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Are modern chemosynthesis-based communities a 'glimpse of antiquity'? The changing fate of bivalves and brachiopods at ancient methane seeps as recorded in the Middle Palaeozoic of Morocco

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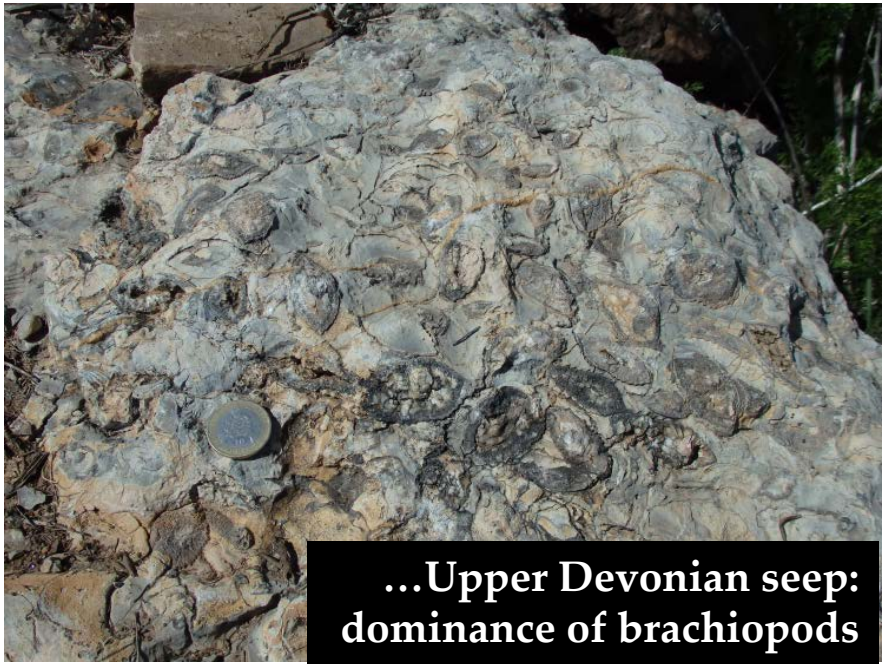
Fossil record of seep and vent ecosystems

The fossil record of chemosynthesis-based communities, one of the most prolific and unique ecosystems of the Earth's oceans, remains poorly constrained. For over two decades, a dominant perception was that general trends in the evolution of chemosynthetic communities paralleled those typifying most marine environments, with the bivalve prevalence starting in the Mesozoic and with Palaeozoic seeps being dominated by brachiopods. This simple view has recently been challanged by descriptions of a new genus of a modiomorphid bivalve, *Ataviaconcha*, from the Middle Palaeozoic of Morocco.

Middle Devonian seep: dominance of bivalves…

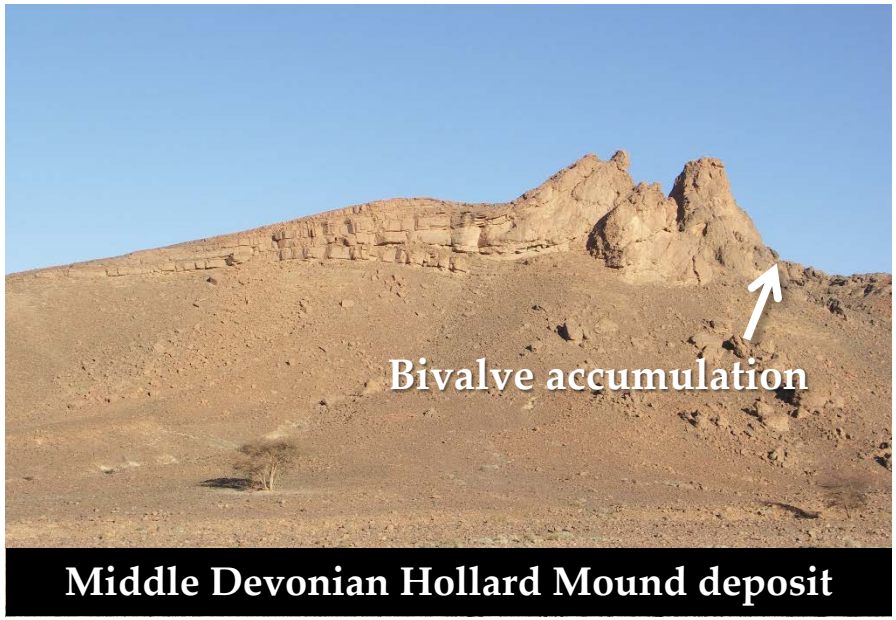


…Upper Devonian seep: dominance of brachiopods

Ataviaconcha bivalves

Ataviaconcha bivalves are known exclusively as forming very dense, nearly monospecific assemblages in two Moroccan seep deposits:

1) Middle Devonian Hollard Mound, eastern Anti-Atlas, first reported by Peckmann et al. (1999), and identified and formally described by Hryniewicz et al. (2017)
2) Upper Silurian El Borj site, Western Meseta, first described by Jakubowicz et al., (2017)



Middle Devonian Hollard Mound deposit

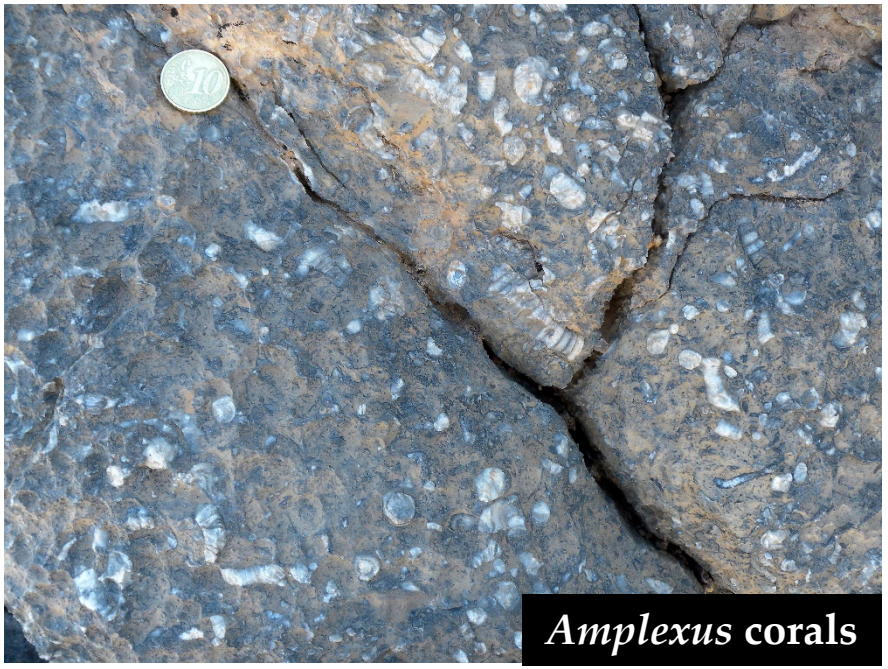
Upper Silurian El Borj deposit

Hollard Mound seep

The stratigraphically younger, but much longer known (first mention in Töneböhn, 1991) occurrence is the Eifelian (Middle Devonian) Hollard Mound. This deposit was identified as a fossil methane seep by Peckmann et al. (1999), and this interpretation was subsequently supported by further studies. Except for the presence of the dense bivalve clusters, this evidence includes:

- Strong depletion in ^{13}C, characteristic of methanogenic carbonates ($\delta^{13}C$ of down to −26‰ V-PDB; Peckmann et al., 1999; Cavalazzi et al., 2007; Jakubowicz et al., 2015)
- Complex paragenetic succession, including abundance of corrosion surfaces, veins and isopachous fibrous cements (Peckmann et al., 1999; Cavalazzi et al., 2012; Jakubowicz et al., 2015)
- The presence of other seep-related organisms: clusters of tube worms (Siboglinidae?; Peckmann et al., 2005) and opportunistic rugose corals (*'Amplexus' florescens*; Berkowski, 2006; Jakubowicz et al., 2013).

