Brachiopods in early Mesozoic cryptic habitats: Continuous colonization, rapid adaptation, and wide geographic distribution

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ABSTRACT

Late Triassic and early Jurassic dikes and fissures in the Dachstein Limestone in the Northern Calcareous Alps harbor mass occurrences of the rhynchonellide brachiopods Sulcirostra juvavica and Halorella amphitoma. To test recent hypotheses about their paleoecology, we characterized these habitats using petrography, carbon stable isotopes, and trace element patterns, and found no evidence for hydrocarbon seepage or hydrothermal venting. Thus the brachiopods lived under normal-marine conditions, in darkness and absence of local photosynthetic primary production, hence relying on the supply of limited and presumably small-sized food washed into the dikes and fissures. Because Halorella and Sulcirostra occur in dikes and fissures since the beginning of their stratigraphic ranges, these rhynchonellides are not relics of formerly widely distributed taxa, but instead are two genera that rapidly adapted to these habitats. Both Halorella and Sulcirostra occur also in late Triassic and early Jurassic deep-water settings such as deep-marine sills and hydrocarbon seeps, indicating that close phylogenetic relationships between submarine cave faunas and deep-sea faunas, as seen today, existed also in the early Mesozoic, albeit among very different taxa. Another analogy to the modern cave fauna is the wide but disjunct geographic distribution of Sulcirostra and Halorella, both found throughout the Tethys and Panthalassa oceans. Our findings support the view that submarine cave habitats were continuously colonized by new taxa throughout Earth’s history.

1. Introduction

Cryptic habitats such as submarine and anchialine caves harbor unique faunal communities, whose evolutionary origins and history are still controversial (Iliffe et al., 1984; Martínez and Gonzales, 2018; Pisera and Gerovasileiou, 2021). These habitats are characterized by perpetual darkness, limited exchange with open waters, and constant temperature. As a consequence, photosynthetic primary production is lacking, food is limited to suspended organic particles that slowly enter from the open ocean, and access of predators is limited (Sket, 1996; Wilkens et al., 2009). The animals in these environments have distinctive adaptations to their unique and patchy habitats (Chiu et al., 2016), yet show broad geographic distributions (Wilkens et al., 2009). Some taxa are endemic on high taxonomic level to these environments, and occupy basal phylogenetic positions among their clades (Yager, 1981; Wilkens, 2017). At least some were proposed to be of ancient or deep-sea origin, and to represent relics of once widely-distributed taxa, whose disjunct present-day distribution is a consequence of plate tectonic separation (Iliffe et al., 1984; Manning and Hart, 1986). However, molecular studies of several cave-dwelling animals indicate broad distributions of homogenous populations (Kano and Kase, 2004; Yorisue et al., 2020) and provided little evidence for tectonic separation of once widespread Tethyan taxa (Botello et al., 2012; Martinez et al., 2013). Furthermore, rapid adaptation to the limited food availability is indicated by the filter-feeding protodrilid annelid Megadrilus pelagicus, which is phylogenetically nested within deposit feeding species (Martinez et al., 2016). Even less is known about fossil examples and the geologic history of such communities (Taylor and Palmer, 1994; Reolid...
and Molina, 2010; Jakubowicz et al., 2014; Berkowski et al., 2019), which could potentially provide insights into the questions of ancient origins, once broad distributions, and the timing of adaptation.

Here we investigate these issues using two fossil brachiopod taxa – *Halorella* and *Sulcirostra* – long known for their disjunct geographic distribution and occurrences in fissures and neptunian dikes in late Triassic to early Jurassic deposits of the Northern Calcareous Alps in Austria. Peculiar about their occurrence is that they are often monospecific, and that the brachiopods are found in life position (Leuchs, 1928). The paleoecology of those occurrences, however, remains elusive. Based on the discovery of mass occurrences of *Halorella* and *Sulcirostra* in methane-seep deposits in Oregon, USA, a relation of the Alpine occurrences to methane-seepage was considered (Peckmann et al., 2011; Peckmann et al., 2013). An analogous monospecific mass occurrence of the rhychonellide brachiopod *Lacunosella* in Oxfordian (late Jurassic) neptunian dikes in Poland has been linked to hydrothermal activity: here the brachiopods were supposed to have lived on abundant organic matter resulting from the mass growth of free-living bacteria (Matyszkiewicz et al., 2016).

