Crustaceans in cold seep ecosystems: fossil record, geographic distribution, taxonomic composition, and biology

Adiël A. Klompmaker¹, Torrey Nyborg², Jamie Brezina³ & Yusuke Ando⁴

¹Department of Integrative Biology & Museum of Paleontology, University of California, Berkeley, 1005 Valley Life Sciences Building #3140, Berkeley, CA 94720, USA. Email: adielklompmaker@gmail.com

²Department of Earth and Biological Sciences, Loma Linda University, Loma Linda, CA 92354, USA. Email: tnyborg06g@llu.edu

³South Dakota School of Mines and Technology, Rapid City, SD 57701, USA. Email: rezinagate@hotmail.com

⁴Mizunami Fossil Museum, 1-47, Yamanouchi, Akeyo-cho, Mizunami, Gifu, 509-6132, Japan. Email: tyuu-destiny53@hotmail.co.jp

This preprint has been submitted for publication in the Topics in Geobiology volume “Ancient Methane Seeps and Cognate Communities”. Specimen figures are excluded in this preprint because permissions were only received for the peer-reviewed publication.

Introduction

Crustaceans are abundant inhabitants of today’s cold seep environments (Chevaldonné and Olu 1996; Martin and Haney 2005; Karanovic and Brandão 2015), and could play an important role in structuring seep ecosystems. Cold seeps fluids provide an additional source of energy for various sulfide- and hydrocarbon-harvesting bacteria, often in symbiosis with invertebrates, attracting a variety of other organisms including crustaceans (e.g., Levin 2005; Vanreusel et al. 2009; Vrijenhoek 2013). The percentage of crustaceans of all macrofaunal specimens is highly variable locally in modern seeps, from 0–>50% (Dando et al. 1991; Levin et al. 2000; Fujikura et al. 2002; Bergquist et al. 2003; Cordes et al. 2006; Cordes et al. 2007; Ritt et al. 2010; Cordes et al. 2010b; Lessard-Pilon et al. 2010; Ritt et al. 2011; Levin et al. 2015; Grupe et al. 2015). Crustacean density is suggested to be higher in/around seeps than in surrounding areas (e.g., Senowbari-Daryan et al. 2007) because there is ample food available and many crustaceans can cope with relatively low oxygen levels at seeps. Some decapod crustaceans have adapted their respiratory system by developing larger appendages (scaphognathites) resulting in increased water flow over the gills per stroke to enhance oxygen uptake (Decelle et al. 2010, for shrimps), and a number of ostracods may increase the water flow over their respiratory surface (Whatley 1991). The composition of decapods from modern cold seeps is dominated by members of the carid shrimp family Alvinocarididae, squat lobsters (Galatheoidea and Chirostyloidea), and true crabs (Brachyura) (Chevaldonné and Olu 1996; Martin and Haney 2005). Ostracod species commonly found at cold seeps are members of the Podocopida and Platycopida (Russo et al. 2012). Other crustaceans such as copepods, amphipods, cumaceans, tanaidaceans, and isopods are also commonly found at seeps (e.g., Humes 1988; Levin et al. 2000; Ritt et al. 2010; Ritt et al. 2011; Degen et al. 2012; Levin et al. 2015).

Crustaceans from fossil cold seeps are less known with a limited number of dedicated studies of seep crustaceans or their inferred traces (Bishop and Williams 2000; Senowbari-Daryan et al. 2007; Peckmann et al. 2007b; Schweitzer and Feldmann 2008; Karasawa 2011; Russo et al. 2012; Wiese et al. 2015; Kiel et al. 2016; Yamaguchi et al. 2016). Consequently, their importance in structuring faunas at these biodiversity hotspots is poorly known, including to what extent seeps of the deep acted as refuges from competition and extinction, the timing of invasion of cold seeps, the degree of endemism, depth preferences, and the longevity of crustacean lineages. Although many of these aspects cannot be answered yet, a first step in addressing these questions is to synthesize the present data. The goal of this paper is to

review the fossil record of crustaceans from cold seeps based on an extensive literature search and quantitative analyses of occurrences. We first discuss general trends and then focus on individual clades of Crustacea that have a fossil record, while also providing information on modern occurrences, composition, and biology for a better framework to understand their ecological and evolutionary role in ancient seep ecosystems.

Institutional abbreviations: AMNH: American Museum of Natural History, New York, USA; GPIBo: Goldfuß-Museum, Steinmann-Institut für Geologie, Mineralogie und Paläontologie, Universität Bonn, Bonn, Germany; GSUB: Geosciences Collection of the University of Bremen at the Faculty 5, Bremen, Germany; LACMIP: Invertebrate Paleontology department, Natural History Museum of Los Angeles, Los Angeles, California, USA; MFM: Mizunami Fossil Museum, Mizunami, Japan; NIWA: National Institute of Water and Atmospheric Research, Wellington, New Zealand; NMB G: Naturhistorisches Museum Basel, Basel, Switzerland; PRI: Paleontological Research Institution, Ithaca, New York, USA; SDSM: Museum of Geology, South Dakota School of Mines, Rapid City, USA; UCMP: University of California Museum of Paleontology, Berkeley, California, USA; USNM: United States National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA; UWBM: Burke Museum, University of Washington, Seattle, Washington state, USA.

Crustaceans in fossil cold seeps – a quantitative analysis

Crustaceans are more commonly present in fossil cold seeps than previously known as suggested by our extensive search into the literature resulting in 306 taxon occurrences. While the percentage of crustaceans of all macrofossils (thus excluding ostracods) is variable from 0–>50% in modern seeps (see above), this percentage is typically low in fossil assemblages, with 0.05% for latest Jurassic–earliest Cretaceous seeps of Spitsbergen (Hryniewicz et al. 2015b), 5.3% in a Late Cretaceous seep from Japan (Jenkins et al. 2007b), 0–0.9% for Late Cretaceous cold seeps from South Dakota (Meehan and Landman 2016), and 0 – < 2.7% for Eocene seeps from Washington state (Goedert and Squires 1990). This result may be in part a reflection of the low preservation potential of crustaceans relative to mollusks (Kidwell and Flessa 1995; Stempien 2005) and varying preservation potentials within marine arthropods (Klompmaaker et al. 2017). Amphipoda, Cumacea, and Copepoda have not been found in fossil seeps because many are comparatively soft-bodied, small, and fragile (e.g., Selden et al. 2010). Isopods, found in concretions, appear to have been living close to seeps during the early Oligocene in Washington state, USA (Wieder and Feldmann 1989; Goedert and Campbell 1995), but confirmed occurrences from within seep limestone bodies are unknown to us.

The taxonomy of crustaceans in fossil seeps is variously known. For ostracods, the taxonomy has been well-resolved for occurrences due to three major studies (Coles et al. 1996; Russo et al. 2012; Yamaguchi et al. 2016). 94% of ostracod body fossil occurrences are identified to at least the genus-level and 73% to the species-level. Conversely, identifications to the genus- and species-level of 57% and 40%, respectively, are found for decapod body fossils.

Research on crustaceans from cold seep deposits has increased markedly: few papers are known to us from before the 1990s, but since then the number of papers per decade has been increasing steadily with a record of 36 papers in this decade (Figure 1). This trend exemplifies the increasing interest in fossil cold seeps in general.

The rate at which decapods can be found at fossil cold seeps has only been quantified for the so-called Late Cretaceous tepee buttes in the US states of South Dakota and Colorado. Bishop and Williams (2000) found 21 brachyuran specimens in 73 working days. Assuming a work day of 8 hours, this results in an average of rate of 0.04 crab specimens per hour. This low number is not representative for decapods in all seeps, in part because ghost shrimps are not included. The other extreme is the very high abundance of *Shinkaia katapsyxis* in an Eocene cold seep in Washington state, which may not be surprising because congeners can be very abundant at modern seeps. Schweitzer and Feldmann (2008) reported 112 carapaces, 107 claw pairs, and tens of pereopods remains in just 22 kg of carbonate rock, although

admittedly these rocks were selected for decapod remains. For comparison, the decapod-rich mid-Cretaceous corallgal reef deposits from Koskobilu in Spain yielded 235 decapods in 36 hours or 6.5 specimens per hour (Klompmaier et al. 2013a), while Danian coral-bryozoan limestones in Denmark yielded 209 specimens (Klompmaier et al. 2016) in 27 hours or 7.7 specimens per hour (field notes AAK).

Crustaceans in fossil seeps are mainly reported from Europe and the United States thus far (90% of occurrences, Figure 2), which is at least in part a reporting bias as is known for marine invertebrates in general (e.g., Wall et al. 2009). Other occurrences are known from New Zealand, Japan, Morocco, South America, Antarctica, Spitsbergen, Greenland, and Nova Zembla (Figure 2). Most occurrences are found close to current or former convergent plate boundaries.

Stratigraphically, most occurrences are found in Cretaceous – Quaternary carbonate rocks (Figure 3). Occurrences are primarily based on body fossils (88%), although coprolites, burrows, and repair scars can be common in certain periods (Figure 3A). Focusing on localities rather than occurrences, shows that the Cretaceous – Neogene yields most crustacean-bearing localities thus far (Figure 3B). Once again, body fossils are the dominant type of crustacean evidence reported (72%). Occurrences are dominated by podocopid ostracods, while decapod crustaceans make up most presences in localities (Figure 3C, 5D). The difference is due to data in Coles et al. (1996), who reported many Quaternary ostracod occurrences from four localities west of Ireland. Numerically, ostracod specimens are the dominant crustaceans reported in fossil cold seeps, with 3411 ostracod specimens compared to the 546 specimens of malacostracans (Decapoda).

Figure 1. The number of papers including fossil crustaceans in cold seeps over the last 100 years.

Figure 2. Fossil cold seep localities containing crustaceans per taxonomic class around the world.

Figure 3. The number of occurrences and localities of crustaceans in cold seeps for each Phanerozoic period per type of evidence and per clade. (a) Number of occurrences per type of evidence. (b) Number of occurrences per clade. (c) Number of localities per type of evidence. (d) Number of localities per clade.

Decapod crustaceans

Modern occurrences and composition.

Extant decapod crustaceans are found in seeps worldwide. The review articles by Chevaldonné and Olu (1996) and Martin and Haney (2005) that include decapod crustaceans in cold seeps, and subsequent studies on cold seeps faunas show that seeps with decapods are primarily found in the Gulf of Mexico (Komai and Segonzac 2005; Cordes et al. 2010b; Coykendall et al. 2017), along the west coast of North America (Sakai and Türkay 1999; Levin et al. 2000; Levin and Michener 2002; Niemann et al. 2013; Levin et al. 2015), in the northwestern Pacific (Chevaldonné and Olu 1996; Fujikura et al. 2002; Sahling et al. 2003; Dong and Li 2015), and New Zealand (Ahyong 2008; Baco et al. 2010). Other occurrences, for example, include off Congo (Macpherson and Segonzac 2005), Chile (Sellanes et al. 2008), Turkey

(Olu-Le Roy et al. 2004), Brazil (Fujikura et al. 2017), the east coast of North America (Van Dover et al. 2003), Barbados (Olu et al. 1996), Spain (Dworschak and Cunha 2007), in the North Sea (Dando et al. 1991), and Denmark (Jensen et al. 1992). Martin and Haney (2005) reported 125 species found in vent and seep environments, and over 30 are known from cold seeps.

Decapods in cold seeps are represented mainly by squat lobsters (Galatheoidea and some Chirostyloidea), king or stone crabs (Lithodidae), true crabs (Brachyura), and shrimps (Caridea, mostly *Alvinocaris* spp., and some Dendrobranchiata) (Chevaldonné and Olu 1996; Martin and Haney 2005). Less commonly reported are burrowing shrimps (Axiidea), hermit crabs (Paguroidea), and lobsters (Astacidea and Polychelida) (Chevaldonné and Olu 1996; Martin and Haney 2005; Sellanes et al. 2008). Endemicity is low among seep decapods (Macpherson and Segonzac 2005; Martin and Haney 2005; Sellanes et al. 2008).

Biology.

Squat lobsters (Galatheoidea and some Chirostyloidea) are predominantly epifaunal benthics with a varied diet. They are suspension and deposit feeders, predators including some cannibals, scavengers, while others consume algae (Lovrich and Thiel 2011). Taxa that live in cold seeps have a varied diet as well. Some seep galatheoids appear to be predators on small heterotrophs and scavengers (Chevaldonné and Olu 1996; MacAvoy et al. 2008), while others may be deposit feeders based on stomach content (Macpherson and Segonzac 2005) or feed on bacteria (Barry et al. 1996). *Munidopsis* sp. from the Gulf of Mexico probably eats hydroids (Becker et al. 2009; Cordes et al. 2010a) and/or a barnacle and a carid shrimp (Cordes et al. 2010a). Another species of *Munidopsis* may consume other decapods and worms (Cordes et al. 2010a). Isotopic evidence suggests that *Munidopsis* sp. from Alaska relied on chemosynthetically-fixed carbon from tropic levels above the primary producers (Levin and Michener 2002). Some have a diet tied to the most abundant primary producers. *Shinkaia crosnieri* scrapes off epibiotic bacteria from their setae as a source of nutrition (Tsuchida et al. 2011), and the same applies for *Kiwa puravida* (Thurber et al. 2011). As for squat lobsters in general (Schweitzer and Feldmann 2010), seep squat lobsters probably did not break molluscan shells given their fairly small claws and their claw morphology.

The other group of anomurans often found in cold seeps, the king crabs (Lithodidae), are epifaunal taxa that prey on vesicomyid and mytilid bivalves and are also deposit-feeders (Hashimoto et al. 1989; Chevaldonné and Olu 1996; Barry et al. 1996). Hashimoto et al. (1989: fig. 10) even showed king crabs fighting over a clam held by the chelipeds by one crab, and we have seen an image of a king crab holding a broken shell. Although king crabs have a generalized diet, non-seep confamilials are suggested to be durophagous predators (Aronson et al. 2015), stomach content does frequently contain mollusks (Abelló 1995; Comoglio and Amin 1999), and experiments show that king crabs can crush mollusk shells (Jørgensen and Primicerio 2007). Lithodids prefer deep and cold waters: only a few taxa live in waters < 200 m, and shallow-water occurrences are restricted to high latitudes (Hall and Thatje 2009a), both of which is related to a low tolerance of high temperatures (Hall and Thatje 2009a; Thatje and Hall 2016).

The true crabs (Brachyura) are represented by a variety of clades at cold seeps including members of Goneplacidae, Atelecyclidae, Cancridae, Homolodromiidae, Trichopeltariidae, Polybiidae, Mathildellidae, and various Geryonidae and Majoidea (Dando et al. 1991; Jensen et al. 1992; Olu-Le Roy et al. 2004; Martin and Haney 2005; Ahyong 2008; Quattrini et al. 2015). These groups tend to be benthic crabs generally not capable of swimming (Hartnoll 1971) and burying/burrowing (Warner 1977; Bellwood 2002). A number of studies have shed light on the diet of crabs in seeps. One study from Monterey Bay seeps off California (Barry et al. 1996) suggested that the spider crab *Chionoecetes bairdi* preys on vesicomyid clams, while the other spider crab, *Chorilia longipes*, would graze on bacteria and clam siphons. Another study suggested that a congeneric from Oregon, *Chionoecetes tanneri*, is a carnivore on macrofauna (Levin and Michener 2002). In the Gulf of Mexico, an atelecyclid crab is heavily dependent on carbon from seeps (MacAvoy et al. 2002), while another study suggested a diet consisting of hydroids and a polychaete for this taxon (Cordes et al. 2010a). The spider crab *Rochinia crassa* was interpreted not to be a major shell-crusher, but would feed on thin-shelled mussels, gastropods,

crustaceans, and hydroids instead (MacAvoy et al. 2002). Members of Goneplacidae, Cancridae, Mathildellidae, Geryonidae, and Majoidea are suggested to be durophagous (Schweitzer and Feldmann 2010) so it is likely that some crabs crushed bivalve shells at seeps. Most crab species (7) associated with seeps are described from New Zealand (Ahyong 2008), and the figured large claws of the males of *Trichopeltarion janetae*, *Neopilumnoplax nieli*, and *Pycnoplax victoriensis* appear suitable for crushing shells.

