Pellets independent of or associated with Bohemian Ordovician body fossils

JANA BRUTHANSOVÁ and PETR KRAFT

Bruthansová, J. and Kraft, P. 2003. Pellets independent of or associated with Bohemian Ordovician body fossils. *Acta Palaeontologica Polonica* 48 (3): 437–445.

Clusters of small cylindrical pellets occur sporadically in Ordovician strata in Bohemia. They are assigned to the ichnogenus *Tomaculum* and occur in lenticular or elongated accumulations. Similar accumulations are associated with body fossils including the cephala of the trilobites *Ormathops atavus*, *Pricyclopyge binodosa*, and *Parabarrandia crassa*. The clusters are situated under the glabella and in the anterior parts of the cephalon but their exact position is variable in different cases. Accumulations of pellets have also been studied inside shells of hyoliths, bellerophontids, and echinoderm thecae. They probably represent the faeces of either scavengers feeding on soft parts or organisms using cephalic shields and other shells as hiding places. An interpretation of these pellets as trilobite eggs is highly improbable.

Key words: Ichnofossils, pellets, palaeoecology, taphonomy, trilobites, Ordovician, Bohemia.

Jana Bruthansová [jana.bruthansova@nm.cz], Department of Palaeontology, National Museum, Václavské nám. 68, 115 79 Prague 1, Czech Republic;
Petr Kraft [kraft@natur.cuni.cz], Charles University, Institute of Geology and Palaeontology, Albertov 6, 128 43 Prague 2, Czech Republic.

Introduction

Clusters of small cylindrical pellets, about 1 mm long and 0.3 mm in diameter occur sporadically in Ordovician strata in Bohemia. They have been found in separate lenticular clusters, elongated rows or associated with body fossils of several animal groups. They have been commonly assigned to the ichnospecies *Tomaculum problematicum* Groom, 1902. Unfortunately, the pellets are not particularly common in museum collections; evidently previous collectors have avoided them. Nevertheless, our study is based on 30 clusters of pellets, of which two thirds are associated with shells of body fossils. The aim of this paper is to describe, characterize their occurrence patterns and interpret the origin of all the specimens.

The investigated material is housed in the palaeontological collections of the National Museum in Prague (NM), Czech Geological Survey (CGU) and Museum of B. Horák in Rokycany (MR).

History of research

Pellets from the Bohemian Ordovician were first described and figured by Barrande (1872) who mentioned several clusters of different sizes, including some associated with trilobites. He assumed most to be eggs of trilobites, although he considered a cluster of pellets within the glabella of *Parabarrandia crassa* (Barrande 1872: pl. 11: 6, 11) to be eggs of a crustacean. Hermite (1878) also described objects similar to those discussed by Barrande. Several years later, Walcott (1879) responded to Barrande's paper and described sections cut through the trilobite *Ceraurus pleurexanthemus*. He identified numerous dark, round and oblong minute spots filling the visceral cavity between the dorsal exoskeleton, hypostoma, and ventral membrane. He also found similar clusters of spots in the sparry infilling of the axial appendages and visceral cavity of the thorax. He explained their presence as due to scattering of organic matter. Because of the mode of aggregation of these objects and close resemblance to the pellets forming the clusters described by Barrande (1872), Walcott judged that both represent the eggs of trilobites. Unfortunately, his description has not been accompanied by illustrations or figures.

Clusters of pellets were formally described in the beginning of 20th century by Groom (1902) as *Tomaculum problematicum*, leaving open the question of their origin. Since then, a faecal-origin attributed to various invertebrates has been the preferred interpretation (e.g., Frič 1908; Thoral 1935; Richter and Richter 1939a, b, 1941; Volk 1941; Péneau 1941; Radig 1964; Scott 1977; Gutiérrez-Marco 1984; Mikuláš 1991; Gutiérrez-Marco et al. 1996). In the older literature some authors did not differentiate between faecal pellets and coprolites whereas others used the latter term.