The aims of this study are: (1) testing the hypotheses of methane seepage or hydrothermal venting for the occurrences of *Halorella* and *Sulcirostra* in the Alpine dikes and fissures using petrographic and geochemical methods, and (2) discussing the implications of our findings for the evolutionary origins of cryptic faunas, focusing on the relict-fauna hypothesis, the adaptation to these habitats, and their distribution pattern.

2. Material and methods

2.1. Field collections

At all sites (Fig. 1) we collected rock samples for thin section preparation, stable isotope analysis, and trace element analysis. Samples of the late Triassic *Halorella amphitoma* were collected at two locations. The Hohe Wand site (47°50.516′N, 16°3.608′E, and an altitude of 825 m) is a small roadside outcrop along Wandeckstraße above the village of Stollhof in Lower Austria, where a c. 30 cm wide neptunian dike with abundant shells in gray matrix passes vertically through the surrounding Dachstein Limestone. The second site is an about 30 cm wide and at least 100 m along and across the hiking trail, is often fractured, and the brachiopods occur in numerous nests. (3) Along Eichstätter Weg (Alpine hiking trail 401) at 47°27.778′N, 12°54.605′E, and an altitude of 2255 m. This fissure starts at its southern end with a large nest with enormous numbers of small *Sulcirostra juvavica*; toward the north, the fissures become thinner and the brachiopods decrease in abundance. (4) Near the turnoff for Eichstätter Weg, at 47°27.652′N, 12°54.706′E, and an altitude of 2229 m. Here two large fissure run in parallel, roughly perpendicular to the hiking path, one of them is filled by pink rather than red sediment containing angular, turbiriniform gastropods, the other is filled by red sediment, shows *Trypanites* borings into the surrounding Dachstein limestone, and contains *Sulcirostra juvavica*. The illustrated fossils are housed in the Swedish Museum of Natural History, palaeontology collection (NRM PAL).

2.2. Petrography and stable isotopes

Nineteen thin sections (sizes of 2.8 × 4.8 and 10 × 15 cm; approximately 40 to 100 μm thickness) of the fossiliferous limestone were prepared. Instead of providing a detailed description of dike and vein fillings, we focus on those properties, which allow for the reconstruction of the paleoecology of the cavity dwelling brachiopods. Some thin sections were partially stained with combined potassium ferricyanide and alizarin red solution. Petrography was conducted with a Zeiss Axio Scope.A1, and photomicrographs were taken with a Canon Eos 1300D. Samples for carbon and oxygen stable isotope analyses were extracted from the rock counterparts from which the thin sections were prepared, using a hand-held microdrill. Carbonate powders were reacted with 100% phosphoric acid at 75 °C using a Kiel III online carbonate preparation line connected to a ThermoFinnigan MAT 252 mass spectrometer at MARUM, University of Bremen. The instrument was calibrated against an in-house standard (SHK Br 2008, ground Solnhofen limestone; δ13C: −0.96‰, δ18O: −4.20‰), which in turn was calibrated against the NBS 19 calcite standard. All values are reported in per mil relative to V-PDB standard (standard deviation smaller than 0.03‰ for δ13C and 0.07‰ for δ18O values), and appropriate correction factors were applied.