Shrimp occurrences in modern seep are dominated by members of Alvinocarididae from the genus *Alvinocaris*. These organisms live on the ocean floor as adults and are variously capable of swimming (Pond et al. 1997; Aguzzi et al. 2007). They are often found in high densities on bivalve beds in seeps (Olu et al. 1996; Van Dover et al. 2003; Komai and Segonzac 2005; Ramirez-Llodra and Segonzac 2006). Substantial progress has been made to unravel the diet of *Alvinocaris*. The diet is best known for *Alvinocaris muricola*: stomach content has revealed diatoms and foraminifera (Komai and Segonzac 2005), but the same species is also a scavenger seen feeding on the tissue of mussels after their shells were broken by a submersible (Ramirez-Llodra and Segonzac 2006). Isotopic analyses of the same species and *A. stactophila* suggest a generalist feeding strategy for both, with low $\delta^{15}\text{N}$ values of *A. muricola* being attributed to a bacterial diet, while higher values for the same species may indicate feeding at higher trophic levels (meiofauna) or organic matter originating from surface waters (Becker et al. 2013). Previous isotopic analyses and subsequent modelling of food webs suggested that *Alvinocaris stactophila* most likely consumed hydroids and sabellid polychaetes and a number of other potential prey, indeed suggesting a generalist-type diet. Even more seems known about alvinocaridids from hydrothermal vents, whose feeding strategies differ from capturing bacteria, scavenging, and preying on confamilials (Pond et al. 1997; Polz et al. 1998; Gebruk et al. 2000; Stevens et al. 2008). Their small chelipeds do not seem suitable to break mollusk shells.

The Axiidea shrimps including ghost shrimps are known to burrow (Dworschak et al. 2012; Kornienko 2013; Hyžný and Klompmaker 2015). They have rarely been reported from modern seeps because they are difficult to observe and catch (Martin and Haney 2005), but are very commonly associated with fossil seeps (see below). Burrowing must be only possible in loose sediments adjacent to the carbonate deposits. Very little is known about the diet of extant axiids associated with seeps. The only remark we are aware of is that by Felder and Kensley (2004), who hypothesized that *Calaxius carneyi* could feed on bacteria. Burrowing shrimps living elsewhere are primarily deposit and suspension feeders consuming detrital material, seaweed, algae, seagrass, and phytoplankton (Dworschak 1987; Stapleton et al. 2001; Shimoda et al. 2007; Kneer et al. 2008; Dworschak et al. 2012), with callianassids being predominantly deposit feeders. For now, we can only assume that the diet of seep axiids is similar to representatives living elsewhere in that small particles caught in suspension or in the substrate are the main source of nutrition. The rare presence of astacid and polychelid lobsters and hermit crabs in seeps does not allow for meaningful generalizations about their diet in seeps.

Fossil record and evolution.

Body fossils

A group that is common in seeps today, but is only reported from three fossil seep localities consisting of four occurrences so far are squat lobsters (Galatheaidea and Chirostyloidea) (Figure 4). *Shinkaia katapsyxis* is described from the Eocene of Washington state (Schweitzer and Feldmann 2008; Kiel 2010a), “*Galathea*” *spitzbergica* and another galatheid species were found in the late Paleocene of Spitsbergen (Hägg 1925; Gripp 1927; Vonderbank 1970; Hryniewicz et al. 2016; pers. obs. AAK), and a possible galatheid appendage was reported from the latest Jurassic–earliest Cretaceous (Tithonian–Berriasian) of again Spitsbergen (Hammer et al. 2011; Hryniewicz et al. 2015b). Galatheoids have a fossil record dating back to the Middle Jurassic (Bathonian) (Van Straelen 1925) with a major diversification in Late Jurassic shallow-water reefs in Europe (Robins et al. 2013; Robins et al. 2016). Other diverse reef assemblages originate from the mid-Cretaceous of Spain (Klompmaker et al. 2012a) and the Eocene–Oligocene of Italy (De Angeli and Garassino 2002). Conversely, only two fossil species of Chirostyloidea

have been confirmed: the Late Cretaceous *Pristinaspina gelasina* (Schweitzer and Feldmann 2000; Ah Yong and Roterman 2014) from siliciclastic rocks of Alaska and the Eocene *Eouropytychus montemagrensis* from a coral limestone of Italy (De Angeli and Ceccon 2012). If the Tithonian-Berriasian decapod is indeed a galatheoid appendage, this diverse group inhabited cold seeps early on in their evolutionary history. Given their fossil record and fairly calcified cuticle, more fossil squat lobsters are expected from fossil cold seep deposits.

The other anomuran group commonly present in modern seeps are king crabs (Lithodidae, phylogenetically nested within the Paguroidea (Noever and Glenner 2017)), but no fossil occurrences from seeps are known thus far. The total number of extant lithodid species known is more than 100 and they occur in predominantly deep waters (Hall and Thatje 2009b; Hall and Thatje 2009a). Only a limited number of fossil occurrences are known: *Paralomis debodeorum* from a middle to late? Miocene concretionary siltstone deposit of New Zealand (Feldmann 1998), *Paralithodes bishuensis* and *Paralomis* sp. from the early Miocene of Japan (Takeda et al. 1986; Mizuno and Takeda 1993; Karasawa et al. 2017), and undetermined lithodid chelae from the early? Miocene of southern Argentina (Feldmann et al. 2011). The age of these occurrences is consistent with estimates from molecular and morphological analyses suggesting an early Miocene origin (Cunningham et al. 1992; Bracken-Grissom et al. 2013). Most fossil occurrences are from the Pacific, which may be consistent with their suggested divergence from shallow-water anomurans in the northern Pacific (Hall and Thatje 2009a; Noever and Glenner 2017). Thus, lithodids are also expected from late Cenozoic cold seeps around the Pacific, particularly given their relatively well-calcified cuticle. Hermit crab (Paguroidea) claws have been found recently in Late Cretaceous seeps from South Dakota.

A fair number of true crabs has been found in fossil seeps so far (Figure 4). One record, referred to a ?goneplacoid or a ?xanthoid (Kiel and Hansen 2015; Luque et al. 2017), is from the early Oligocene of Colombia, whereas four late Cretaceous (Campanian–Maastrichtian) species from the so-called tepee buttes in South Dakota and Colorado have been reported (Bishop and Williams 2000; Meehan and Landman 2016). The latter include lyreidid frog crabs (*Heus foersteri* and *Heus manningi*), the homolid *Latheticocarcinus punctatus*, and the konidromitid *Konidromites bjorki*. New discoveries in seeps from South Dakota include the dakoticancrid *Dakoticancer overanus*, another homolid, the etyid *Secretanella* sp., the necrocarcinid *Elektrocarcinus pierrensis*. Lyreididae and Homolididae are extant, but do not occur in modern cold seeps (Martin and Haney 2005), whereas konidromitids, necrocarcinids, dakoticancrids, and etyids are extinct. The inferred depth from the Late Cretaceous seeps in South Dakota is 100–250 m (Meehan and Landman 2016), an environment in which not many deep-sea decapods are to be expected. The lyreidid frog crabs have a morphology consistent with a burying behavior, implying that these critters lived in soft sediments very close to the hardened limestones. Extant homolids are reported predominantly from waters between 200–500 m (Guinot and Richer de Forges 1995: fig. 74), but they did occur frequently in shallower waters early in their evolutionary history in the Mesozoic (Schweitzer et al. 2004; Feldmann and Schweitzer 2009), probably including the seep record herein. The morphology of *Secretanella* sp. strongly suggests that it was a swimming crab and may have been an occasional inhabitant of seeps. Many more Brachyura are expected from fossil seeps because they are common occurrence in modern seeps, have an extensive fossil record starting in the Jurassic (Klomp maker et al. 2013b; Schweitzer and Feldmann 2015), and have a relatively high preservation potential within the Arthropoda (Klomp maker et al. 2017).

No representatives of shrimps assigned to Alvinocarididae have been found in fossil seeps, but some alvinocaridids (*Hartholfia* spp.) have been reported from the Late Jurassic thin-bedded limestones from Germany (Polz 2007; Schweigert 2011). The assignment of *Hartholfia* to Alvinocarididae was however provisionally (Polz 2007). Indeed, phylogenetic analyses suggest that Alvinocarididae is a derived rather than a basal clade (Bracken et al. 2009; Sudarsky 2016) and the group containing *Alvinocaris* would have radiated as late as the Miocene (Shank et al. 1999). Despite their abundance in modern seeps, it is unlikely that many if any remains will be found due to the low preservation potential of shrimps (Plotnick 1986; Klomp maker et al. 2017).

While modern occurrences of burrowing shrimps (Axiidae and Gebiidea) from seeps are rare, they represent the most commonly found decapod body fossil in fossil seeps (Figure 4). Especially claws of ghost shrimps attributed to Callianassidae are found in the Cretaceous and Cenozoic, including *Callianassa*, *Neocallichirus*, *Glypturus*, *Callianopsis*, and *Calliax* (Peckmann et al. 2002; Peckmann et al. 2007b; Karasawa 2011; Larson et al. 2013; Agirrezabala et al. 2013; Kiel et al. 2013; Nesbitt et al. 2013; Natalicchio et al. 2015; Kiel and Hansen 2015). This difference is caused by the fact that burrowing shrimps are difficult to observe and collect in the ocean bottom today, requiring special methods (Dworschak 2015). As for the frog crabs, it is likely that they lived just outside the hard carbonate rock in the soft sediments surrounding the cold seep. Alternatively, their extensive burrows in initially soft sediments may have served as conduits for seep fluids after which carbonate formation commenced (Wiese et al. 2015; Zwicker et al. 2015). Callianassid claws are found in association with tube structures/burrows in seeps from the mid-Cretaceous (Albian) of Spain (Agirrezabala et al. 2013) and from other fossil deposits (Hyžný and Klompmaker 2015). Much more taxonomic work can be done on ghost shrimps given their common occurrence in fossil seeps.

Figure 4. Occurrence-based pie diagram of decapod body fossils in cold seeps.

Burrows

In addition to the callianassid associated with a burrow mentioned above (Agirrezabala et al. 2013), several burrows attributed to the trace fossil *Thalassinoides* have been reported from fossil seeps. They include burrows from the mid-Cretaceous (Albian) of Spain (Wiese et al. 2015), the latest Cretaceous (Maastrichtian) of the James Ross Basin in Antarctica (Little et al. 2015), the earliest Paleocene (Danian) of California (Blouet et al. 2017), the early Oligocene of Washington state (Zwicker et al. 2015), and the Miocene of New Zealand (Campbell et al. 2008; Troup 2010). *Thalassinoides* burrows contain a variety of decapods including a crab, several lobsters, and ghost shrimps (Neto de Carvalho et al. 2007). However, the majority appear to be associated with callianassids (Neto de Carvalho et al. 2007; Hyžný and Klompmaker 2015). Lobsters are not known from fossil seeps thus far, and are very rare in modern seeps. Callianassids have been found in association with seep burrows and/or are known from the same general area and age. Other than the mid-Cretaceous (Albian) seeps from Spain (Agirrezabala et al. 2013; Wiese et al. 2015), callianassids were also reported from the early Oligocene seeps of Washington state (Goedert and Campbell 1995) and from Late Cretaceous rocks in the James Ross Basin of Antarctica

(Ball 1960; Feldmann et al. 1993). Thus, most burrows in fossil seeps are probably caused by callianassids, a clade that originated in the Early Cretaceous (Hyžný and Klompmaker 2015).

Fecal pellets

Microcoprolites or fecal pellets provide an important additional source of information about the occurrence of crustaceans in fossil cold seeps. Compared to body fossils, they are very abundant and do fossilize in seep limestones. *Palaxius* spp. and *Favreina* spp. are known from fossil seeps. *Palaxius* has been reported from the Late Jurassic (Oxfordian) of France (Senowbari-Daryan et al. 2007), the Late Cretaceous (Cenomanian–Turonian) of Morocco (Smrzka et al. 2017), and the Eocene, Oligocene, and Miocene of Washington state (Peckmann et al. 2007b; Kiel 2010a; Kuechler et al. 2012; Smrzka 2013; Zwickler et al. 2015). *Favreina* is known from the Oxfordian of France (Peckmann et al. 1999; Senowbari-Daryan et al. 2007) and the Eocene of Oregon (Campbell 1995). Crustacean coprolites not assigned to an ichnotaxon originate from the mid-Cretaceous (Albian) of Spain (Agirrezabala et al. 2013), the Cenomanian of Utah (Kiel et al. 2012), and the latest Miocene (Messinian) of Italy (Natalicchio et al. 2013).

Microcoprolites referable to crustaceans ichnotaxonically are produced *at least* by true crabs, glypheid lobsters, galatheoids anomurans, and (callianassid) axiids (Brönnimann 1972; Förster and Hillebrandt 1984; Schweigert et al. 1997). Ascription of coprolites to crustacean species is challenging because multiple species can produce coprolites referable to the same ichnospecies. The stratigraphic ranges of some coprolite ichnospecies span multiple geological periods (Blau et al. 1993; Senowbari-Daryan and Kube 2003; Kietzmann et al. 2010). From fossil seeps, *Palaxius decemlunulatus* is known from the Late Cretaceous to the Miocene, a duration of ~80 my (Kuechler et al. 2012; Smrzka et al. 2017). Crustacean species longevity tends to be shorter, although some exceptions with stratigraphic ranges of up to tens of millions of years are reported (summarized in Klompmaker et al. 2012b). Nevertheless, it is possible to link certain coprolites to crustacean species where they co-occur locally (e.g., Förster and Hillebrandt 1984; Becker and Chamberlain 2006; Feldmann et al. 2015), including in seep deposits (Peckmann et al. 2007b). A search for microcoprolites in seeps older than the Oxfordian has the potential to uncover the timing of crustaceans invading seeps. Inferring the producer of coprolites without accompanying body fossils remains difficult, but the stratigraphic range of decapod clades may be used to narrow down the options.

