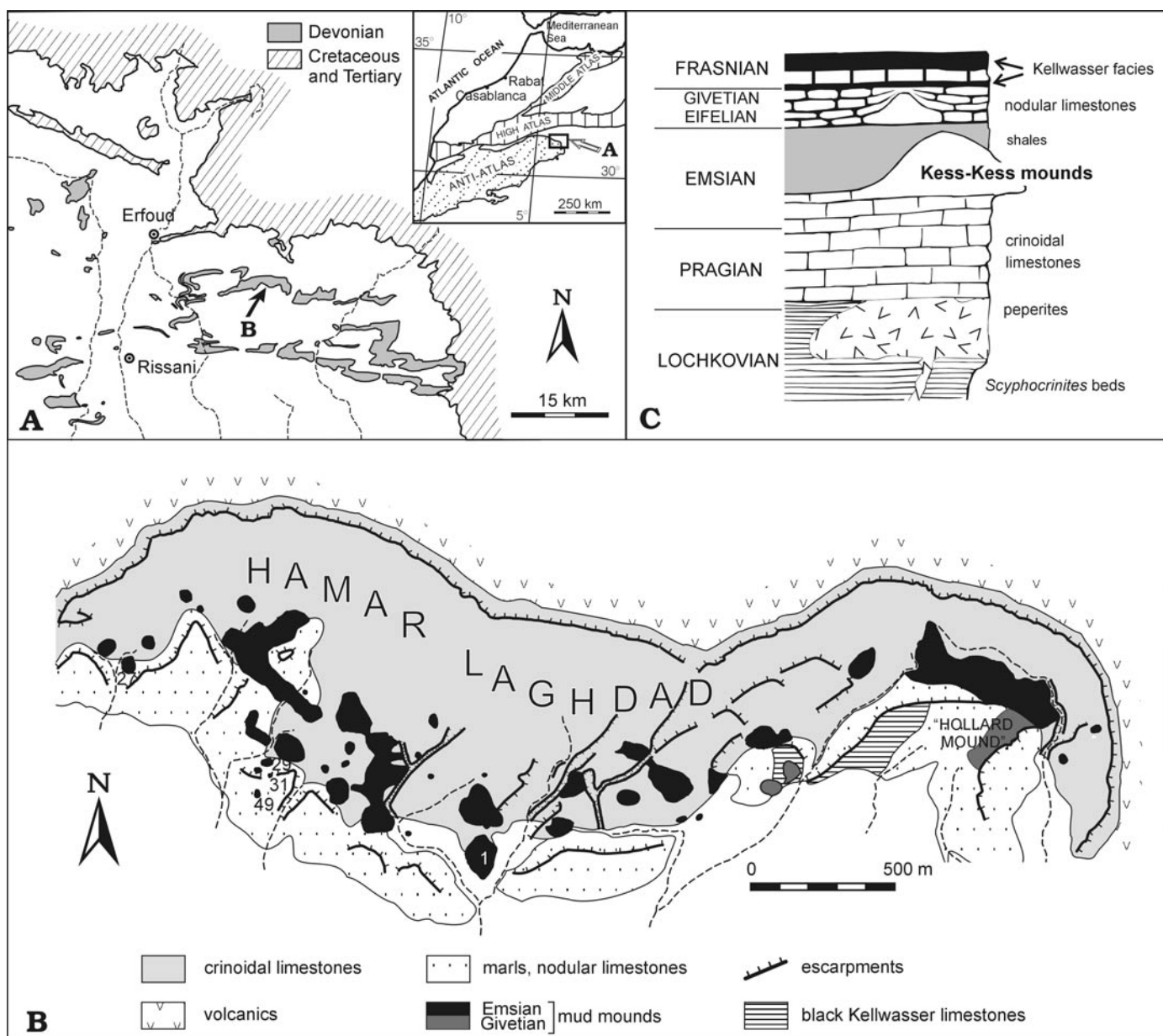


Fig. 1. A. Simplified geologic map of the northeastern Anti-Atlas. Devonian rocks and location of Hamar Laghdad are indicated. B. Detailed geological map of Hamar Laghdad with distribution of particular types of Devonian rocks. Numbered mud mounds are those from which studied corals were collected. C. Schematic stratigraphic log of the Hamar Laghdad. All drawings courtesy of Belka (1998); figure B updated.

reefs, but the first geological description was provided by Massa et al. (1965). Gendrot (1973) identified these structures as mud mounds that were afterwards a subject of many extensive sedimentological and paleontological studies (for review see Brachert et al. 1992; Belka 1994, 1998; Mounji et al. 1998; and Peckmann et al. 1999). The origin of Hamar Laghdad mounds is nowadays interpreted as related to submarine hydrothermal vents (Belka 1994, 1998; Mounji et al. 1998). This contrasts with the most of the other mounds described from the Devonian of North Africa (Wendt 1993; Wendt et al. 1993; and Kaufman 1998), which have rather microbial character.

Hamar Laghdad mounds were formed in the area of submarine volcanic activity at the beginning of the Devonian (Belka 1998). Basaltic lavas covering the sea bottom of the Hamar Laghdad area were covered by thick units of calcareous and marly sediments. The deposition of these sediments was influenced by volcanic activity that was still active on the radially oriented faults as a system of hydrothermal vents (Belka 1998).

