

RESEARCH ARTICLE

Resource partitioning among brachiopods and bivalves at ancient hydrocarbon seeps: A hypothesis

Steffen Kiel¹, Jörn Peckmann^{2*}

1 Swedish Museum of Natural History, Department of Palaeobiology, Stockholm, Sweden, **2** Universität Hamburg, Center for Earth System Research and Sustainability, Institute for Geology, Hamburg, Germany

* joern.peckmann@uni-hamburg.de



OPEN ACCESS

Citation: Kiel S, Peckmann J (2019) Resource partitioning among brachiopods and bivalves at ancient hydrocarbon seeps: A hypothesis. PLoS ONE 14(9): e0221887. <https://doi.org/10.1371/journal.pone.0221887>

Editor: Jürgen Kriwet, University of Vienna, AUSTRIA

Received: June 13, 2019

Accepted: August 16, 2019

Published: September 5, 2019

Peer Review History: PLOS recognizes the benefits of transparency in the peer review process; therefore, we enable the publication of all of the content of peer review and author responses alongside final, published articles. The editorial history of this article is available here: <https://doi.org/10.1371/journal.pone.0221887>

Copyright: © 2019 Kiel, Peckmann. This is an open access article distributed under the terms of the [Creative Commons Attribution License](https://creativecommons.org/licenses/by/4.0/), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Data Availability Statement: All relevant data are in the paper.

Funding: The authors received no specific funding for this work.

Abstract

Brachiopods were thought to have dominated deep-sea hydrothermal vents and hydrocarbon seeps for most of the Paleozoic and Mesozoic, and were believed to have been outcompeted and replaced by chemosymbiotic bivalves during the Late Cretaceous. But recent findings of bivalve-rich seep deposits of Paleozoic and Mesozoic age have questioned this paradigm. By tabulating the generic diversity of the dominant brachiopod and bivalve clades—dimerelloid brachiopods and chemosymbiotic bivalves—from hydrocarbon seeps through the Phanerozoic, we show that their evolutionary trajectories are largely unrelated to one another, indicating that they have not been competing for the same resources. We hypothesize that the dimerelloid brachiopods generally preferred seeps with abundant hydrocarbons in the bottom waters above the seep, such as oil seeps or methane seeps with diffusive seepage, whereas seeps with strong, advective fluid flow and hence abundant hydrogen sulfide were less favorable for them. At methane seeps typified by diffusive seepage and oil seeps, oxidation of hydrocarbons in the bottom water by chemotrophic bacteria enhances the growth of bacterioplankton, on which the brachiopods could have filter fed. Whereas chemosymbiotic bivalves mostly relied on sulfide-oxidizing symbionts for nutrition, for the brachiopods aerobic bacterial oxidation of methane and other hydrocarbons played a more prominent role. The availability of geofuels (i.e. the reduced chemical compounds used in chemosynthesis such as hydrogen sulfide, methane, and other hydrocarbons) at seeps is mostly governed by fluid flow rates, geological setting, and marine sulfate concentrations. Thus rather than competition, we suggest that geofuel type and availability controlled the distribution of brachiopods and bivalves at hydrocarbon seeps through the Phanerozoic.

Introduction

The idea of bivalves replacing brachiopods as the dominant benthic filter feeders over the course of the Phanerozoic is one of the oldest macroevolutionary patterns discussed in paleontology [1–3]. Originally observed in the rich fossil record of shallow marine environments, a

Competing interests: The authors have declared that no competing interests exist.

similar pattern was also seen at deep-sea hydrothermal vents and hydrocarbon seeps [4]. These ecosystems differ radically from all others in being based on chemosynthetic primary production rather than photosynthesis [5]. The evolution of the chemosynthesis-based faunal communities may therefore be buffered from mass extinctions and other disruptions of photosynthesis-based food chains [6–8] and may instead be driven by events affecting the discharge of the reduced chemicals (referred to as geofuels hereafter) that fuel the chemosynthesis-based food chain [9]. The animals that dominate chemosynthesis-based ecosystems show extensive physiological adaptations, commonly involving a symbiosis with chemotrophic bacteria, resulting in faunal communities with a low diversity but high abundance of highly specialized animals [10, 11].

A first compilation of Phanerozoic vent and seep sites with brachiopods and/or bivalves indicated a pattern of a Paleozoic to middle Mesozoic dominance of brachiopods in these ecosystems, and the chemosymbiotic bivalves became dominant from the Late Cretaceous onward [4]. Subsequent research confirmed a number of Paleozoic and early Mesozoic seep deposits dominated by brachiopods, including *Septatrypa* in the Silurian [12], *Dzieduszyckia* in the Devonian [13], *Ibergirhynchia* in the Carboniferous [14], *Halorella* in the Triassic [15], and *Sulcirostra* and *Anarhynchia* in the Jurassic [16–18], supporting this hypothesis. However, also discovered were seep deposits at which inferred chemosymbiotic bivalves were a major faunal element, including the modiomorphid genus *Ataviaconcha* at Silurian and Devonian sites in Morocco [19, 20] and kalenterid and anomalodesmatan genera at Triassic sites in Turkey [21, 22]. These findings challenge the claim of predominantly brachiopod-dominated pre-Cretaceous vents and seeps, and raise the questions why some sites were dominated by brachiopods and others by bivalves.

A further complication in this context is that the feeding strategy (or strategies) of vent and seep-inhabiting brachiopods is essentially unknown. The large size of certain species and brachiopod dominance at some sites may intuitively suggest that they were chemosymbiotic [18, 23, 24]. However, brachiopods are virtually absent from extant vents and seeps, and the few known examples are filter feeder that take advantage of the hard substrate provided by authigenic carbonates exposed at some seeps [25]. Furthermore, the general brachiopod bauplan lacks certain features, such as gills and a closed cardio-vascular system, which are important for hosting chemosymbionts in bivalves or tube worms [26, 27] and make brachiopods ill-suited for coping with the toxicity of hydrogen sulfide. Furthermore, the brachiopods that formed mass occurrences at ancient seeps are not drawn randomly from the brachiopod tree of life but instead belong, with one exception, to a single clade: the Dimerelloidea [28]. The one exception is the genus *Septatrypa* from a Silurian seep deposit in Morocco [12], which belongs to a different rhynchonellate order than the dimerelloids. Because insights into the feeding strategy of seep-dominating brachiopods are only available for the dimerelloids (see below), our study focuses exclusively on members of this clade. One intriguing feature of many seep deposits dominated by dimerelloids is the sheer abundance of the brachiopods, which by far exceeds the abundance of chemosymbiotic bivalves at fossil seep deposits ([13, 15, 17, 29], own observations).

Here we present the hypothesis that dimerelloid brachiopods and chemosymbiotic bivalves coexisted at hydrocarbon seeps during the Paleozoic and Mesozoic by partitioning the locally available geofuels. We propose that the presence, absence, or relative abundance of each clade at a given site was largely controlled by the chemical composition of the seep fluids (the proportions of sulfide, methane, and/or oil), which in turn was influenced by seepage intensity and perhaps seawater sulfate concentrations. Our hypothesis is based on (i) a tabulation of the diversity of the ecologically dominant bivalve and brachiopod genera at seeps through the Phanerozoic; (ii) recent improvements in geochemically assessing the composition of fluids

and the intensity of fluid flow at ancient seeps; and (iii) a set of derivations and assumptions on the paleoecology of the dominant brachiopod and bivalve clades at ancient hydrocarbon seeps.

Approach

Compilation of generic diversity of bivalves and brachiopods

Modern seep communities are characterized by the low diversity but high abundance of a few taxa that are able to take advantage of the unique food resources at seeps [5, 30]. Thus our compilation of brachiopod and bivalve diversity at seeps includes only the ecologically dominant clades instead of the full range of genera known from fossil seep deposits to avoid the results being blurred by chance occurrences or by local taxa fortuitously taking advantage of the abundance of food at a seep site (known as ‘vagrants’ or ‘background taxa’, cf. [31] Sibuet and Olu, 1998). Among bivalves, only chemosymbiotic or in the case of extinct taxa, inferred chemosymbiotic taxa, were included. Although chemosymbiotic bivalves may occasionally be rare, in general they dominate seep deposits numerically (cf. [9] Kiel, 2015; [32] Campbell, 2006).

Among brachiopods, only dimerelloid genera reported from geochemically confirmed seep deposits are included because (i) with a single exception (see below), only dimerelloids occurred at ancient seeps in rock-forming quantities; all other brachiopods reported from ancient seeps (including various terebratulids, i.e. [33–37]) represent minor faunal elements that most likely took advantage of exposed hard substrate [28], and (ii) the feeding strategies of brachiopods at ancient seeps remain unclear except for the dimerelloids, for which some clues are available [38]. The only exception to (i) is *Septatrypa*, which occurs in rock-forming quantities in a Silurian seep deposit from Morocco [12]. This genus belongs to a different rhynchonellate order than the dimerelloids, hence we refrain from extending the feeding strategy inferred from the Cretaceous dimerelloid *Peregrinella* to this Silurian genus.

The dataset includes 42 bivalve and seven brachiopod genera; their stratigraphic distributions, life habits (epifaunal, semi-infaunal, and infaunal), and all relevant references are shown in Table 1. To assess a potential sampling bias, we also compiled the number of seep-bearing rock units at which these taxa were found (Table 2), as done in a previous quantitative study on seep faunas [8].

Proxies for fluid chemistry and flow intensity at ancient seeps

Criteria used to reconstruct the composition of seep fluids and seepage intensity are based on the mineralogy and microfabric of authigenic carbonate and sulfide minerals, stable isotope signatures of authigenic minerals, and lipid biomarkers [133–140]. This set of methods, however, does not allow to reliably discern methane-seep and oil-seep deposits. The use of lipid biomarkers seems an obvious approach for such discrimination, but is hampered by the facts that (i) sulfate-driven anaerobic oxidation of methane occurs at oil seeps too [141] and (ii) the prokaryotes responsible for anaerobic degradation of oil components in marine settings (i.e. sulfate-reducing bacteria; [142]) may yield similar biomarkers like the sulfate-reducing bacteria involved in anaerobic oxidation of methane. Even more problematic, the great abundance of oil components in some seep deposits tends to mask the lipid biomarkers reflecting local biogeochemical processes [143]. Such masking by oil-derived components is a particular problem for the recognition of possible ancient oil-seep deposits, since the timing of oil ingress (syngenetic vs. epigenetic) is commonly difficult to constrain [13]. The sheer presence of pyrobitumen (i.e. metamorphosed oil) in ancient seep limestones is consequently not sufficient proof for oil seepage. These problems prompted the development of an inorganic geochemical

Table 1. Dimerelloid brachiopod genera and (inferred) chemosymbiotic bivalve genera in ancient hydrocarbon-seep deposits. New brachiopod and bivalve genera established since Mike Sandy’s review of dimerelloid brachiopods as seep-inhabitants in 1995 [23] are marked by an asterisk (*); see section ‘Diversity pattern’ for reasoning.

