

A meeting in the cave: Taphonomy and ecology of scutelluid trilobites in the Devonian Hamar Laghdad elevation, eastern Anti-Atlas, Morocco

Zdzisław Belka ^{a,*}, Raimund Feist ^b, Jolanta Dopieralska ^c, Stanisław Skompski ^d

^a Isotope Research Unit, Adam Mickiewicz University, Krygowskiego 10, 61-680 Poznań, Poland

^b Institut des Sciences de l'Evolution, Université Montpellier 2, Montpellier, France

^c Poznań Science and Technology Park, Adam Mickiewicz University Foundation, Rubież 46, 61-612 Poznań, Poland

^d Faculty of Geology, University of Warsaw, Zwirki i Wigury 93, 02-089 Warsaw, Poland

ARTICLE INFO

Editor: S Shen

Keywords:

Trilobites
Taphonomy
Ecology
Mounds
Devonian
Morocco

ABSTRACT

Densely packed accumulations of scutelluid trilobite sclerites, found in subseafloor vent fissures and cavities within the Devonian Hamar Laghdad elevation (Anti-Atlas, Morocco), were investigated to understand their taphonomic, ecological, and behavioural significance. The assemblages are monospecific and composed of disarticulated exuviae, with a predominance of pygidia and no complete trilobite carapaces. Two Pragian-age lumachelles, deposited in subseafloor cavities within bioclastic packstones, are dominated by *Platiscutellum massai*, while five Emsian-age lumachelles occurring in fissures within the Kess-Kess mounds contain *Cavetia furcifera*. This study provides key insights into the moulting behaviour, life habits, and palaeoecological preferences of scutelluid trilobites during the Early Devonian. Morphological features indicate that both trilobite species were adapted to open marine environments, ruling out a permanent cave-dwelling lifestyle. The assemblages are interpreted as the result of mass moulting behaviour within subseafloor fissures and cavities. Size-frequency data suggest synchronised, size-segregated moulting events. Although a reproductive function for these aggregations remains speculative, parallels with modern arthropods suggest that mass moulting may have conferred both protective and reproductive advantages. These findings reinforce the interpretation that the mass gathering of trilobites, particularly during ecdysis, may have been an adaptive strategy in response to ecological pressures in Early Devonian marine environments. The preferred concave-up orientation of sclerites suggests passive gravitational settling within fissures and cavities, rather than transport by horizontal currents, while the breakage of smaller sclerites points to reworking by episodic hydrothermal fluid discharge.

1. Introduction

Shelly accumulations of trilobite remains (lumachelles) are occasionally found filling cavities, pockets and neptunian dykes within various Palaeozoic carbonate buildups. These accumulations often consist of monospecific assemblages characterised by their morphological similarity. Among them, the illaenids and scutelluids have dominated since the Ordovician (e.g., [Mikulic, 1981](#)). Homeomorphic trends are particularly evident in scutelluids, which adapted to carbonate mound habitats ([Fortey and Owens, 1997](#)). Spectacular monospecific accumulations of densely packed sclerites from these environments have been described, including *Eobronteus* from the Upper Ordovician Boda Limestone in Sweden ([Suzuki and Bergström, 1999](#)), *Ekwanoscutellum* from Silurian exhumed reefs in Ontario ([Westrop and Rudkin, 1999](#)) and

North Greenland ([Hughes and Thomas, 2008, 2011](#)), and *Radioscutellum* from reef-core environments of the Pragian Koneprusy Limestone in Bohemia ([Chlupáč, 1983; Šnajdr, 1960](#)). However, the origin of such accumulations remains poorly understood.

The Hamar Laghdad elevation in eastern Anti-Atlas, southern Morocco ([Figs. 1 and 2](#)), renowned for its spectacular Early Devonian mud mounds and fauna (e.g., [Aitken et al., 2002](#); [Belka, 1998](#); [Belka et al., 2018](#); [Berkowski, 2004](#); [Berkowski et al., 2019](#); [Hryniewicz et al., 2017](#); [Jakubowicz et al., 2013, 2014](#)), is also the site of a rich trilobite fauna. Assemblages of clustered trilobites, composed of scutelluid trilobite remains, have already been the subject of paleontological studies in the past (e.g., [Alberti, 1981, 1982](#)). However, most of these reports were based on material collected from the debris, thus providing only limited information on the ecology and taphonomy of scutelluid

* Corresponding author.

E-mail address: zbelka@amu.edu.pl (Z. Belka).

trilobites in the Devonian of Hamar Laghdad.

In this study, by elucidating the circumstances of deposition, taphonomy, and the morphological particularities of the fauna characterising the Hamar Laghdad trilobite accumulations, we aim to discuss the phenomenon of their monospecific segregation, as well as possible instances of cryptic behaviour, as suggested by Belka et al. (2015). Because trilobites possess sclerites of varying sizes and shapes, they represent highly valuable material for taphonomic research, allowing for the straightforward identification of sorting patterns and their underlying causes.

2. Geological background

The Hamar Laghdad elevation is located in the eastern Anti-Atlas in southern Morocco (Fig. 1), where a thick Palaeozoic succession, overlying the northern margin of the Sahara Craton, is perfectly exposed. During the Devonian, this area formed part of a broad shelf extending across the northwestern continental margin of Gondwana (Dopierańska, 2009; Wendt, 1985). Its depositional and tectonic evolution was controlled by regional east-west trending strike-slip faults, which influenced subsidence patterns and locally triggered submarine volcanic activity (Belka et al., 1997). The Hamar Laghdad ridge represents the remnant of a seafloor elevation formed during the Early Devonian by a submarine eruption of basaltic lava (Aitken et al., 2002; Belka, 1998;



Fig. 2. Panoramic view of the Hamar Laghdad elevation, showing the perfectly exposed Early Devonian Kess-Kess mounds.

Brachert et al., 1992). This elevation subsequently became a site of carbonate production with extensive crinoid and brachiopod colonisation, associated with post-volcanic hydrothermal seepage that persisted from the late Pragian to the early Frasnian (Belka, 1998; Belka et al., 2018; Franchi et al., 2014; Mounji et al., 1998). A complex system of synsedimentary faults acted as conduits for hydrothermal fluid migration to the seafloor. As a result, large, spectacular mud mounds (Fig. 2), commonly referred to as the Kess-Kess mounds, developed at the intersections of these faults (Belka, 1998). The mounds are primarily composed of auloporoid boundstones and crinoid packstones. The mound biota does not provide a precise indication of water depth, but the absence of stromatoporoids, calcareous algae, and micritic