The majority of the mud mounds of Hamar Laghdad belong to the so-called Kess-Kess Formation (Brachert et al. 1992) of Emsian (Zlichovian) age. They have been formed on the upper part of a thick-bedded crinoidal limestone, a unit of

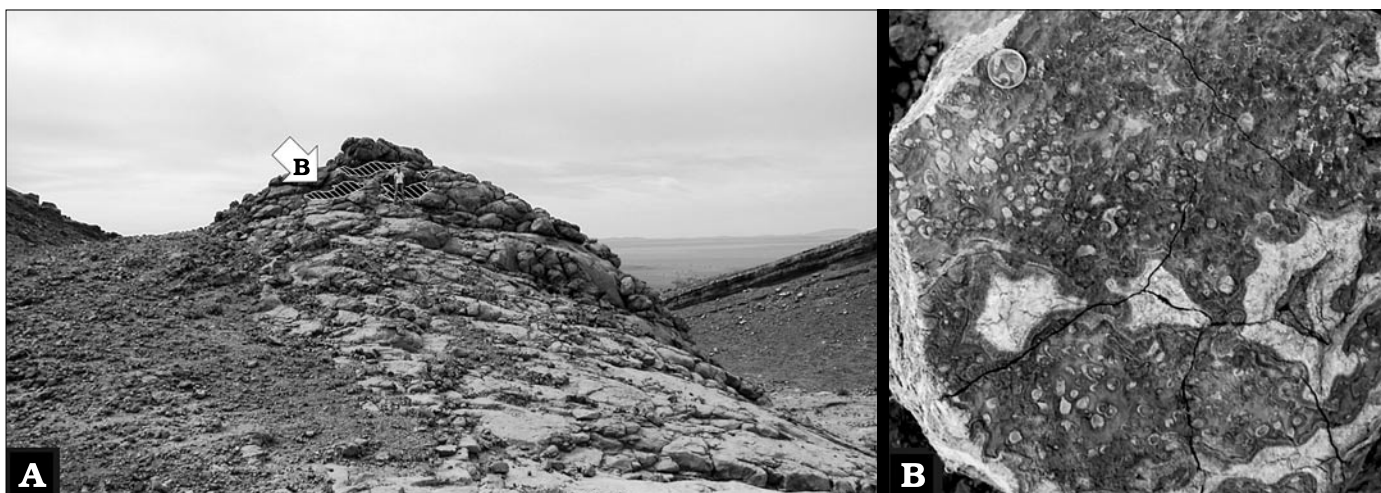


Fig. 2. **A.** Mound 27, western part of Hamar Laghdad. Black shaded patches indicate the outlets of venting chimneys. Note human figure for scale. **B.** Boulder with rugose coral meadows of *Hamarophyllum belkai* gen. et sp. nov. derived from the close vicinity of the vent outlet. Coin for scale.

Pragian age, that is up to 180 m thick (Fig. 1C). The crinoidal limestone directly covers a laccolithic body of volcanic rocks composed of basalts and peperites (Alberti 1982; Belka 1998), which are laterally replaced by Lochkovian *Scyphocrinites* beds (Fig. 1C).

The Kess-Kess Formation is covered first by nodular limestone and then by shale intercalated with marly limestone of Emsian (Dalejan) age. The thickness of the nodular limestone and shale unit is variable and depends on the distance from the mud mounds. The maximum thickness of about 50–60 m is noted between the mounds; the minimums 5–10 m just near the top of the mound. Outside the Hamar Laghdad mud-mound area this unit is thicker (about 180 m). Shale beds are gradually replaced upward by Eifelian and Givetian limestone. All these deposits are covered by black “kellwasser” limestone of the Frasnian to Famennian age. In the eastern part of Hamar Laghdad several mounds including structure called “Hollard mound”, of the next generation occur within the Eifelian, Givetian and Frasnian deposits. They were probably formed during the latest stages of the volcanic activity. The lithology and biotic structure of these mounds are very similar to the Emsian mud mounds, but the taxonomic content is different. The detailed description of these structures will be presented elsewhere.

Emsian mud mounds

The uppermost unit of the Kess-Kess Formation consists of thick-bedded crinoidal limestone (intermound facies) and mud mounds. The transition between mound and intermound facies is gradual, being best distinguishable in the intermitence between the slopes of mounds and the flat surface of the ancient seafloor. One may observe gradual increase of the thickness of crinoidal limestone beds and concurrent decrease of mud content and tabulate coral detritus within the

beds in favor of the crinoidal detritus. Mud mound facies are composed mostly of skeletal wackestone and mudstone riddled by stromatactis cavities and packstone intercalations. Intermound facies are represented by crinoidal packstones with higher proportion of nektonic elements (mostly nautiloids, see Brachert et al. 1992).

Detailed description of mounds and intermound facies as well as their biotic components were given by Brachert et al. (1992) who documented microfacial changes and biota both within the mound surface and intermound facies as well as the mound-intermound transition. All mounds possess within their bodies numerous cavities and neptunian dykes related to hydrothermal vent activity (Belka 1998) being interpreted here as venting fields.