NEOGENE	
Dimerelloid brachiopods:	none.
Infaunal bivalves:	<i>Acharax</i> [39], <i>Anodontia</i> [40], <i>Channelaxinus</i> * [41], <i>Cubatea</i> * [42], <i>Elliptiolucina</i> *, <i>Elongatolucina</i> * [43], <i>Isorropodon</i> [44], <i>Lucinoma</i> , <i>Meganodontia</i> * [41], <i>Megaxinus</i> [45], <i>Myrteopsis</i> , <i>Nipponothracia</i> *, <i>Pegaphysema</i> [43], <i>Pliocardia</i> [46], <i>Solemya</i> [47], <i>Thyasira</i> [48].
Semi-infaunal bivalves:	<i>Archivesica</i> [41], <i>Callogonia</i> [49], <i>Calyptogena</i> [50], <i>Conchocele</i> [42, 47], <i>Gigantidas</i> * [51], <i>Notocalyptogena</i> * [52], <i>Pleurophopsis</i> (= <i>Adulomya</i>) [42, 53, 54].
Epifaunal bivalves:	<i>Bathymodiolus</i> [41, 51].
PALEOGENE	
Dimerelloid brachiopods:	none.
Infaunal bivalves:	<i>Acharax</i> [42, 55], <i>Amanocina</i> *, <i>Cubatea</i> *, <i>Elliptiolucina</i> *, <i>Elongatolucina</i> * [43, 56], <i>Epilucina</i> [57], <i>Lucinoma</i> [58], <i>Maorityas</i> [59], <i>Nipponothracia</i> * [43], <i>Nucinella</i> [55], <i>Nymphalucina</i> [43], <i>Pliocardia</i> [42], <i>Rhacothyas</i> * [33], <i>Solemya</i> [60], <i>Thyasira</i> [59].
Semi-infaunal bivalves:	<i>Conchocele</i> [59], <i>Hubertschenckia</i> [44], <i>Pleurophopsis</i> [42].
Epifaunal bivalves:	<i>Bathymodiolus</i> , <i>Idas</i> , <i>Vulcanidas</i> * [60].
LATE CRETACEOUS	
Dimerelloid brachiopods:	none.
Infaunal bivalves:	<i>Acharax</i> [61], <i>Amanocina</i> * [43], <i>Cubatea</i> * [43], <i>Miltha</i> [61], <i>Myrtea</i> [61], <i>Nucinella</i> [62], <i>Nymphalucina</i> [43], <i>Solemya</i> [63, 64], <i>Tehamatea</i> * [43], <i>Thyasira</i> [48, 59].
Semi-infaunal bivalves:	<i>Caspiconcha</i> * [65, 66], <i>Conchocele</i> [59, 63].
Epifaunal bivalves:	none.
EARLY CRETACEOUS	
Dimerelloid brachiopods:	<i>Peregrinella</i> [29, 38].
Infaunal bivalves:	<i>Acharax</i> [67], <i>Amanocina</i> * [43], <i>Cretaxinus</i> * [68], <i>Cubatea</i> * [43], <i>Nucinella</i> [67–69], <i>Solemya</i> [64, 68, 70], <i>Tehamatea</i> * [43], <i>Thyasira</i> [59].
Semi-infaunal bivalves:	<i>Caspiconcha</i> * [65].
Epifaunal bivalves:	none.
JURASSIC	
Dimerelloid brachiopods:	<i>Anarhynchia</i> [18], <i>Cooperrhynchia</i> [71], <i>Sulcirostra</i> [17].
Infaunal bivalves:	<i>Acharax</i> [67], <i>Beauvoisina</i> * [43], <i>Nucinella</i> [68], <i>Solemya</i> [68], <i>Tehamatea</i> * [37].
Semi-infaunal bivalves:	<i>Caspiconcha</i> * [65].
Epifaunal bivalves:	none.
TRIASSIC	
Dimerelloid brachiopods:	<i>Halorella</i> [15, 21].
Infaunal bivalves:	<i>Nucinella</i> [15], <i>Aksumya</i> * [22].
Semi-infaunal bivalves:	<i>Terzileria</i> *, <i>Kasimlara</i> * [22].
Epifaunal bivalves:	none.
CARBONIFEROUS	

(Continued)

Table 1. (Continued)

Dimerelloid brachiopods:	<i>Ibergirhynchia</i> * [72].
Infaunal bivalves:	'solemyid' [14].
Semi-infaunal bivalves:	none.
Epifaunal bivalves:	none.
DEVONIAN	
Dimerelloid brachiopods:	<i>Dzieduszyckia</i> [13].
Infaunal bivalves:	<i>Dystactella</i> [20].
Semi-infaunal bivalves:	<i>Ataviaconcha</i> * [20].
Epifaunal bivalves:	none.

<https://doi.org/10.1371/journal.pone.0221887.t001>

Table 2. Seep-bearing rock units or equivalents, sorted into the same geologic time bins as the genera in Table 1; Fm = Formation.

Site(s)	Rock unit or equivalent	Reference
NEOGENE		
Fukaura town	Akaishi Fm	[50]
Ogasawara's slumped block	Aokiyama Fm	[47]
Stirone River seep complex	Argille Azzurre Fm	[73]
LACM loc. 6132, USGS M2790	Astoria Fm	[44]
Akanuda Limestone	Bessho Fm	[74]
Bexhaven, Karikarihuata, Moonlight North, Rocky Knob, Tauwhareparae, Waipiro	Bexhaven Limestone	[51]
Liog-Liog Point	Bata Fm	[75]
Takangshan quarry	Gutingkeng Fm	[76]
Ikegami	Hayama Fm	[77]
Shimo-sasahara, near Yatsuo	Higashibessho Fm	[46]
Oinomikado & Kanehara 1938 loc.	Higashiyama Oil field	[47]
Saitama conglomerate	Hiranita Fm	[78]
Nagasawa & Oyamada's 1996 loc.	Hongo Fm	[47]
Kamada's Honya loc.	Honya Fm	[47]
Cantera Portugalete	Husillo Fm	[42]
Haunui, Ugly Hill, Wanstedt	Ihungia Series	[79]
slumped blocks, YDFAB 1993	Ikedo Fm	[47]
Joban coal field	Kabeya Fm	[80]
Doguchi Bridge	Kawazume Fm	[47]
Izura Kanko Hotel	Kokozura Fm	[49]
Matsudai, Sugawa	Kurokura Fm	[81]
Freeman's Bay, Godineau River, Jordan Hill	Lengua Fm	[42]
Casa Cavalmagra, Case Rovereti, Castellvecchio, Le Colline, Montepetra	Marnoso-arenacea Fm	[41]
Kanie's 1991 juvenile <i>Calyptogena</i> loc.	Misaki Fm	[47]
Morai, Otatsume's 1942 loc.	Morai Fm	[47]
loc. M2 of Shikama & Kase, 1976	Morozaki Group	[47]
Limestone nodule in Kochi	Muroto Fm	[82]
Ozaki 1958 loc.	Naari Fm	[83]

(Continued)

Table 2. (Continued)

Site(s)	Rock unit or equivalent	Reference
Nadachi Signal Station	Nadachi Fm	[84]
Amano et al 1994 loc.	Nanbayama Fm	[47]
Nakanomata seep deposit	Nodani Fm	[85]
Rekifune seep	Nupinai Fm	[86]
Kanno & Akatsu 1972 loc.	Nupinaigawa mudstone	[47]
Yokohama City	Ofuna Fm	[47]
Kita-Kuroiwa	Ogaya Fm	[74]
Sakurai's 2003 loc.	Ogikubo Fm	[47]
Hayashi's 1973 localities	Ohno Fm	[47]
Ogasawara 1986 Akita loc.	Onnagawa Fm	[47]
Huso Clay Member	Pozon Fm	[87]
Quinault seep	Quinault Fm	[88]
Hayashi & Miura's 1973 loc.	Ryusenji Fm	[47]
Buton asphalt deposit	Sampalokossa Beds	[89]
Matsumoto & Hirata's 1972 Shizuoka loc.	Setogawa Group	[82]
Oshima	Shikiya Fm	[90]
Kawaguchi/Kotto	Shiramazu Fm	[91]
SOFZ—Baths Cliffs fauna	SOFZ	[87]
Joban coal field	Taira Fm	[80]
Kanno & Ogawa 1964 loc.	Takinoue Fm	[92]
Kanno's 1967 Tokyo loc.	Tateya Fm	[47]
Oinomikado & Kanehara's 1938 loc.	Teradomari Fm	[47]
Sasso delle Streghe	Termina Fm	[41]
Abisso Mornig, Casa Carnè, Casa Piantè	Tossignano marls	[41]
Tanaka's Matsumoto City loc.	Uchimura Fm	[47]
Katto & Masuda's 1978 pyrite loc.	Uematsu Fm	[47]
Matsumoto's 1966 & 1971 Shizuoka locs.	Wappazawa Fm	[47]
Kanehara's 1937 loc.	Yunagaya and Shirado Groups	[93]
PALEOGENE		
Fossildalen	Basilika Fm	[35]
Buje petrol station	Central Istria flysh	[94]
Diapiric mélange, Joes River	Diapiric melange	[87]
Angela Elmira asphalt mine	Elmira Asphalt	[95]
Bear River (LACMIP loc. 5802)	equivalent of Lincoln Creek Fm	[96]
Belen	Heath shales	[95]
LACMIP loc. 12385, CSUN loc. 1583	Humptulips Fm	[96]
LACMIP loc. 17101	Jansen Creek Member	[60]
Rock Creek Oregon, Vernonia-Timber Road	Keasey Fm	[97]
CR2, UWBM loc. B-7451, LACMIP loc. 5843, LACMIP loc. 16504, SR1-SR4	Lincoln Creek Fm	[60, 98–100]
Bullman Creek, LACMIP loc. 6958, Shipwreck Point	Makah Fm	[58, 59, 101]
Cima Sandstone lentil	Moreno Fm	[102]
Kami-Atsunai railway station	Nuibetsu Fm	[103]
Urahoru concretion	Oomagari Fm	[47]
Palmar-Molinera-Road	Palmar-Molinera	[95]
Huberschenkia-loc. (Yayoi site)	Poronai Fm	[104]

(Continued)

Table 2. (Continued)

Site(s)	Rock unit or equivalent	Reference
East Twin River, LACMIP locs. 15621, 6295, Whiskey Creek	Pysht Fm	[59, 100, 101, 105]
North Slope	Sagavanirktok Fm	[32]
Kiritachi	Sakasagawa Fm	[59]
Tanami	Shimotsuyu Fm	[55]
Columbia River, UWBM loc. B-7446	Siltstone of Shoalwater Bay	[60]
West Fork of Grays River	Siltstone of Unit B	[59]
Lomitos	Talara Fm	[95]
Wagonwheel seep CSUN loc. 1580	Wagonwheel Fm	[57]
LATE CRETACEOUS		
Awanui GS 688, Waipiro I, Waipiro III	East Coast Allochthon	[69]
Guenoc Ranch	Great Valley Group	[64]
Maeshima	Himenoura Group	[59]
Seymour Island	Lopez de Bertodano Fm	[63]
Romero Creek	Moreno Fm	[64]
Sada Limestone	Nakamura Fm	[106]
Omagari lens, Yasukawa seep	Omagari Fm	[107, 108]
Tepee Buttes	Pierre Shale	[109]
Snow Hill Island	Snow Hill Island Fm	[63]
Alton Sink, North & South Cottonwood Wash	Tropic Shale	[110]
Obira-cho	Yezo Supergroup	[61]
EARLY CRETACEOUS		
Sassenfjorden carbonates near Freiberg	Agardhfjellet Fm	[111]
Eagle Creek	Beskidy Range	[112]
Yongzhu bridge	Budden Canyon Fm	[65]
Bonanza Creek	Chebo Fm	[113]
Bonanza Creek	Chisana Fm	[114]
Prince Patric & Ellef Ringnes isl&s	Christopher Fm	[115]
Bear Creek, Foley Canyon, Rocky Creek	Crack Canyon Fm	[64]
Awanui I & II	East Coast Allochthon	[69]
Novaya Zemlya III sandy limestone	float	[116]
Little Indian Valley	Franciscan Complex	[64]
Gravelly Flat	Gravelly Flat Fm	[64]
East Berryessa, Knoxville, Rice Valley, West Berryessa, Wilbur Springs	Great Valley Group	[64]
Baska	Hradiště Fm	[117]
Cold Fork of Cottonwood Creek	Lodoga Fm	[118]
Musenalp	Musenalp	[119]
Ispaster	Ogella unit	[120]
W. Kuban	Oubine Valley	[121]
Planerskoje	Planerskoje section	[122]
East of Lhasa	Sangxiu Fm	[123]
Sinaia Beds	Sinaia Fm	[124]
Koniakov, Koniakover Schloss, Raciborsko	Upper Grodziszczce beds	[29, 125]
Curnier, Rottier	Vocontien Basin	[38]
Kuhnpasset Beds	Wollaston Forland	[70]
Ponbetsu, Utagoesawa	Yezo Supergroup	[66, 126]