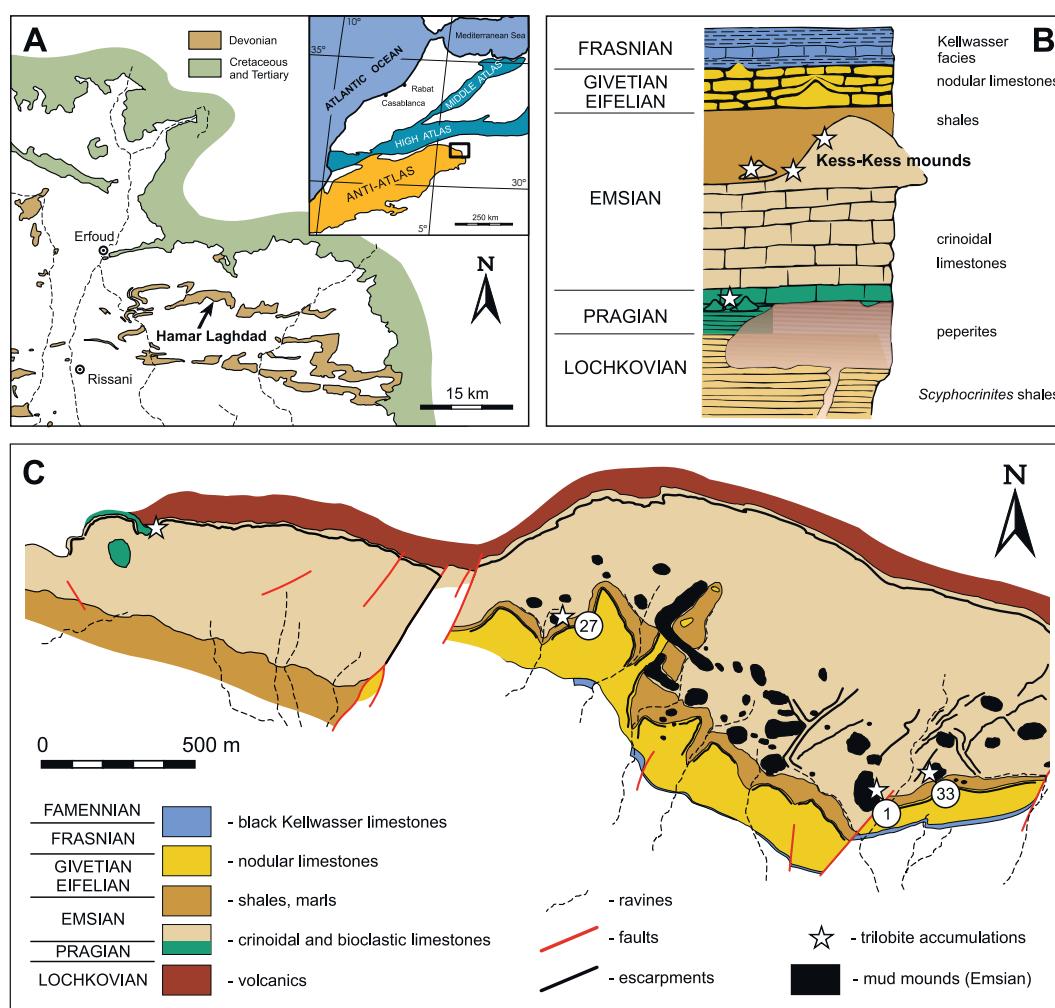


Fig. 1. A. Simplified geological map of the eastern Anti-Atlas. Devonian rocks and location of Hamar Laghdad are indicated (from Belka, 1998). Inset shows regional geology and location of the study area. B. Schematic stratigraphic column of the Hamar Laghdad elevation (from Belka, 1998; modified) with the stratigraphic position of the investigated trilobite accumulations (marked by asterisks). C. Geological map of the western and central parts of the Hamar Laghdad area. The location of the studied trilobite accumulations is indicated by asterisks and mound numbers (for more precise information, see the text).

envelopes around carbonate grains suggests that the Kess-Kess mounds grew in a deep-water environment.

One of the characteristic features of the Kess-Kess mounds is the presence of numerous cavities, which are fragments of larger open spaces, now mostly filled with internal sediments, as well as calcite cements (Belka et al., 2018). These open spaces originally formed a complex system of fissures and chimneys connected to the seafloor. Their irregular shapes suggest chemical corrosion, rather than tectonic control, as the mechanism of their formation. It is proposed that both the dissolution of the carbonate host rock and the precipitation of mud mound carbonates resulted from the mixing of hydrothermal fluids and seawater (Belka et al., 2018, and references therein). During mound formation, dissolution occurred in zones dominated by hydrothermal fluid-rich mixtures, while carbonate precipitation progressed as the vent fluids were diluted by seawater.

The carbonates of the Kess-Kess mounds are highly fossiliferous. A characteristic feature of the mound community is the clear differentiation between the fauna that lived on the mound surfaces and the vent biota, which were restricted to chimneys and the zones surrounding vent outlets (Berkowski, 2006). On the mound surfaces, there are numerous small tabulate corals and crinoids, associated with subordinate dacryconarids, rugose corals, brachiopods, and various trilobites (Berkowski, 2004). In contrast, the vent fauna around the vent outlets consists of small rugose corals, large tabulate corals, crinoids, ostracods, gastropods, sponges, and monoplacophorans (Belka and Berkowski, 2005; Berkowski, 2006; Berkowski et al., 2019). Additionally, the internal sediments (micritic and fine-grained laminated carbonates) filling the system of subseafloor fissures and chimneys contain rich accumulations of scutelluid trilobites and orthoconic cephalopods (Feist and Belka, 2018). Conodont fauna indicate that the mounds grew during the Emsian *inversus* Zone (Belka et al., 2018). The carbonates infilling the vents at the tops of the mounds are of the same age, while those situated at the base of the mounds sometimes contain conodont fauna indicative of the Emsian *serotinus* Zone, showing they are slightly younger.

3. Previous studies

The occurrence of scutelluid trilobites in the Lower Devonian of Hamar Laghdad was first reported by Termier and Termier (1950). However, it was Alberti (1970, 1981) who discovered fragments of scutelluid lumachelles and provided a taxonomic description of the fauna. Brachert et al. (1992) noted that *Scutellum* lumachelles can be found at the tops and flanks of some mounds. In brief notes, Belka et al. (2003) and Belka et al. (2015) mentioned the presence of several tens of scutelluid *Cavetia* lumachelles, both near the summits and on the flanks of numerous Kess-Kess mounds. These lumachelles accumulated inside the mounds, in relatively large, inactive channels and voids, during periods when hydrothermal activity had ceased (Belka et al., 2018).

Feist and Chatterton (2015) were the first to investigate in detail a scutelluid lumachelle found in situ within a vent channel in Mound 27. This sclerite accumulation was composed of a large number of spinose remains of *Sagittapeltis belkai*, associated with a few remains of another scutelluid, *Cavetia*, probably linked to a neighbouring monospecific *Cavetia* accumulations within the same mound, and isolated sclerites belonging to proetids and odontopleurids. The excessively spinose remains of *Sagittapeltis* were randomly dispersed. External parts of the exoskeleton, such as palpebral and occipital spines, thoracic pleurae, and pygidial spines, were generally broken off, and their long, tube-like remains constituted a larger portion of the elements. Randomly stacked, often broken sclerites point to increased hydrodynamic influence during deposition. Feist and Chatterton (2015) suggested that high individual numbers of this species might have gathered seasonally for reproduction and moulting near the cavity outlets, possibly attracted by nutrient abundance and the proximity of protective crevices. They also proposed that the sclerites may have been transported by currents and gravity flows to their final resting places, rather than having simply fallen apart

during or after ecdysis.

Feist and Belka (2018) described another known multispecies accumulation of trilobites in the Lower Devonian of Hamar Laghdad, which fills a vent outlet at the base of Mound 1. Interestingly, this accumulation occurred only a short distance from two vent channels filled with monospecific *Cavetia* lumachelles. This unexpectedly diverse trilobite assemblage was predominantly composed of harpetid sclerites, with an admixture of 24 % odontopleurids (including one miraspide), 8 % scutelluids (*Cavetia*), 2 % aulacopleurids (including one otarionine), and 1 % proetids (including one eremiproetine). All trilobite remains were dissociated exoskeletal parts, presumably representing a death assemblage of taxa that shared the same habitat.

4. Materials and methods

In total, several dozen vent conduits and fissures were found on the Hamar Laghdad elevation, filled with spectacular trilobite lumachelles containing thousands of scutelluid trilobites. Unfortunately, intensive commercial fossil collecting in the eastern Anti-Atlas has led to the destruction of exposures rich in trilobite assemblages in the Hamar Laghdad area. For this reason, we present here only the locations of seven selected dykes containing monospecific scutelluid accumulations, in an effort to help prevent further damage in the future.

Two of the scutelluid lumachelles analysed were found within Pragian bioclastic crinoidal packstones (Fig. 1B), which overlie Lochkovian volcanoclastic rocks in the westernmost part of the Hamar Laghdad area (Figs. 1C, 3A). They occur within the sedimentary infill of dykes that fill meter-scale secondary cavities in the Pragian carbonates (Fig. 1C). The irregular form of the cavities and the presence of hydrothermal calcite cements lining their walls suggest that the cavities formed through dissolution by hydrothermal fluids. The sedimentary infill is predominantly composed of carbonate mudstone containing large orthoconic cephalopods. In both dykes, single trilobite lumachelle layers—up to 35 cm thick—are intercalated. The primary micritic matrix is only partially preserved; in most cases, it has been replaced by coarse calcite cements formed through hydrothermal processes after the deposition of the sedimentary infill. The rare polygnathid conodont fauna recovered from the lumachelles suggests a late Pragian or earliest Emsian age.