Venting fields in the Emsian mounds

The outlets of venting systems are filled with sediment younger than the mound’s host rock. The cavities and fissures located mostly in the topmost parts of the mounds are in fact outlets of hydrothermal channels irregularly forked within the main body of the mound (Fig. 2A). The outlets are irregular in shape making fissures or lens-like structures. The sediment deposited around vents, consisting mostly of wackestones, does not differ markedly from the sediment of the mud mound body, apart from the increase of stromatactis cavities and different kinds of large banded calcite cements. Contrasting to this, the biotic components change successively from the outlet. The following zonation in the coral distribution was herein established:

(1) The sediment closely surrounding outlet of the vent (zone of 30–60 cm wide) contains assemblages consisting of numerous solitary nondissepimented Rugosa belonging to one species *Hamarophyllum belkai* sp. nov. (see Systematic description and Fig. 2B) and rare Tabulata such as auloporid

colonies of *Bainbridgia* and sporadic small colonies of *Favosites*.

(2) About 1m apart from the vent outlets small rugosans disappear and the large bush-like colonies of auloporids (*Bainbridgia*) predominate. Among them small patches of favositid or thamnoporid colonies are embedded.

(3) Approximately 2–3 m apart from the outlet, auloporids with small corallites (*Bainbridgia*) are replaced by auloporids with larger corallites (mostly *Schlueterichonus* and *Aulocystis*).

This zonation disappears when the distance from a vent is larger than 4–5 m and the distribution of biotic components becomes irregular as stated in Brachert et al. (1992). The absence of crinoids very common on the mound flanks and the intermound facies and presence of nest accumulations of ostracods are other striking characters of the biota surrounding venting outlets.

Deposits that filled the cavities of vents differ in age and content. The lowermost part of the infilling consists almost solely of trilobite (scutellids) exuviae (Alberti 1981) and/or polychaete tubes (Belka et al. 2003). Trilobite accumulations are up to 30 cm thick and spread laterally 0.5–2 m. That part of the infillings is covered by muddy laminated sediment containing large number of orthoconic nautiloids in some places replaced by numerous accumulations of small brachiopods.

Solitary rugosa of venting fields in the Emsian Hamar Laghdad mud mounds

Rugose corals occurring in the area of Hamar Laghdad are variously distributed. They occur both in the Emsian and Givetian mounds and within the covering marly deposits. They are extremely rare or even absent within the mound and intermound facies deposited away from the venting cavities but they are very numerous around the outlets of venting systems now exhumed as sediment-filled neptunian dykes. Hence, the area of their occurrence within the mound facies is restricted to nest associations around the vents.

Numerous monospecific rugosan assemblages consisting of *Hamarophyllum belkai* gen et sp. nov. have been discovered in mounds nr 1, 27, 29, 31, and 49 in the middle and western part of the Hamar Laghdad ramp (Fig. 1B). The occurrence of all these populations is restricted to the upper parts of the mounds. They form a structure resembling “coral meadows” growing around cavities within the host rock of the mound (Figs. 2B and 3A). All the coral skeletons are arranged in life position; only sometimes they are slightly bent or knocked over from the position of natural growth. Their calices are mostly oriented toward the cavities or fissures, now filled with younger sediment or ce-

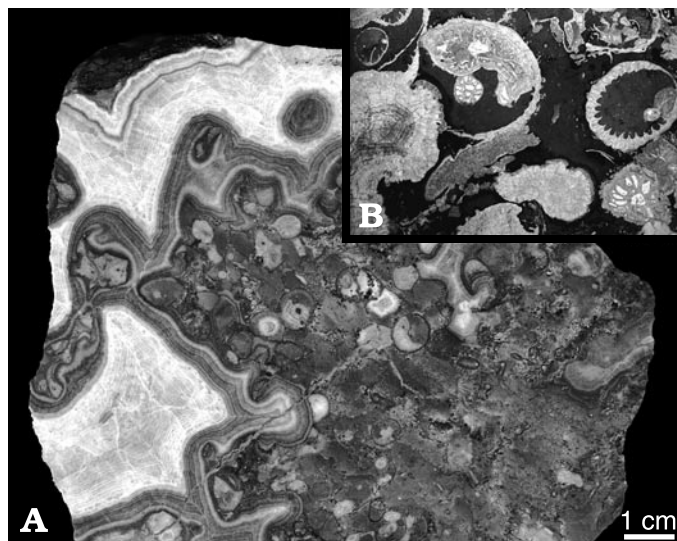


Fig. 3. A. Polished sample from venting field on mound 1 showing densely packed specimens of *Hamarophyllum belkai* gen et sp. nov.; on top-left part of the figure large banded cements are visible. B. Thin section of the sample A with numerous transverse sections of solitary rugosans showing calice-in-calice growth.

ments. Skeletons are densely but irregularly packed (10–40 specimens/10 cm²). The closest distances between corallites vary from several centimeters down to zero, when external walls of two or three skeletons are in direct contact (Fig. 3A, B).