Repair scars

A final evidence for the presence of crustaceans in cold seeps are repair scars in mollusks. However, repair scars cannot be attributed unambiguously to crustaceans. Shell damage can also be caused by durophagous gastropods, birds, and fishes in the Meso-Cenozoic (Alexander and Dietl 2003). The depth of cold seeps precludes birds as viable predators, and predatory gastropods that can break shells such as *Murex*, *Busycon*, *Sinistrofulgur*, and *Busycotypus* (Nielsen 1975; Dietl 2003a; Dietl 2003b) are absent or rare in modern cold seeps (e.g., Sasaki et al. 2010). This leaves predatory fishes as alternatives to crustaceans. They are present in modern cold seeps (Kulm et al. 1986; Juniper and Sibuet 1987; Sellanes et al. 2008; Cordes et al. 2010a), but to what extent they are able to break shells is unknown. Furthermore, damage to infaunal bivalves can be caused by burrowing (Checa 1993; Alexander and Dietl 2005). Specifically, burrowing in an attempt to avoid predators and sediment overburden or erosion resulting in trapped particles and collision with hard objects within the sediments may cause damage commencing at the commissure (Checa 1993; Alexander and Dietl 2005). Burrowing/burying bivalves are present in seep faunas including solemyids, thyasirids, nucinellids, and lucinids (Amano et al., this volume).

Repair scars reported from fossil cold seeps include those in the brachiopod *Sulcirostra paronai* from the Early Jurassic (Sinemurian) of Oregon (Sandy et al. 2005; Sandy 2010); the bivalve *Nucinella gigantea* from the mid-Cretaceous (Cenomanian) of Japan (Kiel et al. 2008); the bivalves *Hubertschenkia ezoensis*, *Bathymodiolus inouei*, and *Conchocele bisecta* from the early Oligocene of Japan (Kiel et al. 2016), the gastropods *Provanna antiqua* and *Turrinosyrinx hickmanae* from the late Oligocene of Washington state (Kiel 2006), and the gastropod *Mohnia vernalis* from the late Pleistocene

of Japan (Amano et al. 2013). In the most extensive study of repair scars in fossil cold seeps thus far, Kiel et al. (2016) showed that substantially higher repair scar frequency (and drilling frequency) in the infaunal thyasirid *C. bisecta* relative to the epifaunal mytilid *B. inouei* and the semi-infaunal vesicomysid *H. ezoensis*. The latter two species are interpreted to have lived closer to the sulfide-rich seepage. Consequently, predatory crabs would have preferentially attacked specimens of *C. bisecta* away from the toxic fluids despite the fact this infaunal species is least accessible to predators. Most damage to *C. bisecta* was found at the ventral margin, which is the deepest point of a shell in life position (Kiel et al. 2016). Although the predation hypothesis remains viable, some of the repaired damages could also have resulted from burrowing, notably divot-shaped scars. Regardless, studying repair scar frequencies in mollusks can be used to infer the presence and potentially the importance of shell-breaking predators in structuring seep communities.

Ostracods

Modern occurrences and composition.

The presence of ostracods in modern cold seeps was most recently summarized by Karanovic and Brandão (2015). Seep ostracods identified to the genus-level are known from the Black Sea near Turkey and the northern part of the Gulf of Mexico, while additional occurrences not identified to low taxonomic levels have been reported off the coast of Norway, again in the Gulf of Mexico, off the west coast of North America, and possibly off Antarctica (Montagna et al. 1987; Sommer et al. 2007; Van Gaeve et al. 2009; Ritt et al. 2010; Bright et al. 2010; Hauquier et al. 2011; Decker et al. 2012; Degen et al. 2012; Portnova et al. 2014).

Ostracods in cold seeps are dominated in terms of diversity and abundance by representatives of Podocopida and to a lesser extent Platycopida (Coles et al. 1996; Ritt et al. 2010; Degen et al. 2012). Ostracod faunas at cold seeps are not endemic at the species-level and consist of a mixture of shallow and deep-water taxa in addition to widely distributed taxa (Karanovic and Brandão 2015). Quaternary seep carbonate mounds west of Ireland contained predominantly upper bathyal ostracods and some shallow-water taxa due to contamination (Coles et al. 1996). These Irish ostracods are much more abundant in cold seeps than at a control site. Ostracod density is higher away from the direct center of the seep site for Norwegian seeps (Decker et al. 2012).

Biology.

Most Podocopida are epifaunal, but *Krithe*, commonly present in cold seeps, is infaunal. *Cytherella*, the platycopid taxon commonly present in cold seeps, has an infaunal life habit (Russo et al. 2012). Feeding modes differ between the orders: while podocopids are detritus feeders, filter feeding is employed by platycopids (Smith and Horne 2002; Russo et al. 2012).

Considerable debate has revolved around the use of ostracods to infer oxygen concentration, which is also of interest here due to relatively low oxygen levels at seep sites. Two proxies have been used: (1) the percentage of platycopids, and (2) the size of the anterior vestibulum of *Krithe/Parakrithe*.

The “Platycopid Signal Hypothesis” (Whatley 1991) proposes that as oxygen levels decrease, the percentage of platycopids of all ostracods increases because these filter-feeding ostracods would be able to move sufficient water along their respiratory surface on the ventral side (Whatley 1990; Whatley 1991; Whatley et al. 2003), further supported by experimental evidence on *Cytherella* (Corbari et al. 2005). Whatley et al. (2003: p. 360) also presented a table for percentages of platycopids and inferred oxygen levels, with medium oxygen concentrations for assemblages consisting of 40–60% platycopid specimens and low oxygen levels for assemblages with > 60% platycopid specimens. This method was used to infer oxygen levels in deep time (Whatley 1991; Boomer and Whatley 1992; Lethiers and Whatley 1994; Whatley 1995). However, the Platycopid Signal Hypothesis was not supported by a re- and new analysis because platycopids are not consistently dominant in oxygen minimum zones today (Brandão 2008; Brandão and Horne 2009) and *Cytherella* was found throughout a Miocene outcrop in Trinidad of varying inferred oxygen levels rather than in the oxygen minimum zone only (Wilson et al. 2014). The fossil

record of seep ostracods is not consistent either with the Platycopid Signal Hypothesis because percentages are low and vary from 0–18.8% (Table 1). Podocopids adapted to low oxygen condition were also abundant in Miocene seep ostracod assemblages (Russo et al. 2012). Rather than a proxy for oxygen levels, Horne et al. (2011) proposed that high percentages of platycopids would indicate oligotrophic nutrient levels because modern platycopids feed on nano- and picoplankton, groups that are dominant in oligotrophic waters.

The size and shape of the anterior vestibulum of the podocopids *Krithe*/*Parakrithe* is hypothesized to be negatively correlated with oxygen concentration (Peypouquet 1975; Peypouquet 1979) in the North Atlantic, and preliminary support was claimed based on one species from Sweden (McKenzie et al. 1989). If correct, this proxy could be used to evaluate oxygen levels in deep time (references in Whatley and Zhao 1993). For fossil seeps, Russo et al. (2012) implied that *Krithe* with large vestibulums were present in Miocene seeps from Italy. However, when re-evaluating this relationship using 12 *Krithe* and four *Parakrithe* species over a 150–4000 m depth range including five water masses varying in oxygen content in the South China Sea, the pattern did not hold up (Whatley and Zhao 1993). Species with four different vestibulum sizes co-occurred in 57% of the samples and the vestibulum of one species reported from a depth range of 2775 m was said not to differ in size. Similar conclusions were reached using fossil and modern North Atlantic species (Coles et al. 1996; Van Harten 1996). Furthermore, considerable variation of anterior vestibulum size in a small range of oxygen concentration was shown within one Holocene species from Brazil (Do Carmo et al. 2009).

Dispersal mechanisms of seep ostracods are poorly known, but Karanovic and Brandão (2015) proposed that they would either hitchhike on other animals such as fishes, or by surviving through the digestive tract of predators.

Table 1. Percentages of platycopid specimens of all ostracods collected from subfossil to fossil cold seeps. Only assemblages of ≥ 10 specimens are incorporated.

Where	Age	# platycopids	Total # ostracods	% platycopids
Mound A (sites 40–41), west of Ireland (Coles et al. 1996)	late Pleistocene - Holocene	1	624	0.2
Mound B (site 18), west of Ireland (Coles et al. 1996)	late Pleistocene - Holocene	13	792	1.6
Mound C (site 25), west of Ireland (Coles et al. 1996)	late Pleistocene - Holocene	61	1124	5.4
Mound D (site 81), west of Ireland (Coles et al. 1996)	late Pleistocene - Holocene	9	664	1.4
SC561/Cals1 W/Cals2 W 15–24, Sarsetta, Italy (Russo et al. 2012)	middle Miocene (Serravallian)	29	154	18.8
UWBM B6781, Washington, USA (Yamaguchi et al. 2016)	late Oligocene	0	33	0.0
UMBM B7897, Washington, USA (Yamaguchi et al. 2016)	early Oligocene	1	11	9.1

Fossil record and evolution.

Ostracods are the most abundant and diverse crustaceans found in fossil seep deposits, with 86% of specimens and 65% of taxon occurrences. The oldest seep ostracods are reported from a hematite facies in an early phase of a Late Silurian seep (Barbieri et al. 2004; Buggisch and Krumm 2005), followed by ostracods outside/above the central zone of a Middle Devonian seep (Hryniewicz et al. 2017) and ostracods in a brachiopod seep limestone from the Late Devonian (Peckmann et al. 2007a). All occurrences are from Morocco and not identified further. The only seep ostracod occurrences from the Mesozoic are Jurassic in age and originate from a variety of countries: Russia (Nova Zembla) (Hryniewicz et al. 2015a), France (Rolin et al. 1990; Gaillard et al. 1992; Peckmann et al. 1999), Germany (Teichert and Luppold 2013), Antarctica (Kelly et al. 1995), and Argentina (Gómez-Pérez 2001; Gómez-Pérez 2003). None of them are identified further, except for the monospecific German occurrence (*Ogmoconcha amalthei*). More localities and occurrences are known from the Cenozoic (Figure 3). Although ostracods from the Neogene of Italy (Barbieri and Cavalazzi 2005) and the early Miocene of Venezuela (Kiel and Hansen 2015) have not been identified further, three papers have done so in great

detail for Oligocene ostracods from Washington state (Yamaguchi et al. 2016), middle Miocene ostracods from Italy (Russo et al. 2012) and late Pleistocene – Holocene ostracods west of Ireland (Coles et al. 1996). The fact that only three articles have focused on fossil ostracods from cold seeps thus far, and only from the Cenozoic, implies that much more research can be done such as depth estimates (Yamaguchi et al. 2016); taphonomic aspects (e.g., Boomer et al. 2003; Yamaguchi et al. 2016); faunal composition changes through time; degree of endemism in deep time; and diversity, body size, predation, and abundance trends across seeps.

Barnacles

Modern occurrences and composition.

A limited number of barnacles are known from modern cold seeps, with most reported taxa restricted to the Pacific Ocean. Non-parasitic taxa from the Pacific are dominated by the stalked barnacles from the scalpelliform Eolepadidae family (Neolepadinae subfamily) and include *Ashinkailepas kermadecensis* from New Zealand (Buckeridge, 2009); *Ashinkailepas seepiophila* from Japan (Fujikura et al. 2002; Yamaguchi et al. 2004); *Leucolepas longa* from Papua New Guinea (Southward et al. 2002; Southward and Jones 2003; Stecher et al. 2003); *Vulcanolepas parensis* from the Pacific-Antarctic Ridge (Southward, 2005); and possibly *Vulcanolepas osheai* found near New Zealand (Buckeridge 2000; Southward 2005). Other Pacific records include rare occurrences of the scalpelliforms *Arcoscalpellum* sp., *Scalpellum projectum*, *Scalpellum* sp., and an unidentified scalpellid from Chile (Sellanes et al. 2008; Báez and Sellanes 2009; Zapata-Hernández et al. 2014). The latter authors also noted the presence of the lepadiform *Lepas* sp. and three other unidentified species of Cirripedia. Other records from the Pacific include unidentified Cirripedia from the Sea of Okhotsk west of Russia (Sahling et al. 2003), and some other Cirripedia were recovered from inactive parts of seeps west of Costa Rica (Levin et al. 2015, table S1) not included in our analyses. The parasitic rhizocephalan barnacle *Parthenopea australis* infesting the callinassid shrimp host *Vulcanocallix* sp. was found near active cold seeps west off New Zealand (Lörz et al. 2008; Lützen et al. 2009). Other rhizocephalans were encountered on the crabs *Trichopeltarion janetae*, *Neopilumnoplax nieli*, and *Pycnoplax victoriensis* west off New Zealand (Ahyong 2008). The only barnacles associated with seeps outside the Pacific we are aware of are the verrucomorph *Costatoverruca floridana* (Carney 1994; Bergquist et al. 2003; Cordes et al. 2006; Becker et al. 2009; Cordes et al. 2010a) and an unidentified cirriped on the carapace of the spider crab *Rochina crassa* (MacAvoy et al. 2002), both from the Gulf of Mexico.

Biology.

Barnacles are filter or suspension feeders, including modern stalked barnacles living in cold seep environments (e.g., Tunnicliffe and Southward 2004). The biology of *Ashinkailepas seepiophila* and *Leucolepas longa* is best known. The nauplius larvae of *A. seepiophila* have large nutrient reservoirs, nauplius appendages are equipped with long plumose setae for flotation, and larval development of this species is completed within 65 days in the lab (Yorisue et al. 2013). Most specimens of sulphide-adapted stalked barnacle *L. longa* grow on bivalves, but rocks and worm tubes are also used, while their larvae are suitable for long-distance dispersal (Tunnicliffe and Southward 2004). The parasitic barnacles rely on nutrients from its host rather than from a seep directly.

Fossil record and evolution.

To our knowledge, barnacles were only mentioned once in association with a fossil cold seep. Eagle et al. (1999) reported an unidentified barnacle from a bathyal early Miocene concretionary siltstone that may represent a hydrocarbon seep based on the bivalves and unusual foraminifera. None of the three bivalve taxa (*Linucula*, *Jupiteria*, and *Notocallista*) are chemosymbiotic taxa known to inhabit cold seeps (e.g., Kiel 2010), but the first two genera are nuculids, members of which are found at modern seeps and vents (Kiel 2010b). Subsequent stable isotope analyses on foraminifera and a bivalve resulted in highly

negative $\delta^{13}\text{C}$ values consistent with methane seepage and the presence of the possibly endemic, highly abundant benthic foraminifer *Amphimorphinella butonensis* (Hayward et al. 2011).

Neolepadinae appears to be a clade that originated fairly late in the evolutionary history of cirripeds, with the stem and crown node estimated to occur within the Cretaceous (Pérez-Losada et al. 2008). Members of this subfamily also inhabit true hydrothermal vents (Newman et al. 2006; Buckeridge et al. 2013; Herrera et al. 2015), implying that a Cretaceous age origin for these barnacles inhabiting cold seeps is unlikely. This hypothesis is supported by a more recent phylogenetic analysis including most of the extant seep barnacles suggesting a late Cenozoic origin of seep barnacles (Herrera et al. 2015, fig. 3). Representatives of the other but extinct subfamily within the Eolepadidae, Eolepadinae, are not known from fossil seep deposits (e.g., Buckeridge and Grant-Mackie 1985).

Balanomorph barnacles, very common in the fossil record of shallow marine deposits (e.g., Foster and Buckeridge 1987; Gale and Sørensen 2015), appear absent from modern and fossil cold seeps and are rarely in modern hydrothermal vents (Yamaguchi and Newman 1990; Yamaguchi and Newman 1997).