Gutiérrez-Marco et al. (1996) interpreted specimens of *T. problematicum* as coprolites of arthropods, possibly trilobites. Gutiérrez-Marco (1984) described the new ichnospecies *Cilindrotomaculum melendezi* from the Llanvirn of Spain. Observed inside mollusc shells, these ichnofossils were interpreted as coprolites probably of polychaetan annelids. Horný (1998a, b) mentioned the pellets infilling

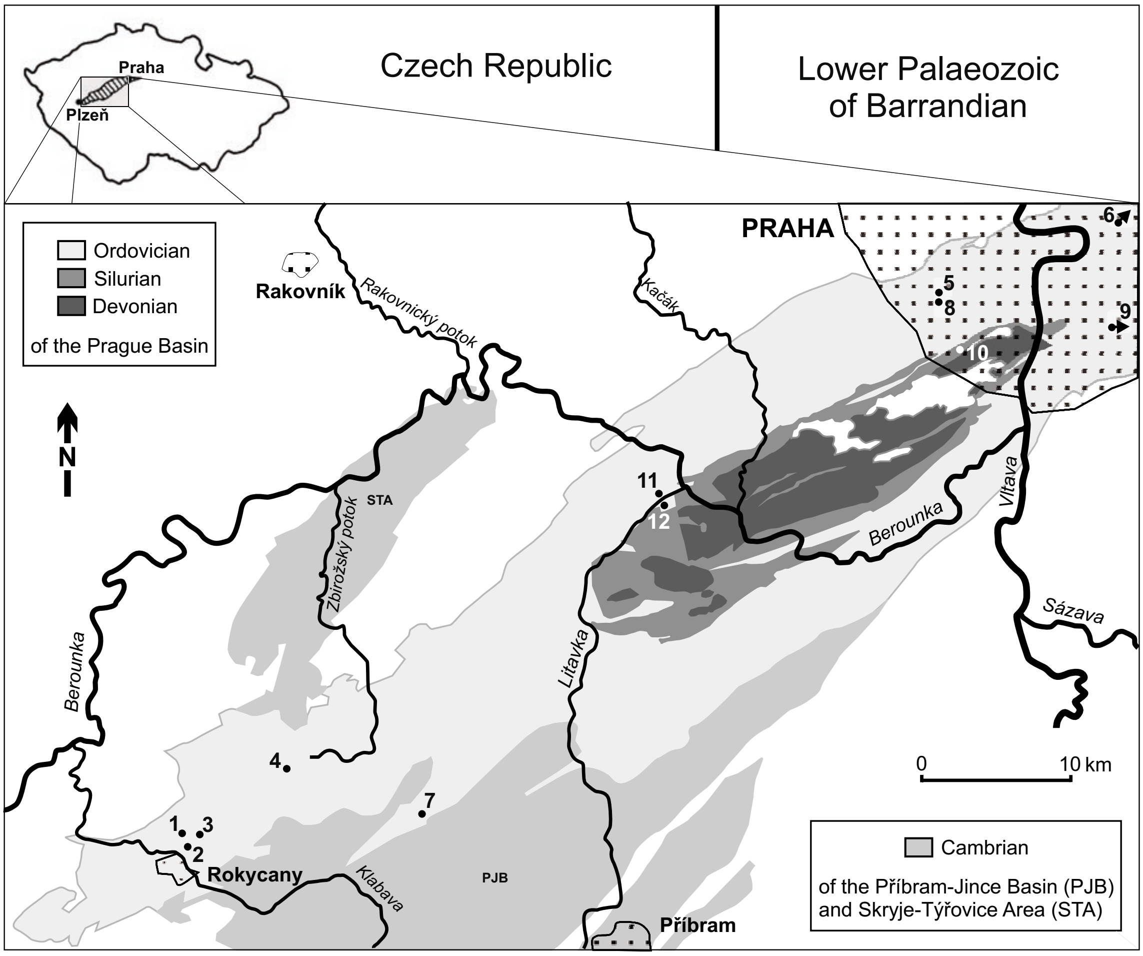

Fig. 1. Map showing the sample localities and position of localities. Šárka Formation: 1, Osek; 2, Díly; 3, Borek; 4, Těškov; 5, Praha-Šárka; 6, Popovice near Brandýs nad Labem. Dobrotivá Formation: 7, Svatá Dobrotivá; 8, Praha-Šárka (pole u vily). Zahořany Formation: 9, Dubeč. Bohdalec Formation: 10, Nová Ves. Králův Dvůr Formation: 11, Králův Dvůr, 12; Lejškov.

mollusc shells and interpreted them as faecal pellets of infaunal inhabitants of empty shells. Hofmann (1972) described pellets from the Lower Ordovician of Québec, which were found in the branching burrows. He preferred a faecal origin, although he noted the less probable alternative that the tunnels represent nests containing eggs.

Recently, Eiserhardt et al. (2001) published a comprehensive revision of *Tomaculum* and restricted this ichnogenus to clusters of pellets formed on the sediment surface. Pellet clusters of other origin or isolated pellets are of different systematic classification. They supposed *Tomaculum* pellets to be coprolites of epibenthic animals with excremental behaviour similar to gastropods.