Calice-in-calice growth

The striking feature of *Hamarophyllum belkai* gen. et sp. nov. assemblage, clearly visible on polished surfaces and in thin sections is the occurrence of young individuals in the empty calices of mature, dead specimens. Among all observed proximal parts of the studied specimens 78% grow within such calices (Fig. 4). More than one individual is commonly observed, growing within an empty calice of mature corallite (Fig. 3B). Such a situation was often repeated when the guest specimen died, making an impression of subsequent rejuvenations. Rejuvenation is a typical

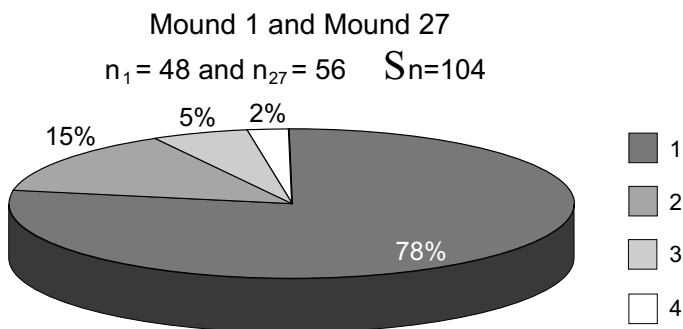


Fig. 4. Percentage of individuals of *Hamarophyllum belkai* gen. et sp. nov. growing: (1) in the calice of dead individuals, (2) on the external wall, (3) on other organic hard parts, (4) directly on the sediment.

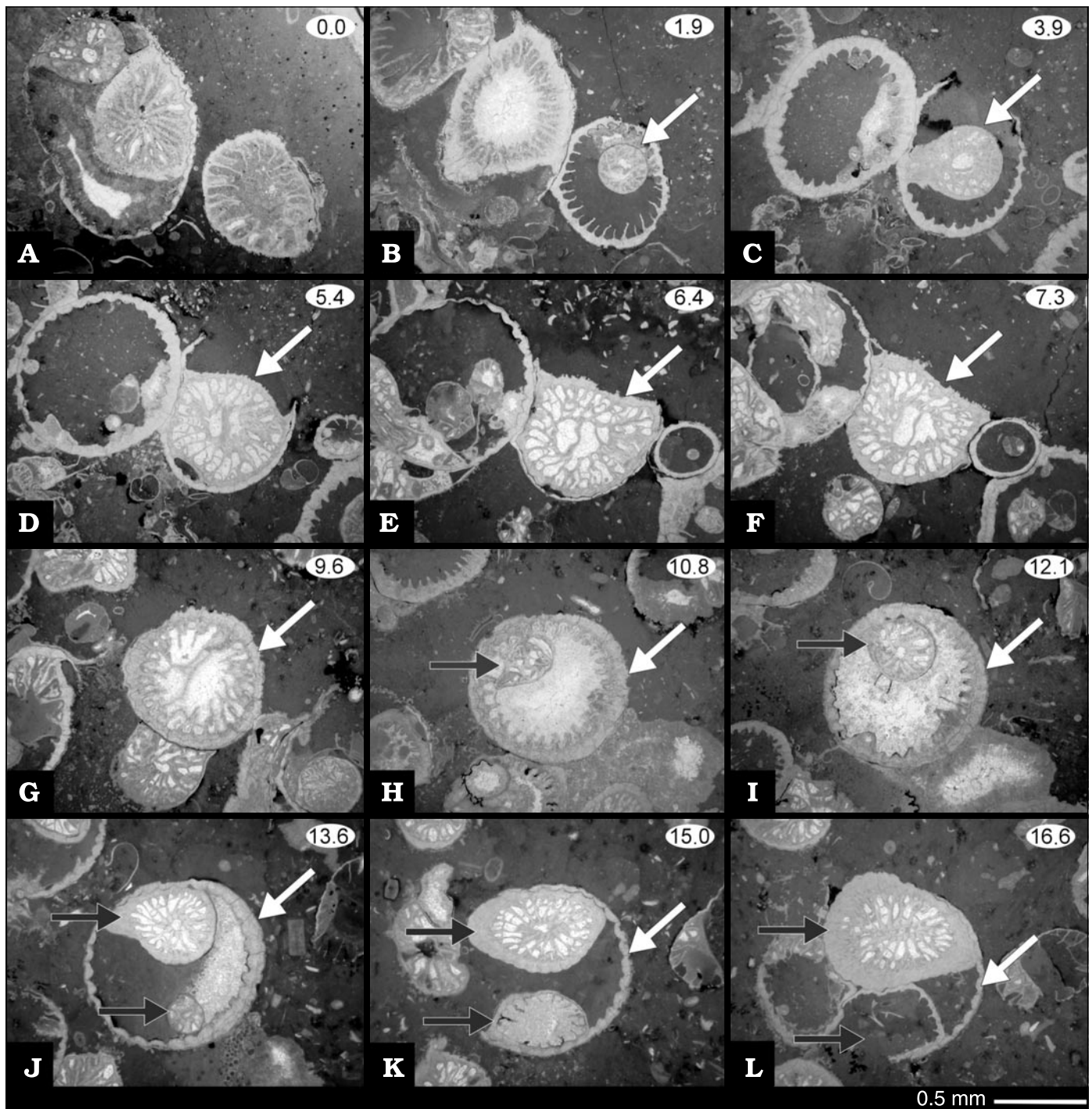


Fig. 5. *Hamarophyllum belkai* gen. et sp. nov. A–L. Serial transverse thin sections of successive stages of “calice in calice” growth. White arrows indicate the development of one specimen (paratype UAM Tc/B HD27/4/1) in the calice of dead individual. Black arrows show double “calice in calice” growth within the empty calice of the specimen previously developed (white arrow). Numbers in white ellipses show the distances (in mm) of successive thin sections from A.