Ataviaconcha bivalves

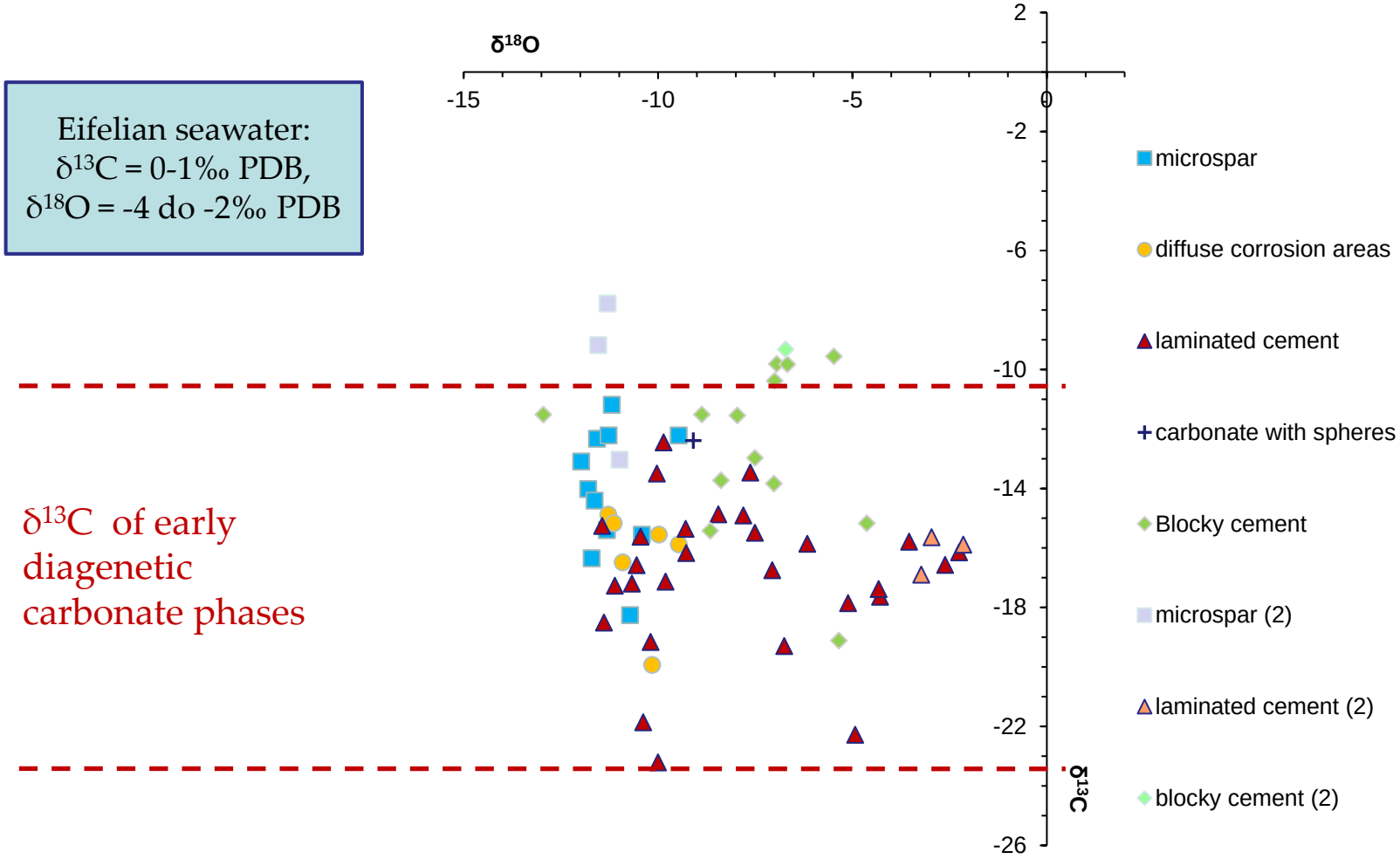


***Amplexus* corals**

Hollard Mound: stable isotopes

Eifelian seawater:
$\delta^{13}C$ = 0-1‰ PDB,
$\delta^{18}O$ = -4 do -2‰ PDB

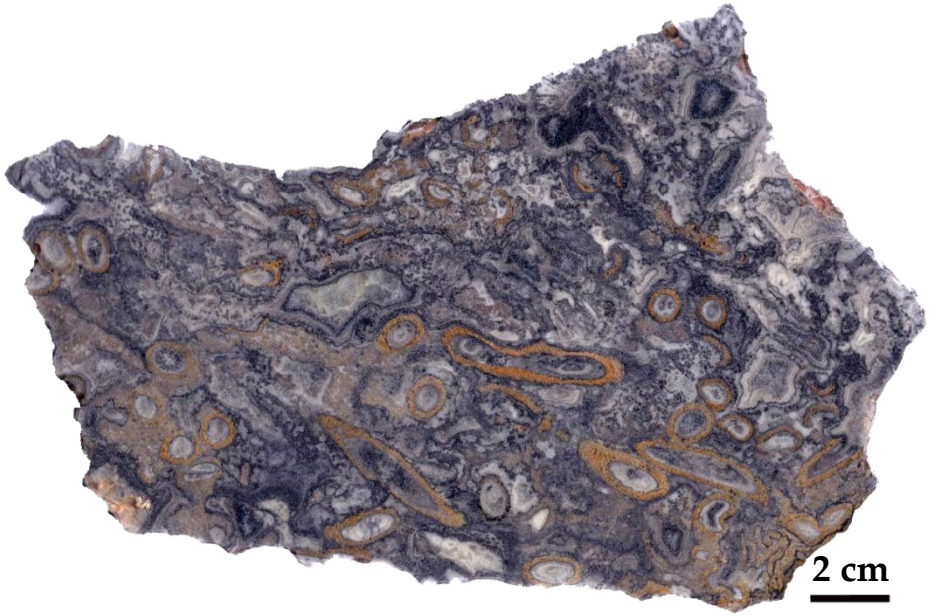
$\delta^{13}C$ of early diagenetic carbonate phases



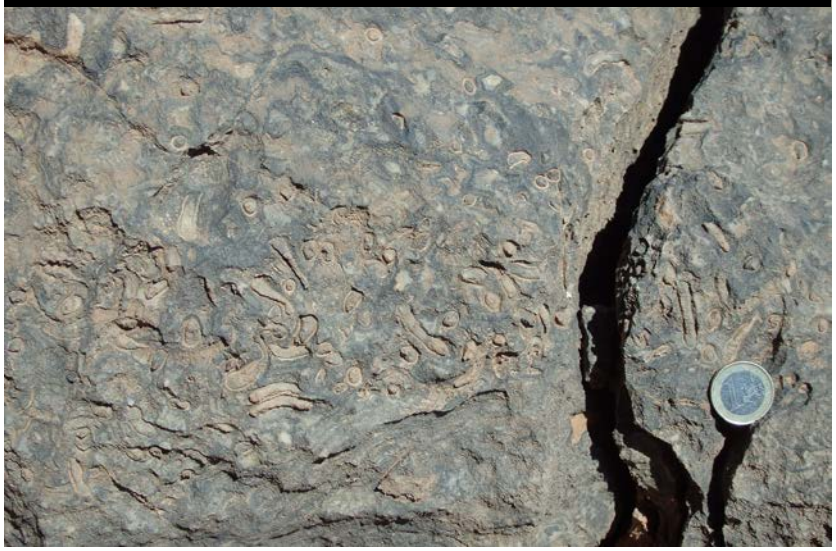
Jakubowicz M., Dopieralska J., Bełka Z. 2015. Tracing the origin and composition of fluids at an ancient hydrocarbon seep (Hollard Mound, Middle Devonian, Morocco) . . . *Geochim Cosmochim Acta*, 156: 50-74

