Fauna, palaeoecology and ecotypes of the Early Cretaceous sediment hosted hydrothermal vent environment of Zengővárkony (Mecsek Mountains, Hungary)

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ABSTRACT

The fossil biota of the upper Valanginian–lower Hauterivian sediment hosted vent (SHV) environment of Zengővárkony comprises 39 species, 55 genera and higher taxa representing seven phyla. Thirteen of these taxa are reported from Zengőrvárkony as new species or new subgenera/genera, and this high endemicity is linked to a unique palaeoenvironment. The palaeoenvironment is developed in an outer shelf epicontinental setting on an elevated block or slope, and is linked to a small sedimentary iron-ore body interbedded with pillow lavas being a result of ferriferous exhalations and biogenic processes. Biogeographically, the brachiopods indicate the Sub-Tethyan domain. Serial sectioning of brachiopods revealed a taxon-dependent rich and diverse microfauna (sponges, foraminifers, gastropods) preserved inside the shells. Internally preserved microfauna in brachiopods reveals differentiation among preventive strategies. It implies different preventive efficiencies of alternative defence strategies of higher brachiopod taxa. The unique Zengővárkony SHV environment attracted both nektonic and benthic organisms by creating different ecotopes around the hydrothermally driven bottom environment. This environment belongs to the group of rare, shelfal, hydrothermally influenced palaeoenvironments formed on continental crust. Water depth was most probably between 100 and 150 m. Recent observations from a similar modern volcanic built-up, and its effects on the marine environment located on continental crust around the Aeolian Islands (Tyrrhenian Sea) support the recognition of this fossil SHV environment and helps to understand better its bathymetry, ecological conditions and ore-formation.

1. Introduction

Discovery of the Recent marine hydrothermal vents in 1979, quickly followed by their recognition in the fossil record (Haymon et al., 1984), brought these unique palaeoenvironments into the main stream of geoscience. Recognition of Recent and fossil deep-sea hydrothermal vents is relatively easy as they have depth-controlled and vent-related fauna. Some twenty-plus years later, the number of fossil and recent vent localities recognized increased to 59 worldwide (13 vents versus 46 seeps; Campbell, 2006 Table 1), and a simple connection between the vent-dependency of organisms and their depth is revealed: the deeper the vent site, the more vent-related organisms occur. The number of vent-obligate taxa continuously increases with water depth. It is 0–1.4% at less than 100 m water depth, while it increases to 40% at 800 m, and up to 50–80% at 1500 m and deeper (Tarasov et al., 2005), which is in

line with other observations. According to Desbruyères et al. (2000) the relative number of hydrothermal vent-related species at 850 m water depth is 30%, while it increased to 70% at 3500 m. These "classic" hydrothermal vents are formed on normal or thinned oceanic crust associated with strong heat and fluid fluxes in several thousand-meter water depth.

In shallow marine (<200 m) settings, however, vent localities (sensu Dando, 2010) did not possess strong endemism and contain only a few vent-dependent taxa, and therefore, their recognition based on the fossil record is still ambiguous. Aside from the oceanic crust hydrothermally influenced settings, many environments of this type appear on continental crust linked to rifting (e.g. Red Sea hydrothermal field, see Wang et al., 2015). It is noteworthy that intra-plate hydrothermal vents are very rare and account for only 1% of the totally 521 active recent vent sites (Beaulieu et al., 2013, p. 4897). In the later census of Beaulieu and

Table 1

Higher taxa of macrofossils with numbers of specimens and percentages in the Zengővárkony fauna examined in the present paper.

Higher taxa	number of specimens	percentage
Ammonoidea	12	5.2
Belemnoidea	13	6.0
Brachiopoda	154	66.5
Crinoidea	1	0.4
Echinoidea (body fossil and spines)	47	20.2
Gastropoda	3	1.3
Porifera	1	0.4
Total	231	100

Note, that the numerous echinoid spines (46 specimens) are included in this chart but it is not possible to determine the number of individual animals represented by them.

Szafrański (2020) 722 localities are listed including 55 hydrothermal vents with less than 150 m water depth but listed without differentiated basement. This implies that recognition of hydrothermally influenced fossil faunas from shallow marine settings is difficult, accidental and dubious. The majority of research was concentrated on high temperature deep-sea hydrothermal vent sites, and only of a handful studies were focused on low temperature, sediment-hosted hydrothermal vents (SHV, see Bell et al., 2016).

In the past few decades we have better understood the role and importance of hydrothermal vents in the fossil record, and the interpretation of hydrothermally influenced settings has broadened toward shallow marine locations with low temperature hydrothermal activities. A typical example for this kind of shallow marine setting is the recent Palaeochori Bay at Milos Island (Greece) from where Dando et al. (1995) and Aliani et al. (1998) described a low temperature outgassing locality with special fauna at 25 m water depth. Here, the species richness of sessile epibenthic animals is remarkable by attaining 50–125 species (Cocito et al., 2000). It became obvious that even in shallow marine settings, the species diversity is increased near the vents, although there are no obligate vent-associated species in these environments (Bianchi et al., 2011). Both macro- and microfauna are richly represented at the shallow marine hydrothermal vent site of the Tyrrhenian Sea (Panieri et al., 2005).

In the absence of vent-obligate taxa in shallow marine hydrothermally influenced sediments, only indirect evidence and a broader geological framework can help to identify sediment hosted vents in ancient shallow marine settings. There are some animal groups in the fossil record that are appropriate for this kind of deciphering. Rhynchonellide brachiopods were continuous constituents in fossil hydrothermal vent communities from the Late Devonian to the Early Cretaceous (Little, 2002). Their general size increase may refer to special environments (e.g. hydrothermal vents), which could be tested by carbon and nitrogen stable isotope fingerprints (Paull et al., 1985). We may note however, that different, but also unique environments (e.g. stromatactis mud-mounds, Lazar et al., 2011) are favourable for general size increase in brachiopods. Today, brachiopods also appear in hydrothermal fields of shallow marine settings, however only as cryptic constituents of the fauna (Cocito et al., 2000).

At present, we understand better the enigmatic shallow marine, intra-plate hydrothermal vent environments and their faunas, although their specific components are only sporadic constituents of Recent hydrothermal vent habitats.

Only five Recent intra-plate shallow hydrothermal vent faunas are known (Beaulieu et al., 2013, p. 4897), and their fossil predecessors are not fully delineated. Recognition of this kind of fauna is primarily based on direct evidence (stable isotope measurements, volcanic activity) and indirect signals (size distribution of fossil populations, diversity, and specimen richness). But without documented Recent analogues it is even more difficult to properly identify them. From the fossil record, the only one intraplate hydrothermal vent locality is known from Early Carboniferous age at Silvermines, Ireland; however, this locality did not provide macrofossils and the water depth of its depositional environment not known (Boyce et al., 2003).

Although the Early Cretaceous volcanics of the Mecsek Mountains were already discovered in the 19th century by Hofmann (in Böckh, 1876), the small iron-ore body at Zengővárkony was only recognized in the 1930s by a private entrepreneur determining magnetic inclination measurements. The Early Cretaceous iron-ore related environment at Zengővárkony, its fauna and geological interpretation remained problematic for decades. But even from its discovery, the fauna attracted the attention of geologists because of its remarkable features. Almost all experts who dealt with the fauna described new taxa, attaining so far 13 species including: six Crustacean microcoprolite species (Palik, 1965), three new brachiopod species (Bujtor and Vörös, 2019), two crinoid species and a subgenus (Szörényi, 1959), and two anthozoan genera/ species (Kolosváry, 1954). Sztrókay (1952) was the first to recognize microfossils that he considered as remnants of Dasycladacean algae. Later on, Pantó et al. (1955) reported a rich microfossil content, which was subsequently regarded as crustacean microcoprolites by Palik (1965). These researchers already considered that the iron-ore body was the by-product of volcanic exhalations, and ferriferous solutions traveling through the volcanic basement (Pantó, 1961). Mining activity ceased in the mid-1950s due to limited access and poor quality of the ore and only some 24,850 tons of iron-ore was excavated (Molnár, 1961).

In the 1960s, geological mapping in the area brought some new discoveries. Fülöp (in Hetényi et al., 1968) was the first to report macrofossils from the region (gastropods, ammonites, belemnites, brachiopods, echinoids, and crinoids) and considered their age as Late Valanginian. He also mentioned the presence of some microfossils (*Tintinnopsella carpathica* (Murgeanu and Filipescu) and a *Globigerina* sp.) but no benthic foraminifera. Bujtor (2006) reported a rich brachiopod assemblage with remarkable size increase. As Callender and Powell (1992) discussed the significance of these faunal characteristics (monotypic and large-sized brachiopod populations) for the recognition of vents/seeps, Bujtor (2007) proposed a possible vent/seep origin of the Zengővárkony assemblage, however carbon and oxygen stable isotope measurements did not support it. He also attempted to interpret the environment and placed it into a broader geological context. Later on, Jáger and Molnár (2009) reported black smoker chimneys from the Dezső Rezső Valley, however the same authors later considered these features as poorly preserved remnants of hydrothermal sediments (Jáger et al., 2012). Primary fluid inclusions from calcite among the hydrothermal sediments, indicate a mean temperature value of 129 °C (Jáger et al., 2012), which is in accordance with the supposed low-temperature character of these hydrothermal deposits.

Bujtor et al. (2013) reported some previously unknown belemnite and dinoflagellate taxa, and interpreted the environment to be of outer-shelf Mediterranean-Tethyan type. He used belemnites and dinoflagellate cysts to decide the more precise age of the succession and concluded a late Valanginian to earliest Hauterivian age, that confirmed the earlier dating by Fülöp (in Hetényi et al., 1968). Bujtor and Szinger (2018) analysed the microfauna of the Zengővárkony locality and reported poorly preserved benthic foraminifera including: *Epistomina* sp., *Glomospira* sp., *G.* cf. *gordialis* (Jones and Parker, 1860), *Lenticulina* sp., *Nodosaria* sp., *Spirillina* sp., *Trocholina* sp., and the planktonic *Hedbergella* sp. Furthermore, Bujtor and Szinger (2018) recognized diactine-type criccorhabd and rhax sponge spicules from the locality.

Based on the rich microcoprolite fauna, Bujtor and Szinger (2018) analysed the size distribution of three microcoprolite species, and reported their size ranges including intraspecific variation from juvenile to adult stages. Most recently, Bujtor and Vörös (2019) described new brachiopod taxa including *Dictyothyropsis vogli*, *Zittelina hofmanni* and *Smirnovina ferraria*. Based on new and older collections Vörös and Bujtor (2020) reported a small but endemic brachiopod fauna of 9 species together with some, from Zengővárkony previously unknown brachiopods (*Fortunella* cf. *fortunae* Calzada, 1985; *Karadagella* sp. aff. *bilimeki*

(Suess, 1858); *Monticlarella remesi* Nekvasilová, 1977). The assemblage has Sub-Tethyan affinity in contrast to the endemic brachiopod assemblage. These new findings and the recognition of the Recent counterpart of this environment requires a summary and evaluation of our knowledge on the Zengővárkony SHV.

This paper is focused on the following purposes: (1) recording a remarkably rich microfossil assemblage revealed in brachiopod shells by serial sectioning; (2) reporting the abundant foraminiferal assemblage; (3) reporting new faunal distribution data; (4) summarizing the knowledge on this unique palaeoenvironment based on research since the 1950s; (5) providing a new outline of a Cretaceous hydrothermally driven, shallow marine, intra-plate sediment hosted fossil vent (SHV) community. The paper also provides a reinterpretation of this fossil environment in the light of a new discovery of a similar Recent environment from the Tyrrhenian Sea by Ferretti et al. (2019). Enough research data has been accumulated over the last 70 years to allow us to summarize knowledge on this Cretaceous Hungarian SHV environment and its fauna. The locality seems exhausted and new material is not expected to appear in the near future. In this paper we recognize for the first time an intra-plate, shallow marine, sediment hosted vent ecosystem in the fossil record, belonging to the SHV family.

2. Materials and methods

The macrofossil material from Zengővárkony included in this study, comprises 231 specimens. The majority of these were collected by one of the authors (L.B.) and his co-workers, 22 specimens were present in the old collection of the Mining and Geological Survey of Hungary. In previous papers 162 specimens were described in detail (Bujtor, 2006; Bujtor, 2012a, 2012b, 2013; Bujtor and Vörös, 2019; Vörös and Bujtor, 2020; Bujtor et al., 2013). The remaining 49 specimens are the subject of the present study. Table 1 shows a list of the macrofossil taxa with respective specimen numbers and percentages. The material described herein (some 250 macrofossil specimens) was collected during various field trips in a period of 24 years from 1989 to 2018 under strict stratigraphic control.