Tomaculum problematicum Groom, 1902 has been recorded from different palaeogeographical areas. In peri-Gondwana, it is known from the Arenig of Spain (Thoral 1935), Llanvirn of Spain (Gutiérrez-Marco et al. 1996; Radig 1964), Portugal (Couto et al. 1986), Germany (Koch 1999), etc. (for complete list see Eiserhardt et al. 2001). From the Bohemian Ordovician it has been described and/or figured from the Šárka Formation (Barrande 1872), Dobrotivá Formation (Mikuláš 1991) and Králův Dvůr Formation (Barrande, 1872).

Pellet specimens from Bohemia and their occurrence patterns

All the studied specimens come from the Ordovician of the Prague Basin (Barrandian area, Central Bohemia, Czech Republic) (Fig. 1). They have been recorded from the Middle and Upper Ordovician. However, they do not occur throughout; they are known only from a few stratigraphical levels: the Šárka Formation (Darriwilian, Llanvirn), Dobrotivá Formation (Dobrotivian, upper Llanvirn/lower Caradoc), Zahořany Formation (upper Berounian, upper Caradoc) and Králův Dvůr Formation (Kralodvorian, lower Ashgill) (Fig. 2). The studied specimens occur in shales or in siliceous nodules and are always preserved in three-dimensionally, regardless of the enclosing lithology.

In the course of our investigations clusters of small cylindrical pellets of different size have been studied; only some are figured here. Several patterns of occurrence are distinguished (lists of specimens are stratigraphically and subsequently geographically ordered):