(Continued)

Table 2. (Continued)

Site(s)	Rock unit or equivalent	Reference
JURASSIC		
Sassenfjorden carbonates	Agardhfjellet Fm	[111]
Gateway Pass Limestone Bed	Atoll Nunataks Fm	[127]
Novaya Zemlya I & II	float	[116]
Charlie Valley	Fransiscan Complex	[64]
NW Berryessa, Stony Creek	Great Valley Group	[64]
Copper Island	Inklin Fm	[18]
Seneca	Keller Creek Fm	[17]
Paskenta	Stony Creek Fm	[128]
Beauvoisin	Terres Noires Fm	[129]
TRIASSIC		
Terziler and Dumanlı	Kasimlar shales	[21]
Graylock Buttes	Rail Cabin mudstone	[15]
CARBONIFEROUS		
Tentes Mound	Calcaires de l'Iraty	[130]
Ganigobis	Ganigobis Shale Member	[131]
Iberg seep	Iberg reef	[14]
DEVONIAN		
Sidi Amar	Devonian-Carboniferous mélange	[13]
Hollard Mound	<i>Pinacites</i> limestone	[132]

<https://doi.org/10.1371/journal.pone.0221887.t002>

proxy for oil seepage. Molybdenum to uranium ratios in conjunction with rare earth element contents of seep limestones have been shown to allow oil-seep and methane-seep deposits to be discriminated [144]. The application of this proxy resulted in the confirmation that Late Devonian limestones from Morocco with the dimerelloid brachiopod *Dzieduszyckia* formed at oil seeps. Future work will have to reveal if some of the other seep limestones with dimerelloids, for which the presence of pyrobitumen was documented, are oil-seep deposits as well.

Another crucial aspect for our reconstruction of the adaptation of bivalves and brachiopods to seep ecosystems concerns the mode in which methane was predominantly oxidized (i.e. anaerobic vs. aerobic methanotrophy). It seems straightforward that episodes of low seawater sulfate concentration favor the release of methane into bottom waters [9, 145], with less methane being oxidized at the sulfate-methane transition zone and more methane available for aerobic methane-oxidizing bacteria. Interestingly, also the mode of seepage (i.e. advective vs. diffusive) is likely to affect the relative proportions of anaerobic and aerobic methanotrophy. Although possibly counterintuitive at first glance, it has been shown that more methane tends to permeate the barrier at the sulfate-methane transition zone formed by sulfate-driven anaerobic oxidation of methane at diffusive seeps compared to advective seeps [146–148]. This circumstance agrees with the observation of more abundant biomarkers of aerobic methanotrophic bacteria in seep deposits reflecting diffusive seepage (Natalicchio et al., 2015) and the inferred affinity of *Peregrinella* to diffusive seepage and aerobic methanotrophy [38]. Likewise, seeps with advective flow will tend to be characterized by high concentrations of hydrogen sulfide—resulting from pronounced sulfate-driven anaerobic oxidation of methane at the sulfate-methane transition zone—whereas at seeps with diffusive flow more methane will be oxidized with molecular oxygen by aerobic methanotrophs.

Assumptions on chemosymbiosis in fossil bivalves

For the sake of our hypothesis, we assume that all bivalve clades that dominated seep deposits before the Cenozoic era were hosting thiotrophic (i.e. sulfide-oxidizing) symbionts only. For most clades, including the Solemyidae, Nucinellidae, Thyasiridae, and Lucinidae, this is a fair assumption based on the actualistic principle: members of these families host thiotrophic symbionts only [149]. The only bivalve clade known to harbor methanotrophic symbionts is the Bathymodiolinae [150, 151]. A detailed study on their evolutionary history [152] showed that the path to methanotrophic symbiosis is difficult: first, only 13 out of 52 investigated species harbor methanotrophs; second, intracellular rather than extracellular symbiont location seems to be required to host methanotrophs; and third, methanotrophic symbiosis was acquired fairly recently in the evolutionary history of the bathymodiolins (in the early Miocene), while the original thiotrophic symbiosis goes much further back in time [152]. Remarkable in this context is that other bivalve families with intracellular symbionts have apparently not developed methanotrophic symbiosis, despite having a similarly long (Vesicomidae; cf. [153] Kiel, 2010) or much longer evolutionary history (Solemyidae, Lucinidae; cf. [20] Hryniewicz et al., 2017; [154] Taylor et al., 2011).

Inferring chemosymbiosis or even symbiotic types is much harder in extinct taxa such as the modiomorphids—a clade commonly found at ancient vents and seep [20, 155]—because there is presently no way to proof chemosymbiosis in the fossil record. However, some clues may be drawn from the geologic history of the modiomorphid/kalenterid genus *Caspiconcha*, which is found in many Late Jurassic to Late Cretaceous seep deposits around the world [66, 70, 122]. *Caspiconcha* was common during most of the Early Cretaceous but declined in abundance and eventually disappeared after marine sulfate concentrations—and hence sulfide availability at seeps—dropped in the Aptian [9, 66, 145]. If *Caspiconcha* had had methanotrophic symbionts, it should not have been affected by the low sulfate concentrations; on the contrary, it should have thrived due to the higher availability of methane at seeps (see above). But *Caspiconcha* responded to the mid- to Late Cretaceous low sulfate concentrations in a way expected for a taxon with thiotrophic symbionts. Based on this observation, we assume that *Caspiconcha*, and seep-inhabiting modiomorphids/kalenterids during the Phanerozoic in general, had thiotrophic rather than methanotrophic symbionts. Furthermore, because virtually all extant bivalves taking up geofuels for their symbionts from pore water have thiotrophic symbionts [11, 149], the infaunal and semi-infaunal lifestyle of the inferred chemosymbiotic bivalves at pre-Cenozoic seeps suggests that they relied on thiotrophy rather than methanotrophy.

The resource partitioning hypothesis: Outline and arguments

Diversity pattern

The bivalve genera at seeps are of low diversity during the Paleozoic followed by a continuous increase in diversity since the Triassic (Fig 1). Prior to the Cenozoic, this increase in diversity is mostly among infaunal genera, plus a few semi-infaunal ones; epifaunal bivalves appeared only in the Cenozoic (Fig 1). The continuous rise in bivalve diversity at seeps, at least since the Mesozoic, appears to mirror the general Phanerozoic increase in bivalve diversity [2]. But the low diversity of semi-infaunal and epifaunal bivalves at seeps and their rapid diversification in the Cenozoic are unlike the general Phanerozoic pattern of bivalve ecospace occupation with its similar proportions of infaunal, semi-infaunal, and epifaunal taxa in the Mesozoic and Cenozoic [156]. This bias toward infaunal taxa might result from our focus on chemosymbiotic bivalves. Indeed, the bivalve diversification pattern at seeps is quite similar to that of the most diverse clade of shallow-water chemosymbiotic bivalves—the Lucinidae [157]—which also

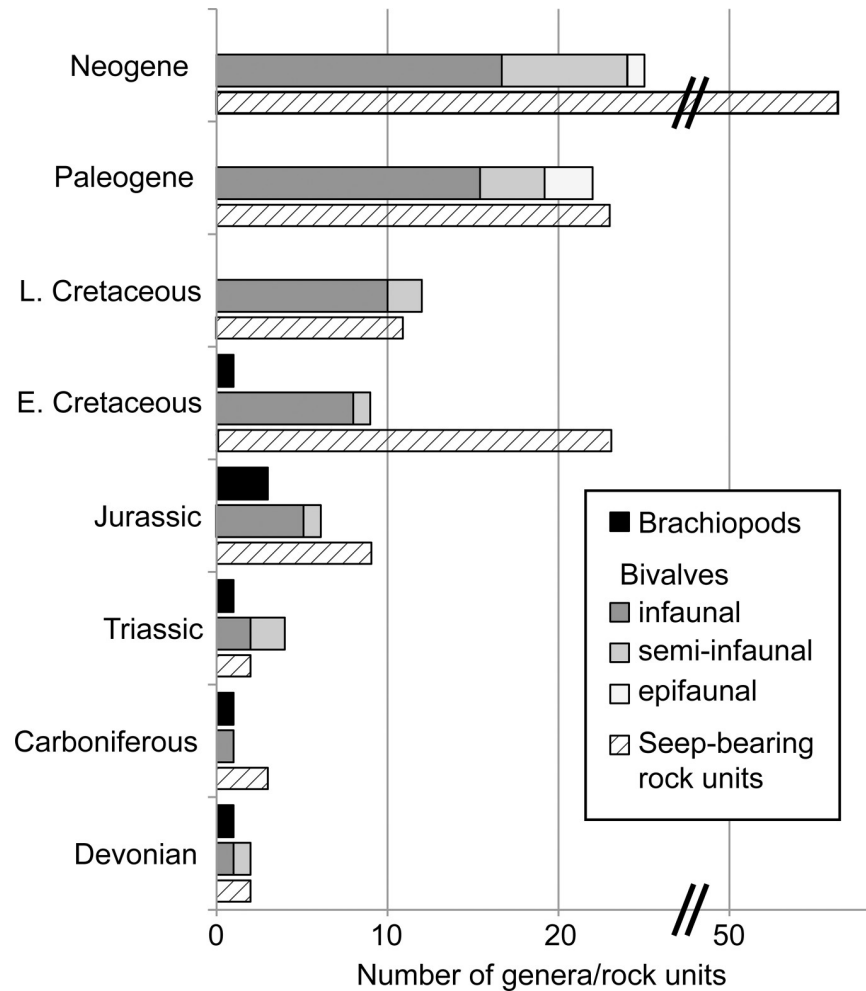


Fig 1. Phanerozoic generic diversity of chemosymbiotic bivalves and dimerelloid brachiopods at hydrocarbon seeps, and the number of seep-bearing rock units. Note break in scale and that the Permian was omitted because no confirmed seep deposits have been reported from this period to date. E. = Early, L. = Late.

<https://doi.org/10.1371/journal.pone.0221887.g001>

shows low diversity during the Paleozoic and a continuous increase starting in the Mesozoic [158]. One may thus argue that bivalve diversity at seeps follows the diversity of chemosymbiotic bivalves in shallow water. Epifaunal and semi-infaunal chemosymbiotic bivalves such as bathymodiolins and vesicomyids are virtually absent from shallow water [149] and appear to be a unique feature of vent and seep environments.

Although this trend in increasing generic diversity among bivalves is roughly mirrored by an increase in the number of seep-bearing rock units (Fig 1), this pattern does not hold when seen in detail: (i) there is an increase in bivalve diversity from the Early to the Late Cretaceous despite a >50% decrease in the number of seep-bearing rock units; (ii) there are roughly identical numbers of seep-bearing rock units in the Early Cretaceous and in the Paleogene, but almost twice as many bivalve genera in the Paleogene; (iii) the number of seep-bearing rock units doubles from the Paleogene to the Neogene, accompanied by only a minor increase in bivalve diversity. Thus, we are confident that the observed pattern in bivalve diversity at seeps represents a real phenomenon, rather than being a sampling bias, although it is clear that the Paleozoic and early Mesozoic are still undersampled and likely contained higher numbers of bivalves at seeps.