The majority of scutelluid accumulations analysed in the study were found in neptunian dykes developed within the Emsian Kess-Kess mounds. The outlets of the dykes are predominantly located on summits of these mounds or at their bases (Belka et al., 2018; Feist and Belka, 2018). The scutelluid accumulations occur as several-centimetre-thick lumachelle layers within the sedimentary infill of the dykes, usually no deeper than 1–5 m below the surface of the vent outlets. The dykes are typically well-bedded and composed of laminated lime mudstone or wackestone. Five scutelluid lumachelles located within three Mounds—1, 27, and 33 (see Fig. 1 for location)—were selected for detailed study. All contain hundreds of disarticulated sclerites. No complete trilobite carapaces were identified. The sclerites are well-preserved and physically undeformed but are often incomplete due to breakage. They are embedded in micritic or fine-grained carbonate sediment, which occasionally contains isolated styliolinids and minute fragments of ostracod, brachiopod, and gastropod shells. The rather flat pygidial shields are closely stacked and packed together like the pages of a book, arranged parallel to the surfaces of the vent outlets. The high degree of sclerite compaction has been enhanced by dewatering, as indicated by sheet cracks oriented parallel to the bedding. The associated conodont fauna indicates the Emsian *inversus* Zone.

The seven selected scutelluid accumulations were examined both taxonomically and biometrically. Since trilobite remains were preserved only as disarticulated sclerites, the maximum width of the pygidium was used as the most reliable measure of overall trilobite size in the biometric analysis. This choice was based on the fact that scutelluid pygidia are typically the largest element of the trilobite exoskeleton and are more often preserved complete than other parts. Moreover, pygidia are

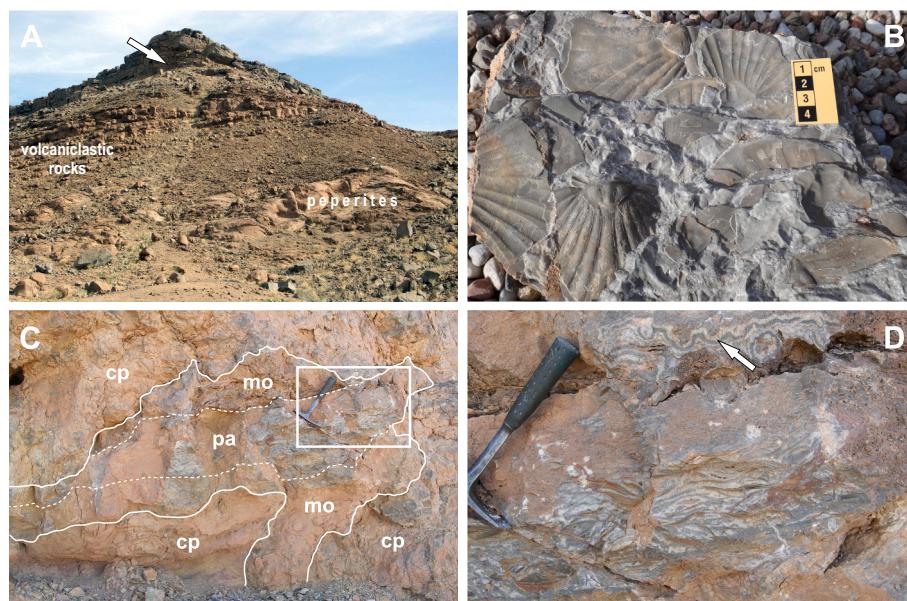


Fig. 3. Pragian monospecific *Platyscutellum massai* lumachelles in the Hamar Laghdad elevation. **A.** View of the northern slope of western Hamar Laghdad, showing Lochkovian volcanic and volcaniclastic rocks, with the location of the Pragian trilobite accumulations indicated by an arrow. **B.** Upper surface view of a block from the *Platyscutellum* accumulation. **C.** Cross-sectional view of an m-size secondary cavity within the Pragian crinoidal limestones, filled with trilobite lumachelle and cephalopod limestone. cp – crinoidal packstone; mo – mudstone with large orthoconic cephalopods; pa – *Platyscutellum* accumulation. The framed area is enlarged in **Fig. 3D**. **D.** Lumachelle consisting of large sclerites of *Platyscutellum massai* in cross-section. White areas are filled with calcite cements. The cavity wall is lined by hydrothermal calcite cements (indicated by an arrow).

wider than they are long, relatively flat, and usually symmetric—features that facilitate easier and more accurate measurement on the rock surface. In total, approximately 650 pygidia were evaluated. Measurements were taken to the nearest 1 mm and grouped into 5 mm class intervals. In earlier studies investigating the size-frequency distribution of trilobite pygidia, class intervals of 1 or 2 mm were typically used (e.g., Sheldon, 1988). However, these studies focused on small trilobites whose pygidia rarely exceeded 2–3 cm in width. In contrast, the large scutelluids analysed here, with pygidial widths frequently over 5 cm, were assessed using 5 mm class intervals, following the approach of Westrop and Rudkin (1999).

5. Composition of trilobite accumulations

5.1. Pragian assemblages

Both scutelluid lumachelles found in cavities within the Pragian limestones contain almost exclusively hundreds of large, disarticulated sclerites of *Platyscutellum massai* Alberti, 1981. Only rarely are a few isolated remains of *Kolihapeltis*, *Eremiproetus* and *Reedops* associated. Other fossils are virtually absent; only a single orthocone cephalopod was observed. The lumachelles are characterised by densely packed and closely superposed layers of both cranidia and pygidia. Numerous free cheeks, hypostoma, rostra and thoracic sclerites are also present, though in relatively low numbers; these sclerites are often broken. In both lumachelles, the pygidia predominantly (64 % and 67 %) show a concave-up attitude, and are mostly well preserved. Their number appears to exceed that of the cranidia. These *Platyscutellum* lumachelles closely resemble the *Ekwanoscutellum* accumulations described by Westrop and Rudkin (1999) from the Silurian of northern Ontario. However, in the latter, the sclerites consisted mainly of pygidia, with only a few cranidia, and the number of other *Ekwanoscutellum* sclerites was very low.

The investigated pygidia of *Platyscutellum massai* do not exhibit any noticeable directional orientation within the lumachelle layers. However, it should be noted that even under the influence of directional current flow, oval-shaped objects—such as the pygidia of *Platyscutellum*,

which have the outline of a truncated ellipse—are difficult to orient directionally. The *Platyscutellum* assemblages are dominated by large pygidia and show a striking absence of small individuals (defined as those with pygidium widths less than 4 cm). Their size-frequency distributions display a slightly negative skew and exhibit characteristic “peaks” in two size classes (Fig. 5).

5.2. Emsian assemblages

The five investigated scutelluid lumachelles occurring within the Kess-Kess mounds are monospecific coquinas composed of the large-tailed *Cavetia furcifera* (Hawle and Corda, 1847). Examination of the assemblages reveals a slight predominance of pygidia over cranidia. Other sclerites—such as free cheeks, rostra, and hypostomes—are also present but occur in relatively smaller numbers. The majority of pygidia (62–71 %) exhibit a concave-up attitude but do not display any directional alignment. Associated cranidia and other sclerites likewise show no preferred orientation.

The five *Cavetia* lumachelles differ significantly in the spectrum of sclerite sizes. This is surprising, as three of them originated from the same mound and were accumulated only a short distance apart. These trilobite accumulations vary in the range of pygidial maximum widths and the shapes of their size-frequency distributions (Fig. 6). Additionally, there is a general scarcity of smaller individuals (with pygidia less than 2 cm wide). Two *Cavetia* lumachelles from Mound 27 (a and b) exhibit distributions with slight bimodality, showing a trough between 4.5 and 5 cm. The third lumachelle from the same mound (27c) is dominated by sclerites representing individuals from only one, smaller mode. In contrast, pygidia in the *Cavetia* accumulations from Mounds 1 and 33 display a more normal distribution, although that of the latter is notably negatively skewed.