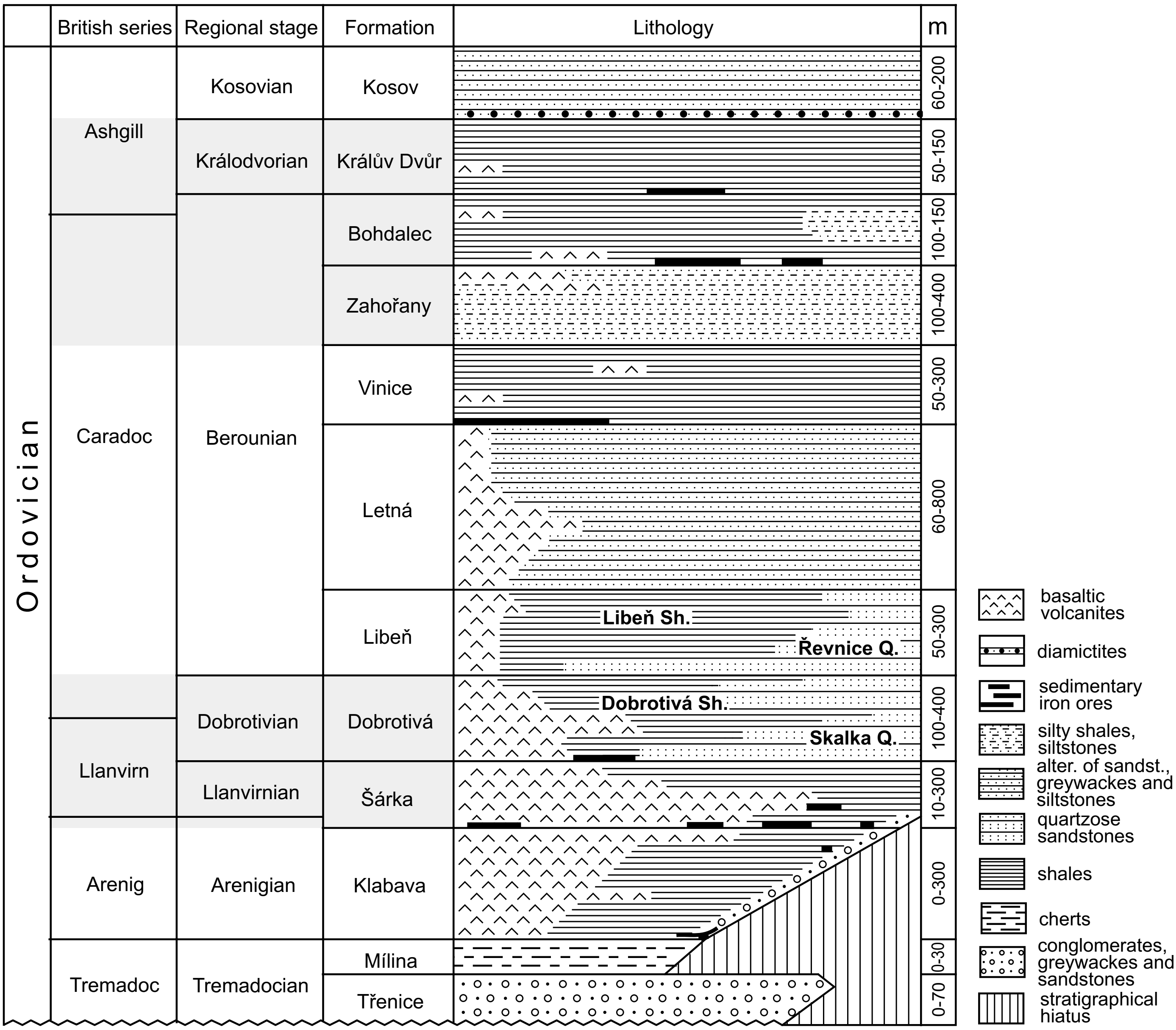

Fig. 2. The Ordovician stratigraphy in the Prague Basin with shaded stratigraphic levels of occurrences of pellets.

A. Pellets in isolated lenticular clusters

This group is represented only by one specimen. The cluster is an irregular, lenticular accumulation of pellets showing no elongation.

NM L 23514. Locality Králův Dvůr; Králův Dvůr Formation; dark shale. This specimen was figured and described by Barrande (1872: pl. 18: 32–33) and together with two other clusters of pellets was interpreted as the trilobite eggs (see above). About 30 cylindrical pellets are visible on the surface of shale in an accumulation 12.0 mm long and 6.0 wide. Pellets are 2.3–2.5 mm long and 0.8–0.9 mm wide. The long axis of most of them is parallel with the bedding plane but they show no apparent prevailing orientation. Their surface is smooth.