2.3. Rare earth element analysis

Thin sections used for laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) were polished and had a thickness of approximately 80 to 100 μm to ensure long ablation periods and good statistics of the analysis. Laser ablation was performed using a 193 nm ArF excimer laser (Analyte G2, Photon Machines) coupled to an Element 2 (ThermoFisherScientific) single collector mass spectrometer. Laser spot size was set to 110 μm at a 5 Hz repetition rate and a fluence of 3 to

Fig. 1. Locations of the three sampling areas Steinernes Meer, Tennengebirge, and Hohe Wand in the Northern Calcareous Alps in Austria.
4 J/cm². Gas flow rates were 1.1 l/min for He and 0.9 l/min and 1.1 l/min for the Ar-auxiliary and sample gas, respectively. Cooling gas was set to a flow rate of 16 l/min. Prior to analyses, the system has been tuned on the NIST 612 reference material measuring 139La, 232Th, and 232ThO for high sensitivity and stability and low oxide rates (232ThO/232Th < 0.1%) during ablation.

Overall measurement time for a single spot analysis was 60 s, with 20 s for background and 40 s for peak signal. The washout time between two spots was set to 15 s. A total of 48 elements were analyzed using 43Ca as internal standard element and NIST 612 as external reference material (Jochum et al., 2011).

Distance between single laser spots of each profile was 130 μm. Groups of about 25 unknowns were bracketed with 3 NIST 612 calibration standards. Data has been processed using the Glitter software (Griffin et al., 2008). Due to known analytical problems analyzing carbonates with LA-ICP-MS (Jochum et al., 2012), the MACS-3 carbonate reference material provided by the United States Geological Survey was measured along with the samples for validation of the data. Obtained MACS-3 (n = 10) trace element concentrations generally match the range of values given in previous work (Chen et al., 2011; Jochum et al., 2012; Wu et al., 2018; Jochum et al., 2019; GeoRem database version 29, Jochum et al., 2005).

3. Results

3.1. Fauna

The late Triassic Neptunian dike near Scheiblingkogel in the Tennenengebirge massif is filled by Halorella amphitoma (Fig. 2A, 3A, C) and Halorelloidea rectifrons (Figs. 2B). Halorella amphitoma occurs in virtually monospecific masses in red or gray sediment, shells reach a width of 45 mm, are mostly articulated, and a few specimens show shell injuries or growth disruptions. Halorelloidea rectifrons occurs in yellowish sediment (Fig. 2B) often associated with gastropods. Although there is no sharp boundary between the two facies, the two species do not mix. Thus although Halorella amphitoma and Halorelloidea rectifrons are found in the same dike, within the dike their occurrence is spatially distinct.

The early Jurassic fissures in the Steinernes Meer massif are dominated by the brachiopod Sulcrostra juvavica (Fig. 2C, 3B, D). The shells reach 15 mm in maximum dimension, are commonly articulated, and occur both in pockets and dispersed throughout the fissures. The only other fossil remains are occasional smooth-shelled ostracods, rare high-spired gastropods, fecal pellets, and Trypanites borings.

3.2. Petrography and stable isotopes

The dikes and fissures in the Dachstein Limestone have many features in common, yet they also show some marked differences. Sediment ingress into dikes occurred episodically over prolonged periods of time, both predating and postdating the precipitation of early marine cement. Reddish and yellowish carbonate sediment fill the dikes to different degrees; both varieties of sediment occur within dikes at the Funtensee locality (Fig. 4A-C), whereas no sediment was observed in the samples collected from the Hohe Wand locality. Closed, articulated brachiopod shells contain geopetal sediment infill at all localities except Hohe Wand. At the Scheiblingkogel locality, patches of articulated Halorella amphitoma shells without geopetal infills occur, and inner shell surfaces are entirely lined with early fibrous cement. The majority of the shells are articulated, with the shell microstructure commonly well preserved (Fig. 4D, E) or occasionally recrystallized (Fig. 4B). At all study sites, much of the dike volume is filled by early fibrous cement. This cement is closely associated with brachiopod shells, having precipitated on the internal and, to a lesser degree, on the external surfaces of shells (Fig. 4D, E). The formerly fibrous rim cement is recrystallized to different degrees. Locally this rim cement reveals a reticulate pattern (Fig. 4F), a pattern suggested to result from the recrystallization of fibrous aragonite to calcite (Aïssaoui, 1985; Peckmann et al., 2007).