Seep-dwelling dimerelloids are of low diversity during the Paleozoic, show a slight increase during the Jurassic and disappear after the Early Cretaceous (Fig 1). This pattern does not mirror the general Phanerozoic brachiopod diversity pattern of Paleozoic dominance, end-Permian decline, and low post-Paleozoic diversity [2]. Two observations indicate that this pattern is not significantly affected by sampling biases: first, despite the large number of seep-bearing rock units in the Early Cretaceous, there is only a single dimerelloid genus at seeps in this epoch. Second, since the first review of dimerelloid genera as potential seep-inhabiting brachiopods in 1995 [23], only a single new dimerelloid genus has been described: the Carboniferous *Ibergirhynchia* [72]. During the same time interval, 18 new genera of seep-inhabiting bivalves have been described, including nine from the Mesozoic and Paleozoic (indicated by asterisks in Table 1). This indicates that despite being undersampled, the relative proportions of brachiopod and bivalve genera at Paleozoic and early Mesozoic seeps shown in Fig 1 are fairly robust. The diversity pattern also does not confirm the paradigm that vents and seeps were dominated by brachiopods during the Paleozoic and most of the Mesozoic and that chemosymbiotic bivalves took over only in the Late Cretaceous [4]. Instead, dimerelloid brachiopods and chemosymbiotic bivalves have coexisted at seeps for nearly half of the Phanerozoic (Late Devonian to Late Cretaceous, ~240 million years [19]). This raises the question whether chemosymbiotic bivalves have indeed “exploited these habitats better than brachiopods” ([4] Campbell and Bottjer, 1995, p. 323).

Ecology of seep-inhabiting brachiopods

At modern seeps, coexisting taxa tend to be spatially separated because different organisms require different types and amounts of geofuels, and the distribution of these geofuels is in turn controlled by flow rates and the resulting geochemical gradients [31, 159]. For example, among two species of vesicomid clams at seeps in Monterey Canyon, *Archivesica kilmeri* requires 10 times higher ambient sulfide concentrations than *Calyptogena pacifica*, and consequently *C. pacifica* occupies the periphery of the seep where sulfide flux is low, whereas *A. kilmeri* lives in the sulfide-rich center of the seep [160]. Analogous faunal distribution patterns in relation to geochemical gradients can be traced into the fossil record: mollusks at Cretaceous seeps show similar zonation as their modern analogs [108, 109], and predation scar frequencies in Oligocene chemosymbiotic bivalves are inversely related to the different, assumed sulfide requirements of these species, most likely because the more sulfidic areas were avoided by predators and hence the bivalves with the highest sulfide requirements were spared from predation [161].

The Cretaceous seep-inhabiting dimerelloid brachiopod *Peregrinella* provides a particularly intriguing case of a geochemically controlled distribution pattern: *Peregrinella* was shown to have grown to much larger size at seeps with slow, diffusive fluid flow compared to sites with strong, advective fluid flow [38]. Because advective fluid flow releases more sulfide to the seabed than diffusive flow [146, 159], this pattern was interpreted as evidence that sulfide-rich seep sites were not ideal for *Peregrinella* and that bacterial, aerobic methane oxidation might have played a more prominent role in its nutrition [38]. That study used the abundance of early diagenetic fibrous cement in the seep limestone as a proxy for seepage intensity—with cement abundance positively correlated with seepage intensity [135]—and the authors pointed out that various other dimerelloids, including the very large *Dzieduszyckia*, lived at sites with very abundant seep cement (*Anarhynchia* even at an ancient hydrothermal vent site), and concluded that different dimerelloids might have had different feeding strategies [38].

Contrary to this claim, here we argue that seep-inhabiting dimerelloids in general relied on hydrocarbon-oxidizing bacteria for nutrition, rather than on sulfide oxidation. The presence

of methane and oil in the water column results in rapid growth of bacterioplankton that takes advantage of these energy sources [162, 163]. We put forward the hypothesis that dimerelloids thrived by feeding on the abundant bacterioplankton at seeps where high amounts of hydrocarbon geofuels effused into bottom waters. To the best of our knowledge, there is no present-day example of a species at seeps with this feeding strategy. The closest modern analogs are probably certain species of stalked barnacles (Cirripedia) living at vents in the West Pacific Ocean [164] and near the Antarctic Peninsula [165], which are adapted to feeding on very fine particles such as bacteria and fine debris [164]. In the following, we go through all pre-Cretaceous (that is: pre-*Peregrinella*) instances of dimerelloids at hydrocarbon seeps to outline our arguments for (i) fluid composition and flow intensity at each site, and (ii) their implications for the dimerelloids' preference for hydrocarbons over sulfide.

Cooperrhynchia. The Late Jurassic dimerelloid *Cooperrhynchia* is known from a single deposit only, where it is not superabundant but instead occurs in patches ([71] Sandy and Campbell, 1994; SK, own observation). The most common chemosymbiotic bivalve at this site is a solemyid [67], a group known to tolerate only low sulfide concentrations [159]. Similarly, the scarcity of ^{13}C -depleted crocetane and the presence of ^{13}C -depleted biphytane in the deposit with *Cooperrhynchia* [166] is typical of seep limestones that resulted from diffusive seepage [135], which would have come along with low sulfide concentrations close to the seabed.

Anarhynchia. This is the only dimerelloid genus yet known from both seeps and vents. An Early Jurassic seep deposit in northern British Columbia is dominated by *Anarhynchia smithi* and contains virtually no other fossils [18]. Despite the presence of early diagenetic fibrous cement, *Anarhynchia smithi* probably lived in a low-sulfide environment. It occurred during a geologic time interval known for its particularly low seawater sulfate concentration [167], which most likely resulted in reduced sulfide availability at seeps (cf. [9] Kiel, 2015; [145] Wortmann and Paytan, 2012) and hence also increased methane availability. Also of Early Jurassic age is a hydrothermal vent deposit in the Franciscan Complex in California, USA, at which *Anarhynchia* cf. *gabbi* is quite common [16, 168]. This occurrence at a hydrothermal vent site undoubtedly indicates that *Anarhynchia* was able to live at or near a strong sulfide source. But this does not necessarily contradict our hypothesis: hydrothermal vents are known to emit considerable amounts of methane, to the extent that for example the Rainbow, Snake Pit, and Logatchev vent sites on the Mid-Atlantic Ridge are inhabited by *Bathymodiolus* species hosting both thiotrophic and methanotrophic symbionts [169, 170].

Sulcirostra. Also of Early Jurassic age are seep deposits with *Sulcirostra* in eastern Oregon, USA; these are monospecific mass occurrences of *Sulcirostra paronai* that apparently lack bivalves and other fossils [17]. Analogously to the reasoning for the seep-inhabiting *Anarhynchia* above that lived in a low-sulfate ocean, we consider these occurrences low-sulfide environments. The great abundance of early diagenetic fibrous cement on the other hand is in accord with advective seepage, which is in favor of high sulfide production; but such production was necessarily still limited by the sulfate concentration of pore waters. Maybe even more interestingly, the *Sulcirostra* deposit contains pyrobitumen and its authigenic carbonate phases are only moderately ^{13}C -depleted ($\delta^{13}\text{C}$ values as low as -23.5‰), both agreeing with oil seepage [17].

Halorella. An argument for a preference for low-sulfide, diffusive seeps with abundant hydrocarbons in the bottom water analogous to that for *Peregrinella* can be made for the Triassic dimerelloid *Halorella*. In seep deposits in Oregon, *Halorella* occurs in rock-forming quantities, reaches almost 10 cm in size, and chemosymbiotic bivalves are rare or absent [15]. In contrast, in seep deposits in Turkey, *Halorella* is rare to common but never abundant, it never exceeds 45 mm in size, and it co-occurs with abundant inferred chemosymbiotic bivalves,

including two species of Kalenteridae and one anomalodesmatan [21, 22]. Assuming that the abundant inferred chemosymbiotic bivalves relied on thiotrophy rather than methanotrophy, this indicates a stronger sulfide flux at the seeps with abundant bivalves compared to those without. Consequently, also *Halorella* appears to have preferred seeps with less sulfide and more methane or other hydrocarbons.

***Ibergirhynchia*.** Early Carboniferous limestones with a mass occurrence of the dimerelloid *Ibergirhynchia* on top of a drowned atoll reef probably represent the most unusual Phanerozoic seep deposit reported to date [14]. Oil—as indicated by the presence of abundant pyrobitumen in the reef and seep limestones—passed through fissures of the Devonian atoll reef and fueled a chemosynthesis-based community on top of the reef. Migration of abundant oil through the Iberg reef apparently occurred in the latest early Carboniferous when the potential source rock, the Middle Devonian Wissenbach black shale, was in the oil window [171]. Due to the lack of a sedimentary cover, a large amount of the emitted geofuels necessarily entered the bottom water and consequently favored bacterioplankton growth, which, in turn, would have been suitable for the filter-feeding brachiopods.

***Dzieduszyckia*.** The Moroccan deposit with *Dzieduszyckia* contains abundant early diagenetic fibrous cement [13]. If the seepage fluids had been dominated by methane, such a pattern would suggest a sulfide-rich environment; a context similar to that of the *Sulcistrostra* deposits of eastern Oregon. However, the presence of pyrobitumen and trace metal patterns reveal that the Upper Devonian limestone with *Dzieduszyckia* represents an oil-seep deposit [13, 144]. At oil seeps, where both oil and accessory methane escape the seabed, these geofuels facilitate bacterioplankton growth [162, 163], resulting in conditions favorable for the colonization by dimerelloid brachiopods. The Middle Devonian Hollard Mound seep deposit is also typified by abundant early diagenetic fibrous cement [132], but contains a mass occurrence of modiomorphid bivalves (*Atavioconcha*) instead of dimerelloids [19]. Unlike the *Dzieduszyckia* oil-seep deposit, thermogenic or abiogenic methane, deriving from the underlying volcanics, have been inferred as dominant geofuels of the Hollard Mound seep [172, 173]. The patterns found for the Devonian seep deposits consequently agree with the hypothesized resource partitioning between hydrocarbon-dependent brachiopods and sulfide-dependent bivalves.

In summary, there are several lines of evidence suggesting that, unlike most bivalves, dimerelloid brachiopods at Paleozoic and Mesozoic seeps were dependent on hydrocarbon rather than sulfide oxidation. Although we have made a strong case for filter-feeding on bacterioplankton for dimerelloid brachiopods, we cannot exclude the possibility that dimerelloids hosted episymbiotic bacteria on the surface of the lophophore instead of feeding on bacterioplankton. However, we do not consider this further because (i) such adaptation is unknown from living brachiopods, (ii) it would be very difficult to prove based on fossil evidence, and (iii) it does not change or add much to our hypothesis. Like episymbiosis, endosymbiosis cannot be fully excluded either. A few animals with symbionts oxidizing short-chain alkanes are known [174]. Yet, because of the lack of features in the brachiopod bauplan that are essential for endosymbiosis in other groups of animals, we consider it unlikely that the seep-dwelling dimerelloids harbored chemosymbiotic bacteria in their soft tissue.