B. Pellets in isolated rows

Seven specimens were studied. The pellets form rows of different lengths and shapes. The arrangement of pellets in rows is mostly chaotic showing no prevailing orientation. Some pellets overlie each other. No apparent original wall surrounding the rows has been observed.

MR 9614. Locality Rokycany; Šárka Formation; siliceous nodule (Fig. 5G). The row of some 25 pellets determines the shape of the nodule. Pellets reaching 2.3–2.5 mm in length and 0.8–0.9 mm in diameter occur in the 16.0 mm long and 6.5 mm wide row. The pellets show some orientation. At both ends of the row there is a tendency for their long axes to be parallel with the long axis of the row. However, in the central part of the row, pellets are markedly par-

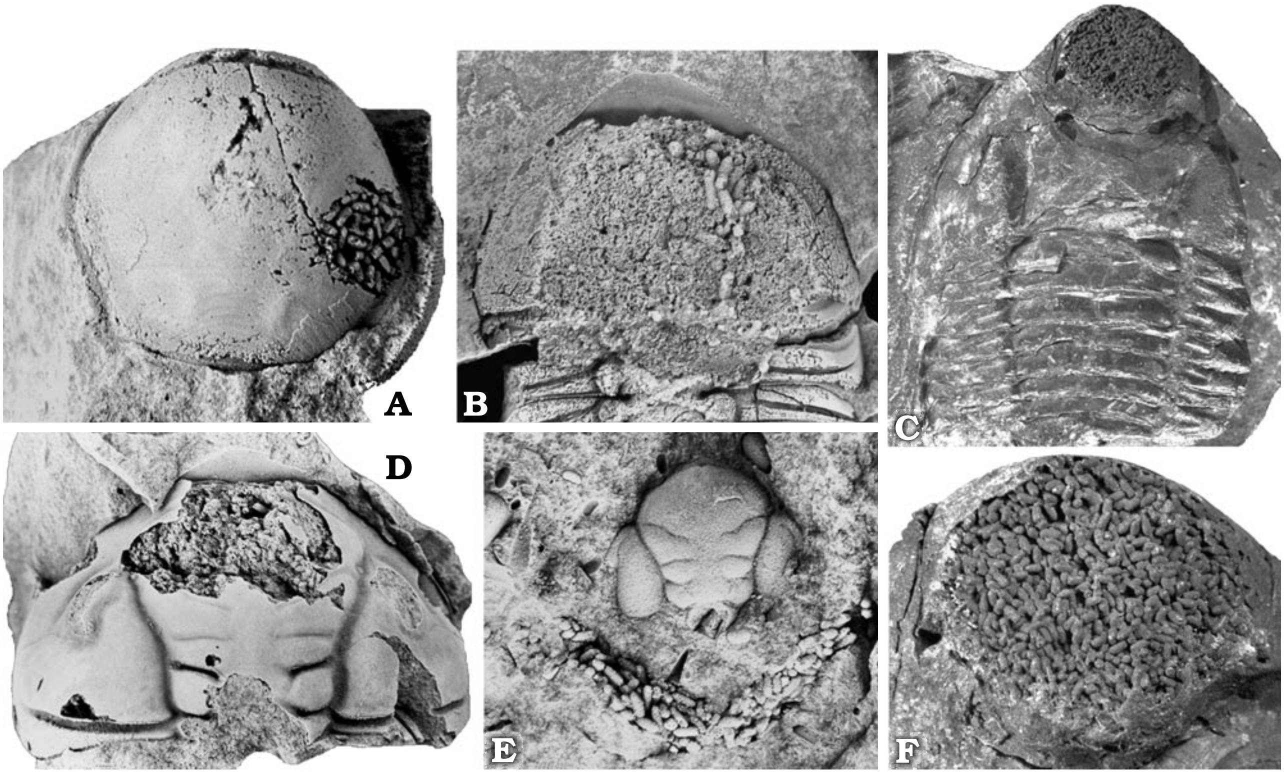

Fig. 3. Clusters of pellets, especially associated with trilobites (**A**–**D**, **F**). **A**. *Pricyclopyge binodosa* (Salter, 1859); incomplete cephalon with the accumulation of pellets visible in the lateral part of the glabella; NM L 35062; Osek; Šárka Formation; × 4.7. **B**. *Ormathops atavus* (Barrande, 1872); cephalon with part of thorax and pellets; MR 529; Osek; Šárka Formation; × 2.5. **C**, **F**. *Parabarrandia crassa* (Barrande, 1872); NM L 16862; Sv. Dobrotivá; Dobrotivá Formation. **C**. Cephalothorax with hundreds of pellets in the anterior part of cephalon; × 1.4. **F**. Detail of the anterior part of cephalon with pellets; × 3.6. **D**. *Ormathops atavus* (Barrande, 1872); cephalon with pellets in its anterior part; NM L 36007; Díly; Šárka Formation; × 2.7. **E**. *Tomaculum problematicum* Groom, 1902; S-shaped accumulation of pellets; the nearby trilobite cranidium is *Ormathops atavus*; NM L 23513; Osek; Šárka Formation; × 3.5. All specimens from the Ordovician of the Prague Basin, Czech Republic.

allel with their long axes perpendicular to the axis of the row.

NM L 23513. Locality Osek; Šárka Formation; siliceous nodule (Fig. 3E). This slightly curved limonitized accumulation was figured by Barrande (1872: pl. 18: 30–31). It is composed of several tens of minute cylindrical pellets. There is an incomplete cephalon of the trilobite *Ormathops atavus* (Barrande, 1872) situated near this row. The overall length of the row is 16.5 mm and the average width ranges between 2.0–3.0 mm. The pellets are small, 1.1–1.2 mm long and 0.5 mm in diameter.