6. Interpretation & discussion

6.1. Depositional site

Although the investigated Pragian and Emsian scutelluid

assemblages contain sclerites from two different species, their general characteristics and modes of occurrence are, in many respects, nearly identical. Most notably, the accumulation of disarticulated trilobite sclerites in the absence of complete trilobites is striking. Also characteristic is the preferential accumulation of scutelluid sclerites in vent fissures of mounds and undersea cavities, whereas occurrences of scutelluid trilobites on the surfaces of the Kess-Kess mounds or in sediments deposited on the surrounding sea floor are generally very rare. These observations raise the question of whether the trilobite sclerites are preserved in situ or were redeposited and subsequently accumulated in fissures, pockets, and cavities.

The first scenario seems unlikely when we consider that the number of free cheeks, rostra, and hypostomes in the examined lumachelles is unbalanced relative to the number of pygidia and cranidia. On the other hand, the complete redeposition of all lumachelle components also appears improbable, given the size distribution of these sedimentary elements. All lumachelles exhibit a bimodal composition. On the one hand, they contain large trilobite sclerites measuring several centimetres; on the other, micritic or fine-grained carbonate sediment. Notably, there is a complete absence of intermediate-sized granular and bioclastic components, as well as benthic fauna or their skeletal fragments, which were abundant on the mound surfaces around vent outlets (Belka et al., 2015; Belka et al., 2018). As already mentioned above, only isolated stylolinids and minute fragments (less than 1 mm) of ostracod, brachiopod, and gastropod shells occur occasionally. Furthermore, if redeposition of the sclerites and carbonate sediment had occurred, the lumachelles would exhibit normal grading patterns, as commonly observed in the infills of neptunian dykes and subseafloor fissures where gravitational transport has taken place (e.g., Mišk et al., 1994; Smart et al., 1988).

In our opinion, the preferred concave-up orientation of pygidia may suggest an alternative scenario. This orientation typically results from the gravitational sinking of concave objects in water, such as trilobite pygidia or bivalve shells (Allen, 1984; Hesselbo, 1987; Lask, 1993). Furthermore, it indicates that the sclerites were not subjected to unidirectional horizontal currents during or after deposition.

The most plausible scenario is that trilobites congregated in the upper parts of fissures and subaqueous cavities, close to their outlets, where disarticulated sclerites fell freely into deeper parts of the vent system. Gravitational redeposition within the fissures likely accounts for the observed sorting. However, many small sclerites are fragmented, implying a more energetic redepositional process. We interpret this as the result of episodic hydrothermal fluid discharge within the vent system. Supporting evidence includes hydrothermal cements lining conduit walls and occurring within the sedimentary infill of associated dykes and fissures. Flow measurements at modern hydrothermal vents indicate velocities of several cm/s at low-temperature diffuse sites, and 1–2 m/s at focused high-temperature discharges (Germanovich et al., 2015). A fluid inclusion study of calcite cements within the infill of neptunian dykes in the Kess-Kess mounds revealed a wide range of homogenization temperatures (T_h), from 75 °C to 295 °C (Belka et al., 2018). These data allow us to assume that hydrothermal fluids could have been expelled upward at flow velocities of up to several tens of cm/s. During such a flow, trilobite sclerites were too large to be transported upward to the seafloor and settled relatively slowly once displaced from the main flow stream by turbulence. In this scenario, smaller sclerites would have been most vulnerable to damage as they fell and collided with the rock walls of the vent conduits.

6.2. Life habit of scutelluid trilobites

The spectacular concentrations of sclerites from scutelluid trilobites found in subseafloor fissures and cavities on the Hamar Laghdad elevation are certainly not accidental and are undoubtedly related to the life habits of these trilobites. One of the key questions is whether scutelluid trilobites preferentially occupied niches within the mound structures and were, at least during part of their life cycle, cave dwellers.

Alternatively, a more likely scenario is that scutelluids entered these cavities only periodically, during moulting and reproductive periods. Cryptic behaviour of trilobites in cavities within limestone build-ups has been reported by Suzuki and Bergström (1999), Feist (2001), and Chatterton et al. (2003), among others. Blind forms may have been permanent cave dwellers (Glaeser and Paulus, 2015), whereas sighted forms might have entered fissures and cavities temporarily for shelter or during moulting periods. If permanent cave-dwelling trilobites were present, one would expect to find associations including entire exoskeletons, juvenile growth stages, and individuals with small, blind or reduced eyes, and smooth morphologies. However, this is not the case with the scutelluid accumulations found in the fissures and cavities of the Hamar Laghdad elevation.

Among the most distinctive morphological characteristics of both species is the development of relatively large, functional visual organs. The Emsian species *Cavetia furcifera* possesses eyes with thousands of lenses arranged on a reniform (kidney-shaped) visual surface (Fig. 4F), providing an almost panoramic field of view, including backward over the thorax. The strongly dorsoventrally vaulted visual area allows downward-directed vision beyond the steeply sloping librigenae. On the ventral side, the hypostomes exhibit prominent maculae bearing numerous lenses, which are commonly interpreted as light-sensitive organs. The presence of such highly developed visual structures clearly reflects an adaptation to life in the photic zone, where light penetrates to reach benthic habitats. In addition, *Cavetia* displays a high degree of spinosity, with spines developed on its peripheral regions and the axial occipital lobe, likely serving as protective structures (Feist and Chatterton, 2015). Its relatively long cephalic spines are not aligned in a horizontal plane, as seen in most other scutelluids, but are instead upraised and curved, occupying a considerable three-dimensional space. This morphology would likely hinder locomotion in confined environments such as cavities. Therefore, based on the specific functional morphologies of the sclerites composing the *Cavetia* lumachelles, we exclude the possibility that these trilobites had a permanent cave-dwelling lifestyle. Similarly, a permanent cave-dwelling lifestyle for the Pragian species *Platyscutellum massai* is very unlikely, despite these trilobites having comparatively smaller eyes, shorter visual surfaces, and lacking spines. Their very large size would have posed a significant obstacle to movement within relatively small, enclosed undersea spaces.

It is important to add that the trilobite fauna of the two multispecies accumulations discovered within the Kess-Kess mounds is entirely composed of sighted taxa, which also display a relatively high degree of spinosity, particularly on peripheral parts and on the axial occipital lobe (Feist and Belka, 2018; Feist and Chatterton, 2015). The proetids exhibit rather long eyes; odontopleurids have prominent lenses; the globular eyes of aulacopleurids contain hundreds of minute, densely packed lenses covered by a cuticular membrane; harpetids display exceptionally large lenses; and the scutelluid *Sagittapeltis* possesses eyes with thousands of lenses. *Sagittapeltis* is particularly remarkable among trilobites for its 26 long spines, which extend beyond the cephalic margin and, in the case of the pygidial spine, reach the length of the entire body. *Ioporussia* and *Ceratocephala* also possess long cephalic spines, and in the latter, the five pygidial spines are barbed with secondary spines. All these features indicate that a permanent cave-dwelling lifestyle can be excluded for these trilobite taxa.

6.3. Moulting behaviour

Although the investigated lumachelles were deposited in the vent fissures and subseafloor cavities at Hamar Laghdad, the scutelluid remains are not associated with the vent fauna—such as thermophilic corals, gastropods, monoplacophorans, sponges, and ostracods—present at the outlets of the vents during periods of hydrothermal venting (Belka and Berkowski, 2005; Olempska and Belka, 2010). This suggests that trilobites periodically gathered in the fissures of the vent system when hydrothermal activity was probably temporarily inactive. However,