character for deep-water solitary rugosans that became temporarily and partly buried within the sediment in soft, muddy bottom environments. An occurrence of several young specimens in the empty calice made an impression of offsetting i.e. the colony formation. Both these impressions are inconsistent with patterns revealed by serial transverse

thin sections (Fig. 5). Tracing successive stages of ontogeny one may easily show that all young specimens grew on the calical floor or are attached to naked septa or to the internal side of wall of the empty calice (Fig. 5). These observations have been supported by the longitudinal sections where several steps of settlement are visible (Fig. 6). These

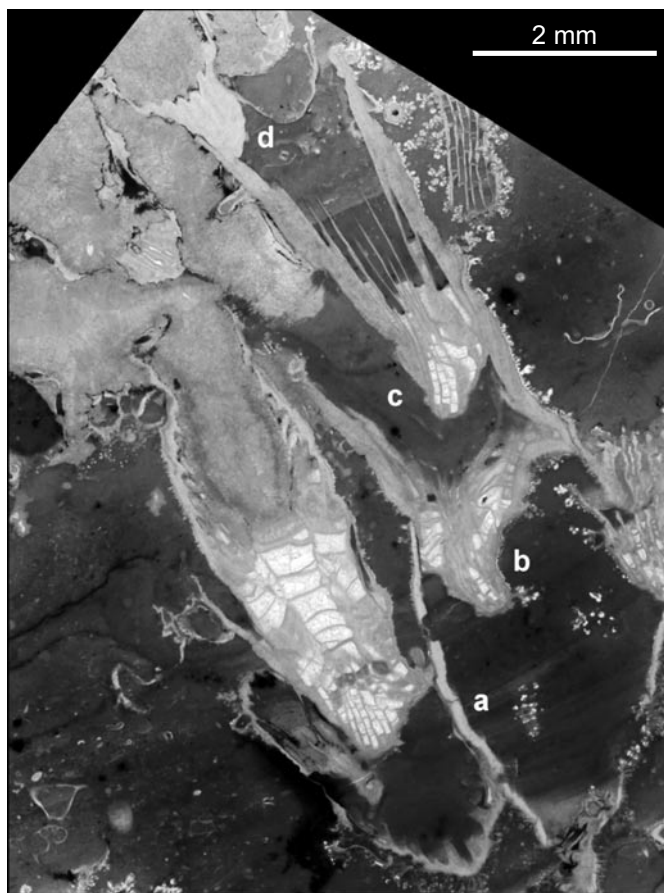


Fig. 6. Longitudinal section of *Hamarophyllum belkai* gen. et sp. nov. corals illustrating "calice-in-calice" growth. a–d indicate successive generations of corals.

observations show clearly that the phenomenon of "calice-in-calice" growth had nothing to do with true coloniality or rejuvenescence.

Among the newly settled specimens only one (Fig. 5K) or two could win the space competition within a calice and could then reach the adult growth stage. The majority of specimens died prior to achieving the mature stage (Fig. 5K).

The "calice-in-calice" growth is very rare among solitary corals in the fossil record, and never occurs at a large scale. The recent solitary scleractinian *Desmophyllum* found at the depth of 636 m in the Pacific Ocean near the coast of Chile (Jarosław Stolarski personal communication) reveal a similar pattern.

Sediment-coral interplay

The sediment infilling the space between corallites is fine-grained and delicately laminated. It contains several, mostly not broken, organic remnants i.e. small tabulate skeletons (auloporids and favositids), articulated ostracod carapaces, small gastropods, and rarely sponges, tentaculids or articulated segments of trilobites. The isotope and Rare Earth Elements composition of large fibrous cements surrounding the "coral meadows" (Fig. 3A, B) indicates the influence of hydrothermal fluids in their origin (Philipp Eisenmann personal communication). The large cements completely destroyed the rugose coral skeletons within the zone of cementation, whereas those skeletons that are only touched, or are in a close proximity to the large fibrous cements, do not show any significant differences in their preservation state (Fig. 3A, B). Thus, it is easy to recognize that the cement postdates the age of rugosan meadows formation.

Calices as the place for recolonization

The calices of dead individuals are deep, in some cases filled by ostracod carapaces (Fig. 7A). Mostly, carapaces occur in spaces between the septa (Fig. 7B) in the bottom part of the calice. In other cases, the infilling of empty calice began with early cement that grew directly on the inner skeletal structures of the calice and was followed by late blocky calcite cements (Fig. 7C). This phenomenon is difficult to explain directly. One may presume only that the empty calice was covered by a kind of mat made by sponges, bacteria, or other soft-bodied organisms preventing it from the sediment infilling. Fine-grained sediment infilling the lowermost part of the calice is observed very rarely. Most frequently cements sur-