Conclusions

- Crustaceans are much more common in fossil seeps than previously known, and are found on each continent.
- Decapod crustaceans are represented by body fossils and traces (coprolites, repair scars in mollusks, and burrows), whereas only body fossils of ostracods and barnacles are known.
- Traces of decapods have the potential to detect their presence when body fossils are lacking.
- Ostracods have the longest stratigraphic record in fossil seeps starting in the Silurian. Seep barnacles have been found only once in the fossil record thus far. Decapod crustaceans are present in seeps from Jurassic onwards.
- While modern seep decapods are dominated by galatheid squat lobsters, alvinocaridid shrimps, king crabs, and true crabs, the fossil record consists primarily of callianassid ghost shrimps and true crabs thus far. Preservation and recognition are likely to have influenced this discrepancy.
- The relatively unexplored fossil record of seep crustaceans provides many opportunities for systematic and paleoecological research.

Acknowledgements

We thank Andrzej Kaim for the invitation to work on this exciting topic and for items of literature. For various reasons, we express our gratitude to (in alphabetical order by family name): Simon Brandão, Tim-Yam Chan, Erica Clites, Katsunori Fujikura, Krzysztof Hryniewicz, Azusa Ikuta, Yasumitsu Kanie, Hiroaki Karasawa, Steffen Kiel, Neil Landman, Ryuichi Majima, Michael Sandy, Sally Shelton, and Chau-Chang Wang. This work was presented at the 9th International Crustacean Congress in Washington D.C. in May 2018, with support of an NSF Travel Grant (#1802718). Reviewers.....

References

- Abelló P (1995) Note on the diet of *Lithodes ferox* (Anomura: Lithodidae) off Namibia. South Afr J Mar Sci 15:273–277 . doi: 10.2989/025776195784156304
- Agirrezabala LM, Kiel S, Blumenberg M, Schäfer N, Reitner J (2013) Outcrop analogues of pockmarks and associated methane-seep carbonates: A case study from the Lower Cretaceous (Albian) of the Basque-Cantabrian Basin, western Pyrenees. Palaeogeogr Palaeoclimatol Palaeoecol 390:94–115 . doi: 10.1016/j.palaeo.2012.11.020

573 Aguzzi J, Ramirez-Llodra E, Telesnicki G, Camps M (2007) Day-night activity rhythm of the cold seep
 574 shrimp *Alvinocaris stactophila* (Caridea: Alvinocarididae) from the Gulf of Mexico. J Mar Biol Assoc
 575 UK 87:1175–1180 . doi: 10.1017/S0025315407057311

576 Ah Yong ST (2008) Deepwater crabs from seamounts and chemosynthetic habitats off eastern New
 577 Zealand (Crustacea: Decapoda: Brachyura). Zootaxa 1708:1–72

578 Ah Yong ST, Roterman CN (2014) Pristinaspiniidae, a new family of Cretaceous kiwaiform stem-lineage
 579 squat lobster (Anomura, Chirostyloidea). Scr Geol 147:125–133

580 Alexander RR, Dietl GP (2003) The fossil record of shell-breaking predation on marine bivalves and
 581 gastropods. In: Kelley PH, Kowalewski M, Hansen TA (eds) Predator-Prey Interactions in the Fossil
 582 Record. Kluwer Academic/Plenum Publishers, New York, Boston, Dordrecht, London, Moscow, pp 141–
 583 176

584 Alexander RR, Dietl GP (2005) Non-predatory shell damage in Neogene Western Atlantic deep-
 585 burrowing bivalves. Palaios 20:280–295

586 Amano K, Hasegawa S, Ishihama S (2013) Molluscan fossils from core samples collected from off Joetsu
 587 during MD179 cruise. J Jpn Assoc Pet Technol 78:92–96

588 Amano K, Kiel S (2007) Fossil vesicomysid bivalves from the North Pacific region. The Veliger 49:270–
 589 293

590 Aronson RB, Smith KE, Vos SC, McClintock JB, Amsler MO, Moksnes P-O, Ellis DS, Kaeli J, Singh H,
 591 Bailey JW, Schiferl JC, van Woesik R, Martin MA, Steffel BV, Deal ME, Lazarus SM, Havenhand JN,
 592 Swalethorp R, Kjellerup S, Thatje S (2015) No barrier to emergence of bathyal king crabs on the
 593 Antarctic shelf. Proc Natl Acad Sci 112:12997–13002 . doi: 10.1073/pnas.1513962112

594 Baco AR, Rowden AA, Levin LA, Smith CR, Bowden DA (2010) Initial characterization of cold seep
 595 faunal communities on the New Zealand Hikurangi margin. Mar Geol 272:251–259 . doi:
 596 10.1016/j.margeo.2009.06.015

597 Báez P, Sellanes J (2009) Nuevo registro de *Scalpellum projectum* (Crustacea: Cirripedia: Thoracica:
 598 Scalpellidae) para el talud continental de Chile. Lat Am J Aquat Res 37:247–251 . doi: 10.3856/vol37-
 599 issue2-fulltext-11

600 Ball HW (1960) Upper Cretaceous Decapoda and Serpulidae from James Ross Island, Graham Land.
 601 Falkl Isl Depend Surv Sci Rep 24:1–30, pls. 1–7

602 Barbieri R, Cavalazzi B (2005) Microbial fabrics from Neogene cold seep carbonates, Northern
 603 Apennine, Italy. Palaeogeogr Palaeoclimatol Palaeoecol 227:143–155 . doi: 10.1016/j.palaeo.2005.04.026

604 Barbieri R, Ori GG, Cavalazzi B (2004) A Silurian cold-seep ecosystem from the Middle Atlas, Morocco.
 605 PALAIOS 19:527–542 . doi: 10.1669/0883-1351(2004)019<0527:ASCEFT>2.0.CO;2

606 Barry JP, Gary Greene H, Orange DL, Baxter CH, Robison BH, Kochevar RE, Nybakken JW, R DL,
 607 McHugh CM (1996) Biologic and geologic characteristics of cold seeps in Monterey Bay, California.
 608 Deep Sea Res I 43:1739–1762 . doi: 10.1016/S0967-0637(96)00075-1

609 Becker EL, Cordes EE, Macko SA, Fisher CR (2009) Importance of seep primary production to *Lophelia*
 610 *pertusa* and associated fauna in the Gulf of Mexico. Deep-Sea Res I 56:786–800 . doi:
 611 10.1016/j.dsr.2008.12.006

612 Becker EL, Cordes EE, Macko SA, Lee RW, Fisher CR (2013) Using stable isotope compositions of
613 animal tissues to infer trophic interactions in Gulf of Mexico lower slope seep communities. PLoS ONE
614 8:e74459 . doi: 10.1371/journal.pone.0074459

615 Becker MA, Chamberlain JA (2006) Anomuran microcoprolites from the lowermost Navesink Formation
616 (Maastrichtian), Monmouth County, New Jersey. Ichnos 13:1–9 . doi: 10.1080/10420940500511645

617 Bellwood O (2002) The occurrence, mechanics and significance of burying behaviour in crabs
618 (Crustacea: Brachyura). J Nat Hist 36:1223–1238 . doi: 10.1080/00222930110048891

619 Bergquist DC, Ward T, Cordes EE, McNelis T, Howlett S, Kosoff R, Hourdez S, Carney R, Fisher CR
620 (2003) Community structure of vestimentiferan-generated habitat islands from Gulf of Mexico cold seeps.
621 J Exp Mar Biol Ecol 289:197–222 . doi: 10.1016/S0022-0981(03)00046-7

622 Bishop GA, Williams AB (2000) Fossil crabs from tepee buttes, submarine seeps of the Late Cretaceous
623 Pierre Shale, South Dakota and Colorado, U.S.A. J Crustac Biol 20:286–300 . doi: 10.1163/1937240X-
624 90000031

625 Blau J, Grün B, Gießen MS (1993) Crustaceen-Koprolithen aus der Trias der westlichen Tethys (Lienzer
626 Dolomiten, Österreich; Pragser Dolomiten, Italien) und vom Gondwana-Westrand (oberes Magdalenatal,
627 Kolumbien, Südamerika). Paläontol Z 67:193–214 . doi: 10.1007/BF02985878

628 Blouet J-P, Imbert P, Foubert A (2017) Mechanisms of biogenic gas migration revealed by seep carbonate
629 paragenesis, Panoche Hills, California. AAPG Bull 101:1309–1340 . doi: 10.1306/10171616021

630 Boomer I, Horne DJ, Slipper IJ (2003) The use of ostracods in palaeoenvironmental studies, or what can
631 you do with an ostracod shell? Paleontol Soc Pap 9:153–180

632 Boomer I, Whatley R (1992) Ostracoda and dysaerobia in the Lower Jurassic of Wales: the reconstruction
633 of past oxygen levels. Palaeogeogr Palaeoclimatol Palaeoecol 99:373–379 . doi: 10.1016/0031-
634 0182(92)90024-Y

635 Bracken HD, De Grave S, Felder DL (2009) Phylogeny of the infraorder Caridea based on mitochondrial
636 and nuclear genes (Crustacea: Decapoda). Decapod Crustac Phylogenetics 28:281–305

637 Bracken-Grissom HD, Cannon ME, Cabezas P, Feldmann RM, Schweitzer CE, Ah Yong ST, Felder DL,
638 Lemaitre R, Crandall KA (2013) A comprehensive and integrative reconstruction of evolutionary history
639 for Anomura (Crustacea: Decapoda). BMC Evol Biol 13:128 . doi: 10.1186/1471-2148-13-128

640 Brandão SN (2008) First record of a living Platycopida (Crustacea, Ostracoda) from Antarctic waters and
641 a discussion on *Cytherella serratula* (Brady, 1880). Zootaxa 1866:349–372

642 Brandão SN, Horne DJ (2009) The Platycopid Signal of oxygen depletion in the ocean: A critical
643 evaluation of the evidence from modern ostracod biology, ecology and depth distribution. Palaeogeogr
644 Palaeoclimatol Palaeoecol 283:126–133 . doi: 10.1016/j.palaeo.2009.09.007

645 Bright M, Plum C, Riavitz LA, Nikolov N, Martinez Arbizu P, Cordes EE, Gollner S (2010) Epizooic
646 metazoan meiobenthos associated with tubeworm and mussel aggregations from cold seeps of the
647 northern Gulf of Mexico. Deep-Sea Res II 57:1982–1989 . doi: 10.1016/j.dsr2.2010.05.003

648 Brönnimann P (1972) Remarks on the classification of fossil anomuran coprolites. Paläontol Z 46:99–103
649 . doi: 10.1007/BF02989556

650 Buckeridge JS (2009) *Ashinkailepas kermadecensis*, a new species of deep-sea scalpelliform barnacle
 651 (Thoracica: Eolepadidae) from the Kermadec Islands, southwest Pacific. *Zootaxa* 2021:57–65

652 Buckeridge JS (2000) *Neolepas osheai* sp. nov., a new deep-sea vent barnacle (Cirripedia: Pedunculata)
 653 from the Brothers Caldera, south-west Pacific Ocean. *N Z J Mar Freshw Res* 34:409–418 . doi:
 654 10.1080/00288330.2000.9516944

655 Buckeridge JS, Grant-Mackie JA (1985) A new scalpellid barnacle (Cirripedia: Thoracica) from the
 656 Lower Jurassic of New Caledonia. *Géologie Fr* 1:15–18

657 Buckeridge JS, Linse K, Jackson JA (2013) *Vulcanolepas scotiaensis* sp. nov., a new deep-sea
 658 scalpelliform barnacle (Eolepadidae: Neolepadinae) from hydrothermal vents in the Scotia Sea,
 659 Antarctica. *Zootaxa* 3745:551 . doi: 10.11646/zootaxa.3745.5.4

660 Buggisch W, Krumm S (2005) Palaeozoic cold seep carbonates from Europe and North Africa—an
 661 integrated isotopic and geochemical approach. *Facies* 51:566–583 . doi: 10.1007/s10347-005-0005-5

662 Campbell KA (1995) Dynamic development of Jurassic-Pliocene cold-seeps, convergent margin of
 663 western North America. Dissertation, University of Southern California

664 Campbell KA (2006) Hydrocarbon seep and hydrothermal vent paleoenvironments and paleontology:
 665 Past developments and future research directions. *Palaeogeogr Palaeoclimatol Palaeoecol* 232:362–407 .
 666 doi: 10.1016/j.palaeo.2005.06.018

667 Campbell KA, Francis DA, Collins M, Gregory MR, Nelson CS, Greinert J, Aharon P (2008)
 668 Hydrocarbon seep-carbonates of a Miocene forearc (East Coast Basin), North Island, New Zealand.
 669 *Sediment Geol* 204:83–105 . doi: 10.1016/j.sedgeo.2008.01.002

670 Carney RS (1994) Consideration of the oasis analogy for chemosynthetic communities at Gulf of Mexico
 671 hydrocarbon vents. *Geo-Mar Lett* 14:149–159 . doi: 10.1007/BF01203726

672 Checa A (1993) Non-predatory shell damage in Recent deep-endobenthic bivalves from Spain.
 673 *Palaeogeogr Palaeoclimatol Palaeoecol* 100:309–331

674 Chevaldonné P, Olu K (1996) Occurrence of anomuran crabs (Crustacea: Decapoda) in hydrothermal vent
 675 and cold-seep communities: a review. *Proc Biol Soc Wash* 109:286–298

676 Coles GP, Ainsworth NR, Whaley RC, Jones RW (1996) Foraminifera and Ostracoda from Quaternary
 677 carbonate mounds associated with gas seepage in the Porcupine Basin, offshore Western Ireland. *Rev Esp*
 678 *Micropaleontol* 28:113–151

679 Comoglio LI, Amin OA (1999) Feeding habits of the false southern king crab *Paralomis granulosa*
 680 (Lithodidae) in the Beagle Channel, Tierra del Fuego, Argentina. *Sci Mar* 63:361–366 . doi:
 681 10.3989/scimar.1999.63s1361

682 Corbari L, Mesmer-Dudons N, Carbonel P, Massabuau J-C (2005) *Cytherella* as a tool to reconstruct
 683 deep-sea paleo-oxygen levels: the respiratory physiology of the platycopid ostracod *Cytherella* cf.
 684 *abyssorum*. *Mar Biol* 147:1377–1386 . doi: 10.1007/s00227-005-0040-3

685 Cordes EE, Becker EL, Fisherb CR (2010a) Temporal shift in nutrient input to cold-seep food webs
 686 revealed by stable-isotope signatures of associated communities. *Limnol Oceanogr* 55:2537–2548 . doi:
 687 10.4319/lo.2010.55.6.2537

688 Cordes EE, Becker EL, Hourdez S, Fisher CR (2010b) Influence of foundation species, depth, and
689 location on diversity and community composition at Gulf of Mexico lower-slope cold seeps. *Deep-Sea*
690 *Res II* 57:1870–1881 . doi: 10.1016/j.dsr2.2010.05.010

691 Cordes EE, Bergquist DC, Predmore BL, Jones C, Deines P, Telesnicki G, Fisher CR (2006) Alternate
692 unstable states: Convergent paths of succession in hydrocarbon-seep tubeworm-associated communities. *J*
693 *Exp Mar Biol Ecol* 339:159–176 . doi: 10.1016/j.jembe.2006.07.017

694 Cordes EE, Carney SL, Hourdez S, Carney RS, Brooks JM, Fisher CR (2007) Cold seeps of the deep Gulf
695 of Mexico: Community structure and biogeographic comparisons to Atlantic equatorial belt seep
696 communities. *Deep-Sea Res I* 54:637–653 . doi: 10.1016/j.dsr.2007.01.001