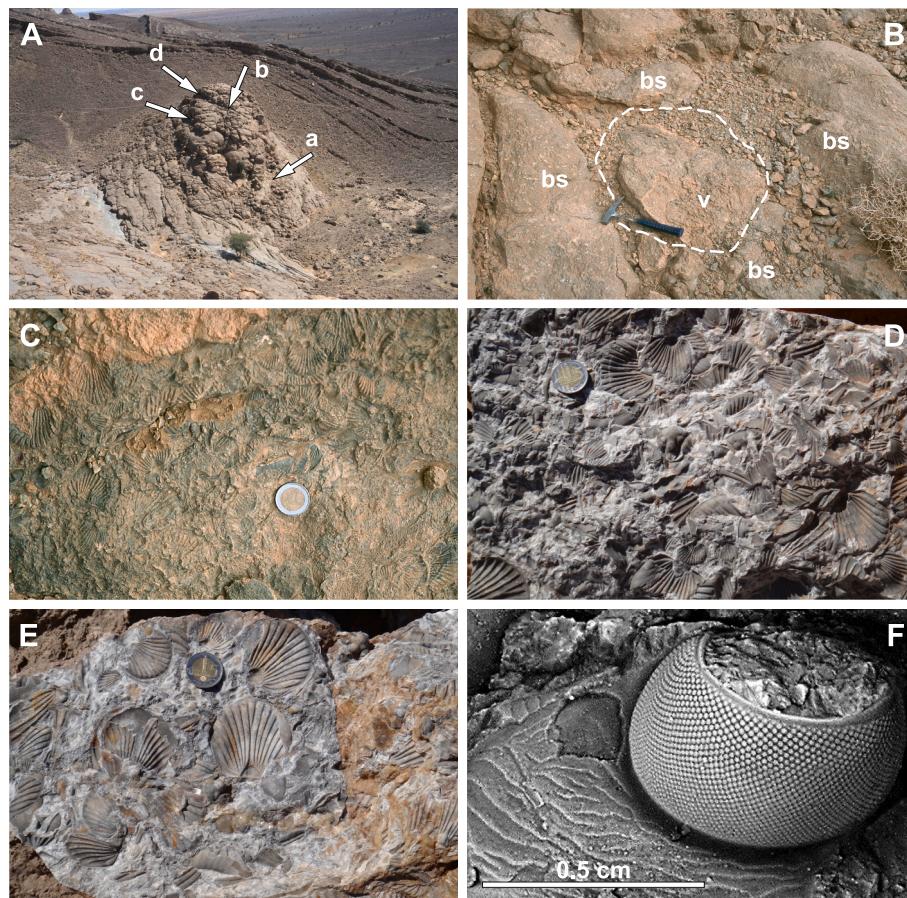


Fig. 4. A. Emsian mound 27 (see Belka et al., 2018 for location), of 30 m in height, displaying vent outlets with scutelluroid infills: a, b, c – monospecific *Cavetia* lumachelles; d – *Sagittapeltis* lumachelle described by Feist and Chatterton (2015). B. Vent outlet filled with *Cavetia furcifera* lumachelle (v) within auloporoid bafflestones (bs) at the base of mound 27. Detail of vent outlet “a” shown in Fig. 4A. C. Enlarged fragment of the lumachelle with partially oriented specimens of *Cavetia*, from the sedimentary infill shown in Fig. 4B. D. Fresh rock surface showing randomly oriented *Cavetia* sclerites, mostly inverted pygidial fragments, cranidia, hypostomes, and librigenae; located 10 cm underneath the surface shown in Fig. 4C. E. Monospecific *Cavetia* lumachelle, showing sclerites of predominantly inverted pygidial fragments bedded in parallel, cranidia and librigenae; from the vent outlet “b” shown in Fig. 4A. F. *Cavetia furcifera*, adaxial part of librigena with high eye of circular outline with strongly vaulted visual surface carrying about 3000 lenses, from outlet “c” shown in Fig. 4A. Coins and hammer for scale (coin diameter is 25 mm).

there is no evidence of a potential food source in the fissures and cavities where scutelluid trilobites assembled. Since no complete trilobites have been found—only their disarticulated sclerites—it appears that moulting was the principal reason for the mass gathering of trilobites in these fissures and cavities.

Trilobites, like all other arthropods do, were shedding their skeletons at periodic intervals (for an overview, see Daley and Drage, 2016; Henningsmoen, 1975). Clustered trilobite assemblages attributed to synchronous mass moulting events have been reported several times (e.g., Corrales-García et al., 2020; Ebbestad et al., 2013; Karim and Westrop, 2002; Paterson et al., 2007; Speyer and Brett, 1985). Some of these assemblages were found in the infills of fissures and pockets within reef and mound structures (Feist and Chatterton, 2015; Suzuki and Bergström, 1999; Westrop and Rudkin, 1999).

As stated previously, only monospecific *Cavetia* lumachelles have been found in most Kess-Kess mounds, except in Mounds 1 and 27 (Fig. 1), where such lumachelles occur within just a few metres of fissures containing multispecies accumulations, in which *Cavetia furcifera* sclerites are only a minor component (Feist and Belka, 2018). This suggests that, at least for individuals of this species, the choice of moulting site was not random and led to species separation and the formation of monospecific sclerite accumulations. Similar moulting behaviour in trilobites has been observed in Upper Ordovician buildups in Sweden by Suzuki and Bergström (1999). The absence of clustered

scutelluid assemblages outside of fissures and cavities at Hamar Laghdad suggests that these trilobites did not commonly form large groups that moved together, but rather assembled in large groups intermittently prior to synchronous ecdysis. Other strong arguments indicating that the formation of *Cavetia* and *Platyscutellum* accumulations was closely related to moulting behaviour include the size-frequency data (Figs. 5–6). Particularly notable are the scarcity or absence of sclerites from small individuals, the limited representation of the full range of *Cavetia* size classes in individual accumulations, and the presence of characteristic “peaks” in specific size classes. Such peaks in the size-frequency distribution of trilobites are generally interpreted as corresponding to successive instars (Brezinski, 1986; Busch and Swartz, 1985; Feist et al., 2009; Palmer, 1957). Similar patterns can be observed in accumulations of exuviae from modern Alaskan Tanner crabs, which undergo mass annual migrations to moult en masse in the same locations (Stone, 1999). The absence of sclerites from small individuals—a feature commonly observed in various trilobite exuviae accumulations—may suggest that scutelluid larvae passed through several unmineralized (and possibly planktic) stages, similar to those seen in modern benthic arthropods (e.g., Lewis, 1951). Sheldon (1988) considered other possible explanations for the lack of sclerites from smaller trilobites in moulting aggregations. These include the possibilities that they (1) had disproportionately thin exoskeletons, (2) resorbed their exoskeletons entirely at ecdysis, or (3) had their exuviae consumed. A striking feature

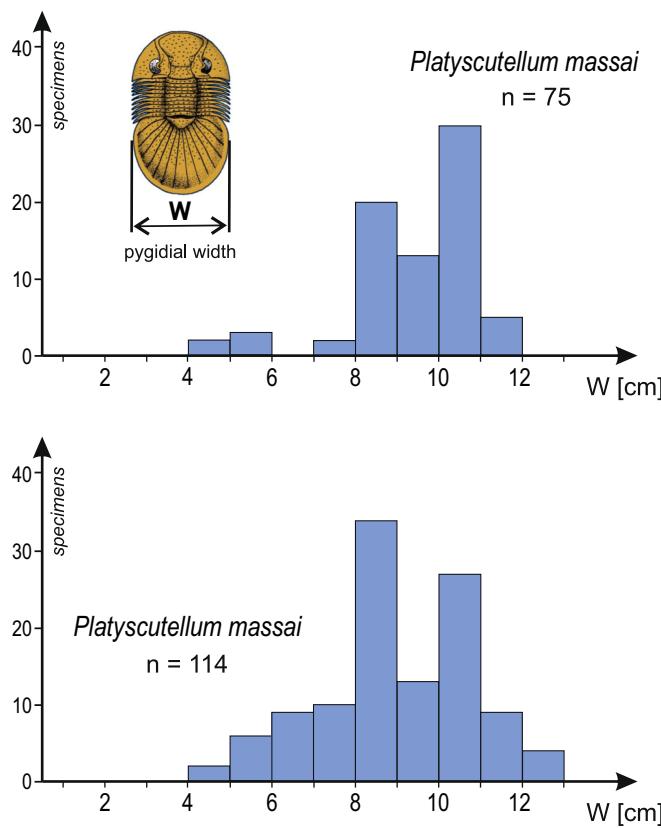


Fig. 5. Size-frequency distributions of pygidial widths for two *Platyscutellum massai* lumachelles. Note the absence of small individuals and the overrepresentation of individuals in two specific size classes.