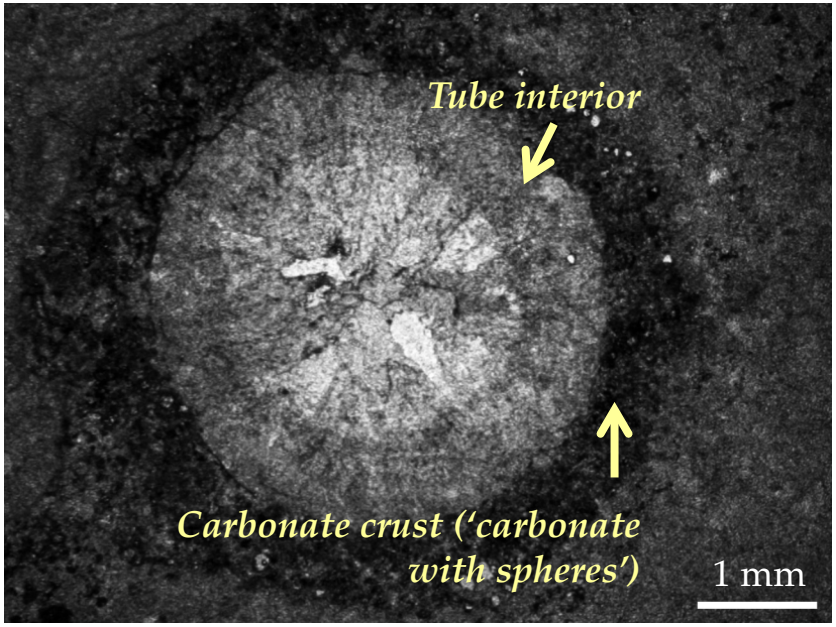
The Hollard Mound: tube worms?

- 'The oldest seep-related vestimentiferans?' (Peckmann et al., 2005)
- Poorly preserved, mostly only due to encrustation by carbonate crusts