Perhaps contrary to the scenario proposed here might be the lack of brachiopod-dominated seeps during the mid-Cretaceous to early Eocene period of low marine sulfate concentrations [9, 145]. If our scenario is correct, this time interval should have been favorable for dimerelloid brachiopods at seeps. The only explanation we can offer is that dimerelloids went extinct in the Barremian with the disappearance of *Peregrinella* [38], so that simply no suitable brachiopods were around to take advantage of the methane-rich seeps. This hypothesis is based on the following lines of evidence:

- i. the inclusion of the Cretaceous to present-day Cryptoporidae in the dimerelloids is questionable, so that *Peregrinella* is probably indeed the geologically youngest dimerelloid [175];
- ii. save for the Silurian *Septatrypa*, only dimerelloids have been able to dominate fossil seep sites, indicating that they possessed some pre-adaptation to successfully invade this habitat;
- iii. although other brachiopods, namely various terebratulids, have been found at fossil seeps [28, 33, 34, 37], they never formed mass occurrences like dimerelloids, and hence did not fill the same ecologic niche as dimerelloids;
- iv. the stratigraphic ranges of seep-inhabiting dimerelloids rarely overlap; this is particularly obvious for the three very large-sized genera *Dzieduszyckia*, *Halorella*, and *Peregrinella*, which are considered phylogenetically closely related ([28] Sandy, 2010, fig 9.6 therein) but are separated stratigraphically by 80 to 130 million years. This suggests that the genera discussed above represent repeated and temporarily very successful radiations into seep environments, which must be derived from as-yet unknown 'ghost dimerelloids' that may have been small and may have lived in cryptic or erosional settings (as suggested earlier for dimerelloids, cf. [176] Ager 1965).

Thus, the apparently only brachiopod lineage with the ability (or a trait) to colonize and to become a dominant member of vent and seep communities became extinct during the Early Cretaceous. This could explain why no brachiopod mass occurrences have been found at seeps during the theoretically favorable 'low sulfate interval' in the mid-Cretaceous to early Eocene. Furthermore, this also argues against the possibility that in the Cenozoic brachiopods were outcompeted at seeps by epifaunal bivalves or by bivalves with methanotrophic symbionts.

An analogous case of partitioning of resources instead of competition for them was recently made for Phanerozoic shallow-water brachiopods and bivalves in general [3]. This allows us to put forward the following scenario: resource partitioning controlled the evolutionary relationship between brachiopods and bivalves both in shallow marine habitats as well as at deep-water hydrocarbon seeps. But in seep environments, the animals were partitioning resources whose availability was controlled by fluid composition and flow intensity rather than by photosynthetic primary production, and hence the Phanerozoic diversity pattern of seep-dwelling animals differs from that of their shallow water relatives.

Conclusions

The diversity patterns of brachiopods and chemosymbiotic bivalves at seeps through the Phanerozoic indicate an interesting combination of evolutionary trajectories. The diversity of infaunal chemosymbiotic bivalves at seeps mirrors their diversity in shallow-marine environments, whereas epifaunal and semi-infaunal chemosymbiotic bivalves are unique to vent and seep ecosystems and are not found in shallow water. Brachiopod diversity at seeps is unlike the global shallow-marine trend, is unrelated to the diversity of seep-dwelling bivalves, and instead indicates long-term coexistence of the two clades. Therefore, bivalves and brachiopods have probably not been competing for the same resources but instead partitioned the food sources resulting from the two most common categories of geofuels in seepage fluids: (i) hydrogen sulfide and (ii) methane and oil-derived components. Chemosymbiotic bivalves mostly relied on sulfide-oxidizing symbionts for nutrition, for the brachiopods bacterial aerobic oxidation of methane and of other hydrocarbons played a more prominent role. The distribution and availability of hydrogen sulfide and methane at seeps is governed by geochemical gradients and ocean chemistry, which in turn should ultimately have controlled whether bivalves or brachiopods dominated hydrocarbon seeps, both in space and through geologic time.

Acknowledgments

We thank Krzysztof Hryniewicz (Warsaw) and three anonymous reviewers for their critical reading of the manuscript and its earlier versions.

Author Contributions

Conceptualization: Steffen Kiel, Jörn Peckmann.

Data curation: Steffen Kiel, Jörn Peckmann.

Formal analysis: Steffen Kiel, Jörn Peckmann.

Investigation: Steffen Kiel, Jörn Peckmann.

Methodology: Steffen Kiel, Jörn Peckmann.

Writing – original draft: Steffen Kiel, Jörn Peckmann.

Writing – review & editing: Steffen Kiel, Jörn Peckmann.

References

1. Agassiz L. Essay on classification. London: Longman, Brown, Green, Longmans, & Roberts, and Trübner & Co.; 1859. 381 p.
2. Gould SJ, Calloway CB. Clams and brachiopods—ships that pass in the night. *Paleobiol.* 1980; 6(4):383–96.
3. Payne JL, Heim NA, Knope ML, McClain CR. Metabolic dominance of bivalves predates brachiopod diversity decline by more than 150 million years. *Proc R Soc B.* 2014; 281:20133122. <https://doi.org/10.1098/rspb.2013.3122> PMID: 24671970
4. Campbell KA, Bottjer DJ. Brachiopods and chemosymbiotic bivalves in Phanerozoic hydrothermal vent and cold seep environments. *Geology.* 1995; 23(4):321–4.
5. Van Dover CL. The ecology of deep-sea hydrothermal vents. Princeton: Princeton University Press; 2000. 424 p.
6. Tunnicliffe V. The nature and origin of the modern hydrothermal vent fauna. *Palaios.* 1992; 7:338–50.
7. Van Dover CL, German CR, Speer KG, Parson LM, Vrijenhoek RC. Evolution and biogeography of deep-sea vent and seep invertebrates. *Science.* 2002; 295:1253–7. <https://doi.org/10.1126/science.1067361> PMID: 11847331
8. Kiel S, Little CTS. Cold seep mollusks are older than the general marine mollusk fauna. *Science.* 2006; 313:1429–31. <https://doi.org/10.1126/science.1126286> PMID: 16960004
9. Kiel S. Did shifting seawater sulfate concentrations drive the evolution of deep-sea vent and seep ecosystems? *Proc R Soc B.* 2015; 282:20142908. <https://doi.org/10.1098/rspb.2014.2908> PMID: 25716797
10. Fisher CR. Ecophysiology of primary production at deep-sea vents and seeps. In: Uiblein R, Ott JA, Stachowitch M, editors. Deep-sea and extreme shallow-water habitats: affinities and adaptations. *Bio-systematics and Ecology Series.* 1996; 11:313–36.
11. Dubilier N, Bergin C, Lott C. Symbiotic diversity in marine animals: the art of harnessing chemosynthesis. *Nat Rev Microbiol.* 2008; 6:725–40. <https://doi.org/10.1038/nrmicro1992> PMID: 18794911
12. Barbieri R, Ori GG, Cavalazzi B. A Silurian cold-seep ecosystem from the Middle Atlas, Morocco. *Palaios.* 2004; 19:527–42.
13. Peckmann J, Campbell KA, Walliser OH, Reitner J. A Late Devonian hydrocarbon-seep deposit dominated by dimerelloid brachiopods, Morocco. *Palaios.* 2007; 22:114–22.
14. Peckmann J, Gischler E, Oschmann W, Reitner J. An Early Carboniferous seep community and hydrocarbon-derived carbonates from the Harz Mountains, Germany. *Geology.* 2001; 29(3):271–4.
15. Peckmann J, Kiel S, Sandy MR, Taylor DG, Goedert JL. Mass occurrences of the brachiopod *Halorella* in Late Triassic methane-seep deposits, Eastern Oregon. *J Geol.* 2011; 119:207–20.
16. Little CTS, Herrington RJ, Haymon RM, Danelian T. Early Jurassic hydrothermal vent community from the Franciscan Complex, San Rafael Mountains, California. *Geology.* 1999; 27(2):167–70.

17. Peckmann J, Sandy MR, Taylor DG, Gier S, Bach W. An Early Jurassic brachiopod-dominated seep deposit enclosed by serpentinite, eastern Oregon, USA. *Palaeogeogr, Palaeoclimat, Palaeoecol.* 2013; 390:4–16.
18. Pálffy J, Kovács Z, Price GD, Vörös A, Johannson GG. A new occurrence of the Early Jurassic brachiopod *Anarhynchia* from the Canadian Cordillera confirms its membership in chemosynthesis-based ecosystems. *Canadian Journal of Earth Sciences.* 2017; 54:1179–93.
19. Jakubowicz M, Hryniewicz K, Belka Z. Mass occurrence of seep-specific bivalves in the oldest-known cold seep metazoan community. *Scientific Reports.* 2017; 7:14292. <https://doi.org/10.1038/s41598-017-14732-y> PMID: 29085054
20. Hryniewicz K, Jakubowicz M, Belka Z, Dopieralska J, Kaim A. New bivalves from a Middle Devonian methane seep in Morocco: the oldest record of repetitive shell morphologies among some seep bivalve molluscs. *J Syst Palaeont.* 2017; 15(1):19–41.
21. Kiel S, Krystyn L, Demirtaş F, Koşun E, Peckmann J. Late Triassic mollusk-dominated hydrocarbon-seep deposits from Turkey. *Geology.* 2017; 45(8):751–4.
22. Kiel S. Three new bivalve genera from Triassic hydrocarbon seep deposits in southern Turkey. *Acta Palaeont Pol.* 2018; 63(2):221–34.
23. Sandy MR. A review of some Palaeozoic and Mesozoic brachiopods as members of cold seep chemosynthetic communities: "unusual" palaeoecology and anomalous palaeobiogeographic pattern explained. *Földtani Közlöny.* 1995; 125(3/4):241–58.
24. Little CTS, Maslennikov VV, Gubanov AP. Two Palaeozoic hydrothermal vent communities from the southern Ural Mountains, Russia. *Palaeont.* 1999; 42(6):1043–78.
25. Barry JP, Greene G, Orange DL, Baxter CH, Robinson BH, Kochevar RE, et al. Biologic and geologic characteristics of cold seeps in Monterey Bay, California. *Deep-Sea Res I.* 1996; 43(11–12):1739–62.
26. Fisher CR. Chemoautotrophic and methanotrophic symbioses in marine invertebrates. *Reviews in Aquatic Sciences.* 1990; 2(3, 4):399–436.
27. Fisher CR. Toward an appreciation of hydrothermal-vent animals: their environment, physiological ecology, and tissue stable isotope values. In: Humphris SE, Zierenberg RA, Mullineaux LS, Thomson RE, editors. *Seafloor Hydrothermal Systems: Physical, Chemical, Biological, and Geochemical Interactions.* Geophysical Monographs Series 91. 91. Kopie ed. Washington, DC: Blackwell; 1995. p. 297–316 (Geophysical Monograph Series).
28. Sandy MR. Brachiopods from ancient hydrocarbon seeps and hydrothermal vents. In: Kiel S, editor. *Vent The and Biota Seep.* Topics in Geobiology. 33. Heidelberg: Springer; 2010. p. 279–314.
29. Campbell KA, Bottjer DJ. *Peregrinella*: an Early Cretaceous cold-seep-restricted brachiopod. *Paleobiol.* 1995; 24(4):461–78.
30. Olu K, Lance S, Sibuet M, Henry P, Fiala-Médoni A, Dinet A. Cold seep communities as indicators of fluid expulsion patterns through mud volcanoes seaward of the Barbados Accretionary Prism. *Deep-Sea Res I.* 1997; 44:811–41.
31. Sibuet M, Olu K. Biogeography, biodiversity and fluid dependence of deep-sea cold-seep communities at active and passive margins. *Deep-Sea Res II.* 1998; 45:517–67.
32. Campbell KA. Hydrocarbon seep and hydrothermal vent paleoenvironments and paleontology: Past developments and future research directions. *Palaeogeogr, Palaeoclimat, Palaeoecol.* 2006; 232:362–407.
33. Hryniewicz K, Amano K, Bitner MA, Hagström J, Kiel S, Klomp maker AA, et al. A late Paleocene fauna from shallow-water chemosynthesis-based ecosystems in Spitsbergen, Svalbard *Acta Palaeont Pol.* 2019; 64(1):101–41.
34. Kaim A, Bitner MA, Jenkins RG, Hikida Y. A monospecific assemblage of terebratulide brachiopods in the Upper Cretaceous seep deposit of Omagari, Hokkaido, Japan. *Acta Palaeont Pol.* 2010; 55(1):73–84.
35. Hryniewicz K, Bitner MA, Durska E, Hagström J, Hjálmarsdóttir HR, Jenkins RG, et al. Paleocene methane seep and wood-fall marine environments from Spitsbergen, Svalbard. *Palaeogeogr, Palaeoclimat, Palaeoecol.* 2016; 462:41–56.
36. Campbell KA, Francis DA, Collins M, Gregory MR, Nelson CS, Greinert J, et al. Hydrocarbon seep-carbonates of a Miocene forearc (East Coast Basin), North Island, New Zealand. *Sediment Geol.* 2008; 204:83–105.
37. Sandy MR, Hryniewicz K, Hammer Ø, Nakrem HA, Little CTS. Brachiopods from Late Jurassic-Early Cretaceous hydrocarbon seep deposits, central Spitsbergen, Svalbard. *Zootaxa.* 2014; 3884(6):501–32. <https://doi.org/10.11646/zootaxa.3884.6.1> PMID: 25543805