of the size-frequency data is, first of all, the markedly different distribution characteristics among individual assemblages. While the *Platyscutellum* lumachelles exhibit similar and essentially normal distributions, with a slight negative skew and significant peaks in two size-classes (Fig. 5), the size distributions in *Cavetia* lumachelles vary between individual locations, even within the same mound (Fig. 6). The mean size, distribution shapes, and the wide range of sizes differ at particular fissures. These data suggest that when *Cavetia furcifera* aggregated for moulting, individuals segregated based on size. This indicates that these trilobites preferentially selected locations where the largest numbers of similarly sized individuals were present. In our opinion, this may have been a strategy to protect vulnerable individuals post-moult, when the absence of a hardened exoskeleton could expose them to cannibalism by larger conspecifics. Another possibility is that the mass aggregation of *Cavetia furcifera* in fissures reflected reproductive behaviour. Examples of synchronous moulting and mating are known in various modern crustaceans (for examples, see Haug et al., 2013; Sainte-Marie and Hazel, 1992; Stone, 1999). In malacostracean crustaceans, both moulting and gametogenesis are controlled by the same hormone (Raviv et al., 2008). Mass moulting coupled with mating has also been proposed for trilobites (Błażejowski et al., 2016; Brett et al., 2011; Brett et al., 2012; Gutierrez-Marco et al., 2009; Karim and Westrop, 2002; Speyer and Brett, 1985). Whether the supposed synchronised moulting described here was in fact linked to mating remains speculative. However, there is no doubt that synchronised mass moulting observed in Early Devonian scutelluids provided a selective advantage, as the gregarious behaviour of many individuals in close proximity reduces predation pressure on any one individual.

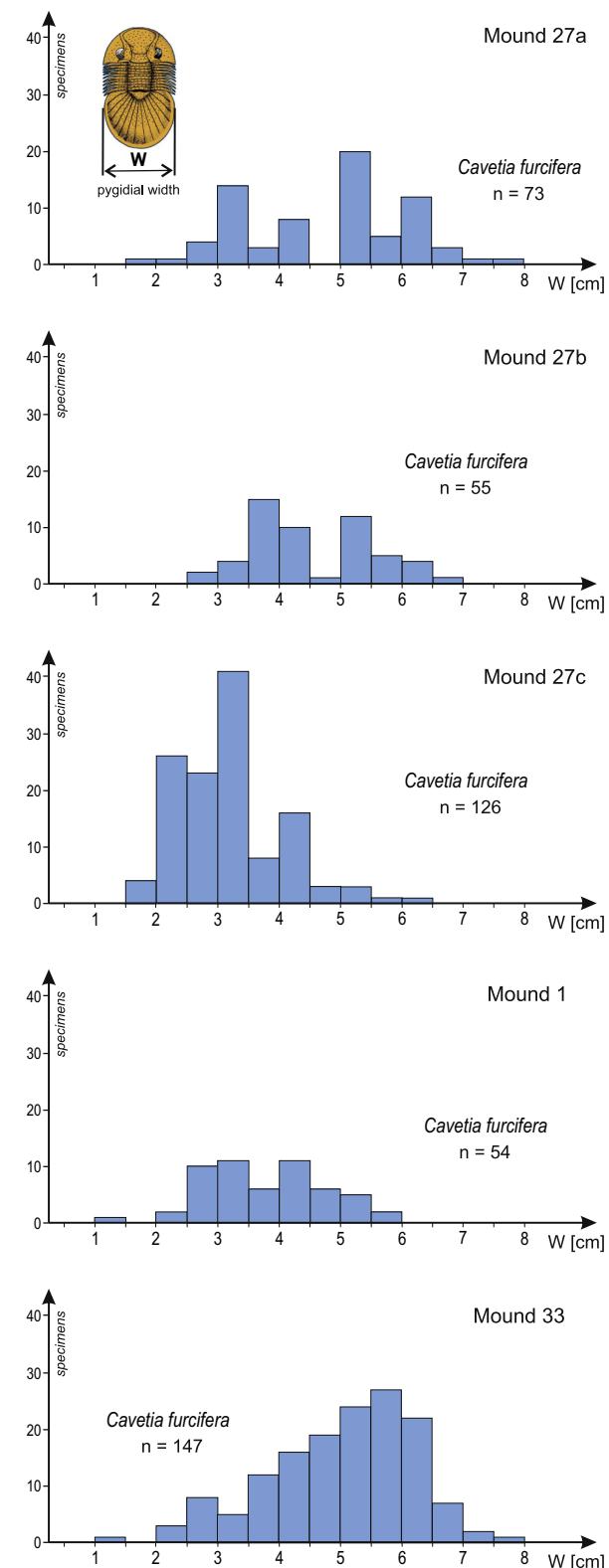


Fig. 6. Size-frequency distributions of pygidial widths for four *Cavetia furcifera* lumachelles from different vent outlets and mounds. For the location of the mounds, see Fig. 1.

7. Conclusions

The Early Devonian trilobite accumulations preserved within subseafloor fissures and cavities of the Kess-Kess elevation at Hamar

Laghdad (Morocco) provide significant insights into the behaviour, ecology, and taphonomy of scutellid trilobites *Cavetia furcifera* and *Platyscutellum massai*. These assemblages are characterised by a conspicuous absence of complete specimens and by a dominance of disarticulated exuviae, indicating mass moulting as the primary cause of accumulation. The evidence strongly suggests that these trilobites did not inhabit the vent cavities permanently but instead assembled there periodically, most likely during synchronous moulting events. Morphological features of both *Cavetia* and *Platyscutellum* species, such as well-developed eyes, large body size, and, in the case of *Cavetia furcifera*, pronounced spinosity, are inconsistent with life in subseafloor aphotic environment. These taxa were certainly adapted to illuminated marine conditions and likely used the vent cavities only temporarily, for shelter during moulting or reproductive phases. The lack of smaller specimens and the size segregation observed within the *Cavetia* assemblages suggest non-random site selection, possibly to limit predation or coordinate reproductive activity. While a definitive link between moulting and mating cannot be confirmed, it remains a plausible explanation for the observed patterns, aligning with behaviour seen in some modern arthropods.

The preferred concave-up orientation of pygidia, the bimodal nature of the sedimentary infill, and the lack of normal grading argue against current-driven redeposition and instead suggest gravitational settling within vent systems, potentially aided by intermittent hydrothermal discharge. Fragmentation of smaller sclerites further supports the interpretation of episodic, moderately turbulent fluid flow during the deposition of these lumachelles.

Taken together, the studied accumulations reveal complex behavioural adaptations in Early Devonian trilobites, including synchronised moulting, possible size-based aggregation, and temporary use of vent-associated cavities for refuge. Such behaviours likely provided advantages, particularly by reducing the risk of predation when animals are vulnerable to predators, and have contributed significantly to our understanding of trilobite paleoecology in hydrothermal environments.

CRediT authorship contribution statement

Zdzisław Belka: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Raimund Feist:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation. **Jolanta Dopieralska:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization. **Stanisław Skompski:** Writing – review & editing, Writing – original draft, Methodology, Investigation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The work was supported by the Polish National Science Centre, grant No. 2013/11/B/ST10/00243 and by the German Research Council (DFG), grant No. Be 1296/7. In addition, we are greatly indebted to the representatives of the Ministry of Energy Transition and Sustainable Development (Rabat, Morocco), Ahmed Benlakhdim, Khalid El Hmidi and Aissam El Khelifi for the work permit and logistic advice. Special thanks go to Blazej Berkowski and Michal Jakubowicz (both Adam Mickiewicz University, Poznań) for their assistance in the field and discussions. We are grateful to Prof. Shuzhong Shen, the journal's editor, Prof. Steve Westrop, and an anonymous reviewer for their insightful comments that improved the manuscript.

Data availability

Data will be made available on request.