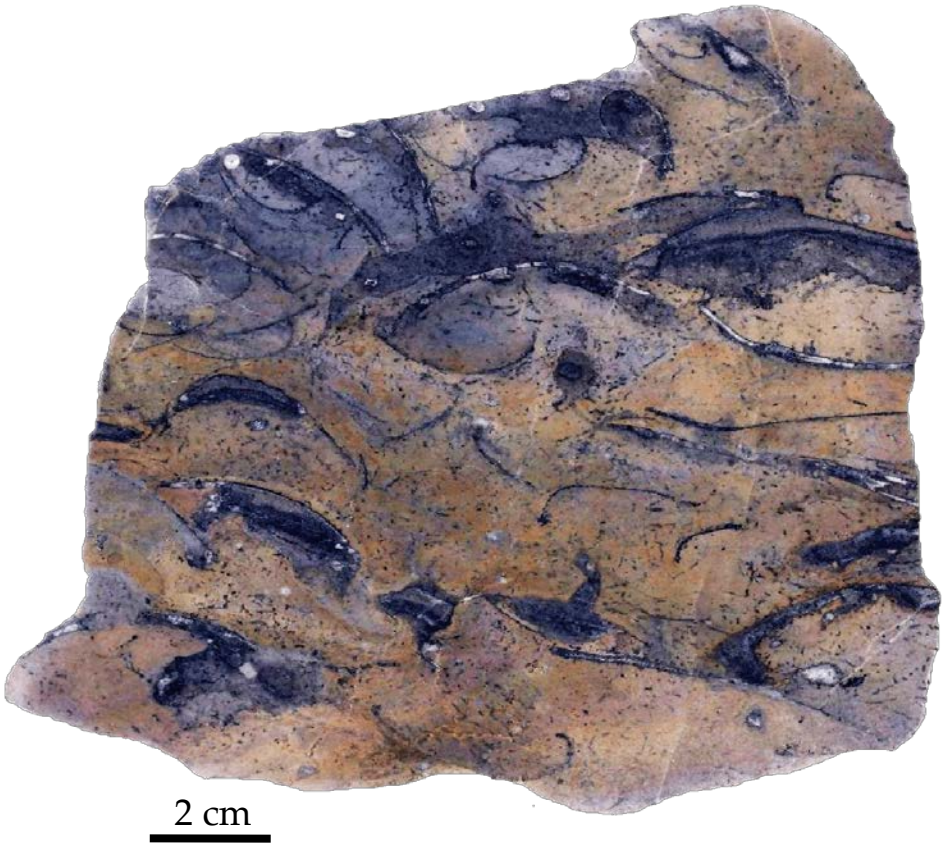
'Tube worm limestone', field view

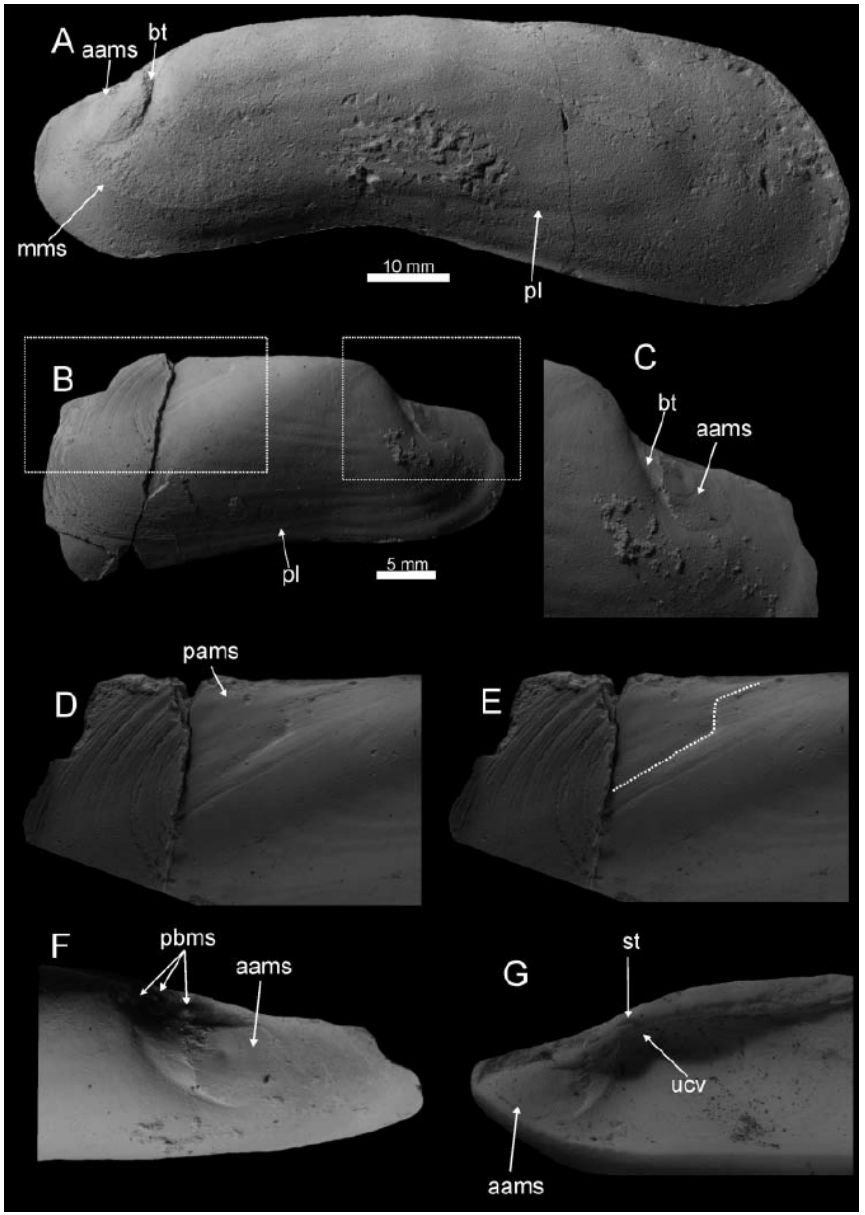




Hollard Mound bivalves

- The species *Ataviaconcha wendti* Hryniewicz et al., 2017



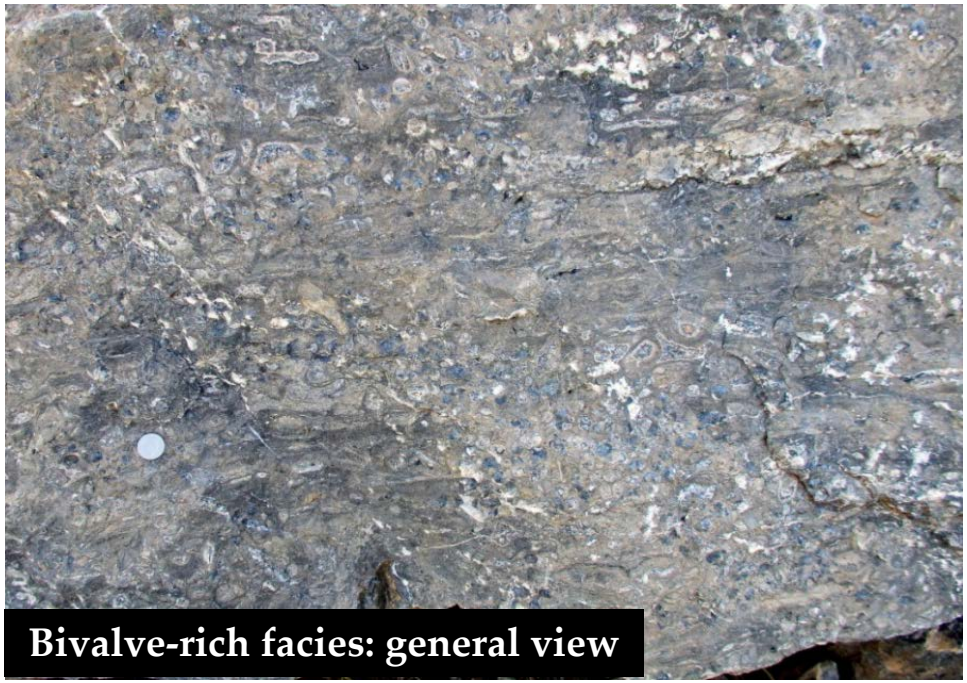


Hryniewicz K., Jakubowicz M. et al.. 2017. New bivalves from a Middle Devonian methane seep in Morocco: the oldest record of repetitive shell morphologies among some seep bivalve molluscs. *J Syst Palaeo*, 15(1): 19-41

Hollard Mound seep

The older, upper Silurian deposit was known from the study of Ager (1976), but its seep-related origin was first proposed by Barbieri et al. (2004). Recently, this interpretation was confirmed by Jakubowicz et al. (2017), who provided evidence that the unusually heavy carbon isotope isotope composition of the El Borj carbonates is explained by its revised stratigraphy, placing the seep formation within a late Ludfordian, very strong positive excursion in the cabon isotope composition of seawater. Except for the bivalves, unrecognised until the study of Jakubowicz et al., (2017), the evidence for seep-related origin of this deposit includes:

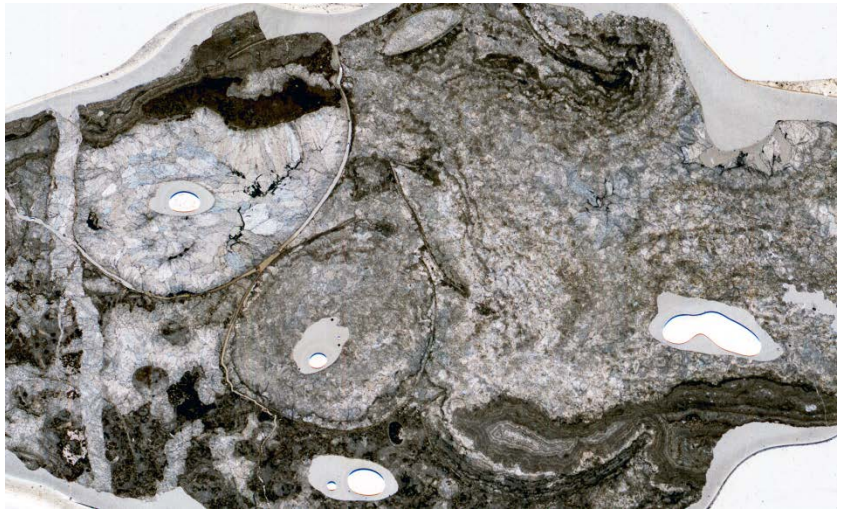
- $\delta^{13}C$ values up to 12‰ lower than the signal of coeval marine-equilibrated carbonates (Jakubowicz et al., 2017)
- Complex paragenetic succession, including abundance of corrosion surfaces and isopachous fibrous cements (Barbieri et al., 2004; Buggisch and Krumm, 2005; Jakubowicz et al., 2017)
- Mass occurrence of atrypid brachiopods underlying the bivalve-rich facies, likely attracted by abundance of seepage-related nutrients (cf., Barbiert et al., 2004)