38. Kiel S, Glodny J, Birgel D, Bulot LG, Campbell KA, Gaillard C, et al. The paleoecology, habitats, and stratigraphic range of the enigmatic Cretaceous brachiopod *Peregrinella*. PLoS ONE. 2014; 9(10): e109260. <https://doi.org/10.1371/journal.pone.0109260> PMID: 25296341
39. Taviani M, Angeletti L, Ceregato A. Chemosynthetic bivalves of the family Solemyidae (Bivalvia, Protobranchia) in the Neogene of the Mediterranean Basin. J Paleont. 2011; 85(6):1067–76.
40. Kiel S, Sami M, Taviani M. A serpulid-*Anodontia*-dominated methane-seep deposit from the Miocene of northern Italy. Acta Palaeont Pol. 2018; 63(3):569–77.
41. Kiel S, Taviani M. Chemosymbiotic bivalves from Miocene methane-seep carbonates in Italy. J Paleont. 2017; 91(3):444–66.
42. Kiel S, Hansen BT. Cenozoic methane-seep faunas of the Caribbean region. PLoS ONE. 2015; 10(10):e0140788. <https://doi.org/10.1371/journal.pone.0140788> PMID: 26468887
43. Kiel S. Lucinid bivalves from ancient methane seeps. J Moll Stud. 2013; 79(4):346–63.
44. Amano K, Kiel S. Fossil vesicomid bivalves from the North Pacific region. Veliger. 2007; 49(4):270–93.
45. Kiel S, Taviani M. Chemosymbiotic bivalves from the late Pliocene Stirone River hydrocarbon seep complex in northern Italy. Acta Palaeont Pol. 2018; 63(3):557–68.
46. Amano K, Hamuro T, Hamuro M, Fujii S. The oldest vesicomid bivalves from the Japan Sea borderland. Venus. 2001; 60(3):189–98.
47. Majima R, Nobuhara T, Kitazaki T. Review of fossil chemosynthetic assemblages in Japan. Palaeogeogr, Palaeoclimat, Palaeoecol. 2005; 227:86–123.
48. Amano K, Little CTS, Campbell KA, Jenkins RG, Saether KP. Paleocene and Miocene *Thyasira* sensu stricto (Bivalvia: Thyasiridae) from chemosynthetic communities from Japan and New Zealand. Nautilus. 2015; 129(2):43–53.
49. Amano K, Ando H. Giant fossil *Acharax* (Bivalvia: Solemyidae) from the Miocene of Japan. Nautilus. 2011; 125(4):207–11.
50. Amano K, Jenkins RG. Fossil record of extant vesicomid species from Japan. Venus. 2011; 69(3–4):163–76.
51. Saether KP, Little CTS, Campbell KA, Marshall BA, Collins M, Alfaro AC. New fossil mussels (Bivalvia: Mytilidae) from Miocene hydrocarbon seep deposits, North Island, New Zealand, with general remarks on vent and seep mussels. Zootaxa. 2010; 2577:1–45.
52. Amano K, Saether KP, Little CTS, Campbell KA. Fossil vesicomid bivalves from Miocene hydrocarbon seep sites, North Island, New Zealand. Acta Palaeont Pol. 2014; 59(2):421–8.
53. Amano K, Miyajima Y, Jenkins RG, Kiel S. The Neogene biogeographic history of vesicomid bivalves in Japan, with two new records of the family. Nautilus. 2019; 133(2):48–56.
54. Amano K, Kiel S. Fossil *Adulomya* (Vesicomidae, Bivalvia) from Japan. Veliger. 2011; 51(2):76–90.
55. Amano K, Jenkins RG, Sako Y, Ohara M, Kiel S. A Paleogene deep-sea methane-seep community from Honshu, Japan. Palaeogeogr, Palaeoclimat, Palaeoecol. 2013; 387:126–33.
56. Gill FL, Little CTS. A new genus of lucinid bivalve from hydrocarbon seeps. Acta Palaeont Pol. 2013; 58(3):573–8.
57. Squires RL, Gring MP. Late Eocene chemosynthetic? bivalves from suspect cold seeps, Wagonwheel Mountain, central California. J Paleont. 1996; 70(1):63–73.
58. Goedert JL, Campbell KA. An Early Oligocene chemosynthetic community from the Makah Formation, northwestern Olympic Peninsula, Washington. Veliger. 1995; 38(1):22–9.
59. Hryniewicz K, Amano K, Jenkins RG, Kiel S. Thyasirid bivalves from Cretaceous and Paleogene cold seeps. Acta Palaeont Pol. 2017; 62(4):705–28.
60. Kiel S, Amano K. The earliest bathymodiolin mussels: Evaluation of Eocene and Oligocene taxa from deep-sea methane seep deposits in western Washington State, USA. J Paleont. 2013; 87(4):589–602.
61. Kiel S, Amano K, Jenkins RG. Bivalves from Cretaceous cold-seep deposits on Hokkaido, Japan. Acta Palaeont Pol. 2008; 53(3):525–37.
62. Amano K, Jenkins RG, Hikida Y. A new gigantic *Nucinella* (Bivalvia: Solemyoidea) from the Cretaceous cold-seep deposit in Hokkaido, northern Japan. Veliger. 2007; 49(2):84–90.
63. Little CTS, Birgel D, Boyce AJ, Crame JA, Francis JE, Kiel S, et al. Late Cretaceous (Maastrichtian) shallow water hydrocarbon seeps from Snow Hill and Seymour Islands, James Ross Basin, Antarctica. Palaeogeogr, Palaeoclimat, Palaeoecol. 2015; 418:213–28.

64. Kiel S, Campbell KA, Elder WP, Little CTS. Jurassic and Cretaceous gastropods from hydrocarbon-seeps in forearc basin and accretionary prism settings, California. *Acta Palaeont Pol.* 2008; 53(4):679–703.
65. Jenkins RG, Kaim A, Little CTS, Iba Y, Tanabe K, Campbell KA. Worldwide distribution of modiomorphid bivalve genus *Caspiconcha* in late Mesozoic hydrocarbon seeps. *Acta Palaeont Pol.* 2013; 58(2):357–82.
66. Jenkins RG, Kaim A, Hikida Y, Kiel S. Four new species of the Jurassic to Cretaceous seep-restricted bivalve *Caspiconcha* and implications for the history of chemosynthetic communities. *J Paleont.* 2018; 92(4):596–610.
67. Kaim A, Jenkins RG, Tanabe K, Kiel S. Mollusks from late Mesozoic seep deposits, chiefly in California. *Zootaxa.* 2014; 3861(5):401–40. <https://doi.org/10.11646/zootaxa.3861.5.1> PMID: 25283419
68. Hryniewicz K, Little CTS, Nakrem HA. Bivalves from the latest Jurassic-earliest Cretaceous hydrocarbon seep carbonates from central Spitsbergen, Svalbard. *Zootaxa.* 2014; 3859:1–66. <https://doi.org/10.11646/zootaxa.3859.1.1> PMID: 25283172
69. Kiel S, Birgel D, Campbell KA, Crampton JS, Schiøler P, Peckmann J. Cretaceous methane-seep deposits from New Zealand and their fauna. *Palaeogeogr, Palaeoclimat, Palaeoecol.* 2013; 390:17–34.
70. Kelly SRA, Blanc E, Price SP, Witham AG. Early Cretaceous giant bivalves from seep-related limestone mounds, Wollaston Forland, Northeast Greenland. In: Harper EM, Taylor JD, Crame JA, editors. *The evolutionary biology of the Bivalvia.* 177. Kopie, pdf ed. London: Geological Society of London, Special Publication; 2000. p. 227–46.
71. Sandy MR, Campbell KA. New rhynchonellid brachiopod genus from Tithonian (Upper Jurassic) cold seep deposits of California and its paleoenvironmental setting. *J Paleont.* 1994; 68(6):1243–52.
72. Gischler E, Sandy MR, Peckmann J. *Ibergirhynchia contraria* (F.A. Roemer, 1850), an Early Carboniferous seep-related rhynchonellid brachiopod from the Harz Mountains, Germany—a possible successor to *Dzieduszyckia*? *J Paleont.* 2003; 77(2):293–303.
73. Cau S, Franchi F, Roveri M, Taviani M. The Pliocene-age Stirone River hydrocarbon chemoherm complex (Northern Apennines, Italy). *Marine Petrol Geol.* 2015; 66(3):582–95.
74. Amano K, Jenkins RG, Aikawa M, Nobuhara T. A Miocene chemosynthetic community from the Ogaya Formation in Joetsu: evidence for depth-related ecologic control among fossil seep communities in the Japan Sea back-arc basin. *Palaeogeogr, Palaeoclimat, Palaeoecol.* 2010; 286(3–4):164–70.
75. Kase T, Isaji S, Aguilar YM, Kiel S. A large new *Wareniconcha* (Bivalvia: Vesicomidae) from a Pliocene methane seep deposit in Leyte, Philippines. *Nautilus.* 2019; 133(1):26–30.
76. Wang S-W, Gong S-Y, Mii H-S, Dai C-F. Cold-seep carbonate hardgrounds as the initial substrata of coral reef development in a siliciclastic paleoenvironment of southwestern Taiwan. *Terrest Atmos Ocean Sci.* 2006; 17:405–27.
77. Kanie Y, Sakai T. Chemosynthetic thraciid bivalve *Nipponothracia*, gen. nov. from the Lower Cretaceous and Middle Miocene mudstones in Japan. *Venus.* 1997; 56(3):205–20.
78. Hirayama K. Molluscan Fauna from the Miocene Hiranita Formation, Chichibu Basin, Saitama Prefecture, Japan. *Tohoku University, Science Reports, 2nd series (Geology).* 1973; Special Volume 6 (Hatai Memorial Volume):163–77.
79. Saether KP. A taxonomic and palaeobiogeographic study of the fossil fauna of Miocene hydrocarbon seep deposits, North Island, New Zealand [PhD]. Auckland: University of Auckland; 2011.
80. Aoki S. Mollusca from the Miocene Kabeya Formation, Joban coal-field, Fukushima Prefecture, Japan. *Science Reports of the Tokyo Kyoiku Daigaku, Section C.* 1954; 17:23–40.
81. Amano K, Kiel S. Taxonomy and distribution of fossil *Archivesica* (Vesicomidae, Bivalvia) in Japan. *Nautilus.* 2010; 124(4):155–65.
82. Matsumoto E, Hirata M. *Akebiconcha uchimuraensis* (Kuroda) from the Oligocene Formations of the Shimanto terrain. *Bulletin of the National Science Museum Tokyo.* 1972; 15(4):753–60.
83. Ozaki H. Stratigraphical and paleontological studies on the Neogene and Pleistocene formations of the Tyosi District. *Bulletin of the National Science Museum.* 1958; 4(1):1–182.
84. Kanno S, Amano K, Ban H. *Calyptogena (Calyptogena) pacifica* Dall (Bivalvia) from the Neogene system in the Joetsu district, Niigata prefecture. *Trans Proc Palaeont Soc Japan, New Ser.* 1989; 153:25–35.
85. Miyajima Y, Watanabe Y, Yanagisawa Y, Amano K, Hasegawa T, Shimobayashi N. A late Miocene methane-seep deposit bearing methane-trapping silica minerals at Joetsu, central Japan. *Palaeogeogr, Palaeoclimat, Palaeoecol.* 2016; 455:1–15.