Serial sectioning of brachiopods was carried out using a CutRock Grinding machine at the Hungarian Natural History Museum, Budapest, in summer 2018. Line drawings were made by means of a Zeiss stereomicroscope, where brachiopod crural elements and revealed microfossils were also depicted. Composite drawings of entombed microfossils were centred around the crura and sectional drawings are superposed and copied on paper that was scanned, and digitalized. The outline of brachiopod shells of composite drawings are portrayed at their maximum width with the indication of the crura at that width. Eleven brachiopod specimens were serial sectioned, 592 serial drawings were made and 7 composite drawing are presented.

Stable isotope measurements were prepared by Heinrich Taubald at Tübingen University, Germany on a NC 2500 Thermo Quest Delta+XL mass spectrometer. Samples are calibrated according to the NBS 123, NBS 127 and IAEA-S-3 standards. Reproducibility for $\delta^{34}S$ isotope is $+/-$ 0.3‰, and for sulphur content is 5%.

Repositories: Specimens (originals and plaster casts) are housed in the palaeontological collection of the Hungarian Natural History Museum (abbreviated HNHM), Budapest and the Mining and Geological Survey of Hungary (abbreviated MGSH), Budapest; Eötvös Loránd University, Budapest (abbreviated PMEU).

3. Geological setting

The Late Jurassic–Early Cretaceous evolution of the Mecsek Mountains is characterized by significant tectonic changes from a stable and calm basin-type sedimentation toward rifting on a thinned continental margin that resulted in the detachment of the region from the European plate. The Mecsek Mountains belong to the Mecsek Tectonic Zone, which is a part of a greater tectonic unit called the Tisza Megaunit (Haas

and Péró, 2004) situated in the southern part of the Carpathian Basin. This is considered as a microplate (Csontos and Vörös, 2004) that has moved southward during the Mesozoic, but originally it belonged to the northern margin of Tethys (Géczy, 1973) and it retained some of its original European faunal character (Vörös and Bujtor, 2020) with increasing influence of the Tethyan faunal realm showed by ammonites (Főzy, 1993; Bujtor, 1993).

Evidence for the intra-plate volcanic activity was provided by Viczián (1966), who reported occurrence of peperite in samples from a core drilled at Kisbattyán (7 km NW from Zengővárkony, Fig. 1) as the first indication for the presence of mixed volcano-sedimentary rocks from the Early Cretaceous in the Mecsek Mountains. This rare mixed rock is a by-product of hot magma intruding into unconsolidated sediment with high water content (Skilling et al., 2002). Viczián (1966, p. 88) also underlined that the volcanic activity started with under-water lava outflows. This was supported by Bilik (1974), who regarded the age of the under-water lava pillows as early to middle Valanginian. K/Ar radiometric dating is roughly in line with this age, but provided a younger range of 105–130 Ma (Harangi and Árva-Sós, 1993). The volcanism equivocally refers to continental crust origin related to a continental rift structure (Embey-Isztin, 1981).

Continental rifting (Harangi, 1994; Huemer, 1997) started in the Late Jurassic and created mixed volcano-sedimentary deposits (Nagy, 1967; Harangi, 1989, 1994) but was not restricted only to the Mecsek Mountains. Volcanic rocks are reported from boreholes located distant from the Mecsek Tectonic unit, as far as 200 km away (Bilik, 1983). The volcanic activity built up a palaeovolcano (Viczián, 1966; Császár and Turnšek, 1996), which had its centre within 20 km from Zengővárkony to the NW (Wein, 1961, 1965).

The Cretaceous sedimentary cycle of the Mecsek Mountains had started with calm, hemipelagic, bathyal sedimentation of fine grained, poorly to unstratified yellowish, Maiolica-type limestone (Márévár Limestone Fm.), deposition of which commenced in the Tithonian and continued through the J/K boundary. The volcanic activity intensified in the Berriasian and reached its acme in the Valanginian and built up the ankaramite–alkaline basaltic basement of volcanic rocks and pillow lavas (Mecsekjánosi Basalt Fm.). These basaltic rocks enveloped completely recrystallized carbonate xenoliths of sedimentary origin (Demény and Harangi, 1996). As the volcanic activity ceased, changing sedimentation started including deposition of coarse-grained conglomerates (the Magyaregregy Conglomerate Fm.) and their heteropic facies (the Hidasivölgy Marl Fm. and Apátvarasd Limestone Fm.). These sediments of different composition were deposited in a hemipelagic basin, and represent the Early Cretaceous from Berriasian (Bujtor et al., 2020) to Barremian (Császár, 2002), but at Zengővárkony only the earliest Hauterivian is proven (Bujtor et al., 2013).

Interpretation of the Zengővárkony palaeoenvironment and its position in a wider geological context was problematic. Before the concept of plate tectonics, there was no attempt to interpret this unique development. A new synthesis of the Cretaceous geological evolution of the region was provided by Császár (1992, 2002) who brought the Early Cretaceous development of the Mecsek Mountains into a broader context. Bércziné et al. (1996) included the Zengővárkony area in a palaeogeographic reconstruction, and pointed out that it was located in a shallower environment (somewhere on the basin slope), but they did not discuss the iron-ore deposit and its genesis.

Bujtor (2007) proposed a genetic model that linked the iron-ore deposit to Late Jurassic–Early Cretaceous volcanism in the region. Jáger and Molnár (2009) reported remnants of black smoker chimneys from Dezső Rezső Valley, however, Jáger et al. (2012) suggested that they were hydrothermal sediments rather than of black smoker origin. Jáger et al. (2012) regarded inter-pillow sediments and rich microcoprolite associations reported from other localities in the Mecsek Mountains as sunk wood-fall colonizations by mud-shrimps. These authors based their interpretation on localities (Kisbattyán, Kisújbánya, Magyaregregy) from the Mecsek Mountains other than Zengővárkony,
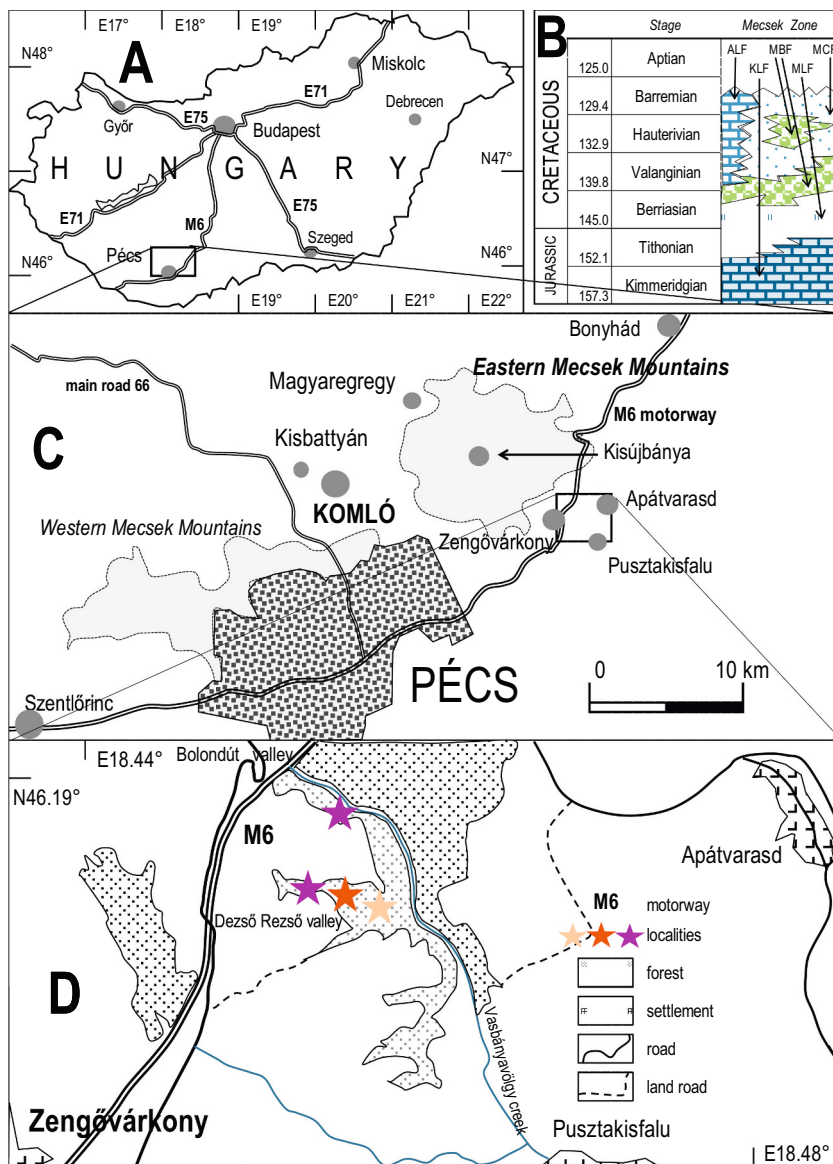
and did not provide biostratigraphic evidence for synchronous timing. New data on SHV (Bell et al., 2016) and more importantly a Recent analogous environment from the shallow hydrothermal vent fields of the Tyrrhenian Sea (Ferretti et al., 2019) delivered the last pieces to complete the interpretation of the enigma of the Zengővárkony fossil environment.

4. Studied sections

Geological evaluation of the iron ore-related formations was contemporaneous with the start of mining activity in the early 1950s. Almost all of the reported localities are connected to the former mining activity in the Zengővárkony region (Molnár, 1961), and are recognized between the parallel Dezső Rezső and Bolondút valleys (Fig. 1) The localities are natural or artificial sections, sampling points on the valley floor and dumps of the ore mine abandoned in 1956.

4.1. Dezső Rezső Valley outcrops and sampling points on the valley floor

4.1.1. Pillow lavas (Mecsekjánosi Basalt Formation, Fig. 2)

On the SE flank of the valley, eroded sections of some fully altered

Fig. 2. Fully altered pillow lavas (Mecsekjánosi Basalt) in the Dezső Rezső Valley (photo 2013). Note the changing colour of the chilled margin. Coordinates: 46.18537°N, 18.45423°E.

pillow lavas are recognized. The size of the pillows varies from 1 to 1.5 m. Eroded chilled margins of the pillows are clearly visible and outlined by a different colour. Pillows indicate submarine volcanic activity.

4.1.2. Geode zones (46.18526°N, 18.45478°E, Fig. 3)

Within a couple of meters toward east from the fully altered pillow lava section, some artificial outcrops were prepared in order to expose the geometry and spatial arrangement of the volcanic pillows. At the root zones, where the pillows were touching each other, some mineral nests were discovered. Regarding the geometry, only one level of pillow lava outflows was recognized.

4.1.3. Hydrothermal deposits (Fig. 4)

These tubular structures are interpreted as the fossilized transport conduits through which the hydrothermal solutions outflowed on the seabed or degassed into the water. Diameter of the tubes varies between 1 and 4 mm. In some cases, not only the tubes, but also their roots are preserved attached to the volcanic basement.

4.1.4. Limestone beds (Apátvarasd Limestone, Fig. 5)

The outcrop of these beds is situated south of the E65 main road, and was described in detail by Bujtor (2006, 2007, 2011, 2012a, 2012b) and by Bujtor et al. (2013). It exposes the Mecsekjánosi Basalt Fm. and the basal Apátvarasd Limestone Fm. The lower part of the section shows the fully altered volcanic pillow lava and hyaloclastite version of the Mecsekjánosi Basalt Fm. Its submarine origin is revealed by vesicles (1–6 mm in diameter) in the chilled margin of the pillows. A fossiliferous limestone bed rests concordant upon the volcanic surface and alternates with the iron ore beds. The locality yielded: large but fragmentary, allochthonous phylloceratid and lytoceratid ammonites (*Lytoceras subfimbriatum*, cf. Bujtor, 2012b); belemnite rostra (Bujtor et al., 2013); a rich but low diversity brachiopod assemblage (Bujtor, 2006, 2011, 2012b; Bujtor and Vörös, 2019; Vörös and Bujtor, 2020); echinoid spines (Bujtor, 2012b); some internal moulds of poorly preserved gastropods. Thin sections of the ammonite body chambers revealed microfaunal elements, such as foraminifera, echinoderm remains, sponge spicules, and rare crustacean microcoprolites. A metasomatized limestone interbedded with volcanic rocks yielded a rich foraminifera assemblage in thin section, but later collecting of the megafauna destroyed that part of the section.