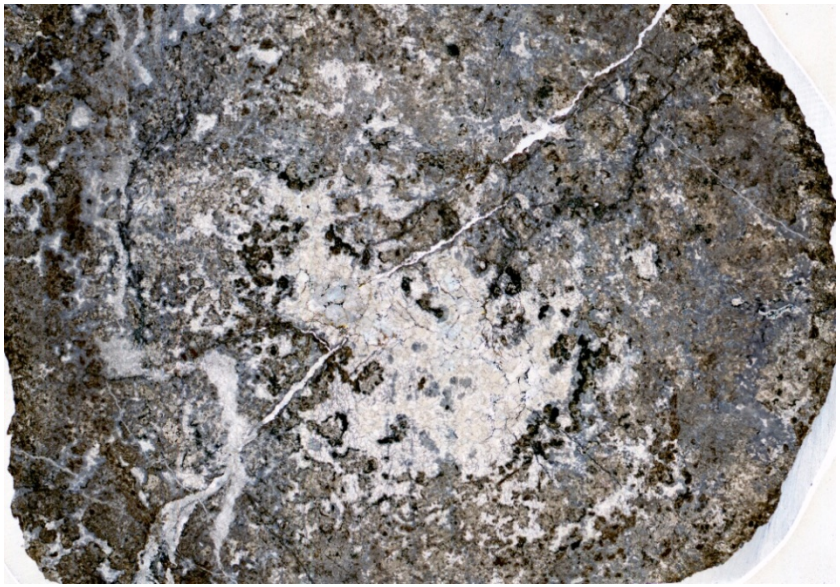


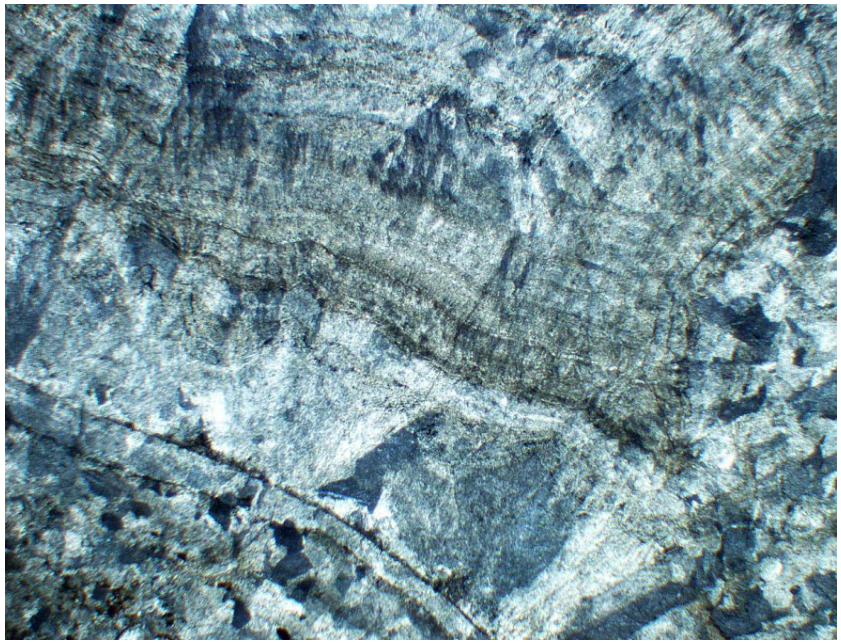
Bivalve-rich facies: general view

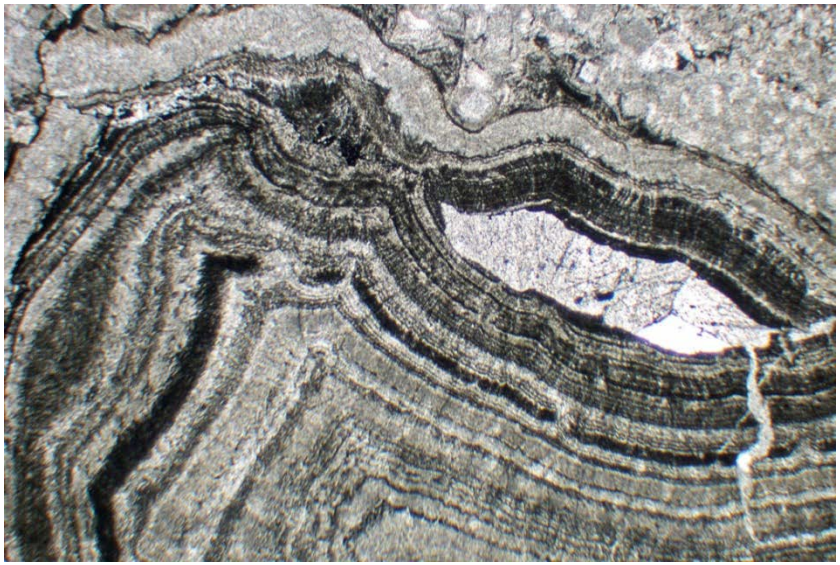
Bivalve-rich facies: close-up

El Borj: microfacies



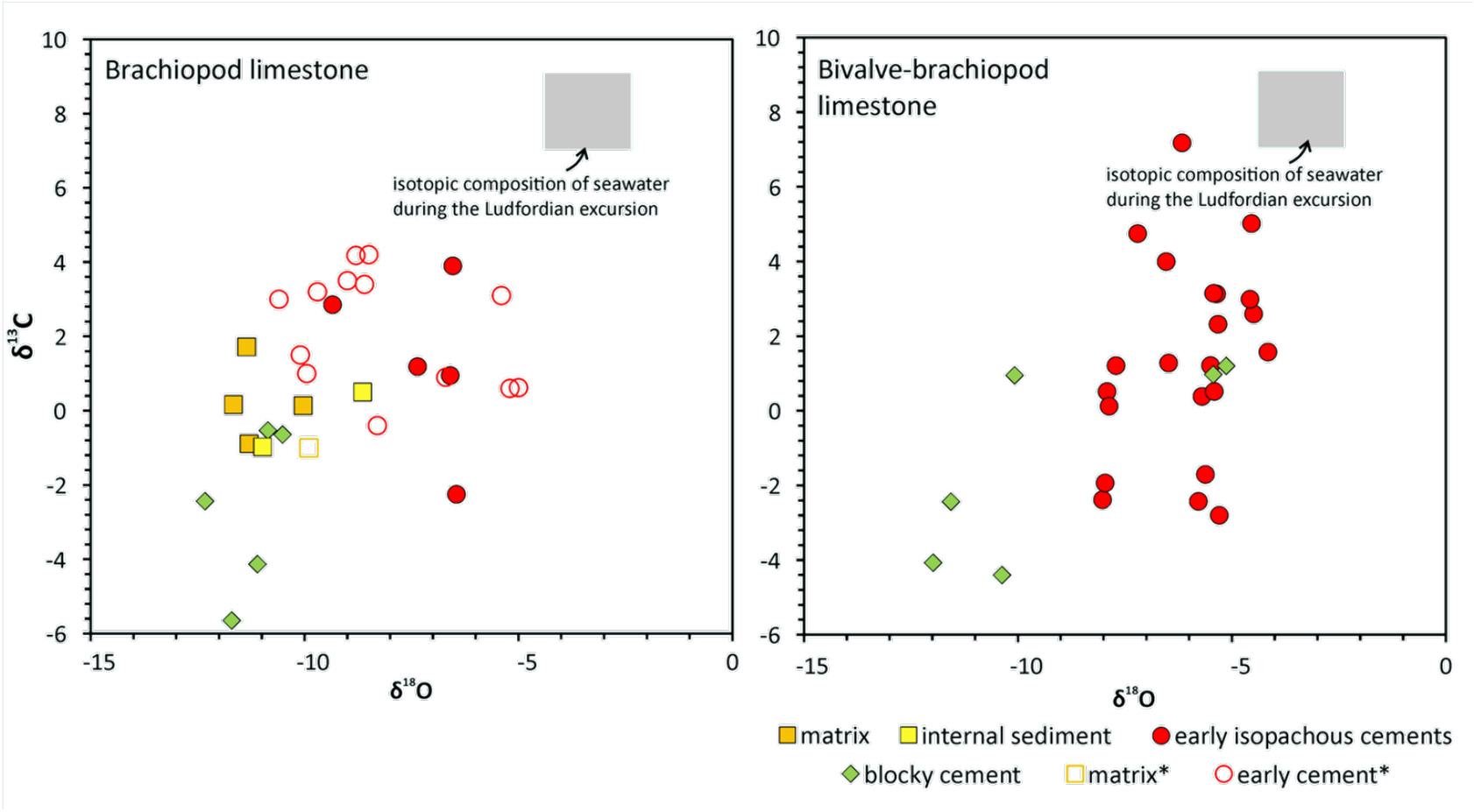






Jakubowicz M., Hryniewicz K., Belka Z. 2017. Mass occurrence of seep-specific bivalves in the oldest-known cold seep metazoan community. *Scientific Reports*, 7: 14292