References

- Aitken, S.A., Collom, C.J., Henderson, C.M., Johnston, P.A., 2002. Stratigraphy, paleoecology, and origin of lower Devonian (Emsian) carbonate mud buildups, Hamar Laghdad, eastern Anti-Atlas, Morocco, Africa. Bull. Can. Petrol. Geol. 50, 217–243. <https://doi.org/10.2113/50.2.217>.
- Alberti, G.K.B., 1970. Trilobiten des jüngeren siluriums sowie des unter- und mitteldevons. II. Abhandlungen der senckenbergischen naturforschenden. Gesellschaft 525, 1–233.
- Alberti, G.K.B., 1981. Scutellidae (Trilobita) aus dem unter-devon des hamar laghdad (Tafilalt, SE-Marokko) und das Alter der "mud mounds" (Ober-Zlichovium bis tiefstes Dalejum). Senckenberg. Leth. 62, 193–204.
- Alberti, G.K.B., 1982. Der Hamar Laghdad (Tafilalt, SE-Marokko), eine bedeutende Fundstätte devonischer Trilobiten. Nat. Mus. 112, 172–182.
- Allen, J.R.L., 1984. Experiments on the settling, overturning and entrainment of bivalve shells and related models. Sedimentology 31, 227–250. <https://doi.org/10.1111/j.1365-3091.1984.tb01961.x>.
- Belka, Z., 1998. Early Devonian Kess-Kess carbonate mud mounds of the eastern Anti-Atlas (Morocco), and their relation to submarine hydrothermal venting. J. Sediment. Res. 68, 368–377. <https://doi.org/10.2110/jsr.68.368>.
- Belka, Z., Berkowski, B., 2005. Discovery of thermophilic corals in an ancient hydrothermal vent community, Devonian, Morocco. Acta Geol. Pol. 55, 1–7.
- Belka, Z., Kazmierzak, M., Kaufmann, B., 1997. Tectonic control on the sedimentation, volcanic activity and the growth of mud mounds in the Palaeozoic of the eastern Anti-Atlas, Morocco, first International Conference on North Gondwanan Mid-Palaeozoic Biodynamics (IGCP Project 421), Vienna, p. 9.
- Belka, Z., Berkowski, B., Eisenmann, P., Dopieralska, J., Skompski, S., 2003. Fauna podmorskich źródeł hydrotermalnych z dewonu Maroka. Prz. Geol. 51, 246.
- Belka, Z., Berkowski, B., Jakubowicz, M., Dopieralska, J., Skompski, S., Feist, R., 2015. Life of the dead mounds: an example from the Devonian mud mounds of Hamar Laghdad (Morocco). In: 31st IAS meeting on Sedimentology, Cracow, 60.
- Belka, Z., Skompski, S., Dopieralska, J., Feist, R., 2018. Flow paths of hydrothermal vent fluids in the Devonian Kess-Kess mounds, Anti-Atlas, Morocco. N. Jb. Geol. Paläont. (Abh.) 290, 49–64. <https://doi.org/10.1127/njgpa/2018/0779>.
- Berkowski, B., 2004. Monospecific rugosan assemblage from the emsian hydrothermal vents of Morocco. Acta Palaeontol. Pol. 49, 75–84.
- Berkowski, B., 2006. Vent and mound rugose coral associations from the Middle Devonian of Hamar Laghdad (Anti-Atlas, Morocco). Geobios 39, 155–170. <https://doi.org/10.1016/j.geobios.2004.11.003>.
- Berkowski, B., Jakubowicz, M., Belka, Z., Król, J.J., Zapalski, M.K., 2019. Recurring cryptic ecosystems in lower to Middle Devonian carbonate mounds of Hamar Laghdad (Anti-Atlas, Morocco). Palaeogeogr. Palaeoclimatol. Palaeoecol. 523, 1–17. <https://doi.org/10.1016/j.palaeo.2019.03.011>.
- Błażejowski, B., Brett, C.E., Kin, A., Radwański, A., Gruszczyński, M., 2016. Ancient animal migration: a case study of eyeless, dimorphic Devonian trilobites from Poland. Palaeontology 59, 743–751. <https://doi.org/10.1111/pala.12252>.
- Brachert, T.C., Buggisch, W., Flügel, E., Hüssner, H.M., Joachimski, M.M., Tourneur, F., Walliser, O.H., 1992. Controls of mud mound formation: the early Devonian Kess-Kess carbonates of the Hamar Laghdad, Anti-Atlas, Morocco. Geol. Rundsch. 81, 15–44. <https://doi.org/10.1007/BF01764537>.
- Brett, C.E., Allison, P.A., Hendy, A.J.W., 2011. Comparative taphonomy and sedimentology of small-scale mixed carbonate/siliciclastic cycles: synopsis of phanerozoic examples. In: Allison, P.A., Bottjer, D.J. (Eds.), Taphonomy: Process and Bias through Time. Springer, Netherlands, Dordrecht, pp. 107–198.
- Brett, C.E., Zambito IV, J.J., Hunda, B.R., Schindler, E., 2012. Mid-Paleozoic trilobite Lagerstätten: models of diagenetically enhanced obrution deposits. Palaios 27, 326–345. <https://doi.org/10.2110/palo.2011.p11-040r>.
- Breznitski, D.K., 1986. An opportunistic upper ordovician trilobite assemblage from Missouri. Lethalia 19, 315–325. <https://doi.org/10.1111/j.1502-3931.1986.tb00746.x>.
- Busch, R.M., Swartz, F.M., 1985. Molting and description of a new homalonotid trilobite from Pennsylvania. J. Paleontol. 59, 1062–1074.
- Chatterton, B.D.E., Collins, D.H., Ludvigsen, R., 2003. Cryptic behaviour in trilobites: cambrian and Silurian examples from Canada and other related occurrences. Spec. Pap. Palaeontol. 70, 157–173.
- Chlupáč, I., 1983. Trilobite assemblages in the Devonian of the Barrandian area and their relations to palaeoenvironments. Geol. Palaeontol. 17, 45–73.
- Corrales-García, A., Esteve, J., Zhao, Y., Yang, X., 2020. Synchronized moulting behaviour in trilobites from the Cambrian Series 2 of South China. Sci. Rep. 10, 14099. <https://doi.org/10.1038/s41598-020-70883-5>.
- Daley, A.C., Drage, H.B., 2016. The fossil record of ecdysis, and trends in the moulting behaviour of trilobites. Arthropod Struct. Dev. 45, 71–96. <https://doi.org/10.1016/j.asd.2015.09.004>.
- Dopieralska, J., 2009. Reconstructing seawater circulation on the Moroccan shelf of Gondwana during the late Devonian: evidence from Nd isotope composition of conodonts. Geochem. Geophys. Geosyst. 10, Q03015. <https://doi.org/10.1029/2008gc002247>.
- Ebbestad, J.O.R., Rushton, A.W.A., Stein, M., Weidner, T., 2013. A paradoxidid moulting ensemble from the Cambrian of Sweden. GFF 135, 18–29. <https://doi.org/10.1080/11035897.2012.737365>.