697 Coykendall DK, Nizinski MS, Morrison CL (2017) A phylogenetic perspective on diversity of
698 Galatheaidea (*Munida*, *Munidopsis*) from cold-water coral and cold seep communities in the western
699 North Atlantic Ocean. *Deep-Sea Res II* 137:258–272 . doi: 10.1016/j.dsr2.2016.08.014

700 Cunningham CW, Blackstone NW, Buss LW (1992) Evolution of king crabs from hermit crab ancestors.
701 *Nature* 355:539–542 . doi: 10.1038/355539a0

702 Dando PR, Austen MC, Burke RA, Kendall MA, Kennicutt MC, Judd AG, Moore DC, O’Hara SCM,
703 Schmaljohann R, Southward AJ (1991) Ecology of a North Sea pockmark with an active methane seep.
704 *Mar Ecol Prog Ser* 70:49–63 . doi: 10.3354/meps070049

705 De Angeli A, Ceccon L (2012) *Eouroptychus montemagrensis* n. gen., n. sp., (Crustacea, Decapoda,
706 Anomura, Chirostylidae) dell’Eocene inferiore (Ypresiano) di Monte Magrè (Vicenza, Italia
707 settentrionale). *Lav Soc Veneziana Sci Nat* 37:19–24

708 De Angeli A, Garassino A (2002) Galatheid, chirostylid and porcellanid decapods (Crustacea, Decapoda,
709 Anomura) from the Eocene and Oligocene of Vicenza (N Italy). *Mem Della Soc Ital Sci Nat E Mus Civ*
710 *Storia Nat Milano* 30:1–40

711 Decelle J, Andersen AC, Hourdez S (2010) Morphological adaptations to chronic hypoxia in deep-sea
712 decapod crustaceans from hydrothermal vents and cold seeps. *Mar Biol* 157:1259–1269 . doi:
713 10.1007/s00227-010-1406-8

714 Decker C, Morineaux M, Van Gaever S, Caprais J-C, Lichtschlag A, Gauthier O, Andersen AC, Olu K
715 (2012) Habitat heterogeneity influences cold-seep macrofaunal communities within and among seeps
716 along the Norwegian margin. Part 1: macrofaunal community structure: Macrofaunal communities at
717 Norwegian cold seeps. *Mar Ecol* 33:205–230 . doi: 10.1111/j.1439-0485.2011.00503.x

718 Degen R, Riavitz L, Gollner S, Vanreusel A, Plum C, Bright M (2012) Community study of tubeworm-
719 associated epizooic meiobenthos from deep-sea cold seeps and hot vents. *Mar Ecol Prog Ser* 468:135–148
720 . doi: 10.3354/meps09889

721 Dietl GP (2003a) Interaction strength between a predator and dangerous prey: *Sinistrofulgur* predation on
722 *Mercenaria*. *J Exp Mar Biol Ecol* 289:287–301 . doi: 10.1016/S0022-0981(03)00047-9

723 Dietl GP (2003b) Coevolution of a marine gastropod predator and its dangerous bivalve prey. *Biol J Linn*
724 *Soc* 80:409–436 . doi: 10.1046/j.1095-8312.2003.00255.x

725 Do Carmo DA, Meireles RP, Suarez PAZ, Mello VM (2009) Size variations of the vestibula of *Krithe*
726 *gnoma* Do Carmo & Sanguinetti, 1999 (Ostracoda): a new procedure for their analysis. Carnets Géologie
727 - Noteb Geol 9:1–9

728 Dong D, Li X (2015) Galatheid and chirostyliid crustaceans (Decapoda: Anomura) from a cold seep
729 environment in the northeastern South China Sea. Zootaxa 4057:91 . doi: 10.11646/zootaxa.4057.1.5

730 Dworschak PC (1987) Feeding behaviour of *Upogebia pusilla* and *Callianassa tyrrenha* (Crustacea,
731 Decapoda, Thalassinidea). Investig Pesq 51:421–429

732 Dworschak PC (2015) Methods collecting Axiidea and Gebiidea (Decapoda): a review. Ann
733 Naturhistorischen Mus Wien Ser B 117:5–21

734 Dworschak PC, Cunha MR (2007) A new subfamily, Vulcanocalliacinae n. subfam., for *Vulcanocalliax*
735 *arutyunovi* n. gen., n. sp. from a mud volcano in the Gulf of Cádiz (Crustacea, Decapoda, Callianassidae).
736 Zootaxa 1460:35–46

737 Dworschak PC, Felder DA, Tudge CC (2012) Infraorders Axiidea de Saint Laurent, 1979 and Gebiidea de
738 Saint Laurent, 1979 (formerly known collectively as Thalassinidea). In: Charmantier-Daures Schram M,
739 Vaupel Klein Forest (†) C (eds) Treatise on Zoology - Anatomy, Taxonomy, Biology. The Crustacea,
740 Volume 9 Part B. Brill, Leiden, pp 109–219

741 Eagle MK, Hayward BW, Grant-Mackie JA, Gregory MR (1999) Fossil communities in an early Miocene
742 transgressive sequence, Mathesons Bay, Leigh, Auckland. Tane 37:43–67

743 East EH (2006) Reconstruction of the fossil mud shrimp *Callianopsis clallamensis*. J Crustac Biol
744 26:168–175 . doi: 10.1651/C-2562.1

745 Felder DL, Kensley BF (2004) A new species of axiid shrimp from chemosynthetic communities of the
746 Louisiana continental slope, Gulf of Mexico (Crustacea: Decapoda: Thalassinidea. Proc Biol Soc Wash
747 117:68–75

748 Feldmann RM (1998) *Paralomis debodeorum*, a new species of decapod crustacean from the Miocene of
749 New Zealand: First notice of the Lithodidae in the fossil record. N Z J Geol Geophys 41:35–38 . doi:
750 10.1080/00288306.1998.9514788

751 Feldmann RM, Schweitzer CE (2009) Revision of Jurassic Homoloidea De Haan, 1839, from the
752 Ernstbrunn and Štramberk limestones, Austria and the Czech Republic. Ann Naturhistorischen Mus Wien
753 Ser A 111:183–205

754 Feldmann RM, Schweitzer CE, Boessenecker RW (2015) A new squat lobster (Decapoda: Anomura:
755 Galatheaidea) from the Pliocene Purisima Formation, California. Ann Carnegie Mus 83:85–93 . doi:
756 10.2992/007.083.0202

757 Feldmann RM, Schweitzer CE, Casadío S, Griffin M (2011) New Miocene Decapoda (Thalassinidea;
758 Brachyura) from Tierra Del Fuego, Argentina: paleobiogeographic implications. Ann Carnegie Mus
759 79:91–123 . doi: 10.2992/007.079.0202

760 Feldmann RM, Tshudy DM, Thomson MRA (1993) Late Cretaceous and Paleocene decapod crustaceans
761 from James Ross Basin, Antarctic Peninsula. Paleontol Soc Mem 28:1–41

762 Förster R, Hillebrandt AV (1984) Das Kimmeridge des Profeta-Jura in Nordchile mit einer *Mecochirus-*
763 *Favreina*-Vergesellschaftung (Crustacea, Decapoda-Ichnogenus). Mitteilungen Bayrischen Staatssamml
764 Paläontol Hist Geol 24:67–84

765 Foster BA, Buckeridge JS (1987) Barnacle palaeontology. Crustac Issues 5:43–62

766 Fujikura K, Hashimoto J, Okutani T (2002) Estimated population densities of megafauna in two
767 chemosynthesis-based communities: a cold seep in Sagami Bay and a hydrothermal vent in the Okinawa
768 Trough. Benthos Res 57:21–30 . doi: 10.5179/benthos1996.57.1_21

769 Fujikura K, Yamanaka T, Sumida PYG, Bernardino AF, Pereira OS, Kanehara T, Nagano Y, Nakayama
770 CR, Nobrega M, Pellizari VH, Shigeno S, Yoshida T, Zhang J, Kitazato H (2017) Discovery of asphalt
771 seeps in the deep southwest Atlantic off Brazil. Deep-Sea Res II. doi: 10.1016/j.dsr2.2017.04.002

772 Gaillard C, Bourseau J-P, Boudeulle M, Paillet P, Rio M, Roux M (1985) Les pseudo-biohermes de
773 Beauvoisin (Drôme); un site hydrothermal sur la marge tethysienne à l'Oxfordien? Bull Société
774 Géologique Fr 1:69–78

775 Gaillard C, Rio M, Rolin Y, Roux M (1992) Fossil chemosynthetic communities related to vents or seeps
776 in sedimentary basins: the pseudobioherms of southeastern France compared to other world examples.
777 PALAIOS 7:451–465 . doi: 10.2307/3514829

778 Gale AS, Sørensen AM (2015) Origin of the balanomorph barnacles (Crustacea, Cirripedia, Thoracica):
779 new evidence from the Late Cretaceous (Campanian) of Sweden. J Syst Palaeontol 13:791–824 . doi:
780 10.1080/14772019.2014.954824

781 Gebruk AV, Southward EC, Kennedy H, Southward AJ (2000) Food sources, behaviour, and distribution
782 of hydrothermal vent shrimps at the Mid-Atlantic Ridge. J Mar Biol Assoc U K 80:485–499

783 Goedert JL, Campbell KA (1995) An Early Oligocene chemosynthetic community from the Makah
784 Formation, northwestern Olympic Peninsula, Washington. The Veliger 38:22–29

785 Goedert JL, Kaler KL (1996) A new species of *Abyssochrysis* (Gastropoda: Loxonematoidea) from a
786 Middle Eocene cold-seep carbonate in the Humptulips Formation, western Washington. The Veliger
787 39:65–70

788 Goedert JL, Squires RL (1990) Eocene deep-sea communities in localized limestones formed by
789 subduction-related methane seeps, southwestern Washington. Geology 18:1182–1185 . doi:
790 10.1130/0091-7613(1990)018<1182:EDSCIL>2.3.CO;2

791 Gómez-Pérez I (2001) Estromatolitos de aguas profundas en la Formación Los Molles (Neuquén,
792 Argentina): ¿chimeneas de metano en el fondo marino jurásico? Rev Asoc Argent Sedimentol 8:1–14

793 Gómez-Pérez I (2003) An Early Jurassic deep-water stromatolitic bioherm related to possible methane
794 seepage (Los Molles Formation, Neuquén, Argentina). Palaeogeogr Palaeoclimatol Palaeoecol 201:21–49
795 . doi: 10.1016/S0031-0182(03)00508-X

796 Gripp K (1927) Beiträge zur Geologie von Spitzbergen. Abh Naturwissenschaftlichen Ver Zu Hambg
797 21:3–38, pls. 1–7

798 Grupe BM, Krach ML, Pasulka AL, Maloney JM, Levin LA, Frieder CA (2015) Methane seep ecosystem
799 functions and services from a recently discovered southern California seep. Mar Ecol 36:91–108 . doi:
800 10.1111/maec.12243

801 Guinot D, Richer de Forges B (1995) Crustacea Decapoda Brachyura: révision de la famille des
802 Homolidae de Haan, 1839. Résultats Camp MUSORSTOM 13:283–517

803 Hägg R (1925) A new Tertiary fauna from Spitsbergen. Bull Geol Inst Univ Upps 20:39–55

804 Hall S, Thatje S (2009a) Global bottlenecks in the distribution of marine Crustacea: temperature
805 constraints in the family Lithodidae. J Biogeogr 36:2125–2135 . doi: 10.1111/j.1365-2699.2009.02153.x

806 Hall S, Thatje S (2009b) Four new species of the family Lithodidae (Crustacea: Decapoda) from the
807 collections of the National Museum of Natural History, Smithsonian Institution. Zootaxa 2302:31–47

808 Hammer Ø, Nakrem HA, Little CTS, Hryniewicz K, Sandy MR, Hurum JH, Druckenmiller P, Knutsen
809 EM, Høyberget M (2011) Hydrocarbon seeps from close to the Jurassic–Cretaceous boundary, Svalbard.
810 Palaeogeogr Palaeoclimatol Palaeoecol 306:15–26 . doi: 10.1016/j.palaeo.2011.03.019

811 Handle KC (2014) Paleoecology of Late Cretaceous methane cold-seeps of the Pierre Shale, South
812 Dakota. Dissertation, City University of New York

813 Hartnoll RG (1971) The occurrence, methods and significance of swimming in the Brachyura. Anim
814 Behav 19:34–50 . doi: 10.1016/S0003-3472(71)80132-X

815 Hashimoto J, Ohta S, Tanaka T, Hotta H, Matsuzawa S, Sakai H (1989) Deep-sea communities
816 dominated by the giant clam, *Calypptogena soyoeae*, along the slope foot of Hatsushima Island, Sagami
817 Bay, Central Japan. Palaeogeogr Palaeoclimatol Palaeoecol 71:179–192 . doi: 10.1016/0031-
818 0182(89)90037-0

819 Hauquier F, Ingels J, Gutt J, Raes M, Vanreusel A (2011) Characterisation of the nematode community of
820 a low-activity cold seep in the recently ice-shelf free Larsen B Area, Eastern Antarctic Peninsula. PLoS
821 ONE 6:e22240 . doi: 10.1371/journal.pone.0022240

822 Hayward BW, Gregory MR, Kennett JP (2011) An extinct foraminifer endemic to hydrocarbon seeps?
823 Geology 39:603–605 . doi: 10.1130/G31974.1

824 Herrera S, Watanabe H, Shank TM (2015) Evolutionary and biogeographical patterns of barnacles from
825 deep-sea hydrothermal vents. Mol Ecol 24:673–689 . doi: 10.1111/mec.13054

826 Horne DJ, Brandão SN, Slipper IJ (2011) The Platycopid Signal deciphered: Responses of ostracod taxa
827 to environmental change during the Cenomanian–Turonian Boundary Event (Late Cretaceous) in SE
828 England. Palaeogeogr Palaeoclimatol Palaeoecol 308:304–312 . doi: 10.1016/j.palaeo.2011.05.034

829 Hryniewicz K, Bitner MA, Durska E, Hagström J, Hjálmarsson HR, Jenkins RG, Little CTS, Miyajima
830 Y, Nakrem HA, Kaim A (2016) Paleocene methane seep and wood-fall marine environments from
831 Spitsbergen, Svalbard. Palaeogeogr Palaeoclimatol Palaeoecol 462:41–56 . doi:
832 10.1016/j.palaeo.2016.08.037

833 Hryniewicz K, Hagström J, Hammer Ø, Kaim A, Little CTS, Nakrem HA (2015a) Late Jurassic–Early
834 Cretaceous hydrocarbon seep boulders from Novaya Zemlya and their faunas. Palaeogeogr
835 Palaeoclimatol Palaeoecol 436:231–244 . doi: 10.1016/j.palaeo.2015.06.036

836 Hryniewicz K, Jakubowicz M, Belka Z, Dopieralska J, Kaim A (2017) New bivalves from a Middle
837 Devonian methane seep in Morocco: the oldest record of repetitive shell morphologies among some seep
838 bivalve molluscs. J Syst Palaeontol 15:19–41 . doi: 10.1080/14772019.2015.1136900

839 Hryniewicz K, Nakrem HA, Hammer Ø, Little CTS, Kaim A, Sandy MR, Hurum JH (2015b) The
840 palaeoecology of the latest Jurassic-earliest Cretaceous hydrocarbon seep carbonates from Spitsbergen,
841 Svalbard. *Lethaia* 48:353–374 . doi: 10.1111/let.12112