4.2. Bolondút Valley tectonically uplifted block (Apátvarasd Limestone)

The section (Fig. 6) is situated on the western flank of the Bolondút Valley, south of the viaduct of the E65 road, and was introduced by Bujtor (2012a, 2012b). The natural outcrop exposes the basal beds of the Apátvarasd Limestone Fm., a red-coloured unstratified limestone interpreted as a tectonically uplifted block. The limestone is partly metasomatized, cut by fractures and commonly penetrated by white, thin calcite veins. It rarely contains patches of goethite but no macrofauna. In thin sections, the microfaunal elements are abundant crustacean microcoprolites, among which *P. decaochetarius*, *P. tetraochetarius*, and *F. hexaochetarius* predominate. Other crustacean microcoprolite ichnospecies, foraminifera, sponge spicules, and shell fragments of brachiopods are accessorial elements to the fauna. The fragmented blocky structure of this uplifted body is also revealed by the occurrence and incidental accumulation of crustacean microcoprolites at different sample points. The fossil content and richness of microcoprolites were significantly various at different sample points referring to the crushed and blocky structure of the uplifted limestone unit (see for details: Bujtor and Szinger, 2018).

5. Results

The Early Cretaceous volcanic activity penetrated the semi- to unconsolidated limy sediments, and outflowed through the soft sediments and created submarine pillow lavas. Between the pillows several generations of minerals grew; some mineral geodes formed in situ, and provided large mineral assemblages (Fig. 3) of calcite, quartz, sometimes amethyst. Parallel to the pillow lava formation, hydrothermal depositions took place, that created tiny, fasciculated tubular structures through which the hydrothermal solutions travelled, outflowed and degassed. Sulphur stable isotope measurements of these sediments show significantly negative data (Table 2), however the samples were weathered for a long time and that may have altered their original isotope ratios. Most probably the negative sulphur isotope data are linked to former microbial activities, which is supported by the observations by Gugliando et al. (2006) on bacterial mats from recent environments on the Aeolian Islands.

Connected with volcanic activity, a nutrient-rich environment developed in the Zengővárkony SHV field, where a remarkably rich micro- and macrofauna flourished, which is presented in details in the following sections.

5.1. Faunal composition

The fauna of the Zengővárkony SHV environment is listed in Table 3. The assemblages are highly diversified by comprising totally 55 genera
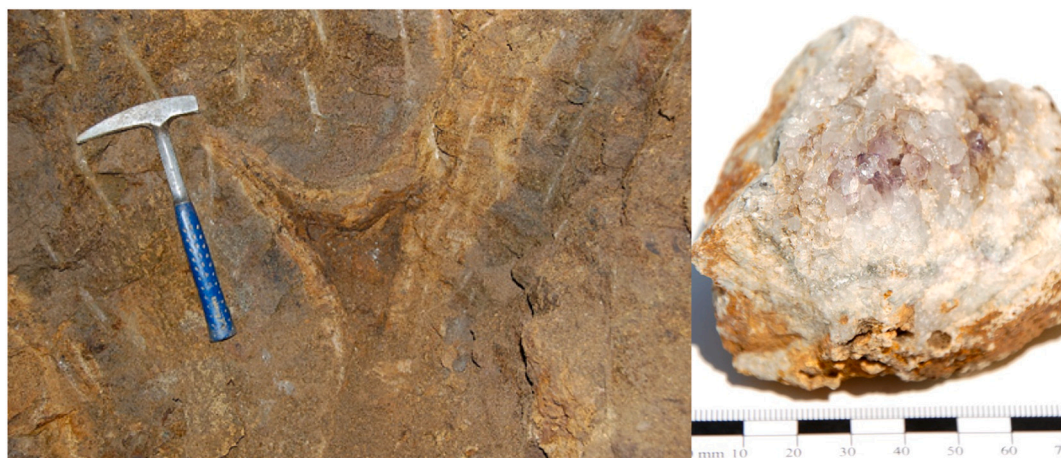

Fig. 3. Pillow lavas and related mineral associations (Mecsekjánosi Basalt) excavated in the Dezső Rezső Valley. Geode zones (left) at the root and junctions between lava pillows (photo 2013) includes calcite, quartz and rarely amethyst. Note the thin and different coloured chilled margins of the attached pillows. Mineral sample (right) collected from the geode zones containing idiomorphic amethyst crystals (Coordinates: 46.18526°N, 18.45478°E).

Fig. 4. Eroded and weathered hydrothermal sediment block collected from the Dezső Rezső Valley floor in 2010. Left photo taken to show the parallel tube arrangement; note the elongated, cylindrical structure of the tubes. Right photo shows a transverse section of the same block. Note the fasciculated structure of the tubes (Sampling point coordinates: 46.18512°N, 18.45528°E).
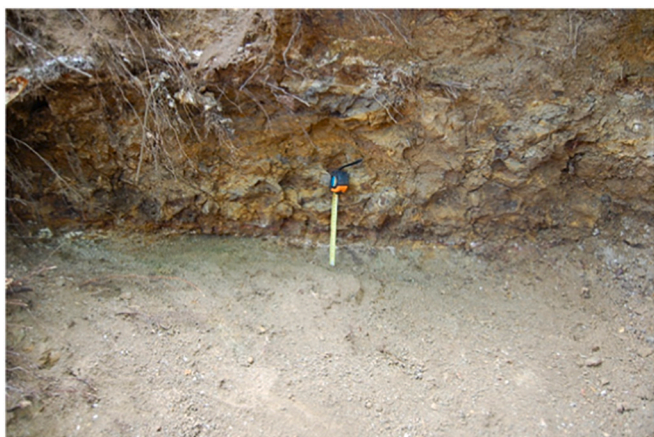

Fig. 5. Section excavated on the NW slope of the Dezső Rezső Valley in 2006. It exposes the Mecsekjánosi Basalt (light greenish grey), and the overlying Apátvarasd Limestone formations. Fossiliferous limestone basal beds (indicated in dark purplish-brown thin bed) resting on the fully altered surface of the ankaramite volcanic body. Coordinates: 46.18545°N, 18.45299°E. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Fig. 6. Tectonically uplifted, fragmented limestone block in the Bolondút Valley (photo 2010). This block is 5 m wide and 2 m tall and the only occurrence of the Apátvarasd Limestone Fm. in the Bolondút Valley. Coordinates: 46.19252°N, 18.45455°E.

or higher taxa and 39 species, which represent 7 animal phyla. 13 taxa from the locality are recorded for the first time in this research and presented in detail in Table 3.

5.1.1. Microfauna

The microfauna of the Zengővárkony environment was previously discussed by Pantó et al. (1955), Palik (1965), Bujtor (2012a, 2012b) and Bujtor and Szinger (2018). A rich and quite diverse Early Cretaceous shallow-marine foraminiferal fauna is reported from the Mecsek Mountains by Vadász (1935). It comprises 35 taxa (Szinger, 2008), and is interpreted to be derived from an atoll environment (Császár and Turnšek, 1996) formed around a volcanic edifice. From the iron ore deposits, the only recorded foraminifera is *Globigerina* sp. reported by Fülöp (in Hetényi et al., 1968).

Dezső Rezső Valley section (Fig. 5) covering the contact between the Mecsekjánosi Basalt and Apátvarasd Limestone formations provided the most diverse microfauna. The Apátvarasd Limestone Formation is basically a biomicritic wackestone and rarely a packstone-textured limestone. The micritic and rarely microsparitic matrix contains variably sized allochemical components with prevailing bioclasts. The limestone is frequently impregnated with ferrigenous material and sometimes goethite flakes are present. Volcanic particles (in some cases plagioclase needle-like minerals) are clearly visible in the matrix. It is also thoroughly penetrated by thinner (0.5–1.5 mm) or thicker (2–5 mm) white calcite veins, which probably belong to several generations of calcite. The numerous thick veins give the rock a breccia-like appearance in thin section. The most abundant bioclasts in the thin sections are sponge skeletal fragments and spicules, but echinoderm and molluscan skeletal fragments, foraminifera, and ostracod(?) remains are also present. A few macrofaunal elements including ammonites, belemnite rostra, and brachiopods were also observed. Frequent traces of bioerosion are typical for these fragments.

5.1.1.1. Foraminifera.
Foraminifera provided the majority of taxa per phylum with 21 genera recognized from thin sections. Nine foraminiferal genera are first recorded by us and reported herein from the Cretaceous of the Mecsek Mountains (Table 2). The foraminiferal assemblage is diverse, and dominated by benthic taxa.

5.1.1.2. Crustacean microcoprolites.
Crustacean microcoprolites from the Zengővárkony locality (Fig. 8.1–8.2) are discussed by Sztrókay (1952), Pantó et al. (1955), Palik (1965), Bujtor (2012a), Bujtor and Szinger (2018). The fauna comprises 9 ichnospecies, which appear to be the most diverse decapod microcoprolite ichnofauna of the Mesozoic reported from a single locality. This fauna is not only diverse, but also
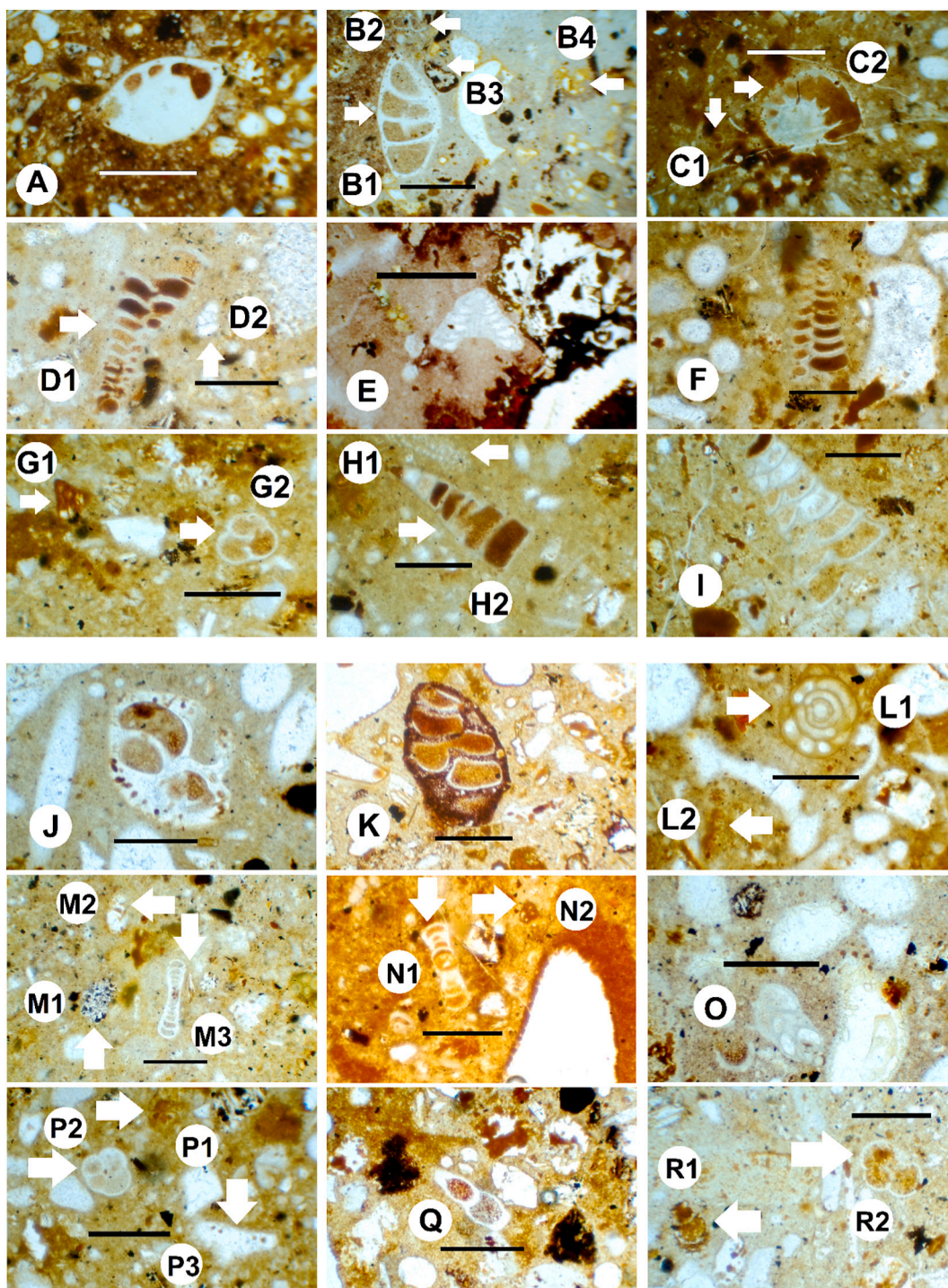
Fig. 7. Thin sections showing species composing the rich and diverse foraminiferal assemblage of the Zengővárkony SHV. A: *Epistomina* sp. B1: *Reinholdella*? sp., B2: *Lagenina* gen. et sp. ind., B3: *Ammobaculites*? sp., B4: *Globigerinina* gen. et sp. ind. C1: *Hedbergella* sp.; C2: *Glavelinella* sp. aff. *brielensis*, D1: *Bolivinella* sp., D2: *Praebulimina* sp. E: *Spirotrocholina* sp. aff. *icerta*. F: *Bolivinella* sp. G1: *Trocholina* sp. aff. *trocholinaeformis*, G2: *Hedbergella* sp. H1: *Cylindrotrocholina* sp. aff. *excelsa*, H2: *Nodosaria* sp. I: *Bolivinella* sp. J: *Reinholdella*? sp. K: *Reophacella* sp. L1: *Meandrospira* sp. aff. *washitensis*, L2: *Reophax* sp. M1: *Haplophragmoides*? sp., M2: *Praebulimina* sp. aff. *carseyae*, M3: *Spirillina* sp. [microspheric]. N1: *Spirillina* sp. [macrospheric], N2: *Trocholina* sp. aff. *trocholinaeformis*. O: *Praebulimina* sp. aff. *carseyae*. P1: *Haplophragmoides*? sp., P2: *Hedbergella* sp., P3: *Trocholina* sp. aff. *trocholinaeformis*. Q: *Nodosaria* sp., R1: *Ammodiscus*? sp., R2: *Hedbergella* sp. Scale bars indicate 500 μm.