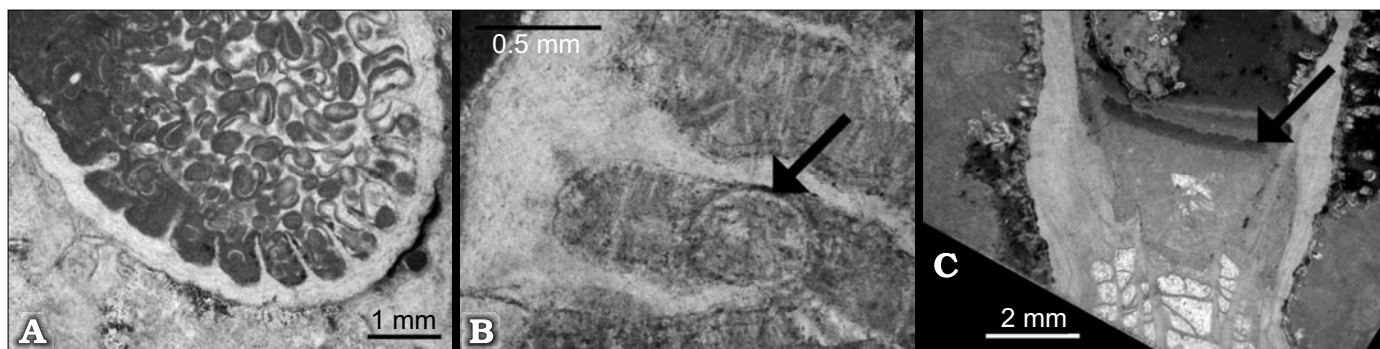


Fig. 7. A. Calice filled with ostracods. B. Ostracod carapaces (arrow) between septa on the calice floor. C. The remnants of the presumably biogenic (sponge?) structure covering the entrance of the calice (arrow).

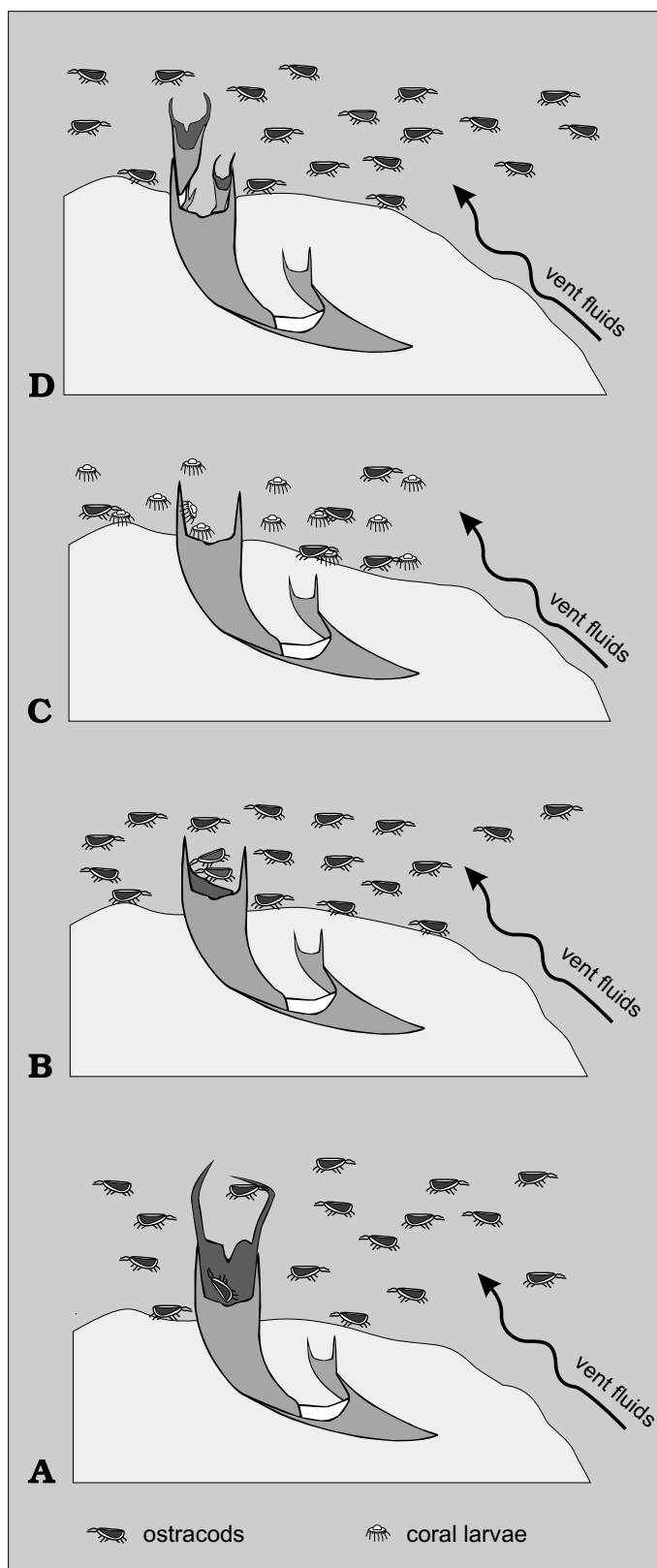


Fig. 8. Reconstruction of presumed life strategy and trophic relation of *Hamarophyllum belkai* gen. et sp. nov. and ostracods. A. Coral feeding on ostracods. B. Ostracods penetrating an empty calice of dead coral. C. Coral planulae dispersal, produced by another corals of the same species, a part of planulae settling inside the empty calice of dead individual. D. Development of young, successful corals only inside the calice of dead individual.

round the youngest parts of the skeletons of the individuals (Fig. 5H, I), attached to the internal structures of the empty calice. In such case fine-grained sediment is infilling the spaces between young skeletons only in the upper part of the host calice (Fig. 5J, K). Most likely, the calices were empty for the time long enough to become a kind of shelter for the coral larvae first and for young individuals growing in there afterwards.