842 Humes AG (1988) Copepoda from deep-sea hydrothermal vents and cold seeps. *Hydrobiologia* 167–
843 168:549–554 . doi: 10.1007/BF00026351

844 Hyžný M, Klompmaker AA (2015) Systematics, phylogeny, and taphonomy of ghost shrimps
845 (Decapoda): a perspective from the fossil record. *Arthropod Syst Phylogeny* 73:401–437

846 Jenkins RG, Kaim A, Hikida Y (2007a) Antiquity of the substrate choice among acmaeid limpets from
847 Late Cretaceous chemosynthesis-based communities. *Acta Palaeontol Pol* 52:369–373

848 Jenkins RG, Kaim A, Hikida Y, Tanabe K (2007b) Methane-flux-dependent lateral faunal changes in a
849 Late Cretaceous chemosymbiotic assemblage from the Nakagawa area of Hokkaido, Japan. *Geobiology*
850 5:127–139 . doi: 10.1111/j.1472-4669.2007.00106.x

851 Jenkins RG, Kaim A, Little CTS, Iba Y, Tanabe K, Campbell KA (2013) Worldwide distribution of the
852 modiomorphid bivalve genus *Caspiconcha* in late Mesozoic hydrocarbon seeps. *Acta Palaeontol Pol*
853 58:357–382

854 Jensen P, Aagaard I, Burke Jr RA, Dando PR, Jørgensen NO, Kuijpers A, Laier T, O’Hara SCM,
855 Schmaljohann R (1992) “Bubbling reefs” in the Kattegat: submarine landscapes of carbonate-cemented
856 rocks support a diverse ecosystem at methane seeps. *Mar Ecol Prog Ser* 83:103–112

857 Jørgensen LL, Primicerio R (2007) Impact scenario for the invasive red king crab *Paralithodes*
858 *camtschaticus* (Tilesius, 1815) (Reptantia, Lithodidae) on Norwegian, native, epibenthic prey.
859 *Hydrobiologia* 590:47–54 . doi: 10.1007/s10750-007-0756-9

860 Juniper S, Sibuet M (1987) Cold seep benthic communities in the Japan subduction zones: spatial
861 organization, trophic strategies and evidence for temporal evolution. *Mar Ecol Prog Ser* 40:115–126 . doi:
862 10.3354/meps040115

863 Kanie Y (1996) Paleoenvironmental study on the chemosynthetic fossil assemblages of the Hayama
864 Formation and the related late Cenozoic assemblages from the Miura-Boso area, south-central Japan.
865 *Fossils* 60:53–58

866 Kanie Y, Asami S, Okada H, Watanabe M (1992) White clam community discovered from fractured
867 claystone of the Miocene Hayama Group, Miura Peninsula, south-central Japan. *Sci Rep Yokosuka City*
868 *Mus* 40:31–35

869 Karanovic I, Brandão SN (2015) Biogeography of deep-sea wood fall, cold seep and hydrothermal vent
870 Ostracoda (Crustacea), with the description of a new family and a taxonomic key to living Cytheroidea.
871 *Deep-Sea Res II* 111:76–94 . doi: 10.1016/j.dsr2.2014.09.008

872 Karasawa H (2011) New axiidean Decapoda from the Albian (Lower Cretaceous) chemosynthetic
873 community of Hokkaido, Japan. *Bull Mizunami Foss Mus* 37:27–29

874 Karasawa H, Mizuno Y, Hachiya K, Ando Y (2017) Reappraisal of anomuran and brachyuran decapods
875 from the lower Miocene Morozaki Group, Japan, collected by the Tokai Fossil Society. *Bull Mizunami*
876 *Foss Mus* 43:47–69

877 Kato M, Oji T, Shirai K (2017) Paleoecology of echinoderms in cold seep environments revealed by
878 isotope analysis in the Late Cretaceous Western Interior Seaway. *PALAIOS* 32:218–230 . doi:
879 10.2110/palo.2016.079

880 Kelly SRA, Blanc E, Price SP, Whitham AG (2000) Early Cretaceous giant bivalves from seep-related
881 limestone mounds, Wollaston Forland, Northeast Greenland. *Geol Soc Lond Spec Publ* 177:227–246 .
882 doi: 10.1144/GSL.SP.2000.177.01.13

883 Kelly SRA, Ditchfield PW, Doubleday PA, Marshall JD (1995) An Upper Jurassic methane-seep
884 limestone from the Fossil Bluff Group forearc basin of Alexander Island, Antarctica. *J Sediment Res*
885 65A:274–282 . doi: 10.1306/D426809A-2B26-11D7-8648000102C1865D

886 Kidwell SM, Flessa KW (1995) The quality of the fossil record: populations, species, and communities.
887 *Annu Rev Ecol Syst* 269–299 . doi: 10.1146/annurev.earth.24.1.433

888 Kiel S (2010a) An Eldorado for paleontologists: the Cenozoic seeps of western Washington State, USA.
889 In: Kiel S (ed) *The Vent and Seep Biota*. Springer Netherlands, Dordrecht, pp 433–448

890 Kiel S (2006) New records and species of molluscs from Tertiary cold-seep carbonates in Washington
891 State, USA. *J Paleontol* 80:121–137 . doi: 10.1666/0022-3360(2006)080[0121:NRASOM]2.0.CO;2

892 Kiel S (2010b) The fossil record of vent and seep mollusks. In: Kiel S (ed) *The Vent and Seep Biota*.
893 Springer Netherlands, Dordrecht, pp 255–277

894 Kiel S, Amano K, Jenkins RG (2016) Predation scar frequencies in chemosymbiotic bivalves at an
895 Oligocene seep deposit and their potential relation to inferred sulfide tolerances. *Palaeogeogr*
896 *Palaeoclimatol Palaeoecol* 453:139–145 . doi: 10.1016/j.palaeo.2016.04.026

897 Kiel S, Amano K, Jenkins RG (2008) Bivalves from Cretaceous cold-seep deposits on Hokkaido, Japan.
898 *Acta Palaeontol Pol* 53:525–537 . doi: 10.4202/app.2008.0310

899 Kiel S, Birgel D, Campbell KA, Crampton JS, Schiøler P, Peckmann J (2013) Cretaceous methane-seep
900 deposits from New Zealand and their fauna. *Palaeogeogr Palaeoclimatol Palaeoecol* 390:17–34 . doi:
901 10.1016/j.palaeo.2012.10.033

902 Kiel S, Hansen BT (2015) Cenozoic methane-seep faunas of the Caribbean region. *PLOS ONE*
903 10:e0140788 . doi: 10.1371/journal.pone.0140788

904 Kiel S, Wiese F, Titus AL (2012) Shallow-water methane-seep faunas in the Cenomanian Western
905 Interior Seaway: No evidence for onshore-offshore adaptations to deep-sea vents. *Geology* 40:839–842 .
906 doi: 10.1130/G33300.1

907 Kietzmann DA, Blau J, Fernández DE, Palma RM (2010) Crustacean microcoprolites from the Upper
908 Jurassic-Lower Cretaceous of the Neuquén Basin, Argentina: systematics and biostratigraphic
909 implications. *Acta Palaeontol Pol* 55:277–284 . doi: 10.4202/app.2009.0094

910 Klompmaker AA, Feldmann RM, Robins CM, Schweitzer CE (2012a) Peak diversity of Cretaceous
911 galatheoids (Crustacea, Decapoda) from northern Spain. *Cretac Res* 36:125–145

912 Klompmaker AA, Feldmann RM, Schweitzer CE (2012b) A hotspot for Cretaceous goniodromitids
913 (Decapoda: Brachyura) from reef associated strata in Spain. *J Crustac Biol* 32:780–801

914 Klompmaker AA, Jakobsen SL, Lauridsen BW (2016) Evolution of body size, vision, and biodiversity of
915 coral-associated organisms: evidence from fossil crustaceans in cold-water coral and tropical coral
916 ecosystems. *BMC Evol Biol* 16:132 . doi: 10.1186/s12862-016-0694-0

917 Klompmaker AA, Ortiz JD, Wells NA (2013a) How to explain a decapod crustacean diversity hotspot in
918 a mid-Cretaceous coral reef. *Palaeogeogr Palaeoclimatol Palaeoecol* 374:256–273 . doi:
919 10.1016/j.palaeo.2013.01.024

920 Klompmaker AA, Portell RW, Frick MG (2017) Comparative experimental taphonomy of eight marine
921 arthropods indicates distinct differences in preservation potential. *Palaeontology* 60:773–794 . doi:
922 10.1111/pala.12314

923 Klompmaker AA, Schweitzer CE, Feldmann RM, Kowalewski M (2013b) The influence of reefs on the
924 rise of Mesozoic marine crustaceans. *Geology* 41:1179–1182 . doi: 10.1130/G34768.1

925 Kneer D, Asmus H, Vonk JA (2008) Seagrass as the main food source of *Neaxius acanthus*
926 (Thalassinidea: Strahlaxiidae), its burrow associates, and of *Corallianassa coutierei* (Thalassinidea:
927 Callianassidae). *Estuar Coast Shelf Sci* 79:620–630 . doi: 10.1016/j.ecss.2008.05.013

928 Komai T, Segonzac M (2005) A revision of the genus *Alvinocaris* Williams and Chace (Crustacea:
929 Decapoda: Caridea: Alvinocarididae), with descriptions of a new genus and a new species of *Alvinocaris*.
930 *J Nat Hist* 39:1111–1175 . doi: 10.1080/00222930400002499

931 Kornienko ES (2013) Burrowing shrimp of the infraorders Gebiidea and Axiidea (Crustacea: Decapoda).
932 *Russ J Mar Biol* 39:1–14 . doi: 10.1134/S1063074013010033

933 Kuechler RR, Birgel D, Kiel S, Freiwald A, Goedert JL, Thiel V, Peckmann J (2012) Miocene methane-
934 derived carbonates from southwestern Washington, USA and a model for silicification at seeps: Miocene
935 seep carbonates. *Lethaia* 45:259–273 . doi: 10.1111/j.1502-3931.2011.00280.x

936 Kulm LD, Suess E, Moore JC, Carson B, Lewis BT, Ritger SD, Kadko DC, Thornburg TM, Embley RW,
937 Rugh WD, Massoth GJ, Langseth MG, Cochran GR, Scamman RL (1986) Oregon subduction zone:
938 venting, fauna, and carbonates. *Science* 231:561–566 . doi: 10.1126/science.231.4738.561

939 Larson NL, Brezina J, Landman NH, Garb MP, Handle KC (2013) Hydrocarbon seeps: unique habitats
940 that preserved the diversity of fauna in the Late Cretaceous Western Interior Seaway. Caspar, Wyoming,
941 p 20

942 Lessard-Pilon S, Porter MD, Cordes EE, MacDonald I, Fisher CR (2010) Community composition and
943 temporal change at deep Gulf of Mexico cold seeps. *Deep-Sea Res II* 57:1891–1903 . doi:
944 10.1016/j.dsr2.2010.05.012

945 Lethiers F, Whatley R (1994) The use of Ostracoda to reconstruct the oxygen levels of Late Palaeozoic
946 oceans. *Mar Micropaleontol* 24:57–69 . doi: 10.1016/0377-8398(94)90011-6

947 Levin LA (2005) Ecology of cold seep sediments: interactions of fauna with flow, chemistry and
948 microbes. *Oceanogr Mar Biol Annu Rev* 43:1–46

949 Levin LA, James DW, Martin CM, Rathburn AE, Harris LH, Michener RH (2000) Do methane seeps
950 support distinct macrofaunal assemblages? Observations on community structure and nutrition from the
951 northern California slope and shelf. *Mar Ecol Prog Ser* 208:21–39 . doi: 10.3354/meps208021

952 Levin LA, Mendoza GF, Grupe BM, Gonzalez JP, Jellison B, Rouse G, Thurber AR, Waren A (2015)
 953 Biodiversity on the rocks: macrofauna inhabiting authigenic carbonate at Costa Rica methane seeps.
 954 PLOS ONE 10:e0131080 . doi: 10.1371/journal.pone.0131080

955 Levin LA, Michener RH (2002) Isotopic evidence for chemosynthesis-based nutrition of macrobenthos:
 956 The lightness of being at Pacific methane seeps. *Limnol Oceanogr* 47:1336–1345 . doi:
 957 10.4319/lo.2002.47.5.1336

958 Little CTS, Birgel D, Boyce AJ, Crame JA, Francis JE, Kiel S, Peckmann J, Pirrie D, Rollinson GK,
 959 Witts JD (2015) Late Cretaceous (Maastrichtian) shallow water hydrocarbon seeps from Snow Hill and
 960 Seymour Islands, James Ross Basin, Antarctica. *Palaeogeogr Palaeoclimatol Palaeoecol* 418:213–228 .
 961 doi: 10.1016/j.palaeo.2014.11.020

962 Lörz A-N, Glenner H, Lützen J (2008) New records of Rhizocephala (Cirripedia) from New Zealand,
 963 including the first rhizocephalan records from hot vents and cold seeps. *Crustaceana* 81:1013–1019 . doi:
 964 10.1163/156854008X354911

965 Lovrich GA, Thiel M (2011) Ecology, physiology, feeding and trophic role of squat lobsters. In: Poore G,
 966 Ahyong ST, Taylor J (eds) *The Biology of Squat Lobsters*. CSIRO Publishing/CRC Press,
 967 Melbourne/Boca Raton, pp 183–222

968 Luque J, Schweitzer CE, Santana W, Portell RW, Vega FJ, Klompmaker AA (2017) Checklist of fossil
 969 decapod crustaceans from tropical America. Part I: Anomura and Brachyura. *Nauplius* 25:e2017025 . doi:
 970 10.1590/2358-2936e2017025

971 Lützen J, Glenner H, Lörz A (2009) Parasitic barnacles (Cirripedia: Rhizocephala) from New Zealand
 972 off-shore waters. *N Z J Mar Freshw Res* 43:613–621 . doi: 10.1080/00288330909510027

973 MacAvoy SE, Carney RS, Fisher CR, Macko SA (2002) Use of chemosynthetic biomass by large,
 974 mobile, benthic predators in the Gulf of Mexico. *Mar Ecol Prog Ser* 225:65–78 . doi:
 975 10.3354/meps225065

976 MacAvoy SE, Carney RS, Morgan E, Macko SA (2008) Stable isotope variation among the mussel
 977 *Bathymodiolus childressi* and associated heterotrophic fauna at four cold-seep communities in the Gulf of
 978 Mexico. *J Shellfish Res* 27:147–151 . doi: 10.2983/0730-8000(2008)27[147:SIVATM]2.0.CO;2

979 Macpherson E, Segonzac M (2005) Species of the genus *Munidopsis* (Crustacea, Decapoda, Galatheididae)
 980 from the deep Atlantic Ocean, including cold-seep and hydrothermal vent areas. *Zootaxa* 1095:1–60

981 Martin JW, Haney TA (2005) Decapod crustaceans from hydrothermal vents and cold seeps: a review
 982 through 2005. *Zool J Linn Soc* 145:445–522 . doi: 10.1111/j.1096-3642.2005.00178.x