very rich in individuals as discussed by Bujtor (2012a). The most abundant species are: *Favreina hexaochetarius*, *Palaxius tetraochetarius* and *P. decaochetarius*. These abundant microcoprolites represent all development phases from juvenile to adult (Bujtor, 2012a).

5.1.1.3. Sponge spicules. Sponge spicules were recorded by Bujtor and

Szinger (2018). Diactine-type cricorrhabd spicules are abundant (Fig. 8.3–8.5), but rhax types also occur. These are transported fragments, in some cases corroded. Diactine-type cricorrhabd spicules are observed frequently inside brachiopod shells during serial sectioning. Procriccotriaene spicules (Fig. 8.5) are reported for the first time from the Mecsek Mountains.

Table 2

Sulphur stable isotope measurements from hydrothermal sediment samples, Dezső Rezső Valley.

Sample	Sulphur concentration (%S)	δ^{34}S %CDT
ZGV-SM 1	0.49	−40.39
ZGV-SM 2	0.64	−36.84
ZGV-SM 3	0.14	−20.84
ZGV-SM 4	0.06	−23.97
ZGV-SM 5	0.48	−33.96
ZGV-SM 6	0.27	−28.16
ZGV-SM 7	0.09	−19.27

Samples are taken from the weathered remnants of hydrothermal sediments collected from the valley floor. CDT: Canyon Diablo Troilite standard.

5.1.1.4. Lithistid Demospongiae. In many cases the specimens are dis-articulated fragments (Fig. 8.6), and may belong to Pleromidae according to A. Pisera (personal comm.).

5.1.1.5. Hexactinellid sponges. Počta (1886) reported *Sporadopyle* species from Bathonian of the Mecsek Mountains. The specimen recorded here (Fig. 8.7) resembles *Sporadopyle* sp. revealed during serial sectioning inside a terebratulide brachiopod.

5.1.2. Macrofauna

The macrofauna from the Dezső Rezső valley comprising nektonic and benthic taxa, was collected from the dumps of the abandoned ore mine, and was first reported by Fülöp (in Hetényi et al., 1968, p. 32) includes: *Rhynchonella malbosi* Pictet, *Rhynchonella sparsicostata* Oppel, *Terebratula* aff. *salevensis* Loriol, *Pleurotomaria* sp., *Neolissoceras grasianum* d'Orbigny, *Olcostephanus astierianus* d'Orbigny, *Neocomites neocomiensis* d'Orbigny, *Duvalia dilatata* Blainville, *Cidaris* sp., *Torynocrinus* sp. This fauna was never described nor illustrated. Later collections confirmed the presence of these taxa except for *Olcostephanus* and *Neocomites*. Bujtor, Janssen, Verreussel (Bujtor et al., 2013), and Vörös (Vörös and Bujtor, 2020) visited the old collection of the MGSH and partly published the fauna collected by Fülöp (in Hetényi et al., 1968). The macrofauna is dominated by a diverse and greater-than-usual brachiopod assemblage of 147 specimens.

5.1.2.1. Ammonites. Ammonites were first reported by Fülöp (in Hetényi et al., 1968) from the dumps of the abandoned ore mine and include: *Neolissoceras grasianum* (d'Orbigny, 1841), *Olcostephanus astierianus* (d'Orbigny, 1840), and *Neocomites neocomiensis* (d'Orbigny, 1841). These findings are however not fully supported by our results. Bujtor (2012b) reported a *Lytoceras subfimbriatum* (d'Orbigny) and a *Neolissoceras grasianum,* while Fig. 9.1 illustrates a reworked, partly dissolved, badly preserved lytoceratid ammonite species. The ammonite preservation is poor as peripheral parts of the fossils are usually corroded, dissolved and fragmentary. The biggest ammonite finding is a fragment belonging to a *Lytoceras* species with circular cross section and 8 cm whorl breadth.

5.1.2.2. Belemnites. Belemnites reported by Fülöp (in Hetényi et al., 1968) and Bujtor et al. (2013, p. 144) include: *Adiakritobelus* (?) sp., *"Belemnites pistilliformis"* Raspail, 1829, *Duvalia* ex gr. *dilatata* (Blainville, 1827), *Hibolithes* ex gr. *subfusiformis* (Raspail, 1829), *Pseudobelus* sp.

5.1.2.3. Nautilids. Bujtor et al. (2019) were the first to report the nautiloidea *Eutrephoceras* ex gr. *boissieri* from the Cretaceous of Zengővárkony, but from a section outside the SHV facies. From the Dezső Rezső Valley locality, Bujtor (2006) mentioned finding a nautiloid specimen, which is described below.

Order Nautilida Agassiz, 1847

Table 3

Faunal composition of the Zengővárkony upper Valanginian–lower Hauterivian SHV.

Higher taxa	Genus/Species	Reference
Foraminifera	[1] *Ammobaculites?* sp.	*this paper*
	[2] *Ammodiscus?* sp.	*this paper*
	[3] *Bolivinella* sp.	*this paper*
	[4] *Cylindrotrocholina* sp. aff. *excelsa* (Ruggieri and Guinta, 1965)	*this paper*
	[5] *Epistomina* sp.	Bujtor and Szinger, 2018, *this paper*
	[6] *Gavelinella* sp. aff. *brielensis* Malapris-Bizouard, 1974	*this paper*
	[7] *Globigerinina* gen. et sp. ind.	*this paper*
	Glomospira sp. = *Meandrospira* sp. aff. *washitensis* Loeblich and Tappan, 1946	Bujtor and Szinger, 2018
	[8] *Glomospira* cf. *gordialis* = *Meandrospira* sp. aff. *washitensis* Loeblich and Tappan, 1946	Bujtor and Szinger, 2018
	[9] *Haplophragmoides?* sp.	*this paper*
	[10] *Hedbergella* sp.	Bujtor and Szinger, 2018; *this paper*
	[11] *Lagenina* gen. et sp. ind.	*this paper*
	[12] *Lenticulina* sp.	Bujtor and Szinger, 2018, *this paper*
	Meandrospira sp. aff. *washitensis* Loeblich and Tappan, 1946	*this paper*
	[13] *Nodosaria* sp.	Bujtor and Szinger, 2018, *this paper*
	Praebulimina? sp.	*this paper*
	[14] *Praebulimina* sp. aff. *carseyae* (Plummer, 1931)	*this paper*
	[15] *Reinholdella?* sp.	*this paper*
	[16] *Reophacella?* sp.	*this paper*
	[17] *Reophax?* sp.	*this paper*
	[18] *Repmanina* [=*Glomospira*] sp. aff. *charoides* (Jones and Parker, 1860)	*this paper*
	[19] *Spirillina* sp. (micro- and macrospheric)	Bujtor and Szinger, 2018, *this paper*
	[20] *Spirotrocholina* sp. aff. *incerta* (Svetovostokova In Myatlyuk, 1953)	*this paper*
	Trocholina sp.	Bujtor and Szinger, 2018
	[21] *Trocholina* sp. aff. *trocholiniformis* (Dieni and Massari, 1966)	*this paper*
Anthozoa	[22] *Discocoenia* sp. aff. *bononiensis* Tomes, 1884	Kolosváry, 1956, 1959
	[23] **Prototrochocyathus valanginicus Kolosváry, 1956**	Kolosváry, 1956, 1959, 1961
	[24] **Thecocyathus mecsekensis Kolosváry, 1956**	Kolosváry, 1956, 1959, 1961
Porifera	[25] diactine-type criccorhabd spicules	Bujtor and Szinger, 2018, *this paper*
	[26] anactine-type rhax spicules	Bujtor and Szinger, 2018
	[27] procriccotriaene spicules	*this paper*
	[28] lithistid demospongiae	Bujtor and Szinger, 2018, *this paper*
	[29] *Sporadopyle* sp.	*this paper*
Arthropoda (microcopr.)	[30] *Favreina belandoi*	Bujtor and Szinger, 2018
	[31] **Favreina dispentochetarius Palik, 1965**	Palik 1965, Bujtor 2012a
	[32] **Favreina hexaochetarius Palik, 1965**	Palik 1965, Bujtor and Szinger, 2018

	[33] *Favreina octoochetarius* **Palik, 1965**	Palik 1965
	[34] *Palaxius darjaensis* Silantiev in Senowbari-Daryan and Silantiev, 1991	Bujtor 2012a
	[35] *Palaxius tetraochetarius* **Palik, 1965**	Palik 1965, Bujtor 2012a, Bujtor and Szinger, 2018
	[36] *Palaxius decaochetarius* **Palik, 1965**	Palik 1965, Bujtor 2012a, Bujtor and Szinger, 2018
	[37] *Palaxius triochetarius* **Palik, 1965**	Palik 1965, Bujtor 2012a
	[38] *Palaxius salataensis* Brönnimann, Cros and Zaninetti, 1972	Bujtor 2012a
Mollusca, Ammonitina	[39] *Lytoceras subfimbriatum* d'Orbigny, 1841	Bujtor 2012b
	[40] *Phylloceras* sp. ind.	*this paper*
	[41] *Neolissoceras grasianum* (d'Orbigny, 1841)	*this paper*
Mollusca, Belemnoidea	[42] "*Belemnites pistilliformis*" Raspail, 1829	Bujtor et al. 2013
	[43] *Adiakritobelus*? sp.	Bujtor et al. 2013
	[44] *Hibolithes* ex gr. *subfusiformis* (Raspail, 1829)	Bujtor et al. 2013
	[45] *Duvalia* ex gr. *dilatata* (Blainville, 1827)	Bujtor et al. 2013
	[46] *Pseudobelus* sp.	Bujtor et al. 2013
Mollusca, Nautiloidea	[47] *Eutrephoceras boissieri* (Pictet, 1866)	*this paper*
Mollusca, Gastropoda	[48] Gastropoda gen. et sp. ind.	*this paper*
Brachiopoda	[49] *Fortunella* cf. *fortunae* Calzada, 1985	Vörös and Bujtor, 2020
	[50] *Lacunosella hoheneggeri* (Suess, 1858)	Bujtor 2006, 2007, Vörös and Bujtor, 2020
	[51] *Monticlarella remesi* Nekvasilová, 1977	Vörös and Bujtor, 2020
	[52] *Moutonithyris moutoniana* (d'Orbigny, 1847)	Bujtor 2006, Vörös and Bujtor, 2020
	[53] *Karadagella* ? aff. *bilimeki* (Suess, 1858)	Vörös and Bujtor, 2020
	[54] *Nucleata veronica* Nekvasilová, 1980	Bujtor 2006, Vörös and Bujtor, 2020
	[55] *Dictyothyropsis vogli* **Bujtor and Vörös, 2019**	Bujtor and Vörös, 2019, *this paper*
	[56] *Zittelina hofmanni* **Bujtor and Vörös, 2019**	Bujtor and Vörös, 2019, *this paper*
	Smirnovina sp.	Bujtor and Vörös, 2019
	[57] *Smirnovina ferraria* **Bujtor and Vörös, 2019**	Bujtor and Vörös, 2019, *this paper*
Echinodermata	[58] *Balanocidaris rysacantha* (Gras, 1848)	Szörényi 1961, 1965; Bujtor 2012b
	Cidaris cherennensis Savin, 1905	Szörényi 1961, 1965; Bujtor 2012b
	[59] *Pseudocidaris clunifera* (Agassiz, 1836)	Szörényi 1961, 1965; Bujtor 2012b
	[60] *Plegiocidaris* sp.	Bujtor, 2013
	[61] *Saccocoma* sp.	*this paper*
	[62] *Torynocrinus (Torynocrinus) granulatus* (Jaekel, 1891)	Szörényi, 1959
	[63] *Torynocrinus (Labiocrinus) labiatus* **Szörényi, 1959**	Szörényi, 1959
	[64] *Phyllocrinus hungaricus* **Szörényi, 1959**	Szörényi, 1959
	phyllocrinid cup	*this paper*