Carbon and oxygen stable isotope compositions were determined for (1) the host rock (i.e. the Dachstein Limestone), (2) sedimentary infill, (3) few brachiopod shells, (4) marine fibrous cement, and (5) late diagenetic cement (Fig. 5), and were found to fall in a narrow range. The δ13C and δ18O values of the Dachstein Limestone range from 0.4 to 2.6‰ and −4.1 to −0.9‰, respectively. Sulcrostra shells yielded δ13C values from 2.5 to 2.7‰ and δ18O values from −2.0 to −1.1‰; note that shells are thin, rendering likely minor contamination of drilled powders by other carbonate microfabrics. The isotope compositions of red sediment (δ13C: 1.5 to 2.7‰; δ18O: −3.2 to −1.2‰) are similar to shells and
fibrous cement ($\delta^{13}$C: 0.7 to 3.0‰; $\delta^{18}$O: 3.1 to 0.8‰), with the exception of one sample of fibrous cement from the Hohe Wand locality reflecting minor $\delta^{13}$C depletion ($\delta^{13}$C: 0.7‰; $\delta^{18}$O: 3.6‰). Equant calcite cement yielded slightly lower $\delta^{18}$O values (5.5 to 2.3‰), but similar $\delta^{13}$C values (–0.3 to 2.9‰).

3.3. Trace elements

Contents of rare earth elements (REE) of the fibrous carbonate cements are mainly in the range below 1 ppm. They are displayed normalized to Post-Archean Australian Shale (PAAS; Fig. 6). The cements show REE patterns featuring a negative cerium (Ce) anomaly but lacking evidence for an europium (Eu) anomaly. The brachiopod shells (not shown) display similar REE patterns.

4. Discussion

4.1. The dike paleoenvironment

The articulated preservation of the thin shells of Halorella amphitoma, Halorelloidea rectifrons, and Sulcirostra juvavica, and geopetal infills indicate only a minor degree of re-deposition or transport. Hence, these communities represent paraautochthonous assemblages. The specimens of Halorella amphitoma in the Scheiblingkogel dike that lack geopetal infills may even have been preserved in life position, as suggested earlier (Walther, 1885; Fischer, 1964; Scholl and Wendt, 1971).

Several species of Paleozoic and Mesozoic rhynchonellide brachiopods are known from hydrocarbon seeps, including members of the genera Halorella and Sulcirostra (Peckmann et al., 2011, 2013). As in most mass occurrences of rhynchonellides at seeps, articulated shells of Halorella amphitoma, Halorelloidea rectifrons, and Sulcirostra juvavica dominate over disarticulated shells in the dikes of the Dachstein Limestone. Another analogy between the brachiopod assemblages at seeps and those within the Alpine dikes is the abundance of fibrous cement, filling many articulated specimens to a large degree. This marine cement formed close to the life span of brachiopods and consequently archives paleoenvironmental conditions at the seafloor or, like in this case, in cryptic environments flushed by seawater. For hydrocarbon seep deposits, fibrous cement growing on and within brachiopod shells is typified by a pronounced $\delta^{13}$C depletion (e.g., Peckmann et al., 2001), reflecting the local production of dissolved inorganic carbon (DIC) by anaerobic oxidation of hydrocarbons including methane. Yet, the $\delta^{13}$C values of fibrous cement of the dike fillings in the Dachstein Limestone – like the values of sedimentary infill and Sulcirostra shells – reflect formation in equilibrium with seawater DIC. The sediment-deprived dikes were probably a rather open system for microbially generated $\delta^{13}$C-depleted DIC compared to sedimentary pore water and very low $\delta^{13}$C values are not to be expected in such an open system. Still, the exclusively high $\delta^{13}$C values of fibrous cement are in sharp contrast with the carbon isotope signatures of the early diagenetic fibrous cement forming at seeps.