Discussion

The “calice-in-calice” phenomenon, described above relies on selective survival of coral larvae (planulae). It is commonly accepted that larvae of solitary rugose corals similarly to the recent corals were free swimming as plankton. On the other hand a part of recent deep-water scleractinians (caryophylliids) produce rather large, benthic larvae, which have restricted ability to swim and settle almost immediately after planulation (Stolarski 1995: 29). Most likely they had a restricted ability to move after settlement and choose the best place of attachment as the recent living coral taxa do. Hence, larvae of a given species possibly settled around their parents’ neighborhood, using all available hard parts of the bottom to attach. But, almost exclusively larvae settled within calices of dead individuals were successful, i.e. could have reached metamorphosis, started to secrete a skeleton and live. The rest of them probably died before metamorphosis and secretion of a skeleton.

The first question is why among successful individuals the majority (78%) occurs within the calice of an extinct individual? The second one is why those numerous populations developed almost only in close neighborhood of venting systems? The questions seem to be connected.

The most probable explanation for the “calice in calice” pattern of growth observed is that larvae used the calices as shelters against either physical (high turbulence of venting fluids) or biological (predators living within the same environment) dangers.

On the other hand these small corals preferred life around fissures where vent fluids came up. This idea is supported by the presence of numerous specimens around vent chimneys and their absence far outside venting systems, on the slopes of mud mounds. It is possible also that this phenomenon resulted from nutrient supply. Corals living in recent environments of venting fields are mostly predators preying on small free-swimming arthropods (Andre Freiwald personal communication). In the thin sections of Devonian samples, taken from venting fields, a huge number of ostracod tests have been found within the sediment around and within coral calices. Thus, it can be speculated that swarms of ostracods living around venting fields and feeding on chemotrophic microorganisms became, the most important food source for corals living around vents (Fig. 8).

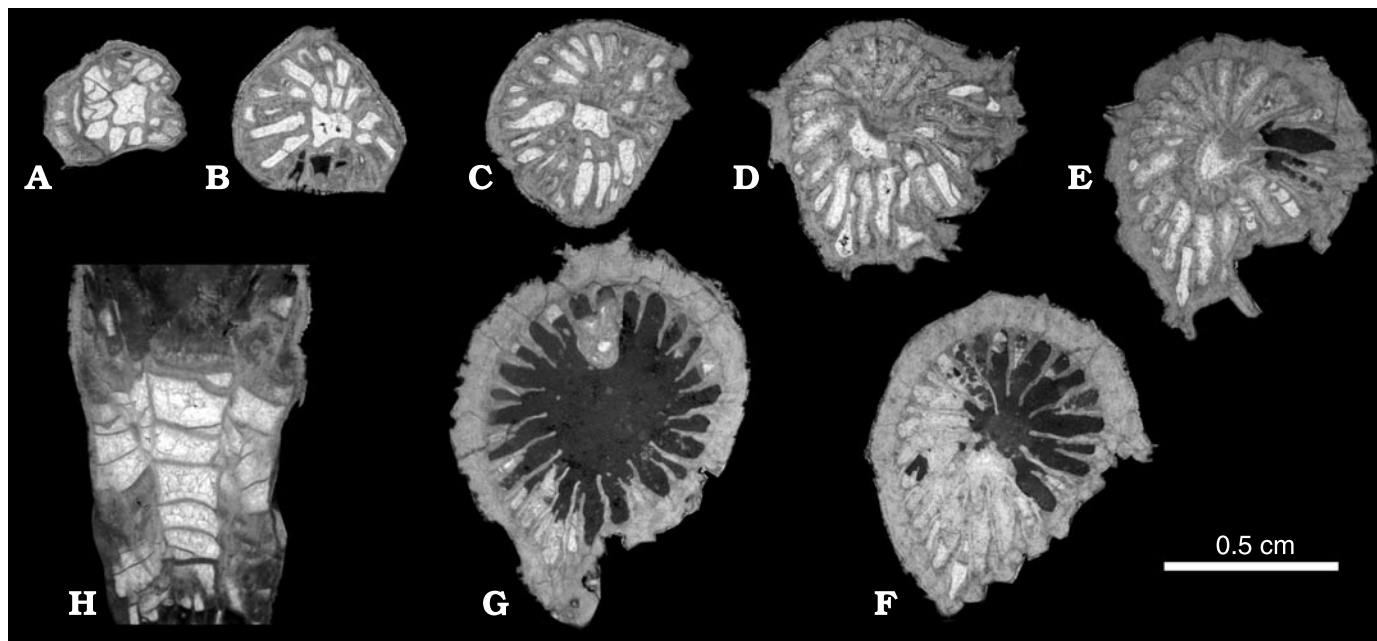


Fig. 9. *Hamarophyllum belkai* gen. et sp. nov. A–G. Holotype UAM Tc/B HD1/1/1, transverse thin sections of successive ontogenetic stages. H. Paratype UAM Tc/B HD27/1/1, longitudinal thin section.

Systematic description

Order Rugosa Milne, Edwards, and Haime, 1850

Family Protozaphrentidae Ivanovskiy, 1959

Subfamily ?Laccophyllinae Grabau, 1928

Genus *Hamarophyllum* nov.

Derivation of the name: After Hamar Laghdad in Morocco—the collecting area.

Type species: *Hamarophyllum belkai*.

Species assigned.—*Hamarophyllum belkai*, *Laccophyllum* sp. of Weyer 1990: 26.

Stratigraphic and geographic occurrence.—Emsian (Zlichovian) mud mounds of Hamar Laghdad and Early or Middle Givetian of the Lower Harz Mountains.