Species/genera indicated by bold are reported for first time from the Zengővárkony environment as new taxa. Taxa in grey shaded boxes are recorded for the first time from the Mecsek Mountains. Earlier foraminifera records are based on Vadász (1935), Balla and Bodrogi (1993), and Szinger (2008). Numbers in brackets refer to the irrespective species, genus or higher taxa reported from the locality.

Superfamily Nautiloidea De Blainville, 1825

Family Nautilidae De Blainville, 1825

Subfamily Nautilinae De Blainville, 1825

Genus *Eutrephoceras* Hyatt, 1894

Type species: Nautilus dekayi Morton, 1834

Eutrephoceras boissieri (Pictet, 1866)

Fig. 9.2–9.4.

1866 *Nautilus Boissieri* Pictet – Pictet, p. 58, pl. 8. figs. 4a–c.

1956 *Eutrephoceras boissieri* (Pictet) – Kummel, p. 379, text-fig. 13b.

1960 *Eutrephoceras boissieri* (Pictet) – Nagy, p. 205.

1971 *Eutrephoceras*? *boissieri* (Pictet) – Nagy, p. 15. [in lit.]

v 2019 *Eutrephoceras* ex gr. *boissieri* (Pictet) – Bujtor et al., p. 21, figs. 3a–b.

Material. One well preserved juvenile specimen, internal mould from ferruginous limestone bed (Apátvarasd Limestone Formation).

Dimensions.

Specimen	D	Wb	Wh	U	Wb/Wh	Wh/D	U/D
ZGV-1/36	36.3	26.1	25.0	3.7	1.04	0.69	0.10

Description. Small sized, fairly well-preserved specimen representing phragmocone. Seven septae seen. Conch inflated, cross section sub-circular, slightly depressed. Umbilicus narrow and shallow. Flanks convex, inflated. Venter smooth, rounded. Suture simple, shallow umbilical lobe. Aperture, sculpture, constrictions not seen.

Remarks. This is a juvenile specimen. Besides its small size the lack of sutural crowding confirms this, too. A contemporaneous species (*E. uitenhagense* Spath, 1930) is reported by Cooper (1981, p. 357) from the late Valanginian of South Africa. Its cross section is similar, but the Zengővárkony specimen has a different suture: there is an initial sinus, and farther around the venter it becomes less prorsiradiate. Its cross section is somewhat wider than the type.

Distribution. The species has a wide stratigraphic distribution from the Hauterivian (possibly even from the Valanginian) to the Campanian. Geographically, it has been reported from France, Switzerland, Algeria, and Hungary (Gerecse Mountains, Transdanubian Range, and the Mecsek Mountains).

Benthic macrofauna

Benthic macrofauna were collected from the dumps of the abandoned ore mine by Fülöp reported in Hetényi et al. (1968). It is dominated by brachiopods, but some crinoids, echinoids and a few poorly
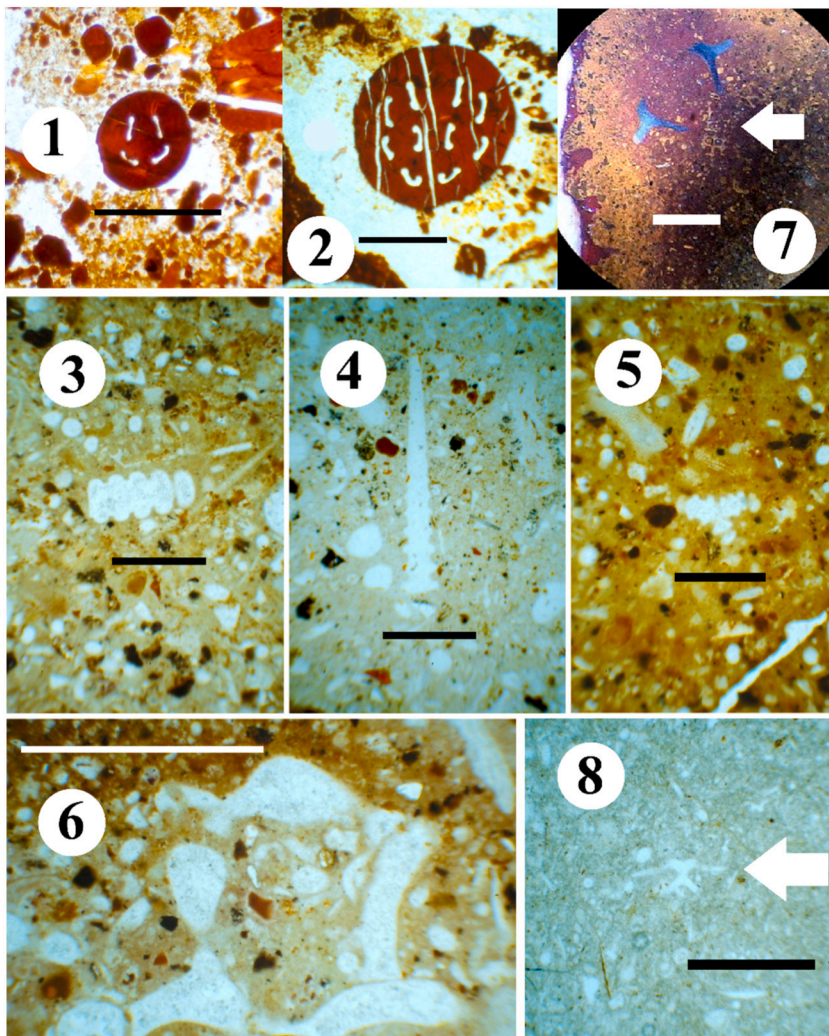
Fig. 8. Microfossils from the Zengővárkony SHV environment (Apátvarasd Limestone Formation). 1, 2. Examples of abundant crustacean microcoprolites represented by 1) *Palaxius tetraochetarius* Palik, 1965 and 2) *Palaxius decaochetarius* Palik, 1965. These microcoprolites are occasionally present in rock-forming quantity. Samples from the Bolondút Valley section (Fig. 6). 3–5. Sponge spicules in thin sections from limestone bed (Apátvarasd Limestone, Zengővárkony, Dezső Rezső valley). 3) short, stubby, and 4) elongated, slender diactine-type cricorrhabd sponge spicules. 5) Procriccotriaene sponge spicule. Samples from the Dezső Rezső Valley section (Fig. 5). 6) Lithistid Demospongiae in thin section from limestone bed (Apátvarasd Limestone, Zengővárkony, Dezső Rezső valley. Fig. 5). 7) *Sporadopyle* sp. from a brachiopod shell (*Moutonithyris moutoniana*, from limestone bed, Apátvarasd Limestone, Zengővárkony, Dezső Rezső Valley; specimen PAL.2019.259.1). Photograph taken during serial sectioning with mobile phone camera. Blue coloured, triangular, spiny shaped structures are the fossilized remains of the crura. Arrow indicates the hexactinellid sponge remain. 8) *Saccocoma* sp. in thin section from the uplifted block in the Bolondút Valley section (Fig. 6); arrow indicates the specimen. Scale bars indicate 0.5 mm (Fig. 1–6 and 8); 2 mm (Fig. 7). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

preserved gastropods were also collected.

5.1.2.4. Anthozoans. The anthozoans collected by József Fülöp during the active mining period (1953–1956), were determined by Kolosváry (1956, 1959, 1961) from thin sections. A 4–6 mm long solitary coral, *Discocoenia* cf. *bononiensis* Tomes, 1884 was described from the basal beds of the iron ore body (Kolosváry, 1956, fig. 1–4; 6–7). From the same beds a new species of Cariophyllidae, *Thecocyathus mecsekensis* n. sp. was reported (Kolosváry, 1956, p. 206, fig. 5, 8). Kolosváry continued the research and reported a new genus and new species of Cariophyllidae: *Prototrochocyathus valanginicus* n. gen. et n. sp. (Kolosváry, 1959, p. 126, fig. 5–8). We did not find these fossils during field work or in thin sections.

5.1.2.5. Brachiopods. Brachiopods were reported by Fülöp (in Hetényi et al., 1968), Bujtor (2006, 2007, 2011), Bujtor and Vörös (2019), and Vörös and Bujtor (2020). The majority of these brachiopods reveal significant size increase compared to dimensions at their type localities as demonstrated by Bujtor (2006) and Bujtor and Vörös (2019). The average size increase varies between 26 and 71% compared to populations from other localities. Fig. 9.5–9.6 demonstrates this significant size increase, which typifies the Zengővárkony SHV system. A rare species (*Dictytothyropsis vogli*) is shown on Fig. 9.7.

5.1.2.6. Crinoids. Crinoids are reported by Szörényi (1959, 1961, 1965), who erected a new species *Phyllocrinus hungaricus,* a new

subgenus *Labiocrinus* and a new species *Torynocrinus (Labiocrinus) labiatus* from the Zengővárkony locality. *Phyllocrinus hungaricus* n. sp. (Szörényi, 1959) pl. IV. fig. 25–28), is however a nomen nudum. A *Phyllocrinus* sp. is shown on Fig. 9.8. *Saccocoma* sp. was also recognized in thin sections (Fig. 8.8).

5.1.2.7. Echinoids. Echinoids are reported by Szörényi (1961, 1965), while Bujtor (2012b, 2013) reported echinoid spines and a *Plegiocidaris* sp. ind. body fossil, too. *Balanocidaris rysacantha* (Gras, 1848), *Pseudocidaris clunifera* (Agassiz, 1836) and *Cidaris cherennensis* Savin, 1905 (Fig. 9.9–9.12) are the echinoid spines associated with other megafossils and collectible on the floor of the Dezső Rezső Valley. It is noteworthy that according to Szörényi (1965, p. 300) *P. cherennensis* Savin, 1905 is an objective junior synonym of *P. clunifera* (Agassiz, 1836).

5.1.2.8. Gastropods. Although Fülöp (in Hetényi et al., 1968) referred to *Pleurotomaria* sp., the three collected gastropod specimens have such poor preservation that their generic assignment has not been possible. Fig. 9.13 depicts a worn, tiny gastropod internal mould that only indicates the presence of its class in the assemblage.