86. Amano K, Kiel S. Two Neogene vesicomid species (*Bivalvia*) from Japan and their biogeographic implications. *Nautilus*. 2012; 126(2):79–85.
87. Gill FL, Harding IC, Little CTS, Todd JA. Palaeogene and Neogene cold seep communities in Barbados, Trinidad and Venezuela: An overview. *Palaeogeogr, Palaeoclimat, Palaeoecol*. 2005; 227:191–209.
88. Campbell KA. Recognition of a Mio-Pliocene cold seep setting from the Northeast Pacific Convergent Margin, Washington, U.S.A. *Palaios*. 1992; 7:422–33.
89. Beets C. Beiträge zur Kenntnis der angeblich oberoligocänen Mollusken-Fauna der Insel Buton, Niederländisch-Ostindien. *Leidsche Geologische Mededeelingen*. 1942; 13(1):255–328.
90. Amano K, Jenkins RG, Ohara M, Kiel S. Miocene vesicomid species (*Bivalvia*) from Wakayama in southern Honshu, Japan. *Nautilus*. 2014; 128(1):9–17.
91. Kanie Y, Kuramochi T. Two new species of the Vesicomidae (*Bivalvia*: Mollusca) from the Pliocene Shiramazu Formation of the Chikura Group in the Boso Peninsula, Japan. *Science Report of the Yokosuka City Museum*. 2001; 48:1–9.
92. Kanno S, Ogawa H. Molluscan fauna from the Momijiyama and Takinoue districts, Hokkaido, Japan. *Science Reports of the Tokyo Kyoiku Daigaku, Section C*. 1964; 8(81):269–94.
93. Kanehara K. Miocene shells from the Joban coal field. *Bulletin of the Imperial Geological Survey of Japan*. 1937; 27(1):1–21.
94. Venturini S, Selmo E, Tarlao A, Tunis G. Fossiliferous methanogenic limestones in the Eocene flysch of Istria (Croatia). *Giornale di Geologia, serie 3a*. 1998; 60:219–34.
95. Kiel S, Peckmann J. Chemosymbiotic bivalves and stable carbon isotopes indicate hydrocarbon seepage at four unusual Cenozoic fossil localities. *Lethaia*. 2007; 40(4):345–57.
96. Goedert JL, Squires RL. Eocene deep-sea communities in localized limestones formed by subduction-related methane seeps, southwestern Washington. *Geology*. 1990; 18:1182–5.
97. Hickman CS. Paleogene marine bivalves of the deep-water Keasey Formation in Oregon, part III: The heteroconchs. *PaleoBios*. 2015; 32(3):1–44.
98. Peckmann J, Goedert JL, Thiel V, Michaelis W, Reitner J. A comprehensive approach to the study of methane-seep deposits from the Lincoln Creek Formation, western Washington State, USA. *Sedimentology*. 2002; 49:855–73.
99. Kiel S. New records and species of mollusks from Tertiary cold-seep carbonates in Washington State, USA. *J Paleont*. 2006; 80(1):121–37.
100. Goedert JL, Squires RL. First Oligocene record of *Calyptogena* (*Bivalvia*: Vesicomidae). *Veliger*. 1993; 36(1):72–7.
101. Kiel S, Goedert JL. Deep-sea food bonanzas: Early Cenozoic whale-fall communities resemble wood-fall rather than seep communities. *Proc R Soc B*. 2006; 273:2625–31. <https://doi.org/10.1098/rspb.2006.3620> PMID: 17002948
102. Schwartz H, Sample JC, Weberling KD, Minisini D, Moore JC. An ancient linked fluid migration system: cold-seep deposits and sandstone intrusions in the Panoche Hills, California, USA. *Geo-Mar Let*. 2003; 23:340–50.
103. Amano K, Jenkins RG. New fossil *Bathymodiolus* (s. l.) (*Mytilidae*, *Bivalvia*) from Oligocene seep-carbonates in eastern Hokkaido, Japan—with remarks on the evolution of *Bathymodiolus* (s. l.). *Nautilus*. 2011; 125(1):29–35.
104. Yokoyama M. Versteinerungen aus der japanischen Kreide. *Palaeontographica*. 1890; 36:159–202.
105. Goedert JL, Thiel V, Schmale O, Rau WW, Michaelis W, Peckmann J. The late Eocene 'Whiskey Creek' methane-seep deposit (western Washington State) Part I: Geology, palaeontology, and molecular geobiology. *Facies*. 2003; 48:223–40.
106. Nobuhara T, Onda D, Kikuchi N, Kondo Y, Matsubara K, Amano K, et al. Lithofacies and fossil assemblages of the Upper Cretaceous Sada Limestone, Shimanto City, Kochi Prefecture, Shikoku, Japan. *Fossils, The Palaeontological Society of Japan*. 2008; 84:47–60.
107. Hikida Y, Suzuki S, Togo Y, Ijiri A. An exceptionally well-preserved seep community from the Cretaceous Yezo forearc basin in Hokkaido, northern Japan. *Paleont Res* 2003; 7(4):329–42.
108. Jenkins RG, Kaim A, Hikida Y, Tanabe K. Methane-flux-dependent lateral faunal changes in a Late Cretaceous chemosymbiotic assemblage from the Nakagawa area of Hokkaido, Japan. *Geobiol*. 2007; 5(2):127–39.
109. Kauffman EG, Arthur MA, Howe B, Scholle PA. Widespread venting of methane-rich fluids in Late Cretaceous (Campanian) submarine springs (Tepee Buttes), Western Interior seaway, U.S.A. *Geology*. 1996; 24(9):799–802.

110. Kiel S, Wiese F, Titus AL. Shallow-water methane-seep faunas in the Cenomanian Western Interior Seaway: No evidence for onshore-offshore adaptations to deep-sea vents. *Geology*. 2012; 40(9):839–42.
111. Hammer Ø, Nakrem HA, Little CTS, Hryniewicz K, Sandy MR, Hurum JH, et al. Hydrocarbon seeps close to the Jurassic-Cretaceous boundary, Svalbard. *Palaeogeogr, Palaeoclimat, Palaeoecol*. 2011; 306:15–26.
112. Remeš M. *Rhynchonella peregrina* bei Freiberg in Mähren. *Verh kk geol Reichsanst*. 1903; 11:223–5.
113. Sun D. Discovery of Early Cretaceous *Peregrinella* (Brachiopoda) in Xizang (Tibet) and its significance. *Palaeontol Cathayana*. 1986; 2:211–27.
114. Sandy MR, Blodgett RB. *Peregrinella* (Brachiopoda; Rhynchonellida) from the Early Cretaceous Wrangellia Terrane, Alaska. In: Copper P, Jin J, editors. *Brachiopods*. Rotterdam: A.A. Balkema; 1996. p. 239–42.
115. Beauchamp B, Savard MM. Cretaceous chemosynthetic carbonate mounds in the Canadian Arctic. *Palaios*. 1992; 7:434–50.
116. Hryniewicz K, Hagström J, Hammer Ø, Kaim A, Little CTS, Nakrem HA. Late Jurassic-Early Cretaceous hydrocarbon seep boulders from Novaya Zemlya and their faunas. *Palaeogeogr, Palaeoclimat, Palaeoecol*. 2015; 436:231–44.
117. Kaim A, Skupien P, Jenkins RG. A new Lower Cretaceous hydrocarbon seep locality from Czech Carpathians and its fauna. *Palaeogeogr, Palaeoclimat, Palaeoecol*. 2013; 390:42–51.
118. Campbell KA, Farmer JD, Des Marais D. Ancient hydrocarbon seeps from the Mesozoic convergent margin of California: carbonate geochemistry, fluids and palaeoenvironments. *Geofluids*. 2002; 2:63–94.
119. Trümpy R. Notizen zur mesozoischen Fauna der innerschweizerischen Klippen (I-II). *Eclogae geol Helvetiae*. 1956; 49:573–91.
120. Agirrezabala LM, Kiel S, Blumenberg M, Schäfer N, Reitner J. Outcrop analogues of pockmarks and associated methane-seep carbonates: a case study from Lower Cretaceous (Albian) of the Basque-Cantabrian Basin, western Pyrenees. *Palaeogeogr, Palaeoclimat, Palaeoecol*. 2013; 390:94–115.
121. Renngarten V. O Kavkaykikh Peregrinellae (Sur les Pérégrinelles du Caucase). *Izvestiia Geologicheskogo Komiteta, Leningrad*. 1924; 42(5–9):119–28.
122. Kiel S, Peckmann J. Paleoecology and evolutionary significance of an Early Cretaceous *Peregrinella*-dominated hydrocarbon-seep deposit on the Crimean Peninsula. *Palaios*. 2008; 23:751–9.
123. Hou H-F, Wang J-X. The discovery of Early Cretaceous *Peregrinella* (Brachiopoda) in Xizang (Tibet). *Bulletin of the Chinese Academy of Geological Sciences*. 1984; 10:207–15.
124. Sandy MR, Lazar I, Peckmann J, Birgel D, Stoica M, Roban RD. Methane-seep brachiopod fauna within turbidites of the Sinaia Formation, Eastern Carpathian Mountains, Romania. *Palaeogeogr, Palaeoclimat, Palaeoecol*. 2012; 323–325:42–59.
125. Ascher E. Die Gastropoden, Bivalven und Brachiopoden der Grodischter Schichten. *Beitr Paläontol Geol Österreich-Ungarns Orients*. 1906; 19:135–72.
126. Kanie Y, Yoshikawa Y, Sakai T, Takahashi T. The Cretaceous chemosynthetic cold water-dependent molluscan community discovered from Mikasa City, central Hokkaido. *Science Report of the Yokosuka City Museum*. 1993; 41:31–6.
127. Kelly SRA, Ditchfield PW, Doubleday PA, Marshall JD. An Upper Jurassic methane-seep limestone from the Fossil Bluff Group forearc basin of Alexander Island, Antarctica. *J Sediment Res*. 1995; A65(2):274–82.
128. Campbell KA, Carlson C, Bottjer DJ. Fossil cold seep limestones and associated chemosymbiotic macroinvertebrate faunas, Jurassic-Cretaceous Great Valley Group, California. In: Graham SA, Lowe DR, editors. *Advances in the Sedimentary Geology of the Great Valley Group, Sacramento Valley, California*. 73. Los Angeles: Pacific Section of the Society of economic Paleontologists and Mineralogists; 1993. p. 37–50.
129. Gaillard C, Rio M, Rolin Y. Fossil chemosynthetic communities related to vents or seeps in sedimentary basins: the pseudobioherms of southeastern France compared to other world examples. *Palaios*. 1992; 7:451–65.
130. Buggisch W, Krumm S. Palaeozoic cold seep carbonates from Europe and North Africa—an integrated isotopic and geochemical approach. *Facies*. 2005; 51:566–83.
131. Himmler T, Freiwald A, Stollhofen H, Peckmann J. Late Carboniferous hydrocarbon-seep carbonates from the glaciomarine Dwyka Group, southern Namibia. *Palaeogeogr, Palaeoclimat, Palaeoecol*. 2008; 257:185–97.