El Borj: stable isotopes

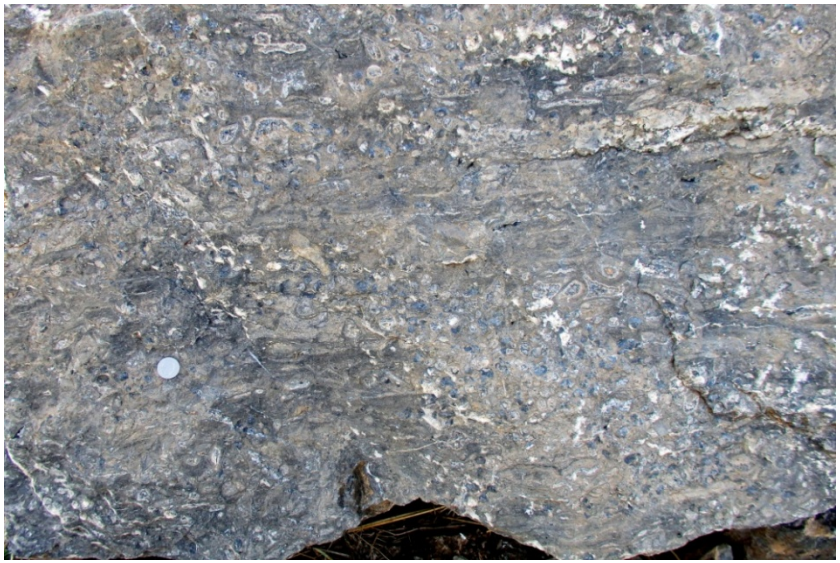


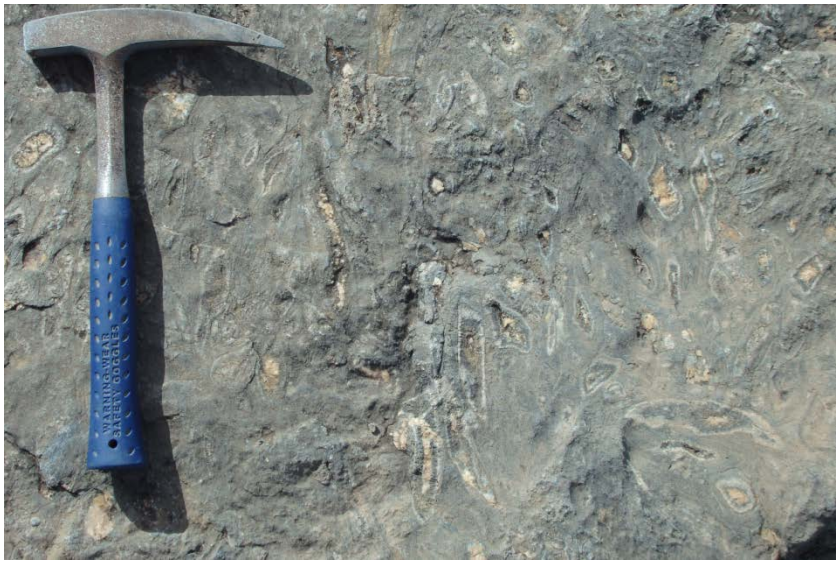
Jakubowicz M., Hryniewicz K., Belka Z. 2017. Mass occurrence of seep-specific bivalves in the oldest-known cold seep metazoan community. *Scientific Reports*, 7: 14292

El Borj: brachiopods

Jakubowicz M., Hryniewicz K., Belka Z. 2017. Mass occurrence of seep-specific bivalves in the oldest-known cold seep metazoan community. *Scientific Reports*, 7: 14292

El Borj: bivalves





Jakubowicz M., Hryniewicz K., Belka Z. 2017. Mass occurrence of seep-specific bivalves in the oldest-known cold seep metazoan community. *Scientific Reports*, 7: 14292

El Borj: bivalves

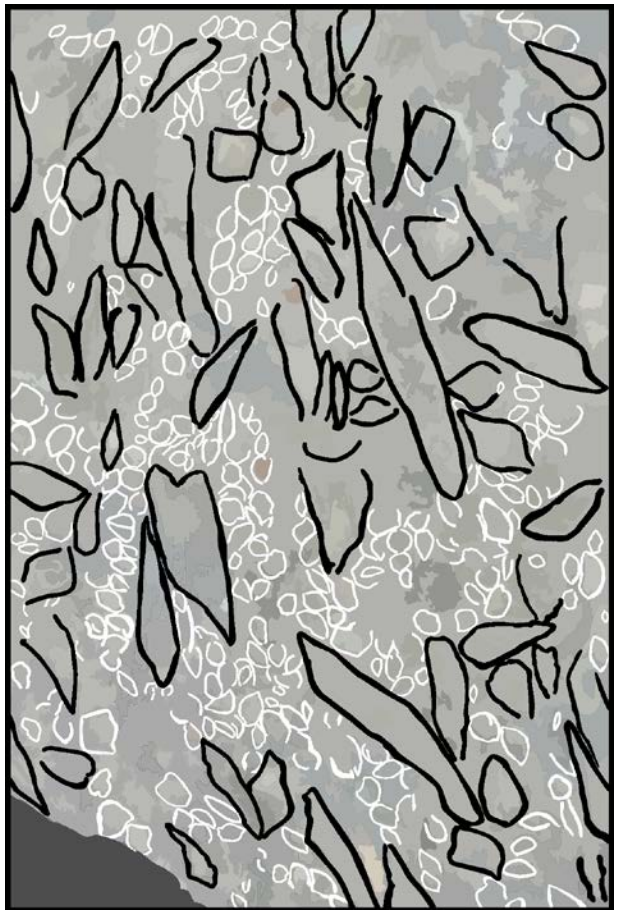





Jakubowicz M., Hryniewicz K., Belka Z. 2017. Mass occurrence of seep-specific bivalves in the oldest-known cold seep metazoan community. *Scientific Reports*, 7: 14292

El Borj: bivalves

The El Borj bivalves are mostly poorly preserved, with irregular outlines due to recrystallisation or dissolution of their shells. As a results, in some portions of the deposit recognising the original shell outlines poses difficulties, which apparently can be held responsible for them being unnoticed in several previous studies.



Jakubowicz M., Hryniewicz K., Belka Z. 2017. Mass occurrence of seep-specific bivalves in the oldest-known cold seep metazoan community. *Scientific Reports*, 7: 14292

El Borj: bivalves

Jakubowicz M., Hryniewicz K., Belka Z. 2017. Mass occurrence of seep-specific bivalves in the oldest-known cold seep metazoan community. *Scientific Reports*, 7: 14292

El Borj: bivalves

Late Silurian bivalve (*Ataviaconcha* sp.) – brachiopod (*Septatrypa lantenoisi*) assemblage from the El Borj methane seep

Jakubowicz M., Hryniewicz K., Belka Z. 2017. Mass occurrence of seep-specific bivalves in the oldest-known cold seep metazoan community. *Scientific Reports*, 7: 14292

Mid-Palaeozoic *Ataviaconcha* vs. modern seep bivalves

Silurian-Devonian *Ataviaconcha*

Jakubowicz et al., 2017 *Sci Rep*

similarity

≠

affinity

©NOAA

Extant
Bathymodiolinae

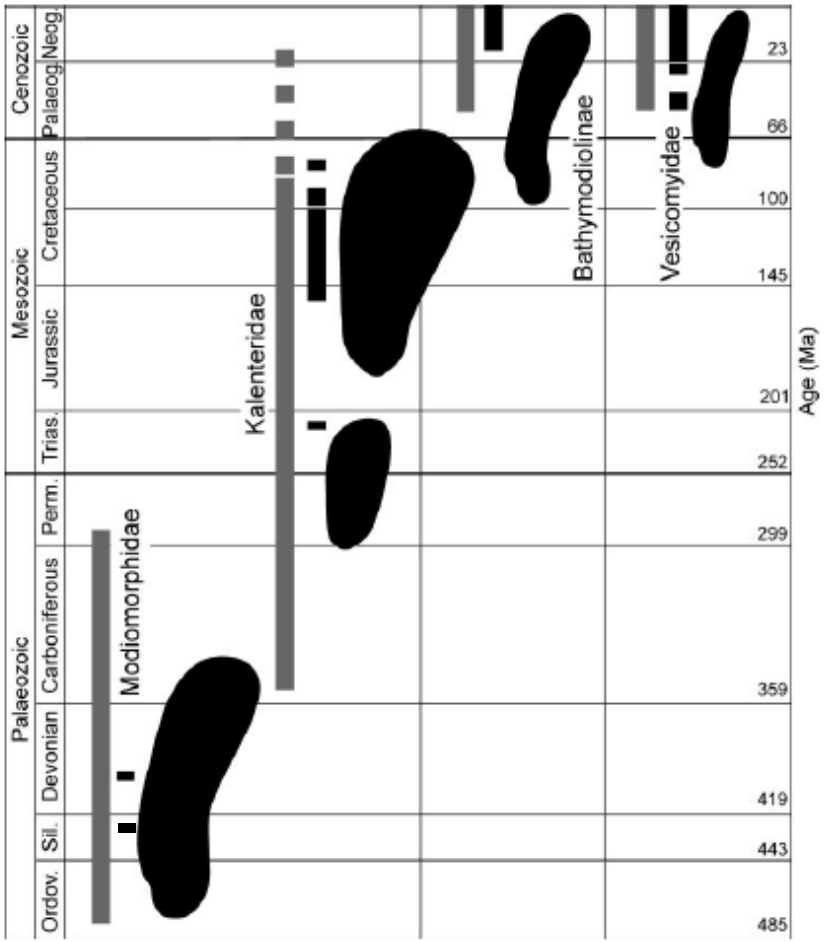
©Krylova & Sahling 2010,
PLoS One 5(4): e9957