5.2. Similar faunas

Faunal composition of the Zengővárkony assemblage is similar to that of the Oxfordian – Kimmeridgian environments of the Bétic Cordilleras (Olóriz et al., 2006) with some differences:
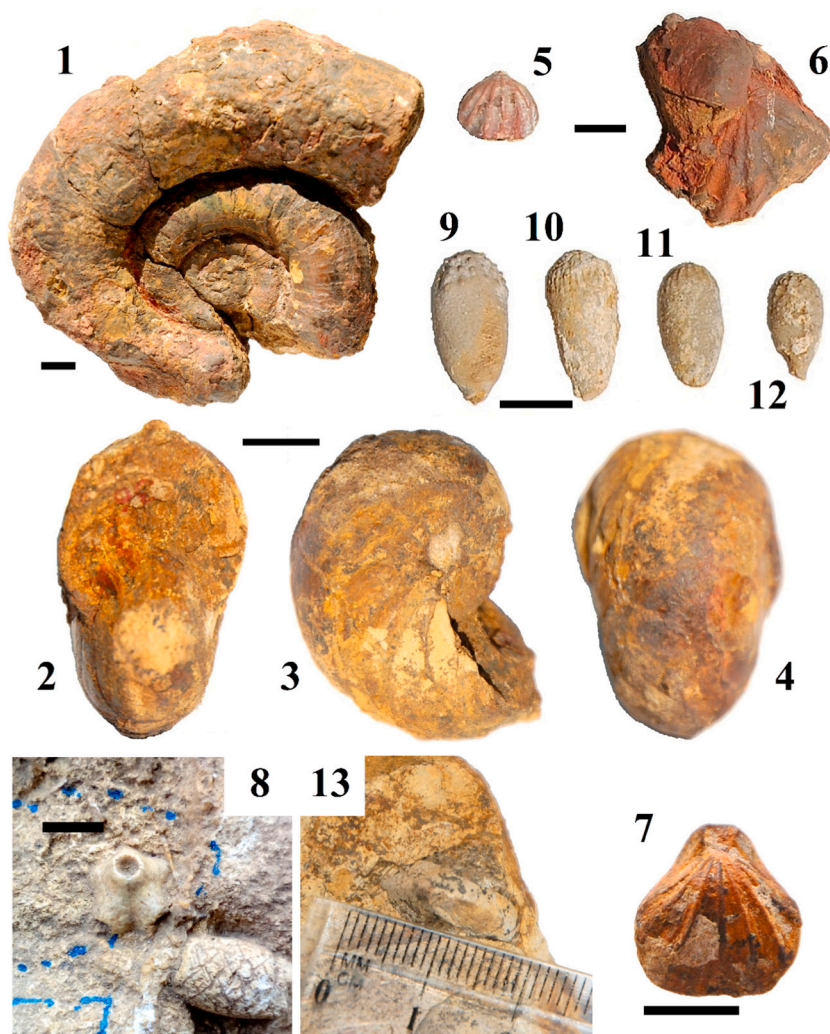
Fig. 9. Macrofaunal elements from the Zengővárkony SHV environment (Apátvarasd Limestone Formation). 1) *Lytoceras subfimbriatum* (d'Orbigny, 1841) from the Dezső Rezső Valley section, basal, red, ferruginous bed (Apátvarasd Limestone, Fig. 5). Lateral view. Note the reworked, fragmentary state and the fine manganese encrustation of the specimen. 2–4. *Eutrephoceras boissieri* (Pictet, 1863–1868) specimen MGSH. ZGV-1/36 from Dezső Rezső Valley, basal, red, ferruginous bed (Apátvarasd Limestone, Fig. 5). 2. apertural view; 3. lateral view; 4. ventral view; 5–6. Remarkable size increase of the brachiopod species *Lacunosella hoheneggeri* (Suess, 1858) from different environments. 5) specimen HNHM INV 2019.2814 from Zengővárkony, lower Berriasian, Dezső Rezső Valley, Kisújbánya Mészkő Formation (Bujtor et al., 2020); 6) specimen 99öu02/V-912 from limestone bed (Fig. 5), upper Valanginian–lowermost Hauterivian, Dezső Rezső Valley, Apátvarasd Limestone Formation from hydrothermally influenced sediments. 7) *Dictyothyropsis vogli* Bujtor and Vörös, 2019; specimen HNHM PAL 2019.2.1. 8. Crinoids from the Zengővárkony SHV environment. Left: weathered crinoid (? *Phyllocrinus* sp. ind.) cup from the Dezső Rezső valley floor; 9–12. Weathered specimens of echinoid spines of *Pseudocidaris clunifera* (Agassiz, 1836) collected from the Dezső Rezső Valley floor; 13. Gastropoda gen. et sp. ind. From Dezső Rezső Valley, basal, red, ferruginous bed, Apátvarasd Limestone (Fig. 5). Scale bars indicate 1 cm. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(1) No bivalves (either infaunal or epifaunal) are recorded at Zengővárkony.

(2) The Zengővárkony fauna reveals a mixture compared to the faunas of well-defined assemblages of different lithofacies representing different depths and environments in the Bétic Cordilleras (Olóriz et al., 2006, fig. 15).

(3) No irregular echinoids are recorded at Zengővárkony, although soft substrate is present.

(4) Only the Zengővárkony SHV fauna shows significant size increases in different fossil groups (Figs. 10, 11).

The typical size increase in some brachiopod populations at Zengővárkony (Fig. 10) is already reported (Bujtor, 2006, 2007; Vörös and Bujtor, 2020), but new evidence for size expansion is provided by echinoids (Fig. 11). The most diverse echinoderm fauna (including crinoids and echinoids) from the Lower Cretaceous in Hungary comes from Borzavár (Zirc, Bakony Mountains) reported by Sieverts-Doreck (1961) and Szörényi (1965). The fauna includes echinoid spines of species also occurring in Zengővárkony. Therefore, biometric comparisons were undertaken, that revealed a significant size increase of the average diameter of the spines of both compared species in the Zengővárkony material: the *Balanocidaris rysacantha* population revealed 154%, while the *Cidaris cherenensis* population showed 141% average diameter increases. These data also support the effect of the nutrient-rich SHV environment, where these animals attained larger size.

As demonstrated above, populations of both brachiopods and echinoids typical of the Zengővárkony SHV show substantial size increases. The earlier observations of Bujtor (2006, 2007) and Bujtor and Vörös (2019) on the general size increases of brachiopod populations of Zengővárkony, are now supported by an additional fossil group; the echinoid spine assemblages showing a similar general size increase.

6. Discussion

The peculiar fauna from Zengővárkony and its palaeoenvironment remained enigmatic without recent counterpart for decades. Bujtor (2007) supposed a possible palaeoenvironment, without a modern counterpart however, it was insufficient to connect it with the associated volcanic regime involving iron ore formation. But now, this enigma appears to be resolved by recognition of the first recent analog to the Zengővárkony fossil system. The analogue is a shallow marine environment where volcanic activity is taking place on thinned continental crust at comparable water depth reported by Ferretti et al. (2019). This environment is recorded from the Aeolian Island Arc of the Tyrrhenian Sea (Italy), where it is developed at a water depth of 100–150 m between active volcanoes (Stromboli and Lipari) around Panarea Island. The environment of the Panarea locality reveals similar microfauna and more surprisingly, it offers a plausible solution for the iron-ore formation at Zengővárkony. At the supposed analogouse water depth, the loose sediment is constituted by dominant ooidal ironstone grains and various skeletal elements as sponge spicules, foraminifera, bryozoans, gastropods and ostracodes (Ferretti et al., 2019, fig. 2). Note that
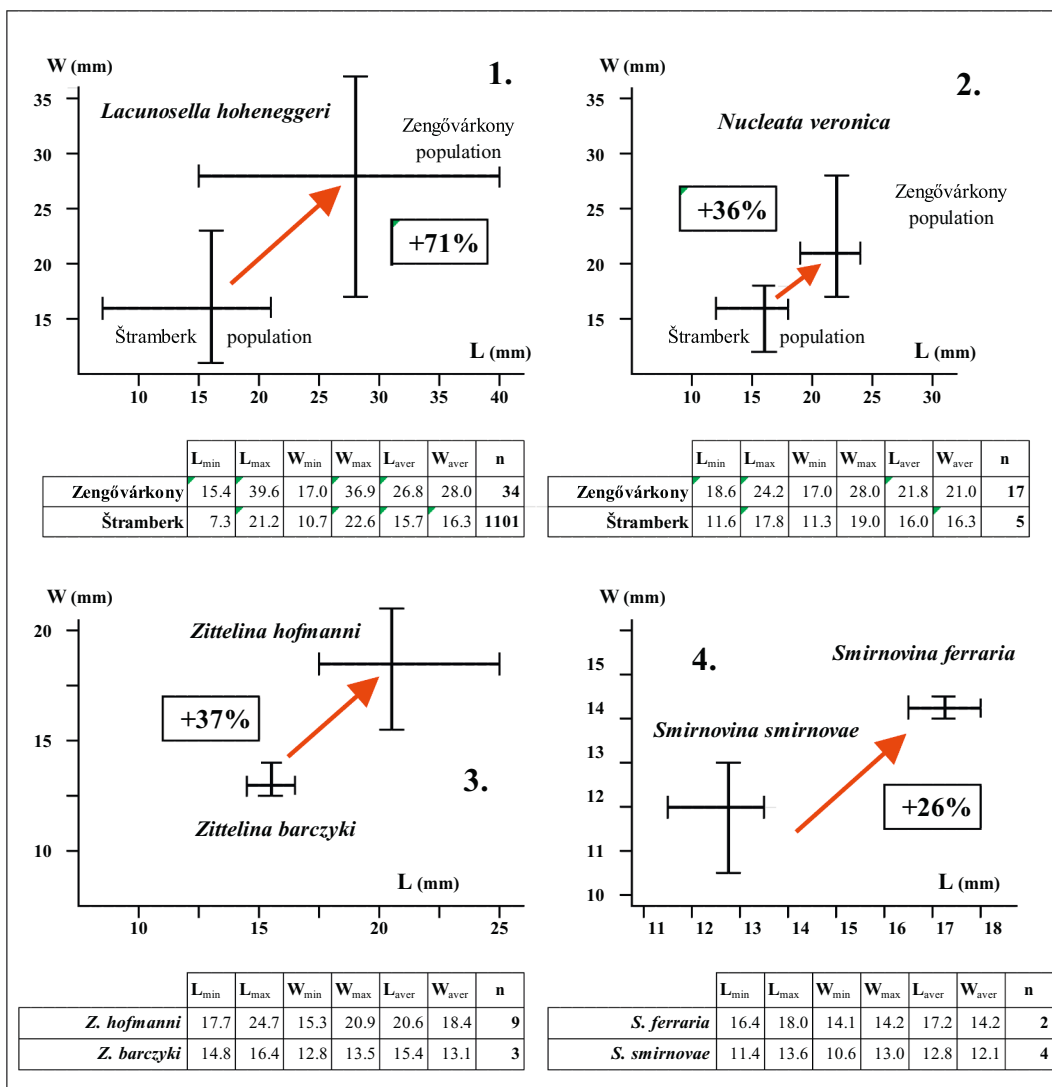
Fig. 10. Significant size increases of brachiopod populations of the Zengővárkony SHV (Apátvarasd Limestone Formation). Regarding *Lacunosella hoheneggeri* and *Nucleata veronica* the dimensions of the Zengővárkony populations are compared to those of the type species populations. Regarding *Zittelina hofmanni* and *Smirnovina ferraria,* their closest sister-species populations. Figure after Bujtor and Vörös (2019).
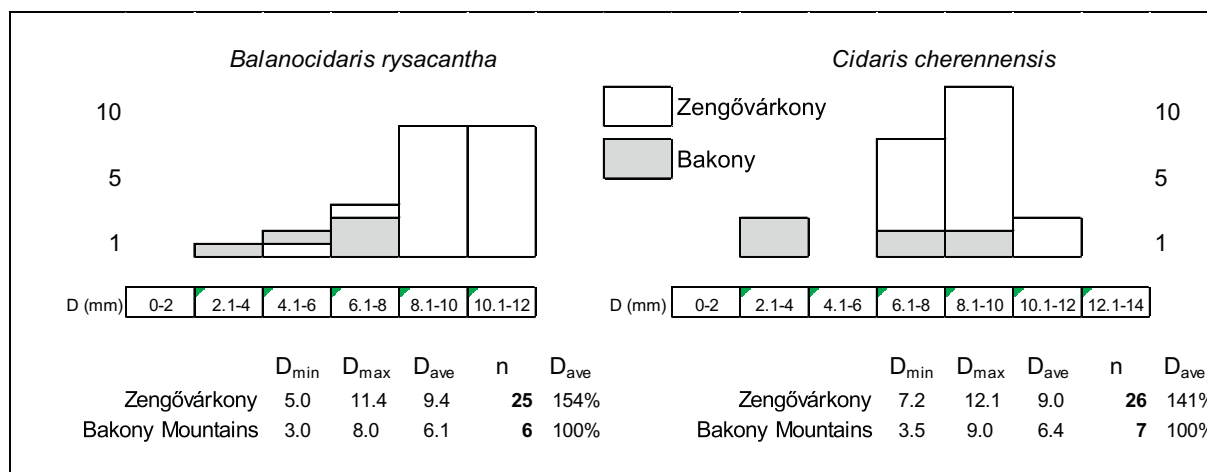

Fig. 11. Different echinoid spine populations from Zengővárkony (Apátvarasd Limestone Formation) compared to those of a locality in the Bakony Mountains. Bakony data from Szörényi (1965). Material used: Zengővárkony specimens MGSH Eb/688–692; Bakony Mountains specimens, MGSH Eb/650–656, Eb/687, Eb/693–694, Eb/699–700, and Eb/781; and the present research. The average dimensions (diameters) of different echinoid spine populations in the Zengővárkony SHV show significant size increase compared to size values from normal marine environments of the Cretaceous in the Bakony Mountains.

bivalves are also missing from this Recent Mediterranean environment. Brachiopods are absent too, however in Recent environments, brachiopods are cryptic constituents of shallow marine hydrothermal field faunas (Cocito et al., 2000), but played an important role at Zengővárkony.