Matyszkiewicz et al. (2016) studied neptunian dikes encountered in massive Oxfordian limestones in the Kraków-Częstochowa Upland in southern Poland. Like the dikes from the Dachstein Limestone, the Oxfordian dikes are typified by a mass occurrence of rhynchonellide brachiopods tentatively identified as Lacunosella sp. The Oxfordian dikes
were penetrated by karst waters and hydrothermal solutions during Cretaceous and Cenozoic times. Based on the neodymium isotopic composition of dike-filling sediments, which is different from the composition of unaltered Oxfordian limestone, Matyszkiewicz et al. (2016) suggested the presence of hydrothermal solutions also during the life span of the rhynchonellides.

Europium (Eu) is a rare earth element (REE), which is known for its potential to trace hydrothermal conditions (Bau, 1991). Most REEs are insensitive to redox conditions with the exception of cerium (Ce) and Eu. In oxidized seawater, dissolved REEs occur as threefold positive charged ions with the exception of Ce, which is oxidized to Ce$^{4+}$ (Moffett, 1990). The latter results in negative Ce anomalies when REEs are normalized to average shale compositions (De Baar et al., 1985). Apart from negative Ce anomalies, seawater is typified by the enrichment of heavy REEs as a consequence of the formation of stable, soluble REE-carbonate complexes (Sholkovitz et al., 1994; Alibo and Nozaki, 1999). The normalized REE patterns of fibrous cement associated with brachiopod shells of the Dachstein Limestone dikes consequently match the REE pattern of seawater (cf. Tostevin et al., 2016). Hydrothermal fluids and the minerals forming from them are typified by positive Eu anomalies (Bau, 1991); Eu$^{3+}$ is reduced to Eu$^{2+}$ under strongly reducing conditions at high temperature. Interestingly, Eu is a more sensitive recorder of the influence of hydrothermalism than, for example, Sr isotopes (Eickmann et al., 2009). Accordingly, the lack of positive Eu anomalies in fibrous
cement is strong evidence for the absence of an influence of hydrothermal waters on brachiopod paleoecology. Similarly, none of the obtained element patterns suggest a hydrocarbon seep setting (cf. Zwicker et al., 2018; Smrzka et al., 2020). However, it needs to be stressed that translucent fibrous cement forming at seeps – unlike seep micrite or yellow fibrous cement – is typically also characterized by seawater-like REE distributions (Himmler et al., 2010; Schier et al., 2021), consequently reflecting an unspecific element signature in this case. To sum up, the lack of evidence for an influence of either hydrocarbon-rich fluids or hydrothermal fluids suggests that Halorella amphitoma, Halorelloidea rectifrons, and Sulcirostra juvavica lived in fully marine habitats and took advantage of the remains of photosynthetic primary production, either particulate organic matter that trickled into their cryptic habitat or dissolved organic carbon that was taken up by the brachiopods (cf. McCammon and Reynolds, 1976).

4.2. Ecology and evolution of Halorella, Sulcirostra, and related “dimerelloid” brachiopods

One distinctive feature of present-day submarine cave fauna is its disjunct but wide distribution (Wilkens et al., 2009). This was considered as either representing a relict distribution, or as the result of continuous colonization paired with rapid adaption and high dispersal capabilities. Another distinctive feature are close phylogenetic relationships of some cave taxa to deep-sea species, spurring the idea of a potential deep-sea origin of this fauna (Iliffe et al., 1984; Manning and Hart, 1986; Sket, 1996; Martínez et al., 2013; Wilkens, 2017). The early Mesozoic submarine cave-dwelling brachiopods Sulcirostra and Halorella provide interesting fossil insights into these questions.