983 McKenzie KG, Majoran S, Emami V, Reymont RA (1989) The *Krithe* problem - first test of
 984 Peypouquet's hypothesis, with a redescription of *Krithe praetexta praetexta* (Crustacea, Ostracoda).
 985 *Palaeogeogr Palaeoclimatol Palaeoecol* 74:343–354 . doi: 10.1016/0031-0182(89)90069-2

986 Meehan KC, Landman NH (2016) Faunal associations in cold-methane seep deposits from the Upper
 987 Cretaceous Pierre Shale, South Dakota. *PALAIOS* 31:291–301 . doi: 10.2110/palo.2015.055

988 Mizuno Y, Takeda M (1993) 6-3. Crustacea. In: *Fossils from the Miocene Morozaki Group - Fossils of*
 989 *Aichi Prefecture*. Tokai Fossil Society, Nagoya, pp 77–90

990 Montagna PA, Bauer JE, Toal J, Hardin D, Spies RB (1987) Temporal variability and the relationship
 991 between benthic meiofaunal and microbial populations of a natural coastal petroleum seep. *J Mar Res*
 992 45:761–789 . doi: 10.1357/002224087788326894

993 Moore GW (1969) New formations on Kodiak and adjacent islands, Alaska. *US Geol Surv Bull*
 994 1274:A27–A35

995 Natalicchio M, Dela Pierre F, Clari P, Birgel D, Cavagna S, Martire L, Peckmann J (2013) Hydrocarbon
 996 seepage during the Messinian salinity crisis in the Tertiary Piedmont Basin (NW Italy). *Palaeogeogr*
 997 *Palaeoclimatol Palaeoecol* 390:68–80 . doi: 10.1016/j.palaeo.2012.11.015

998 Natalicchio M, Peckmann J, Birgel D, Kiel S (2015) Seep deposits from northern Istria, Croatia: a first
 999 glimpse into the Eocene seep fauna of the Tethys region. *Geol Mag* 152:444–459 . doi:
 1000 10.1017/S0016756814000466

1001 Nesbitt EA, Martin RA, Campbell KA (2013) New records of Oligocene diffuse hydrocarbon seeps,
 1002 northern Cascadia margin. *Palaeogeogr Palaeoclimatol Palaeoecol* 390:116–129 . doi:
 1003 10.1016/j.palaeo.2013.05.001

1004 Neto de Carvalho C, Viegas PA, Cachao M (2007) *Thalassinoides* and its producer: populations of
 1005 *Mecochirus* buried within their burrow systems, Boca do Chapim Formation (Lower Cretaceous),
 1006 Portugal. *PALAIOS* 22:104–109 . doi: 10.2110/palo.2006.p06-011r

1007 Newman WA, Yamaguchi T, Southward AJ, Segonzac M (2006) Cirripedia. In: Desbruyères D, Segonzac
 1008 M, Bright M (eds) *Handbook of Deep-sea Hydrothermal Vent Fauna*. Biologiezentrum, Linz, pp 356–368

1009 Nielsen C (1975) Observations on *Buccinum undatum* L. attacking bivalves and on prey responses, with a
 1010 short review on attack methods of other prosobranchs. *Ophelia* 13:87–108 . doi:
 1011 10.1080/00785326.1974.10430593

1012 Niemann H, Linke P, Knittel K, MacPherson E, Boetius A, Brückmann W, Larvik G, Wallmann K,
 1013 Schacht U, Omeregge E, Hilton D, Brown K, Rehder G (2013) Methane-carbon flow into the benthic food
 1014 web at cold seeps – a case study from the Costa Rica subduction zone. *PLoS ONE* 8:e74894 . doi:
 1015 10.1371/journal.pone.0074894

1016 Noever C, Glenner H (2017) The origin of king crabs: hermit crab ancestry under the magnifying glass.
 1017 *Zool J Linn Soc*. doi: 10.1093/zoolinnean/zlx033

1018 Olu K, Sibuet M, Harmegnies F, Foucher J-P, Fiala-Médioni A (1996) Spatial distribution of diverse cold
 1019 seep communities living on various diapiric structures of the southern Barbados prism. *Prog Oceanogr*
 1020 38:347–376 . doi: 10.1016/S0079-6611(97)00006-2

1021 Olu-Le Roy K, Sibuet M, Fiala-Médioni A, Gofas S, Salas C, Mariotti A, Foucher J-P, Woodside J
 1022 (2004) Cold seep communities in the deep eastern Mediterranean Sea: composition, symbiosis and spatial
 1023 distribution on mud volcanoes. *Deep-Sea Res I* 51:1915–1936 . doi: 10.1016/j.dsr.2004.07.004

1024 Peckmann J, Campbell KA, Walliser OH, Reitner J (2007a) A Late Devonian hydrocarbon-seep deposit
 1025 dominated by dimerelloid brachiopods, Morocco. *PALAIOS* 22:114–122 . doi: 10.2110/palo.2005.p05-
 1026 115r

- 1027 Peckmann J, Goedert JL, Thiel V, Michaelis W, Reitner J (2002) A comprehensive approach to the study
1028 of methane-seep deposits from the Lincoln Creek Formation, western Washington State, USA.
1029 *Sedimentology* 49:855–873 . doi: 10.1046/j.1365-3091.2002.00474.x
- 1030 Peckmann J, Sandy MR, Taylor DG, Gier S, Bach W (2013) An Early Jurassic brachiopod-dominated
1031 seep deposit enclosed by serpentinite, eastern Oregon, USA. *Palaeogeogr Palaeoclimatol Palaeoecol*
1032 390:4–16 . doi: 10.1016/j.palaeo.2013.01.003
- 1033 Peckmann J, Senowbari-Daryan B, Birgel D, Goedert JL (2007b) The crustacean ichnofossil *Palaxius*
1034 associated with callianassid body fossils in an Eocene methane-seep limestone, Humptulips Formation,
1035 Olympic Peninsula, Washington: Seep-associated crustacean fossils. *Lethaia* 40:273–280 . doi:
1036 10.1111/j.1502-3931.2007.00026.x
- 1037 Peckmann J, Thiel V, Michaelis W, Clari P, Gaillard C, Martire L, Reitner J (1999) Cold seep deposits of
1038 Beauvoisin (Oxfordian; southeastern France) and Marmorito (Miocene; northern Italy): microbially
1039 induced authigenic carbonates. *Int J Earth Sci* 88:60–75 . doi: 10.1007/s005310050246
- 1040 Pérez-Losada M, Harp M, Høeg JT, Achituv Y, Jones D, Watanabe H, Crandall KA (2008) The tempo
1041 and mode of barnacle evolution. *Mol Phylogenet Evol* 46:328–346 . doi: 10.1016/j.ympev.2007.10.004
- 1042 Peypouquet JP (1975) Les variations des caractères morphologiques internes chez les ostracodes des
1043 genres *Krithe* et *Parakrithe*: relation possible avec le teneur en O₂ dissous dans l’eau. *Bull L’Institut*
1044 *Géologie Bassin Aquitaine* 17:81–88
- 1045 Peypouquet J-P (1979) Ostracodes et paléo-environnements: méthodologie et application aux domaines
1046 profonds du Cénozoïque. *Bull Bur Rech Géologiques Minières* 4:3–79
- 1047 Plotnick RE (1986) Taphonomy of a modern shrimp: Implications for the arthropod fossil record.
1048 *PALAIOS* 1:286–293
- 1049 Polz H (2007) Die Garnelengattung *Harthofia* g. nov. (Crustacea: Decapoda: Pleocyemata: Caridea) mit
1050 zwei neuen Arten aus den Solnhofener Plattenkalken von Eichstätt. *Archaeopteryx* 25:1–13
- 1051 Polz MF, Robinson JJ, Cavanaugh CM, Van Dover CL (1998) Trophic ecology of massive shrimp
1052 aggregations at a Mid-Atlantic Ridge hydrothermal vent site. *Limnol Oceanogr* 43:1631–1638 . doi:
1053 10.4319/lo.1998.43.7.1631
- 1054 Pond DW, Dixon DR, Bell MV, Fallick AE, Sargent JR (1997) Occurrence of 16:2(n-4) and 18:2(n-4)
1055 fatty acids in the lipids of the hydrothermal vent shrimps *Rimicaris exoculata* and *Alvinocaris markensis*:
1056 nutritional and trophic implications. *Mar Ecol Prog Ser* 156:167–174
- 1057 Portnova DA, Mokievsky VO, Haflidason H, Todt K (2014) Metazoan meiobenthos and nematode
1058 assemblages in the Nyegga Region of methane seepage (Norwegian Sea). *Russ J Mar Biol* 40:255–265 .
1059 doi: 10.1134/S1063074014040075
- 1060 Quattrini AM, Nizinski MS, Chaytor JD, Demopoulos AWJ, Roark EB, France SC, Moore JA, Heyl T,
1061 Auster PJ, Kinlan B, Ruppel C, Elliott KP, Kennedy BRC, Lobecker E, Skarke A, Shank TM (2015)
1062 Exploration of the canyon-incised continental margin of the northeastern United States reveals dynamic
1063 habitats and diverse communities. *PLOS ONE* 10:e0139904 . doi: 10.1371/journal.pone.0139904

- 1064 Ramirez-Llodra E, Segonzac M (2006) Reproductive biology of *Alvinocaris muricola* (Decapoda:
1065 Caridea: Alvinocarididae) from cold seeps in the Congo Basin. J Mar Biol Assoc UK 86:1347–1356 . doi:
1066 10.1017/S0025315406014378
- 1067 Ritt B, Pierre C, Gauthier O, Wenzhöfer F, Boetius A, Sarrazin J (2011) Diversity and distribution of
1068 cold-seep fauna associated with different geological and environmental settings at mud volcanoes and
1069 pockmarks of the Nile Deep-Sea Fan. Mar Biol 158:1187–1210 . doi: 10.1007/s00227-011-1679-6
- 1070 Ritt B, Sarrazin J, Caprais J-C, Noël P, Gauthier O, Pierre C, Henry P, Desbruyères D (2010) First
1071 insights into the structure and environmental setting of cold-seep communities in the Marmara Sea. Deep-
1072 Sea Res I 57:1120–1136 . doi: 10.1016/j.dsr.2010.05.011
- 1073 Robins CM, Feldmann RM, Schweitzer CE (2013) Nine new genera and 24 new species of the
1074 Munidopsidae (Decapoda: Anomura: Galatheoidea) from the Jurassic Ernstbrunn Limestone of Austria,
1075 and notes on fossil munidopsid classification. Ann Naturhistorischen Mus Wien Ser A 115:167–251
- 1076 Robins CM, Feldmann RM, Schweitzer CE, Bonde A (2016) New families Paragalatheididae and
1077 Catilloagalatheididae (Decapoda: Anomura: Galatheoidea) from the Mesozoic, restriction of the genus
1078 Paragalathea, and establishment of 6 new genera and 20 new species. Ann Naturhistorischen Mus Wien
1079 Ser A 118:65–131
- 1080 Rolin Y, Gaillard C, Roux M (1990) Ecologie des pseudobiohermes des Terres Noires jurassiques liés à
1081 paléo-sources sous-marines. Le site oxfordien de Beauvoisin (Drôme, Bassin du Sud-Est, France).
1082 Palaeogeogr Palaeoclimatol Palaeoecol 80:79–105 . doi: 10.1016/0031-0182(90)90123-O
- 1083 Russo A, Pugliese N, Serventi P (2012) Miocene ostracodes of cold seep settings from northern
1084 Apennines (Italy). Rev Micropaléontologie 55:29–38 . doi: 10.1016/j.revmic.2011.09.001
- 1085 Sahling H, Galkin SV, Salyuk A, Greinert J, Foerstel H, Piepenburg D, Suess E (2003) Depth-related
1086 structure and ecological significance of cold-seep communities - a case study from the Sea of Okhotsk.
1087 Deep-Sea Res I 50:1391–1409 . doi: 10.1016/j.dsr.2003.08.004
- 1088 Sakai K, Türkay M (1999) A new subfamily, Bathycalliacinae n. subfam., for *Bathycalliax geomar* n.
1089 gen., n. sp. from the deep water cold steps off Oregon, USA (Crustacea, Decapoda, Callianassidae).
1090 Senckenberg Biol 79:203–210
- 1091 Sandy MR (2010) Brachiopods from ancient hydrocarbon seeps and hydrothermal vents. In: Kiel S (ed)
1092 The Vent and Seep Biota. Springer Netherlands, Dordrecht, pp 279–314
- 1093 Sandy MR, Goedert JL, Peckmann J, Taylor D (2005) Brachiopods under attack – evidence of predation
1094 on a mass-occurrence of the rhynchonellid brachiopod *Sulcirostra* from an autochthonous cold-seep
1095 limestone – Early Jurassic of Oregon, U.S.A.
- 1096 Sasaki T, Warén A, Kano Y, Okutani T, Fujikura K (2010) Gastropods from Recent hot vents and cold
1097 seeps: systematics, diversity and life strategies. In: Kiel S (ed) The Vent and Seep Biota. Springer
1098 Netherlands, Dordrecht, pp 169–254
- 1099 Schweigert G (2011) The decapod crustaceans of the Upper Jurassic Solnhofen Limestones: A historical
1100 review and some recent discoveries. Neues Jahrb Für Geol Paläontol - Abh 260:131–140 . doi:
1101 10.1127/0077-7749/2011/0162

- 1102 Schweigert G, Seegis DB, Fels A, Leinfelder RR (1997) New internally structured decapod
1103 microcoprolites from Germany (Late Triassic/Early Miocene), Southern Spain (Early/Middle Jurassic)
1104 and Portugal (Late Jurassic): Taxonomy, palaeoecology and evolutionary implications. *Paläontol Z*
1105 71:51–69 . doi: 10.1007/BF03022546
- 1106 Schweitzer CE, Feldmann RM (2008) New Eocene hydrocarbon seep decapod crustacean (Anomura:
1107 Galatheidæ: Shinkaiinae) and its paleobiology. *J Paleontol* 82:1021–1029 . doi: 10.1666/08-007.1
- 1108 Schweitzer CE, Feldmann RM (2010) The Decapoda (Crustacea) as predators on Mollusca through
1109 geologic time. *PALAIOS* 25:167–182
- 1110 Schweitzer CE, Feldmann RM (2000) First notice of the Chirostylidae (Decapoda) in the fossil record and
1111 new Tertiary Galatheidæ (Decapoda) from the Americas. *Bull Mizunami Foss Mus* 27:147–165
- 1112 Schweitzer CE, Feldmann RM (2015) Faunal turnover and niche stability in marine Decapoda in the
1113 Phanerozoic. *J Crustac Biol* 35:633–649
- 1114 Schweitzer CE, Nyborg TG, Feldmann RM, Ross RLM (2004) Homolidae de Haan, 1839 and
1115 Homolodromiidae Alcock, 1900 (Crustacea: Decapoda: Brachyura) from the Pacific Northwest of North
1116 America and a reassessment of their fossil records. *J Paleontol* 78:133–149 . doi: 10.1666/0022-
1117 3360(2004)078<0133:HDHAHA>2.0.CO;2
- 1118 Selden PA, Huys R, Stephenson MH, Heward AP, Taylor PN (2010) Crustaceans from bitumen clast in
1119 Carboniferous glacial diamictite extend fossil record of copepods. *Nat Commun* 1:1–6 . doi:
1120 10.1038/ncomms1049
- 1121 Sellanes J, Quiroga E, Neira C (2008) Megafauna community structure and trophic relationships at the
1122 recently discovered Concepcion Methane Seep Area, Chile, 36°S. *ICES J Mar Sci* 65:1102–1111 . doi:
1123 10.1093/icesjms/fsn099
- 1124 Senowbari-Daryan B, Gaillard C, Peckmann J (2007) Crustacean microcoprolites from Jurassic
1125 (Oxfordian) hydrocarbon-seep deposits of Beauvoisin, southeastern France. *Facies* 53:229–238 . doi:
1126 10.1007/s10347-006-0096-7
- 1127 Senowbari-Daryan B, Kube B (2003) The ichnogenous *Palaxius* (crustacean coprolite) and description of
1128 *P. hydranensis* n. sp. from the Upper Triassic (Norian part of “Pantokrator” limestone) of Hydra (Greece).
1129 *Paläontol Z* 77:115–122 . doi: 10.1007/BF03004563
- 1130 Shank TM, Black MB, Halanych KM, Lutz RA, Vrijenhoek RC (1999) Miocene radiation of deep-sea
1131 hydrothermal vent shrimp (Caridea: Bresiliidae): evidence from mitochondrial cytochrome oxidase
1132 subunit I. *Mol Phylogenet Evol* 13:244–254 . doi: 10.1006/mpev.1999.0642
- 1133 Shimoda K, Aramaki Y, Nasuda J, Yokoyama H, Ishihi Y, Tamaki A (2007) Food sources for three
1134 species of *Nihonotrypaea* (Decapoda: Thalassinidea: Callinassidae) from western Kyushu, Japan, as
1135 determined by carbon and nitrogen stable isotope analysis. *J Exp Mar Biol Ecol* 342:292–312 . doi:
1136 10.1016/j.jembe.2006.11.003
- 1137 Smith AJ, Horne DJ (2002) Ecology of marine, marginal marine and nonmarine ostracodes. In: Holmes
1138 JA, Chivas AR (eds) *Geophysical Monograph Series*. American Geophysical Union, Washington, D. C.,
1139 pp 37–64