Extant
Vesicomyidae

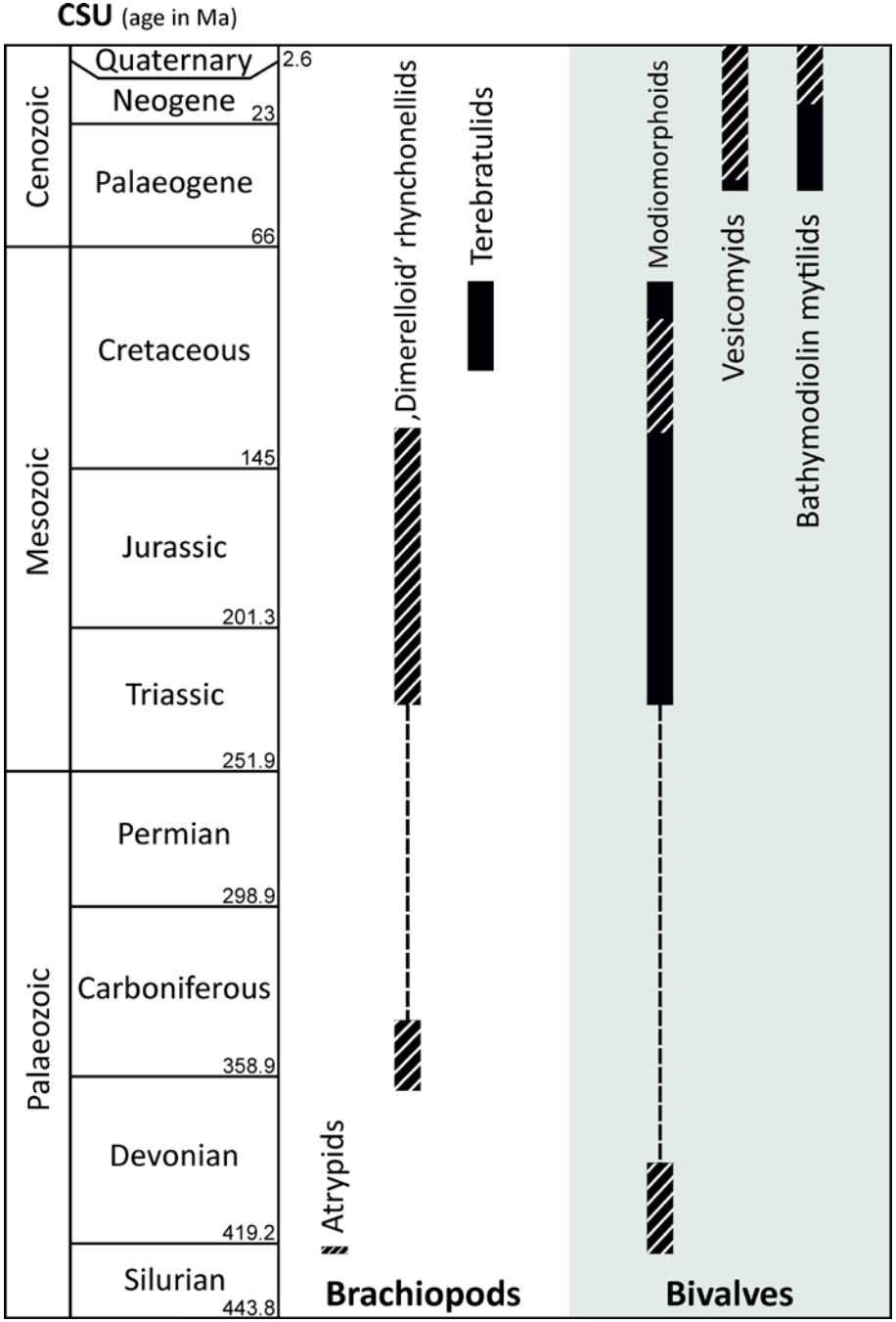
The large, strongly elongated, arcuate shells developed convergently in different groups of seep-related bivalves, representing adaptation to a semi-infaunal lifestyle in seepage-affected environments. Such shells, when oriented with their anterior end shallowly buried in the sediment, and the posterior part exposed, enable simultaneous access to seawater-derived oxygen and interstitial sulphide. Given the high metabolic toxicity of sulphide, the semi-infaunal strategy provides no advantage to non-chemosymbiotic bivalves, and indeed for modern seep bivalves is found exclusively in chemosymbiotic forms. Accordingly, this morphology strongly suggests a chemosymbiotic feeding strategy of *Ataviaconcha* bivalves.

Reccurrence patterns of elongated, incurved shells and tendency to form mass assemblages among seep bivalves

Boomerang-shaped shells in seep-related bivalves.
From: Hryniewicz et al., 2017 *J Syst Pal*



Hryniewicz et al., 2017 *J Syst Pal*



Fossil record of bivalves and brachiopods at seeps. Time periods for which representatives of given lineages formed mass concentrations at seeps are cross-hatched. From: Jakubowicz et al., 2017 *Sci Rep*

Khenifra seep (Famennian, Moroccan Meseta)

It is striking that, following the period of their remarkable success at mid-Palaeozoic seeps, rich, monospecific assemblages of semi-infaunal bivalves disappear from the fossil record of chemosynthetic ecosystems until the middle Mesozoic. Starting from the Late Devonian, a characteristic element of many seep-related communities became brachiopods of the superfamily Dimerelloidea, which recurred in seep assemblages over the next 240 Myr, until the Early Cretaceous. Notably, the oldest dimerelloid occurrance at seeps is also known from Morocco, highlighting the importance of this area for our understanding of the early evolution of chemosynthesis-based communities.

Upper Devonian seep with abundant dimerelloid *Dzieduszyckia*

Conclusions and final remarks

- New descriptions of Silurian and Devonian seep-obligate, modiomorphid bivalves from Morocco question the long-held paradigm that until the middle Mesozoic the shelly faunas of chemosynthesis-based ecosystems were dominated by brachiopods. Conversely, dense clusters of bivalves morphologically strikingly similar to modern seep-specific bivalve taxa inhabited the two oldest known, middle Palaeozoic seep ecosystems. Unlike Palaezoic and Mezozoic seep brachiopods, the mid-Palaeozoic seep bivalves show clear, advanced adaptations to seepage-affected habitats, most likely including their former cooperation with chemosymbionts. **Studies of the mid-Palaeozoic bivalve-dominated seeps provide a new look at the concept of modern chemosynthetic communities as representing a 'glimpse of antiquity' (Newman, 1985), showing that while it is largely not true taxonomically, it clearly is in terms of recurring morphological patterns**.
- The **controls on the changing fate of bivalves vs. brachiopods at seeps remain arguably the most pertinent enigma in studied on pre-Cenozoic record of chemosynthetic communities.** No seep-specialised brachiopods are known from modern oceans and, unlike for the *Ataviaconcha* bivalves, there are no morphological traits that would suggest that fossil brachiopods developed symbioses with chemosynthetic microbes, characteristic for most groups of seep-specialised macroinvertebrates. Preliminary ideas for the origin of these evolutionary trends consider a role of palaeogeographic factors (Campbell & Bottjer, 1995; Peckmann et al., 2011; Jakubowicz et al., 2017) or distinct feeding strategies differentially affected by changing oceanic chemistry (Kiel & Peckmann, 2019).
- Studies on Moroccan palaeoseeps provide one more **illustration of the problems inherent to reconstructing general evolutionary or palaeoecological trends for ecosystems with very fragmentary fossil record**, and drastic revisions that may be required for existing models with even single new discoveries.