Numerous species of Sulcirostra have been described, though many of them are doubtful as they are based on minute differences and fragmentary material, and virtually all described occurrences are highly localized, mono- or oligospecific populations (e.g., Sulser and Furrer, 2008). Geographically, species of Sulcirostra are distributed from the

![Fig. 5. Carbon and oxygen stable isotope plots. A. Neptunian dikes with Halorella amphitoma. B. Fissures with Sulcirostra juvavica; the samples are from all four sites and pooled here by carbonate type, as they did not vary significantly between sites.](image)

![Fig. 6. REE-data of cement carbonates normalized to PAAS.](image)
Tethys to the northeastern Panthalassa Ocean and the paleoenvironments, when known, are restricted to submarine dikes (Cicardi and Gaetani, 1974; for Sulcrostra alpina; herein for S. juvavica), presumably deep-marine sills (S. alpina and S. doesseggeri; Sulser and Furrer, 2008), and deep-marine hydrocarbon seeps (Sulcrostra paronat; Peckmann et al., 2013). Thus, the occurrences of Sulcrostra in submarine caves (and any of the other habitats it has been found in) are not relics of a formerly widespread taxon. Furthermore, Sulcrostra is geologically short-lived genus (Sulser and Furrer, 2008; Sandy, 2010; Kiel and Peckmann, 2019), indicating that it quickly adapted to dark environments with small-sized but in some cases abundant food (bacterio-plankton, planktonic detritus, possibly dissolved organic carbon).

The case of Halorella is similar. Occurrences in neptunian dikes are common both in the Northern Calcareous Alps (Walther, 1885; Fischer, 1964; herein) and their continuation in Slovakia (Channell et al., 2003) and Romania (Lazar et al., 2020). In addition, pockets with mass occurrences are known from hemipelagic calciturbidites of the Northern Calcareous Alps (Lobitzer, 1974; Mandl, 2000; Mandl and Krystyn, 2008). Halorella occurs at hydrocarbon seeps in both northwestern North America and in Turkey, the latter corresponding to the central Tethys (Peckmann et al., 2011; Kiel et al., 2017); however, the nature of the records further east in the Tethys Ocean remains unknown (Ager, 1969). Just like Sulcrostra, Halorella is a geologically relatively short-lived genus (Ager, 1968; Sandy, 2010).

Thus, both Sulcrostra and Halorella reached broad geographic distributions within geologically short time spans, showing that these early Mesozoic cave inhabitants were by no means relics of once widely distributed taxa. Instead, Sulcrostra and Halorella likely possessed broad dispersal capabilities, despite having non-planktotrophic larvae and living in warm oceans (Jablonski and Lutz, 1983; Valentine and Jablonski, 1983). Furthermore, Sulcrostra and Halorella show that the close faunal link between deep-marine and cave environments is not restricted to the modern ocean. Rather, the nature of these habitats, being light-limited and lacking local photosynthetic primary productivity, appears to have facilitated faunal exchange between them throughout Earth’s history.

A distinctive feature of Sulcrostra and Halorella are their long, ventrally curving (ensiform or ciliform) crura (Biernat, 1957; Manenido et al., 2002; Sulser and Furrer, 2008; Sandy, 2010). The crura hold the lophophore – the brachiopods’ feeding apparatus – and the increase in their length most likely is the manifestation of an adaptation in their feeding strategy. Likewise, the increase in size of Halorella populations at seeps with diffusive fluid transport or oil seepage, and hence an abundance of free-living methanotrophic bacteria (cf. Kiel et al., 2014; Kiel and Peckmann, 2019), likely is a further adaptation to the abundant bacterial food in their habitats. These rapid adaptations to the unique nutrient supply in their habitats resemble those seen in present-day cave-dwelling animals (Ilfie et al., 1984; Iliffe and Bishop, 2007; Martinez et al., 2016).

Sulcrostra and Halorella have traditionally been placed in the Dimerelloidea among the rynchonellids (Ager, 1965; Manenido et al., 2002; Sandy, 2010). This superfamily has often been depicted as a long-lived lineage inhabiting, or even being restricted to, habitats with a chemosynthesis-based food web (Sandy, 1995; Sandy, 2010; Pályi et al., 2017; Kiel and Peckmann, 2019). Indeed, well-investigated, in situ-occurrences of several dimerelloid genera represent ancient communities that were based on chemosynthesis. This applies to the Cretaceous Peregrirella, which is known exclusively from seep deposits (Campbell and Bottjer, 1995; Sandy et al., 2012; Kiel et al., 2014), the early Jurassic Analirynchia, known from both seep and vent deposits (Little et al., 1999; Pályi et al., 2017), as well as the early Carboniferous Ibergirhyncha and late Jurassic Cooperirhyncha; the latter two are known from a single seep deposit each (Sandy and Campbell, 1994; Gischler et al., 2003). The Devonian dimerelloid Dzieduszyckia, occurring both at hydrocarbon seeps and in bedded strata in Morocco, was suggested to have had a wider ecological flexibility (Peckmann et al., 2007).