- Feist, R., 2001. Clustered trilobite assemblages formed under shelter: case studies of paleoecological behaviour. Third International Symposium on Trilobites and their Relatives, Oxford, p. 12.
- Feist, R., Belka, Z., 2018. Late Emsian (Devonian) trilobite communities from the Kess-Kess mounds, Hamar Laghdad (Anti-Atlas, Morocco). N. Jb. Geol. Paläont. (Abh.) 290, 277–290. <https://doi.org/10.1127/njgpa/2018/0784>.
- Feist, R., Chatterton, B.D.E., 2015. Kolihaipeltina trilobites, the spiniest scutelluids from the eastern Anti-Atlas (Morocco, early Devonian): evolution, environment and classification. Pap. Palaeontol. 1, 255–287. <https://doi.org/10.1002/spp2.1015>.
- Feist, R., McNamara, K.J., Cröner, C., Leroosey-Aubril, R., 2009. Patterns of extinction and recovery of phacopid trilobites during the Frasnian-Famennian (late Devonian) mass extinction event, Canning Basin, Western Australia. Geol. Mag. 146, 12–33. <https://doi.org/10.1017/S0016756808005335>.
- Fortey, R.A., Owens, R.M., 1997. Evolutionary history. In: Kaesler, R.L. (Ed.), Treatise on Invertebrate Paleontology, part O, Arthropoda, 1. Trilobita, revised. Geological Society of America & University of Kansas Press, Boulder & Lawrence, pp. 349–387.
- Franchi, F., Cavalazzi, B., Pierre, C., Barbieri, R., 2014. New evidences of hydrothermal fluids circulation at the Devonian Kess-Kess mounds, Hamar Laghdad (eastern Anti-Atlas, Morocco). Geol. J. 50, 634–650. <https://doi.org/10.1002/gj.2582>.
- Germanovich, L.N., Hurt, R.S., Smith, J.E., Genn, G., Lowell, R.P., 2015. Measuring fluid flow and heat output in seafloor hydrothermal environments. J. Geophys. Res. Solid Earth 120, 8031–8055. <https://doi.org/10.1002/2015JB012245>.
- Glaeser, G., Paulus, H.F., 2015. The Evolution of the Eye. Springer Cham.
- Gutierrez-Marco, J.C., Sa, A.A., Garcia-Bellido, D.C., Rabano, I., Valerio, M., 2009. Giant trilobites and trilobite clusters from the Ordovician of Portugal. Geology 37, 443–446. <https://doi.org/10.1130/g25513a.1>.
- Haug, J.T., Caron, J.-B., Haug, C., 2013. Demecology in the Cambrian: synchronized molting in arthropods from the Burgess Shale. BMC Biol. 11, 64. <https://doi.org/10.1186/1741-7007-11-64>.
- Hawle, I., Corda, A.J.C., 1847. Prodrom einer monographie der böhmischen Trilobiten. Königl. Böhmisches Gesellsch. Wissenschaft. Abhandlungen 5, 1–176.
- Henningsmoen, G., 1975. Moulting in trilobites. Fossils Strata 4, 179–200. <https://doi.org/10.18261/8200049639-1975-10>.
- Hesselbo, S.P., 1987. The biostratigraphy of Dikelocephalus sclerites: implications for the use of trilobite attitude data. Palaios 2, 605–608. <https://doi.org/10.2307/3514497>.
- Hryniewicz, K., Jakubowicz, M., Belka, Z., Dopierańska, J., Kain, A., 2017. New bivalves from a Middle Devonian methane seep in Morocco: the oldest record of repetitive shell morphologies among some seep bivalve molluscs. J. Syst. Palaeontol. 15, 19–41. <https://doi.org/10.1080/14772019.2015.1136900>.
- Hughes, H.E., Thomas, A.T., 2008. Trilobite associations and taphonomy of the Silurian reefs of eastern North Greenland. Cuadernos Museo GeoMinero 9, 189–194.
- Hughes, H.E., Thomas, A.T., 2011. Trilobite associations, taphonomy, lithofacies and environments of the Silurian reefs of North Greenland. Palaeogeogr. Palaeoclimatol. Palaeoecol. 302, 142–155. <https://doi.org/10.1016/j.palaeo.2010.12.009>.
- Jakubowicz, M., Berkowski, B., Belka, Z., 2013. Devonian rugose coral 'Amplexus' and its relation to submarine fluid seepage. Palaeogeogr. Palaeoclimatol. Palaeoecol. 386, 180–193. <https://doi.org/10.1016/j.palaeo.2013.05.020>.
- Jakubowicz, M., Berkowski, B., Belka, Z., 2014. Cryptic coral-crinoid "hanging gardens" from the Middle Devonian of southern Morocco. Geology 42, 119–122. <https://doi.org/10.1130/g35217.1>.
- Karim, T., Westrop, S.R., 2002. Taphonomy and paleoecology of Ordovician trilobite clusters, Bromide Formation, south-Central Oklahoma. Palaios 17, 394–402. [https://doi.org/10.1669/0883-1351\(2002\)017<394:Tapoot>2.0.Co;2](https://doi.org/10.1669/0883-1351(2002)017<394:Tapoot>2.0.Co;2).
- Lask, P.B., 1993. The hydrodynamic behavior of sclerites from the trilobite Flexicalymene meeki. Palaios 8, 219–225. <https://doi.org/10.2307/3515144>.
- Lewis, J.B., 1951. The phyllosoma larvae of the spiny lobster *Panulirus argus*. Bull. Mar. Sci. Gulf Caribb. 1, 89–103.
- Mikulic, D.G., 1981. Trilobites in Paleozoic carbonate buildups. Lethaia 14, 45–56. <https://doi.org/10.1111/j.1502-3931.1981.tb01073.x>.
- Mišík, M., Sýkora, M., Aubrecht, R., 1994. Middle Jurassic scarp breccias with clefts filled by Oxfordian and Valanginian-Hauterivian sediments, Krasin near Dolna Suca (Pieniny Klippen Belt, Slovakia). Geol. Carpath. 45, 343–356.
- Mounji, D., Bourque, P.A., Savard, M.M., 1998. Hydrothermal origin of Devonian conical mounds (kess-kess) of Hamar Lakhdad Ridge, Anti-Atlas, Morocco. Geology 26, 1123–1126.
- Olempska, E., Belka, Z., 2010. Hydrothermal vent myodocopid ostracods from the Eifelian (Middle Devonian) of southern Morocco. Geobios 43, 519–529. <https://doi.org/10.1016/j.geobios.2010.06.001>.
- Palmer, A.R., 1957. Ontogenetic development of two olenellid trilobites. J. Paleontol. 31, 105–128.
- Paterson, J.R., Jago, J.B., Brock, G.A., Gehling, J.G., 2007. Taphonomy and palaeoecology of the emuellid trilobite Balcoracania dailyi (early Cambrian, South Australia). Palaeogeogr. Palaeoclimatol. Palaeoecol. 249, 302–321. <https://doi.org/10.1016/j.palaeo.2007.02.004>.
- Raviv, S., Parnes, S., Sagi, A., 2008. Coordination of reproduction and molt in decapods. In: Mente, E. (Ed.), Reproductive Biology of Crustaceans. CRC Press, Boca Raton, p. 26.
- Sainte-Marie, B., Hazel, F., 1992. Moulting and mating of snow crabs, *Chionoecetes opilio* (*O. Fabricius*), in shallow waters of the northwestern Gulf of Saint Lawrence. Can. J. Fish. Aquat. Sci. 49, 1282–1293. <https://doi.org/10.1139/f92-144>.
- Sheldon, P.R., 1988. Trilobite size-frequency distributions, recognition of instars, and phyletic size changes. Lethaia 21, 293–306. <https://doi.org/10.1111/j.1502-3931.1988.tb01759.x>.
- Smart, P.L., Palmer, R.J., Whitaker, F., Wright, V.P., 1988. Neptunian dikes and fissure fills: an overview and. In: James, N.P., Choquette, P.W. (Eds.), Paleokarst. Springer, New York, New York, NY, pp. 149–162.
- Šnajdr, M., 1960. Studie o čeledi Scutellidae (Trilobitae). Rozpravy Ústředního ústavu Geol. 26, 1–263.
- Speyer, S.E., Brett, C.E., 1985. Clustered trilobite assemblages in the Middle Devonian Hamilton Group. Lethaia 18, 85–103. <https://doi.org/10.1111/j.1502-3931.1985.tb00688.x>.
- Stone, R.P., 1999. Mass molting of Tanner crabs *Chionoecetes bairdi* in a Southeast Alaska estuary. Alaska Fish. Res. Bull. 6, 19–28.
- Suzuki, Y., Bergström, J., 1999. Trilobite taphonomy and ecology in Upper Ordovician carbonate buildups in Dalarna, Sweden. Lethaia 32, 159–172. <https://doi.org/10.1111/j.1502-3931.1999.tb00536.x>.
- Termier, G., Termier, H., 1950. Paléontologie Marocaine II. Invertébrés de l'ère primaire, IV, Annelides, arthropodes, échinodermes, conularides et graptolithes. Notes et Mémoires. Service des Mines et de la Carte Géol. Maroc 79, 1–279.
- Wendt, J., 1985. Disintegration of the continental margin of northwestern Gondwana: late Devonian of the eastern Anti-Atlas (Morocco). Geology 13, 815–818. [https://doi.org/10.1130/0091-7613\(1985\)13<815:DOTCMO>2.0.CO;2](https://doi.org/10.1130/0091-7613(1985)13<815:DOTCMO>2.0.CO;2).
- Westrop, S.R., Rudkin, D.M., 1999. Trilobite taphonomy of a Silurian reef: Attawapiskat Formation, northern Ontario. Palaios 14, 389–397. <https://doi.org/10.2307/3515464>.