Diagnosis.—Small, solitary coral possessing very deep calice; external wall thick with hardly visible septal furrows; major septa form a continuous aulos; cardinal septum equal to adjacent septa, counter septum may be slightly longer; counter-lateral minor septa (Km) form inconstant triad; most of minor septa contratingent at younger stages, contraclined or free in maturity; tabularium bifiform.

Remarks.—*Hamarophyllum* gen. nov. displays most characters of *Laccophyllum* Simpson, 1900. However, the inconstant position of minor septa forms main and easily distinguishable difference between those genera. Namely, in *Laccophyllum* they are continuously contratingent, whereas in *Hamarophyllum* they may be either contratingent or, especially in mature stages, contraclined or free. Permanent contratingency of minor septa is a typical character for all representatives of the family Protozaphrentidae *sensu* Weyer

(2001) known to date. However, the present observations made on *Hamarophyllum* gen. nov. indicate that this character may be inconsistent during the ontogeny of one specimen, so it is regarded here to be sufficient to create at least a separate genus.

Similar character is also observed in *Laccophyllum* sp. figured by Weyer (1990: 26) described from the Early or Middle Givetian strata (*Amplexus*-kalk) of Buchenberg in Lower Harz Mountains.

Hamarophyllum belkai sp. nov.

Figs. 2B, 3, 5, 6, 9.

?*Laccophyllum* sp. Weyer 1990: 26, fig. 2.

Holotype: Specimen UAM Tc/B HD1/1/1 (Fig. 9A–G).

Paratypes: Specimens UAM Tc/B HD27/4/1 (Fig. 5B–L), UAM Tc/B HD27/1/1 (Fig. 9H).

Type horizon: Emsian (Zlichovian), *Polygnathus inversus* conodont zone.

Type locality: Mud mounds of Hamar Laghdad, Tafilalt, Eastern Anti-Atlas, Morocco.

Derivation of the name: In honor of Professor Zdzisław Belka, who organized expedition to Morocco in 2001 and 2002 where the specimens were found.

Diagnosis.—*Hamarophyllum* with 15–16 wavy major septa at the diameter of 6–8 mm near calice floor. In longitudinal section aular tabulae are widely spaced, horizontal or delicately convex or concave.

Material.—Hundreds of specimens. 21 specimens were sectioned: 47 transverse and 6 longitudinal thin sections have been made.

Description.—Corallites are small and horn-shaped. Calices

are deep, septal furrows and interseptal ridges are observed on the external wall only in mature stages.

External wall is thin in bryophic and neanic stages (Fig. 9A–C) and thick and lamellar in mature stages (Fig. 9D–G). Major septa are long reaching 2/3–4/5 of the corallite radius. They are wavy and rhopaloid, forming a constant and thickened aulos. Aulos is occupying 1/4–1/5 of the corallite diameter (Fig. 9A–E). Cardinal septum is as long as adjacent septa; counter septum may be somewhat elongated. Cardinal fossula is very shallow, and not well marked. Septal splitting of cardinal, counter, or alar septa is not observed. Most of minor septa reach 1/3 length of major septa. They are mostly contratingent, but they may be also contratingent or free especially in mature stages.

Tabularium is biform. Periaular tabellae in position I subhorizontal or slightly declined adaxially, in position II they are declined abaxially, sloping down outward (Fig. 9H).

Tabellae in the aulos are flat not densely packed 4–5/5 mm (Fig. 9H)

Microstructure of wall is lamellar, whereas septal microstructure is not well preserved, contains trabecular relics.

Ontogeny.—The earliest stages are aseptal (circular basal disk). In the six septal stage septa are straight and united in the axis. A minute aulos is formed early, when the next four major septa appear. Minor septa begin to appear when 10–14 major septa are inserted and are mostly contratingent (Fig. 9B). Contratingency of minor septa may disappear in later stages when they become contraclined or free (Fig. 9E). They may be either slightly wavy or straight.

Intraspecific variability.—Displaying mostly in the external shape, which is often caused by the restricted space of growth. The proximal part of the skeleton is radiceform of various shapes depending on the place of attachment. The shape of the transversal section of young skeleton in the calice of extinct individual in place where it is attached at the early stages of ontogeny follows the shape of the empty calice. Internal structures vary in thickness and swellings of major septa and the diameter of aulos, which may be more or less wide in neanic stages.

Occurrence.—Venting fields of Hamar Laghdad mud mounds, Tafilalt, Eastern Anti-Atlas Morocco. Emsian *Polygnathus inversus* conodont zone.

Conclusions

- The presence of monospecific rugosan meadow-like assemblages of *Hamarophyllum belkai* gen. et sp. nov. around venting outlets and their absence or sporadic occurrence outside the venting fields within the mud-mound body suggest that vents offered better life conditions for these corals.
- Better life conditions may be related to higher temperature, which may have stimulated the meadow-like growth

and more probably local increase in nutrient supply, probably ostracods. Hence, the trophic relation between corals and ostracods may be the most important factor responsible for the development of coral meadows.

- Calice-in-calice development of particular individuals resulted from selective survival of coral larvae. The majority of larvae, which settled inside the empty calices seem to have been successful at the beginning of their growth whereas those settling outside may have been exterminated by physical (hot and/or poisoning fluids) or biological (predators) factors. Hence, the calice-in-calice growth may be regarded as pattern of growth typical for the rugose corals that lived around hydrothermal vents.

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