However, the monophyly and integrity of the Dimerelloidea has long been an issue. Already Dagys (1974) questioned the position of Halorellidae within Dimerelloidea, and long stratigraphic gaps between the constituting genera of several dimerelloid families, in particular the large-sized Datieduszyckia, Halorella, and Pergerinilla, had been pointed out (Gischler et al., 2003; Kiel and Peckmann, 2019). In a recent phylogenetic analysis of Permian and Triassic rynchonellid brachiopods (Guo et al., 2021), Halorella und Sulcrostra were placed on two widely separated branches, Halorella together with Halorellidae on a branch with genera traditionally placed among Allorynchidae, Austrochinaeidae, and Norellidae, and Sulcrostra forming a clad with the two dimerelloid genera Carapezza and Rhychnellina, either on a branch of their own, or along with genera traditionally placed in Allorynchidae.

Due to these uncertainties in the phylogenetic relationships of Sulcrostra and Halorella, it is difficult to maintain the view that dimerelloids were a distinct clade whose members continuously or repeatedly colonized chemosynthesis-based habitats. Rather, it appears that adaptations to cope with the specifics of deep-water, chemosynthesis-based, and cave habitats evolved several times independently among rynchonellid brachiopods. For example, morphological features traditionally used to establish family-level relationships among “dimerelloid” genera, such as the long, ensiform crura discussed above, could be homoplasies that evolved repeatedly as adaptation to the particularly small-sized and scarce (submarine caves and other cryptic environments, cf. Wilkens et al., 2009) or abundant (vents/seeps, cf. Kiel and Peckmann, 2019) food particles in these environments. However, regardless of the exact phylogenetic relationships of Halorella and Sulcrostra, our findings support the notion by Jaume et al. (2000, p. 241) that the submarine cave habitat “is being continuously colonised”, just like methane seeps and hydrothermal vents have been continuously colonized by new taxa throughout Earth’s history (Warén and Bouchet, 2001; Kiel and Little, 2006; Kiel and Peckmann, 2019).

5. Conclusions

The identification of mass occurrences of the late Triassic and early Jurassic brachiopods Halorella and Sulcrostra as ancient hydrocarbon-seep deposits spurred the hypothesis that mass occurrences of these two brachiopods in fissures and dikes in the Northern Calcareous Alps might also have been fueled by chemosynthetic primary production. Our stable isotope and element geochemistry data of several such examples in the Tennengebirge, Hohe Wand, and Steinernes Meer in the Austrian Alps provide no evidence that these habitats were influenced by hydrocarbon seepage or hydrothermal venting. Based on these results and further observations on the habitats, and the geographic and geologic ranges of these two genera, we conclude that Halorella and Sulcrostra were able to rapidly adapt to dark habitats with small-sized food particles. Analogous adaptation to, and colonization of, such habitats occurred repeatedly through Earth’s history among rynchonellid brachiopods traditionally classified among the Dimerelloidea. Further analogies to the present-day anchialine cave fauna include close phylogenetic links to deep-sea taxa and broad but disjunct geographic distributions.

Research highlights

• Mesozoic cryptic habitat with dimerelloid brachiopods in Dachstein limestone explored
• No evidence for hydrothermal venting or hydrocarbon seepage
• Halorella and Sulcrostra likely relied on filter-feeding on small-sized particles
• Submarine cryptic habitats were continuously colonized throughout Earth’s history
• Mesozoic cryptic habitat fauna shows links to deep-sea faunas
Declaration of Competing Interest

None.

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Conflicts of interest

There are no conflicts of interest.

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