132. Peckmann J, Walliser OH, Riegel W, Reitner J. Signatures of hydrocarbon venting in a middle Devonian carbonate mound (Hollard Mound) at the Hamar Laghdad (AntiAtlas, Morocco). *Facies*. 1999; 40:281–96.
133. Blumenberg M, Seifert R, Reitner J, Pape T, Michaelis W. Membrane lipid patterns typify distinct anaerobic methanotrophic consortia. *Proc Natl Acad Sci USA*. 2004; 101(30):11111–6. <https://doi.org/10.1073/pnas.0401188101> PMID: 15258285
134. Niemann H, Elvert M. Diagnostic lipid biomarker and stable carbon isotope signatures of microbial communities mediating the anaerobic oxidation of methane with sulphate. *Org Geochem*. 2008; 39:1668–77.
135. Peckmann J, Birgel D, Kiel S. Molecular fossils reveal fluid composition and flow intensity at a Cretaceous seep. *Geology*. 2009; 37(9):847–50.
136. Haas A, Peckmann J, Elvert M, Sahling H, Bohrmann G. Patterns of carbonate authigenesis at the Kouilou pockmarks on the Congo deep-sea fan. *Mar Geol*. 2010; 268:129–36.
137. Feng D, Peng Y, Bao H, Peckmann J, Roberts HH, Chen D. A carbonate-based proxy for sulfate-driven anaerobic oxidation of methane. *Geology*. 2016; 44(12):999–1002.
138. Lu Y, Liu Y, Sun X, Lin Z, Xu L, Lu H, et al. Intensity of methane seepage reflected by relative enrichment of heavy magnesium isotopes in authigenic carbonates: A case study from the South China Sea. *Deep-Sea Res I*. 2017; 129:10–21.
139. Lin Z, Sun X, Lu Y, Strauss H, Xu L, Gong J, et al. The enrichment of heavy iron isotopes in authigenic pyrite as a possible indicator of sulfate-driven anaerobic oxidation of methane: Insights from the South China Sea. *Chem Geol*. 2017; 449:15–29.
140. Lin Z, Sun X, Peckmann J, Lu Y, Xu L, Strauss H, et al. How sulfate-driven anaerobic oxidation of methane affects the sulfur isotopic composition of pyrite: A SIMS study from the South China Sea. *Chem Geol*. 2016; 440:26–41.
141. Naehr T, Birgel D, Bohrmann G, MacDonald IR, Kasten S. Biogeochemical controls on authigenic carbonate formation at the Chapopote “asphalt volcano”, Bay of Campeche. *Chem Geol*. 2009; 266:399–411.
142. Kniemeyer O, Musat F, Sivert SM, Knittel K, Wilkes H, Blumenberg M, et al. Anaerobic oxidation of short-chain hydrocarbons by marine sulphate-reducing bacteria. *Nature*. 2007; 449:898–902. <https://doi.org/10.1038/nature06200> PMID: 17882164
143. Smrzka D, Zwicker J, Misch D, Walkner C, Gier S, Monien P, et al. Oil seepage and carbonate formation: A case study from the southern Gulf of Mexico. *Sedimentology*. 2019: <https://doi.org/10.1111/sed.12516>
144. Smrzka D, Zwicker J, Klügel A, Monien P, Bach W, Bohrmann G, et al. Establishing criteria to distinguish oil-seep from methane-seep carbonates. *Geology*. 2016; 44(8):667–70.
145. Wortmann UG, Paytan A. Rapid variability of seawater chemistry over the past 130 million years. *Science*. 2012; 337:334–6. <https://doi.org/10.1126/science.1220656> PMID: 22822148
146. Knab NJ, Cragg BA, Borowski C, Parkes RJ, Pancost RD, Jørgensen BB. Anaerobic oxidation of methane (AOM) in marine sediments from the Skagerrak (Denmark): I. Geochemical and microbiological analyses. *Geochim Cosmochim Acta*. 2008; 72:2868–79.
147. Knab NJ, Cragg BA, Hornibrook ERC, Holmkvist L, Pancost RD, Borowski C, et al. Regulation of anaerobic methane oxidation in sediments of the Black Sea. *Biogeosciences*. 2009; 6: 1505–18.
148. Niemann H, Fischer D, Graffe D, Knittel K, Montiel A, Heilmayer O, et al. Biogeochemistry of a low-activity cold seep in the Larsen B area, western Weddell Sea, Antarctica. *Biogeosciences*. 2009; 6:2383–95.
149. Taylor JD, Glover EA. Chemosymbiotic bivalves. In: Kiel S, editor. *The Vent and Seep Biota*. Topics in Geobiology. 33. Heidelberg: Springer; 2010. p. 107–36.
150. Childress JJ, Fisher CR, Brooks JM, Kennicutt MCI, Bidigare RR, Anderson AE. A methanotrophic marine molluscan (*Bivalvia*, *Mytilidae*) symbiosis: mussels fueled by gas. *Science*. 1986; 233(4770):1306–8. <https://doi.org/10.1126/science.233.4770.1306> PMID: 17843358
151. Duperron S. The diversity of deep-sea mussels and their bacterial symbioses. In: Kiel S, editor. *The Vent and Seep Biota*. Topics in Geobiology. 33. Heidelberg: Springer; 2010. p. 137–67.
152. Lorion J, Kiel S, Faure BM, Kawato M, Ho SYW, Marshall BA, et al. Adaptive radiation of chemosymbiotic deep-sea mussels. *Proc R Soc B*. 2013; 280(1770):20131243. <https://doi.org/10.1098/rspb.2013.1243> PMID: 24048154
153. Kiel S. The fossil record of vent and seep mollusks. In: Kiel S, editor. *The Vent and Seep Biota*. Topics in Geobiology. 33. Heidelberg: Springer; 2010. p. 255–78.

154. Taylor JD, Glover EA, Smith L, Dyal P, Williams ST. Molecular phylogeny and classification of the chemosymbiotic bivalve family Lucinidae (Mollusca: Bivalvia). *Zool J Linn Soc.* 2011; 163:15–49.
155. Little CTS, Herrington RJ, Maslennikov VV, Morris NJ, Zaykov VV. Silurian hydrothermal vent community from the southern Urals, Russia. *Nature.* 1997; 385:146–8.
156. Mondal S, Harries PJ. Phanerozoic trends in ecospace utilization: The bivalve perspective. *Earth-Science Reviews.* 2016; 152:106–18.
157. Taylor JD, Glover EA. Lucinidae (Bivalvia)—the most diverse group of chemosymbiotic molluscs. *Zool J Linn Soc.* 2006; 148:421–38.
158. Stanley SM. Evolutionary radiation of shallow-water Lucinidae (Bivalvia with endosymbionts) as a result of the rise of seagrasses and mangroves. *Geology.* 2014; 42(9):803–6.
159. Sahling H, Rickert D, Lee RW, Linke P, Suess E. Macrofaunal community structure and sulfide flux at gas hydrate deposits from the Cascadia convergent margin, NE Pacific. *Mar Ecol Prog Ser.* 2002; 231:121–38.
160. Barry JP, Kochevar RE. A tale of two clams: differing chemosynthetic life styles among vesicomyids in Monterey Bay cold seeps. *Cah Biol Mar.* 1998; 39:329–31.
161. Kiel S, Amano K, Jenkins RG. Predation scar frequencies in chemosymbiotic bivalves at an Oligocene seep deposit and their potential relation to inferred sulfide tolerances. *Palaeogeogr, Palaeoclimat, Palaeoecol.* 2016; 453:139–45.
162. LaRock PA, Hyun J-H, Bennison BW. Bacterioplankton growth and production at the Louisiana hydrocarbon seeps. *Geo-Mar Let.* 1994; 14(2–3):104–9.
163. Hazen TC, Dubinsky EA, DeSantis TZ, Andersen GL, Piceno YM, Singh N, et al. Deep-sea oil plume enriches indigenous oil-degrading bacteria. *Science.* 2010; 330(6001):204–8. <https://doi.org/10.1126/science.1195979> PMID: 20736401
164. Newman WA, Yamaguchi T, Southward AJ. Arthropoda, Crustacea, Cirripedia. *Denisia.* 2006; 18:359–68.
165. Rogers AD, Tyler PA, Connelly DP, Copley JT, James R, Larter RD, et al. The discovery of new deep-sea hydrothermal vent communities in the Southern Ocean and implications for biogeography. *PLoS Biology.* 2012; 10(1):e1001234. <https://doi.org/10.1371/journal.pbio.1001234> PMID: 22235194
166. Birgel D, Peckmann J, Klautsch S, Thiel V, Reitner J. Anaerobic and aerobic oxidation of methane at Late Cretaceous seeps in the Western Interior Seaway, USA. *Geomicrobiology Journal.* 2006; 23:565–77.
167. Newton RJ, Reeves EP, Kafousia N, Wignall PB, Bottrell SH, Sha J-G. Low marine sulfate concentrations and the isolation of the European epicontinental sea during the Early Jurassic. *Geology.* 2011; 39(1):7–10.
168. Little CTS, Danelian T, Herrington RJ, Haymon RM. Early Jurassic hydrothermal vent community from the Franciscan Complex, California. *J Paleont.* 2004; 78(3):542–59.
169. Robinson JJ, Polz MF, Fiala-Médoni A, Cavanaugh CM. Physiological and immunological evidence for two distinct C1-utilizing pathways in *Bathymodiolus puteoserpentis* (Bivalvia: Mytilidae), a dual endosymbiotic mussel from the Mid-Atlantic Ridge. *Mar Biol.* 1998; 132:625–33.
170. Pimenov NV, Kalyuzhnaya MG, Khmelena VN, Mityushina LL, Trotsenko YA. Utilization of methane and carbon dioxide by symbiotrophic bacteria in gills of Mytilidae (*Bathymodiolus*) from the Rainbow and Logachev hydrothermal fields on the Mid-Atlantic Ridge. *Microbiology.* 2002; 71(5):587–94.
171. Krebs W. Aspekte einer potentiellen Kohlenwasserstoff-Führung in den devonischen Riffen Nordwestdeutschlands. *Erdöl-Erdgas-Zeitschrift.* 1978; 94:15–25.
172. Jakubowicz M, Dopieralska J, Belka Z. Tracing the composition and origin of fluids at an ancient hydrocarbon seep (Hollard Mound, Middle Devonian, Morocco): a Nd, REE and stable isotope study. *Geochim Cosmochim Acta.* 2015; 156:50–74.
173. Peckmann J, Little CTS, Gill FL, Reitner J. Worm tube fossils from the Hollard Mound hydrocarbon-seep deposit, Middle Devonian, Morocco: Palaeozoic seep-related vestimentiferans? *Palaeogeogr, Palaeoclimat, Palaeoecol.* 2005; 227:242–57.
174. Rubin-Blum M, Antony CP, Borowski C, Sayavedra L, Pape T, Sahling H, et al. Short-chain alkanes fuel mussel and sponge *Cycloclasticus* symbionts from deep-sea gas and oil seeps. *Nature Microbiology.* 2017; 2:17093 <https://doi.org/10.1038/nmicrobiol.2017.93> PMID: 28628098
175. Manceñido MO, Owen EF, Savage NM, Dagys AS. Dimerell006Fidea. In: Williams A, Brunton CH, Carlson SJ, editors. *Treatise on Invertebrate Paleontology, Part H, Brachiopoda, revised, volume 4.* 42002. p. 1236–45.
176. Ager DV. The adaptation of Mesozoic brachiopods to different environments. *Palaeogeogr, Palaeoclimat, Palaeoecol.* 1965; 1:143–72.