Further reading (hyperlinked)

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Mass occurrence of seep-specific bivalves in the oldest-known cold seep metazoan community

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One of the most striking features of modern chemosynthesis-based ecosystems surrounding methane seeps is the presence of abundant chemosymbiotic bivalves. However, such accumulations have rarely been reported from Palaeozoic to mid-Mesozoic seeps, and it is widely thought that general trends in the evolution of chemosynthetic communities paralleled those typifying most marine environments, with the bivalve prevalence starting in the Mesozoic and with Palaeozoic seeps being dominated by brachiopods. Here, we report a discovery of bivalve clusters in the oldest-known methane seep that hosted metazoan fauna, dated to the late Silurian. We identify the bivalves, externally very similar to modern chemosymbiotic forms, as members of the extinct family Modiomorphidae, known previously from a younger, Devonian seep. The bivalves inhabited the seep at a stage of increased fluid flow, when they co-occurred with atrypid brachiopods, and display a set of morphological characteristics suggesting a seep-obligate lifestyle. We conclude that bivalves colonised chemosynthesis-based ecosystems at least as early as brachiopods and apparently first developed specialized lineages able to thrive in seep-related habitats for a prolonged period of time. Rather than being simple ecological successors of brachiopods, rich bivalve communities represent an ancient and recurring theme in the evolution of chemosynthetic assemblages.

Modern ecosystems based on chemical energy sources supplied by methane (cold) seeps and hydrothermal vents stand out as some of the most unique communities found in the deep sea[1–4]. These both nutrient- and toxin-rich settings host prolific, highly-endemic faunas, the most characteristic elements of which include vestimentiferan tube worms and mass concentrations of large bivalves, notably bathymodiolin mussels and vesicomyid clams[3,5,6]. Having developed close symbioses with chemoautotrophic bacteria harboured in their gills, the bathymodiolins and vesicomyids have dominated many seeps and vents since the mid-Palaeogene, the moment often regarded as the onset of modern-type chemosynthetic ecosystems[2,7–10].

Despite three decades of studies that have aimed to better constrain the fossil record of chemosynthesis-based assemblages, the early stages of their evolution remain poorly recognised. As few as six metazoan methane seep ecosystems have been documented for the entire Palaeozoic[7,11], and these were often inhabited by biota with no or unclear affinities to modern seep lineages[2,8,12]. As a result, many key questions regarding the palaeoecology of Palaeozoic seeps remain unanswered, and few attempts have been made so far to delineate general trends in the evolution of the earliest chemosynthetic communities. Probably the most widely held perception has become that, unlike modern, bivalve-dominated seeps, the Palaeozoic to late Mesozoic seep ecosystems were dominated by brachiopods[7,13]. The role of bivalves at seeps until the early Mesozoic was poorly known and considered subordinate, with the notable, yet apparently isolated exception of a single Devonian seep that sustained dense bivalve accumulations, but few, lingulate brachiopods[12,14,15]. Likewise, although the Devonian seep bivalves apparently possessed specialised features indicative of their longer evolution at seeps[12], no molluscs were known from the sole example of an older, Silurian, metazoan-containing seep ecosystem[16]. Nevertheless, the available Palaeozoic record appears too fragmentary to support such broad generalisations. Indeed, even our recognition of the documented Palaeozoic seeps is often very limited and turns out, in some cases, strikingly incomplete.

The latter situation is exemplified by the present study, in which we report the presence of mass accumulations of large bivalves at the oldest-known, Silurian methane seep, an occurrence that remained unnoticed

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Tracing the composition and origin of fluids at an ancient hydrocarbon seep (Hollard Mound, Middle Devonian, Morocco): A Nd, REE and stable isotope study

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Abstract

For the first time, Nd isotope signatures combined with rare earth element (REE) concentrations were used in investigations of ancient seep carbonates. The study was performed on the fossil hydrocarbon seep deposit of the Middle Devonian Hollard Mound (eastern Anti-Atlas, Morocco), where Nd isotopes, REE concentrations, and carbon and oxygen isotope ratios were measured to investigate the origin, former migration pathways and composition of fluids. Relatively high ε_{Nd} values compared to local Eifelian seawater, as well as consistently appearing positive Eu anomalies in MREE-enriched shale-normalized REE patterns of the seep carbonates provided evidence for interaction between the seeping fluids and the Lower Devonian basaltic volcaniclastics underlying the studied seep deposit. Strongly reducing conditions and increased temperature of methane formation could have constituted an additional factor in the Eu-enrichment of the investigated carbonate phases. The presence of exclusively negative Ce anomalies in these carbonates is in line with observations of other workers that seep limestones may not necessarily display positive Ce anomalies indicative of precipitation under anoxic conditions. The negative Ce anomalies are attributed here to mixing between anoxic pore waters and oxic, Ce-depleted seawater, necessary to enable carbonate precipitation at seeps. The methane-rich fluids ascended most likely from below the volcaniclastic unit and inherited the enriched ε_{Nd} signatures and positive Eu anomalies due to fluid–rock interactions during their seepage to the seafloor. The carbon isotope data are most consistent with thermogenic origin of methane, although contribution of abiotic and biogenic methane sources cannot be excluded.

Our results indicate that neodymium isotope and rare earth element analyses constitute one of the most valuable tools for reconstructing former fluid migration patterns. The study shows also that Nd isotopes and Eu anomalies can serve as sensitive tracers of fluid–rock interactions at submarine springs.

Journal of Systematic Palaeontology, 2016
http://dx.doi.org/10.1080/14772019.2015.1136900

Taylor & Francis

New bivalves from a Middle Devonian methane seep in Morocco: the oldest record of repetitive shell morphologies among some seep bivalve molluscs

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(Received 5 June 2015; accepted 18 December 2015)

A fauna of bivalve molluscs is described from methane seep carbonates of the Middle Devonian (c. 390 Ma) Hollard Mound in the eastern Anti-Atlas, Morocco. We describe a new modiomorphid genus *Ataviaconcha* gen. nov. with the type species *Ataviaconcha wendti* sp. nov. This is a very large, semi-infaunal species occurring in large colonies similar to those formed by Recent chemosymbiotic cold-seep and hydrothermal vent bivalves. It is the second modiomorphid bivalve known from Palaeozoic chemosynthesis-based ecosystems, after the roughly coeval *Sibuya ivanovi* Little, Maslennikov, Morris & Gubanov, 1999, from the Sibay hydrothermal vent deposit in the Ural Mountains, Russia. The second and much less numerous bivalve species described in this paper is the solemyid *Dystactella? eisenmanni* sp. nov., belonging to a genus known also from Ordovician to Devonian marine environments distinct from cold seeps and hydrothermal vents. As with other fossil and Recent solemyids, it was an infaunal burrower, most likely living in symbiosis with chemoautotrophic bacteria. These new findings show that bivalves are ancient in chemosynthesis-based ecosystems, thriving there for at least 390 Myr, and that the bivalve-dominated faunas predated the first occurrence of dimerelloid brachiopods at seeps. The early evolutionary adaptation of some bivalves to chemosynthesis-based ecosystems is probably related to a symbiosis-based metabolism allowing efficient exploitation of chemosynthetic food resources. *Ataviaconcha wendti* sp. nov. represents a morphology which recurred several times throughout the following 390 Myr in different bivalve groups that flourished at hydrocarbon seeps. This strongly suggests environmental control on the evolution of adaptations in seep biotas.

http://zoobank.org/urn:lsid:zoobank.org:pub:A83D5CB1-67D2-4D05-8EBC-BFCA6E6845D8

Keywords: bivalves; chemosynthesis-based ecosystems; Devonian; Morocco; Modiomorphidae; Solemyidae

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Thank you for reading!

I'll be happy to address any questions or comments, whether in the discussion section, live chat, or a private correspondence.

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