6.1. Interactions between faunal elements

During serial sectioning of brachiopod specimens collected from the limestone bed (Fig. 5), the most astonishing observation was the varied and occasionally rich entombed microfauna inside the shells. Brachiopod shells very rarely preserve entombed fossils; therefore, their recognized richness requires closer analysis to understand the process of entombment. Fig. 12 shows the fossilized microfauna revealed internally during serial sectioning.

Many constituents of different fossil groups were recognized inside

the brachiopod shells and drawn: foraminifera (the least surprising), diactine type cricorrhabd sponge spicules, lithistid demospongiae, echinoderms, and gastropods. It is noteworthy, that only specimens belonging to the Terebratulida revealed the rich internally preserved microfauna, while specimens belonging to the Rhynchonellida did not contain any observed microfossil remains. Table 4 summarizes the entombed microfossils found within the serially ground brachiopod specimens.

In order to understand the significant differences between the entombed faunal contents of rhynchonellide and terebratulide brachiopods, their different shell structure may help as discussed by Vörös (2010). The endopuncta in terebratulide shells were possibly a helpful adaptation to the increasingly diverse and "crowded" nutrient-rich resources close to the hydrothermal upwellings in the Zengővárkony SHV. These structures excluded the durophagous and shell-drilling brachiopod enemies, while the microfossils more easily entered into
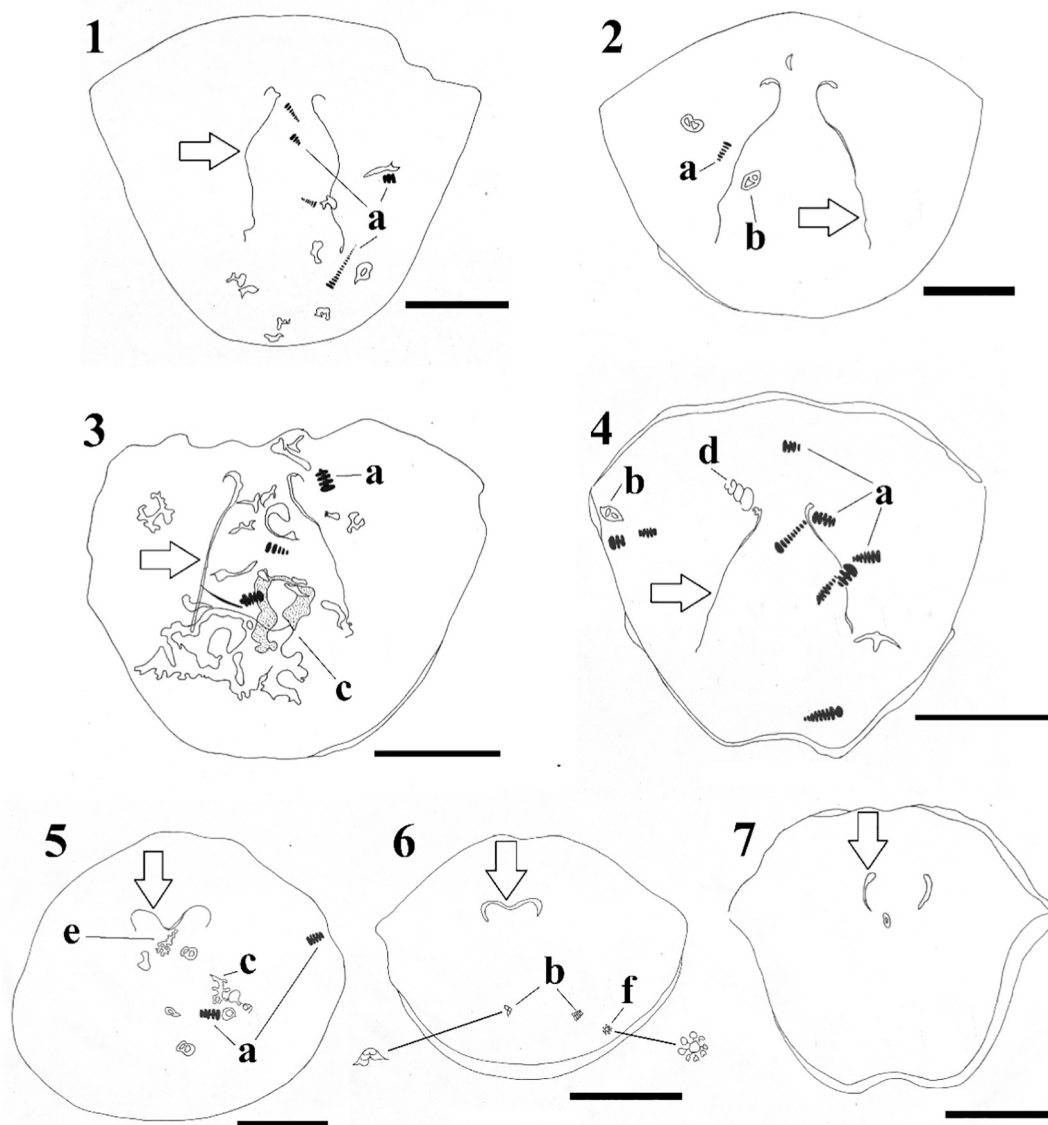

Fig. 12. Combined transverse serial section drawings of sectioned brachiopods. The figure reveals all microfossils that appeared during serial sectioning; brachiopod loops arrowed. 1–3) *Zittelina hofmanni* Bujtor and Vörös, 2019 with specimen numbers: PAL 2019.5.1; PAL 2019.6.1; PAL 2019.7.1, respectively; 4) *Smirnovina ferraria* Bujtor and Vörös, 2019 with specimen number: PAL 2019.8.1; 5, 6) *Moutonithyris moutoniana* d'Orbigny, 1847 with specimen numbers PAL 2019.260.1; PAL 2019.259.1, respectively. 7) *Nucleata veronica* Nekvasilová, 1980 with specimen number PAL 2019.267.1. Scale bars indicate 5 mm. All specimens derived from the Apátvarasd Limestone Formation. Abbreviations: a) diactine cricorrhabd sponge spicules; b) foraminifera; c) lithistid demospongiae; d) gastropod; e) *Sporadopyle* sp.; f) echinoderm remain.

Table 4
Entombed microfossils of the serial sectioned brachiopod specimens. Grey shaded boxes with '+' indicate the entombed fossil types.

		foraminiferas	diactine cricorrhabd spicules	lithistid demospongiae	echinoderm	gastropod	*Sporadopyle*	length of crura in mm	length of shell in mm	length of crura / length of shell	surface of shell	loop type
RHYNCHONELLIDA, Pugnacoidea												
PAL 2019.254.1	*Lacunosella hoheneggeri* (Suess, 1858)							5.25 mm	18.9 mm	27.8%	ribbed	short
PAL 2019.255.1	*Lacunosella hoheneggeri* (Suess, 1858)							4.50 mm	16.3 mm	27.6%	ribbed	short
RHYNCHONELLIDA, Norelloidea												
PAL 2019.258.1	*Monticlarella remesi* Nekvasilová, 1977							3.83 mm	16.9 mm	22.7%	ribbed	short
TEREBRATULIDA, Terebratuloidea												
PAL 2019.259.1	*Moutonithyris moutoniana* (d'Orbigny, 1847)	+	+	+	+	+	+	11.3 mm	35.9 mm	31.5%	smooth	short
PAL 2019.260.1	*Moutonithyris moutoniana* (d'Orbigny, 1847)	+						7.04 mm	20.9 mm	33.7%	smooth	short
TEREBRATULIDA, Discolioidea												
PAL 2019.263.1	*Nucleata veronica* Nekvasilová, 1980							7.0 mm	20.6 mm	34.0%	smooth	short
PAL 2019.267.1	*Nucleata veronica* Nekvasilová, 1980	+						8.5 mm	21.5 mm	39.5%	smooth	short
TEREBRATULIDA, Kingenoidea												
PAL 2019.5.1	*Zittelina hofmanni* Bujtor and Vörös, 2019	+	+	+	+			20.1 mm	24.7 mm	81.4%	smooth	long
PAL 2019.6.1	*Zittelina hofmanni* Bujtor and Vörös, 2019	+	+					14.1 mm	19.1 mm	73.8%	smooth	long
PAL 2019.7.1	*Zittelina hofmanni* Bujtor and Vörös, 2019		+	+	+			15.7 mm	22.6 mm	69.5%	smooth	long
PAL 2019.8.1	*Smirnovina ferraria* Bujtor and Vörös, 2019	+	+			+		11.0 mm	16.4 mm	67.1%	smooth	long

Abundance of entombed microfossils are not indicated but only the absence/presence status. Ribbed shells of rhynchonellides did not contain any entombed fossils. Among smooth shelled Terebratulida there is no difference according to the short or long loop types.

the shells. Possible spatial differences between the populations of rhynchonellide and terebratulide brachiopods around the SHV seems an unlikely solution. The fauna is dominated by rhynchonellides showing significant size increase (Fig. 10.1), which refers also to close proximity to the nutrient resources of the Zengővárkony SHV. The clear separation of the presence/absence of entombed microfossils among brachiopod clades raise the possibility that the entombment did not happen post mortem and accidentally, but was controlled with the different protective mechanisms of the brachiopods.

6.2. Ecological differences among brachiopod taxa

Rhynchonellide and terebratulide brachiopods contain remarkably different internally preserved faunal components (Table 4). During serial sectioning rhynchonellides did not reveal any internally preserved microfossils, although all specimens of these two groups were collected from the same locality and same bed. It would have been related to the different protective mechanisms of brachiopod clades. Ribbed forms are equipped with zigzag deflexions of commissures, which have an important role to prevent the entering of extraneous particles in their body cavity as discussed in details by Rudwick (1964). Size comparisons reveal that independently from the commissure protecting mechanism, brachiopods flourished in the nutrient-rich environment and grew to significantly increased dimensions. This is also in line with a recent observation of Georgieva et al. (2020, p. 12) on sponge communities living at vent peripheries, and showing adaptation to high volume water filtration leading to a unique ability to obtain food sources in the vent periphery. It may also imply that disarticulated sponge skeletal particles can drift by equal chance to different brachiopods, therefore we hypothesize that their entombment may not have related to different ecotypes, but rather controlled by their different protective mechanism.

Regarding brachiopod evolution, this SHV fauna also bears significance. By the end of the Early Cretaceous, brachiopod evolutionary lineages start to be discontinuous (Vörös, 2005, fig. 3, 7). The presence of basiliolid, dyscolioid, and terebratellidinid brachiopods in the fauna

reflects remarkably successful adaptations to the special SHV environment, which may have provided shelters also later in time. Therefore, recognition of similar but younger environments in the future may offer answers on certain discontinuous evolutionary lineages of brachiopods.

6.3. Benthic ecotypes and their substrates

Both soft and hard substrates were present at the Zengővárkony SHV site and hosted rich, diverse fauna of special interest for ecotype considerations. Unconsolidated limy mud created a soft substrate for decapods and benthic foraminifera, while the outflowing pillow lavas provided a hard substrate for brachiopods and crinoids to attach to.