- 1140 Smrzka D (2013) Petrography and geochemistry of Eocene cold-seep carbonates from Washington State,
1141 USA. MS Thesis, University of Vienna
- 1142 Smrzka D, Zwicker J, Kolonic S, Birgel D, Little CTS, Marzouk AM, Chellai EH, Wagner T, Peckmann J
1143 (2017) Methane seepage in a Cretaceous greenhouse world recorded by an unusual carbonate deposit
1144 from the Tarfaya Basin, Morocco. *Depositional Rec* 3:4–37 . doi: 10.1002/dep2.24
- 1145 Sommer S, Gutzmann E, Pfannkuche O (2007) Sediments hosting gas hydrate: oases for metazoan
1146 meiofauna. *Mar Ecol Prog Ser* 337:27–37 . doi: 10.3354/meps337027
- 1147 Southward AJ (2005) Systematics and ecology of a new species of stalked barnacle (Cirripedia:
1148 Thoracica: Scalpellomorpha: Eolepadidae: Neolepadini) from the Pacific-Antarctic Ridge at 38° S.
1149 *Senckenberg Maritima* 35:147–156 . doi: 10.1007/BF03043683
- 1150 Southward AJ, Jones DS (2003) A revision of stalked barnacles (Cirripedia: Thoracica: Scalpellomorpha:
1151 Eolepadidae: Neolepadinae) associated with hydrothermalism, including a description of a new genus and
1152 species from a volcanic seamount off Papua New Guinea. *Senckenberg Maritima* 32:77–93 . doi:
1153 10.1007/BF03043086
- 1154 Southward EC, Schulze A, Tunnicliffe V (2002) Vestimentiferans (Pogonophora) in the Pacific and
1155 Indian Oceans: a new genus from Lihir Island (Papua New Guinea) and the Java Trench, with the first
1156 report of *Arcovestia ivanovi* from the North Fiji Basin. *J Nat Hist* 36:1179–1197 . doi:
1157 10.1080/00222930110040402
- 1158 Squires RL, Goedert JL (1995) An extant species of *Leptochiton* (Mollusca: Polyplacophora) in Eocene
1159 and Oligocene cold-seep limestones, Olympic Peninsula, Washington. *The Veliger* 38:47–53
- 1160 Stapleton KL, Long M, Bird FL (2001) Comparative feeding ecology of two spatially coexisting species
1161 of ghost shrimp, *Biffarius arenosus* and *Trypaea Australiensis* (Decapoda: Callinassidae). *Ophelia*
1162 55:141–150 . doi: 10.1080/00785236.2001.10409481
- 1163 Stecher J, Tunnicliffe V, Türkay M (2003) Population characteristics of abundant bivalves (Mollusca,
1164 Vesicomidae) at a sulphide-rich seafloor site near Lihir Island, Papua New Guinea. *Can J Zool* 81:1815–
1165 1824 . doi: 10.1139/z03-180
- 1166 Stempien JA (2005) Brachyuran taphonomy in a modern tidal-flat environment: Preservation potential
1167 and anatomical bias. *PALAIOS* 20:400–410
- 1168 Stevens CJ, Limén H, Pond DW, Gélinas Y, Juniper SK (2008) Ontogenetic shifts in the trophic ecology
1169 of two alvinocaridid shrimp species at hydrothermal vents on the Mariana Arc, western Pacific Ocean.
1170 *Mar Ecol Prog Ser* 356:225–237 . doi: 10.3354/meps07270
- 1171 Sudarsky S (2016) A phylogenetic analysis of fossil and extant shrimp-like decapods (Dendrobranchiata
1172 and Caridea). MS Thesis, Kent State University
- 1173 Takeda M, Mizuno Y, Yamaoka M (1986) Some fossil crustaceans from the Miocene Morozaki Group in
1174 the Chita Peninsula, central Japan. *Kaseki-No-Tomo Publ Tokai Foss Soc* 28:12–22
- 1175 Taviani M, Angeletti L, Ceregato A, Foglini F, Frogliani C, Trincardi F (2013) The Gela Basin pockmark
1176 field in the strait of Sicily (Mediterranean Sea): chemosymbiotic faunal and carbonate signatures of
1177 postglacial to modern cold seepage. *Biogeosciences* 10:4653–4671 . doi: 10.5194/bg-10-4653-2013

1178 Teichert BMA, Luppold FW (2013) Glendonites from an Early Jurassic methane seep - Climate or
 1179 methane indicators? *Palaeogeogr Palaeoclimatol Palaeoecol* 390:81–93 . doi:
 1180 10.1016/j.palaeo.2013.03.001

1181 Thatje S, Hall S (2016) The effect of temperature on the evolution of per offspring investment in a
 1182 globally distributed family of marine invertebrates (Crustacea: Decapoda: Lithodidae). *Mar Biol* 163:48 .
 1183 doi: 10.1007/s00227-015-2776-8

1184 Thurber AR, Jones WJ, Schnabel K (2011) Dancing for food in the deep sea: bacterial farming by a new
 1185 species of Yeti crab. *PLoS ONE* 6:e26243 . doi: 10.1371/journal.pone.0026243

1186 Troup MJ (2010) Sedimentology and petrology of Miocene cold-seep carbonates in Southern Hawke's
 1187 Bay: geological evidence for past seabed hydrocarbon seepage. Dissertation, The University of Waikato

1188 Tsuchida S, Suzuki Y, Fujiwara Y, Kawato M, Uematsu K, Yamanaka T, Mizota C, Yamamoto H (2011)
 1189 Epibiotic association between filamentous bacteria and the vent-associated galatheid crab, *Shinkaia*
 1190 *crossnieri* (Decapoda: Anomura). *J Mar Biol Assoc U K* 91:23–32 . doi: 10.1017/S0025315410001827

1191 Tunnicliffe V, Southward AJ (2004) Growth and breeding of a primitive stalked barnacle *Leucolepas*
 1192 *longa* (Cirripedia: Scalpellomorpha: Eolepadidae: Neolepadinae) inhabiting a volcanic seamount off
 1193 Papua New Guinea. *J Mar Biol Assoc UK* 84:121–132 . doi: 10.1017/S0025315404008987h

1194 Van Dover CL, Aharon P, Bernhard JM, Caylor E, Doerries M, Flickinger W, Gilhooly W, Goffredi SK,
 1195 Knick KE, Macko SA, Rapoport S, Raulfs EC, Ruppel C, Salerno JL, Seitz RD, Sen Gupta BK, Shank T,
 1196 Turnipseed M, Vrijenhoek R (2003) Blake Ridge methane seeps: characterization of a soft-sediment,
 1197 chemosynthetically based ecosystem. *Deep-Sea Res I* 50:281–300 . doi: 10.1016/S0967-0637(02)00162-0

1198 Van Gaever S, Olu K, Derycke S, Vanreusel A (2009) Metazoan meiofaunal communities at cold seeps
 1199 along the Norwegian margin: Influence of habitat heterogeneity and evidence for connection with
 1200 shallow-water habitats. *Deep-Sea Res I* 56:772–785 . doi: 10.1016/j.dsr.2008.12.015

1201 Van Harten D (1996) The case against *Krithe* as a tool to estimate the depth and oxygenation of ancient
 1202 oceans. In: Mokuilevsky A, Whatley R (eds) *Microfossils and Oceanic Environments*. University of
 1203 Wales Press, Aberystwyth, pp 297–304

1204 Van Straelen V (1925) Contribution à l'étude des Crustacés Décapodes de la période jurassique. *Mém*
 1205 *D'Académie R Belg Sci Ser 2* 7:1–462, pls. 1–10

1206 Vanreusel A, Andersen A, Boetius A, Connelly D, Cunha M, Decker C, Heeschen K, Hilario A, Kormas
 1207 K, Maignien L, Olu K, Pachiadaki M, Ritt B, Rodrigues C, Sarrazin J, Tyler P, Van Gaever S, Vanneste
 1208 H (2009) Biodiversity of cold seep ecosystems along the European margins. *Oceanography* 22:110–127 .
 1209 doi: 10.5670/oceanog.2009.12

1210 Vonderbank K (1970) Geologie und Fauna der Tertiären Ablagerungen Zentral-Spitsbergens. *Nor*
 1211 *Polarinst Skr* 153:5–119, pls. 1–21

1212 Vrijenhoek RC (2013) On the instability and evolutionary age of deep-sea chemosynthetic communities.
 1213 *Deep-Sea Res II* 92:189–200 . doi: 10.1016/j.dsr2.2012.12.004

1214 Wall PD, Ivany LC, Wilkinson BH (2009) Revisiting Raup: exploring the influence of outcrop area on
 1215 diversity in light of modern sample-standardization techniques. *Paleobiology* 35:146–167 . doi:
 1216 10.1666/07069.1

- 1217 Warner GF (1977) The Biology of Crabs. Van Nostrand Reinhold Company, New York
- 1218 Whatley R (1991) The platycopid signal: a means of detecting kenoxic events using Ostracoda. J
1219 Micropalaeontology 10:181–185 . doi: 10.1144/jm.10.2.181
- 1220 Whatley R, Zhao Q (1993) The *Krithe* problem: A case history of the distribution of *Krithe* and
1221 *Parakrithe* (Crustacea, Ostracoda) in the South China Sea. Palaeogeogr Palaeoclimatol Palaeoecol
1222 103:281–297 . doi: 10.1016/0031-0182(93)90146-A
- 1223 Whatley RC (1990) Ostracoda and global events. In: Whaley RC, Maybury C (eds) Ostracoda and Global
1224 Events. Chapman and Hall, London, pp 3–24
- 1225 Whatley RC (1995) Ostracoda and oceanic palaeoxygen levels. Mitteilungen Hambg Zool Mus Inst
1226 92:337–353
- 1227 Whatley RC, Pyne RS, Wilkinson IP (2003) Ostracoda and palaeo-oxygen levels, with particular
1228 reference to the Upper Cretaceous of East Anglia. Palaeogeogr Palaeoclimatol Palaeoecol 194:355–386 .
1229 doi: 10.1016/S0031-0182(03)00333-X
- 1230 Wieder RW, Feldmann RM (1989) *Palaega goedertorum*, a fossil isopod (Crustacea) from late Eocene to
1231 early Miocene rocks of Washington State. J Paleontol 63:73–80 . doi: 10.1017/S0022336000040981
- 1232 Wiese F, Kiel S, Pack A, Walliser EO, Agirrezabala LM (2015) The beast burrowed, the fluid followed –
1233 Crustacean burrows as methane conduits. Mar Pet Geol 66:631–640 . doi:
1234 10.1016/j.marpetgeo.2015.03.004
- 1235 Wilson B, Coimbra JC, Hayek L-AC (2014) Ostracoda (Arthropoda, Crustacea) in a Miocene oxygen
1236 minimum zone, Trinidad, West Indies: A test of the Platycopid Signal Hypothesis. J South Am Earth Sci
1237 54:210–216 . doi: 10.1016/j.jsames.2014.06.003
- 1238 Withers TH (1924) V. - Some decapod crustaceans (*Callianassa* and *Ranina*) from the Oligocene of
1239 Washington State, U.S.A. Ann Mag Nat Hist 14:121–127 . doi: 10.1080/00222932408633095
- 1240 Yamaguchi T, Goedert JL, Kiel S (2016) Marine ostracodes from Paleogene hydrocarbon seep deposits in
1241 Washington State, USA and their ecological structure. Geobios 49:407–422 . doi:
1242 10.1016/j.geobios.2016.06.003
- 1243 Yamaguchi T, Newman WA (1990) A new and primitive barnacle (Cirripedia: Balanomorphs) from the
1244 North Fiji Basin abyssal hydrothermal field, and its evolutionary implications. Pac Sci 44:135–155
- 1245 Yamaguchi T, Newman WA (1997) *Eochionelasmus paquensis*, new species (Cirripedia: Balanomorphs),
1246 from 17°25'S, north of Easter Island: first record of a sessile hydrothermal barnacle from the East Pacific
1247 Rise. J Crustac Biol 17:488–496 . doi: 10.2307/1549443
- 1248 Yamaguchi T, Newman WA, Hashimoto J (2004) A cold seep barnacle (Cirripedia: Neolepadinae) from
1249 Japan and the age of the vent/seep fauna. J Mar Biol Assoc UK 84:111–120 . doi:
1250 10.1017/S0025315404008975h
- 1251 Yorisue T, Kado R, Watanabe H, Høeg JT, Inoue K, Kojima S, Chan BKK (2013) Influence of water
1252 temperature on the larval development of *Neoverruca* sp. and *Ashinkailepas seepiophila* - Implications for
1253 larval dispersal and settlement in the vent and seep environments. Deep-Sea Res I 71:33–37 . doi:
1254 10.1016/j.dsr.2012.10.007

1255 Zapata-Hernández G, Sellanes J, Thurber AR, Levin LA, Chazalon F, Linke P (2014) New insights on the
 1256 trophic ecology of bathyal communities from the methane seep area off Concepción, Chile (~36° S). Mar
 1257 Ecol 35:1–21 . doi: 10.1111/maec.12051

1258 Zwicker J, Smrzka D, Gier S, Goedert JL, Peckmann J (2015) Mineralized conduits are part of the
 1259 uppermost plumbing system of Oligocene methane-seep deposits, Washington State (USA). Mar Pet Geol
 1260 66:616–630 . doi: 10.1016/j.marpetgeo.2015.05.035

1261