Interpillow sediments were previously reported by Jáger et al. (2012). These soft, basically calcareous, fine grained and unconsolidated sediments are the primary ecotypes of the varied shrimp fauna that had left the diverse microcoprolite ichnofauna. The rock forming quantity of crustacean microcoprolites, especially the *Palaxius decaochetarius* suggests a burrowing mode of life of the host animals (Pohl, 1946; Felgenhauer, 1992), because recent crustaceans that produce *Palaxius*-like microcoprolites require soft sediments to prepare their burrows (Dworschak et al., 2012). The connection between ghostshrimps and *Palaxius*-like microcoprolites is supported by the fossil record: an Eocene callianassid body fossil was reported from a methaneseep limestone by Peckmann et al. (2007) associated with the ichnofossil *Palaxius*. In addition, abundant *Lenticulina,* a typical surficial to infaunal genus, also indicates a soft substrate.

Ferretti et al. (2019) reported loose sediments around the modern Panarea volcanic complex with ooidal ironstones, the nuclei of which are sponge spicules (Ferretti et al., 2019, fig. 5.A–E). It seems highly probable that iron-ore genesis would have been a similar process at the Zengővárkony SHV during the Early Cretaceous, and besides sponge spicules the crustacean microcoprolites could have been acted as the nuclei of the ooidal iron ore formation as Naumann (1931) already reported. This is even more plausible due to the fact of the ecological behaviour of ghost shrimps: these decapods are regularly delivering

their fecal pellets from their burrows to the surface (Pohl, 1946) from where a current can sweep them away.

Brachiopods are linked to hard substrates. Most possible, hard substrates are provided by the pillow lava blocks reported by Bujtor (2012b) and smaller volcanic fragments. Size of the pillows are about 1–1.5 m, with clearly visible chilled margins (Fig. 2). The rock-attached and cliff-living crinoids (*Torynocrinus,* cf. Szörényi, 1959) also suggest the presence of hard substrates.

6.4. Nektonic fauna

Agirrezabala and López-Horgue (2017) reported a comparable but younger (Albian) palaeoenvironment from Spain with large–sized ammonites and a rich nektonic fauna. In that palaeoenvironment, abundant and diverse bottom fauna fed by nutrient upwelling linked to chemosynthetic and hydrothermal processes attracted the large sized ammonites to feed. This is apparently the case at Zengővárkony too, as shown by the presence of fragmentary, large–sized lytoceratid ammonites (Wh = 8 cm). Belemnites are also recognized (see Section 5.1.2.2), as possible visitors to the Zengővárkony SHV as well as the nautiloid described herein.

7. Bathymetric significance of fauna

One of the most important questions regarding the intra-plate, shallow marine SHV at Zengővárkony concerns the water depth. The different fossil groups presented in this study, combined with mineralogical and petrographic observations, indicate a consistent bathymetric setting of the depositional environment.

7.1. Foraminifera

The conventional thin sections contain a total of 27 benthic foraminiferal specimens belonging to 20 genera, which are regarded contemporaneous as being collected from the same bed. By considering the thin sections as a single sample, this numbers provide a Fisher alpha diversity index higher than 30, based on the alpha graph published by Murray (2006). This alpha value, has to be regarded as an estimate owing to the biasing effect of the low number of observed specimens. But in spite of this uncertainty, the diversity is still extremely high as the average alpha value in modern normal marine shelf seas is mainly 5–10 and very rarely attains 25–40.

The planktonic group is represented by only 6 specimens of globigerinid taxa, which appears too few to be indicative of an upper bathyal depositional setting. It is generally accepted, that the frequency of planktonic taxa increases from inner neritic through outer neritic to bathyal waters (Emery and Mayers, 1996; Leckie and Olson, 2003). This is also demonstrated by the modern eastern continental shelf and slope of North America (Gibson, 1988), where planktonic species compose 1–10% on the middle shelf, 10–25% on the outer shelf and 25–50% on the upper continental slope. Although the present material contains few planktonic specimens, it seems to fit best with an outer shelf setting, which also corresponds to previous interpretations based on macrofossil groups.

The distribution of morphological groups of foraminifera provides information about adaptation to various environmental habitats in the benthic domain (Jones and Charnock, 1985; Nagy, 1992; Setoyama et al., 2011). In the present material, five morphological groups of the genera indicate the following foraminiferal habitats. 1) Flattened planispiral shape, epifaunal to clinging mode of life: *Ammodiscus*? *Spirillina.* 2) Trochospiral shape, surficial habitat: *Trocholina, Spirotrocholina, Gavelinella, Reinholdella*? *Epistomina.* 3) Subglobular test, immersed habitat: *Meandrospira.* 4) Rounded periphery planispiral shape, surficial to infaunal habitat: *Haplophragmoides*? 5) Elongated tapered test, infaunal habitat: *Ammobaculites, Reophax, Reophacella, Bolivinella, Nodosaria, Praebulimina.*

As shown above, the morphology of the observed genera indicates adaptations to each of the principal foraminiferal habitats by a balanced frequency of surface-dwelling and infaunal components. This, together with the very high species diversity and strong dominance of calcareous taxa indicate normal marine salinity and oxygenation conditions. In addition, the extremely high diversity suggests that rich nutrient supply and increased food productivity created particularly favourable conditions for foraminifera through hydrothermal influence in the outer neritic environment.

Bathymetry of taxa: *Praebulimina carseyae, Epistomina lacunosa, Gavellinella* sp., *Buliminella* sp., and *Pullenia cretacea* refer to a depth greater than 100 m (Carillo et al., 1995). Outer shelf 100–200 m water depth suggested by: *Praebulimina carseyae, Gavellinella compressa, G. spissocostata, Coryphostoma plaitum* and *Pullenia jarvisi* if predominant (Nyong and Olsson, 1984).

7.2. Brachiopoda

Lacunosella seems to be a useful indicator of water depth in the fossil assemblages. Lazar et al. (2011) made an estimation of water depths ranging from 40 to 100 m for Late Jurassic *Lacunosella*-sponge facies associations. Other estimates of water depth for Jurassic occurrences of *Lacunosella* with associated fauna include: with sponges 80–90 m (Herrmann, 1996); with sponges and corals 100 m (Krawczynski, 2008); with ammonoids 80–120 m depth (Olóriz et al., 2006).

7.3. Lithistid Demospongiae

Lithistid Demospongiae are frequent constituents of the microfauna represented by high abundance of disintegrated particles. According to Pisera (1997, p. 28) "Kimmeridgian coral facies with siliceous sponges may be of relatively deep-water origin, i.e., at least 60–70 meters deep, but perhaps even 100 meter[s] deep".

7.4. Vesicle sizes of pillow lavas

According to Bilik (1983), pillow lavas of the Mecsek Mountains were formed at a depth of 100–400 m based on vesicularity indexes (Jones, 1969).

Fig. 13 summarizes the water depths indicated by the different fossil groups and petrology. Based on this evidence the most probable water depth of the Zengővárkony environment was between 100 and 150 m.

8. Comparison with recent analogous environments

Ferretti et al. (2019) reported a special environment off the coast of Panarea (Aeolian Islands) from around 150 m water depth (Romagnoli et al., 2013). This depth and its fauna are closely similar to those of the Zengővárkony environment. The foraminiferal assemblage recorded by Bujtor and Szinger (2018) is similar to that of the hydrothermal environment off Panarea reported by Panieri et al. (2005). In comparing the findings at Zengővárkony with the foraminiferal fauna of the Tyrrhenian Sea locality strengthen the similarity. Panieri et al. (2005, p. 216, Table 4) reported 19 genera 3 of which are in common within the 20 genera from Zengővárkony.

Frequent ooid formation around sponge spicules in modern environments may be a similar process to that of the goethite accumulation around the crustacean microcoprolites in the Cretaceous at Zengővárkony. Also at Panarea, the goethite precipitation is linked to hydrothermal processes as reported by Di Bella et al. (2019). The active submarine volcanic hydrothermal system, with CO_2–dominated and Fe–rich thermal fluids, triggers precipitation of goethite around abiogenic particles (small volcanic grains) and/or biogenic particles (siliceous sponge spicules or crustacean microcoprolites) deposited at the seafloor. The complete absence of crustacean microcoprolites at Panarea is linked to the substrate: there are no soft sediments in the sampling
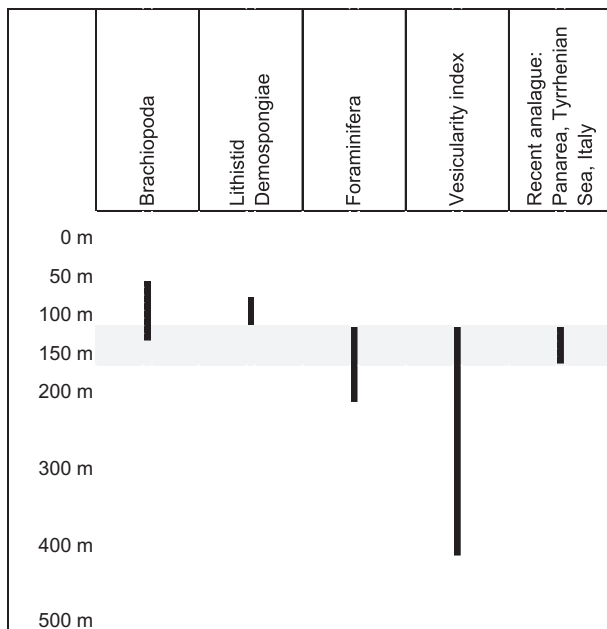
Fig. 13. Bathymetric estimate for the Zengővárkony SHV based on different fossil groups, vesicularity index, and recent analogous environment. Data from Bilik (1983), Lazar et al. (2011), Nyong and Olsson (1984), Peccerillo (2013) and Pisera (1997). The most probable water depth range is indicated by grey shading.

area (cf. Romagnoli et al., 2013, fig. 4.4), which is a precondition for burrowing organisms, while soft substrate areas were present at Zengővárkony.

9. Conclusions

Intra-plate hydrothermal vents are rare, accounting for only 1% of active recent vent sites (Beaulieu et al., 2013 p. 4897), and apparently therefore, their fossil counterparts have not yet been thoroughly investigated. These developments are even more unique as they are not 'classical' high temperature vents with strong fluid transport, but low temperature, sediment-hosted hydrothermal vents (Bell et al., 2016). Summarizing 70 years scientific exploration we conclude, that the Early Cretaceous iron-ore related ecosystem at Zengővárkony (Mecsek Mountains, Hungary) belongs to, and constitutes the first fossil member of the shallow marine intra-plate group.

Recognition of the faunal developments typifying the SHV group of environments is difficult. A combination of both direct and indirect evidence contribute to understanding the kind of ecosystem exemplified by the Zengővárkony SHV:

1) *Submarine volcanic activity* expressed by pillow lavas, peperites, hydrothermal sediments, vesicularity index.
2) *Sulphur stable isotope data* showing unusually negative values, which can indicate former bacterial life close to the hydrothermal fields.
3) *High diversity fauna,* which includes some components displaying an unusual average size increase (e.g., brachiopods and echinoids).
4) *Diverse crustacean microcoprolite ichnofauna,* which in some cases can occur in rock-forming quantities.
5) *Rich taxonomic composition of major faunal groups* such as foraminifera, brachiopods and microcoprolites showing high specimen abundance of certain taxa.
6) *Endemism* among multiple fossil groups (e.g., brachiopods and crustacean microcoprolites).

Oxygen and carbon stable isotope measurements do not appear decisive to recognize the SHV type fossil environment. At the Zengővárkony locality, these stable isotope data did not show significant deviations from normal values. Sulphur isotope measurements however, are significantly negative and may indicate former biological activity, but exposure of samples to weathering might have reduced their reliability and applicability. Discovery of sediment with tubular structures suggests an origin from hydrothermal activity. Based on faunal and lithological evidence the estimated water depth of the Zengővárkony palaeoenvironment was between 100 and 150 m.

At the Zengővárkony SHV, nutrient-rich upwelling is suggested by the populations of *Lacunosella*. This brachiopod tends to be large-sized where it found favourable conditions e.g., hydrothermal vents or stromatactis mud-mounds. In addition, other brachiopod taxa and echinoid spines also reveal size increase, and this phenomenon could be a useful tool to recognize comparable environments in the future. Sediment hosted vents are rare, and occur extremely seldom in shallow marine intra-plate tectonic settings. The unique environment of the Zengővárkony fauna is the first fossil member of this rare group of vent sites.

Declaration of competing interest

None.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2020.110179.

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