MR 9615. Locality Díly; Šárka Formation; siliceous nodule (Fig. 5D). The row is curved, 16.0 mm long and 1.5 mm wide, and contains about 30 minute pellets The pellets are covered by limonite and this mineral marks the limits of the whole accumulation. The pellets are 0.8–1.0 mm long and 0.4–0.5 mm in diameter and show no prevailing orientation.

NM L 36135. Locality Borek-Volduchy; Šárka Formation; siliceous nodule. The row (17.0 mm long and 3.5 mm in diameter) contains some 15 large pellets with a strongly limonitized and weathered surface. The length of the pellets varies from 2.0–3.9 mm and the diameter from 0.9–1.0 mm.

NM L 36138. Locality Těškov; Šárka Formation; siliceous nodule. The preserved part of the row (16.0 mm in length and 7.0 mm in diameter) is formed by at least by 25 large pellets reaching the largest dimensions of all the investigated specimens: 3.0–3.8 mm in length, 0.9–1.1 mm in diameter. Most of the pellets are orientated with their long axis parallel with the elongation of the row.

NM L 36487. Locality Nová Ves; Bohdalec Formation; black shale. Flattened accumulation (probably originally of circular outline), 21.0 × 5.0 mm, comprising several tens of small 3-D pellets. They show no prevailing orientation although they seem to be parallel with the bedding. The pellets have a smooth surface and are 1.8–2.0 long and 0.8–0.9 mm in diameter.

NM L 27724. Locality Lejškov; Králův Dvůr Formation; dark shale. This row, 22.0 mm long and 3–6.5 mm in diameter, contains several tens of minute pellets. This specimen was figured and described by Frič (1908: pl. 10: 12). The space between pellets is secondarily limonitized. Individual pellets are large, reaching lengths of 2.0–2.3, and 0.5–0.6 mm in diameter, with smooth surfaces. Most are parallel to the bedding plane but they show no prevailing orientation.

C. Pellets inside another ichnofossil

Pellets of various sizes are in clusters or dispersed in the infill of tube of ichnofossils with thickened walls. In one case they

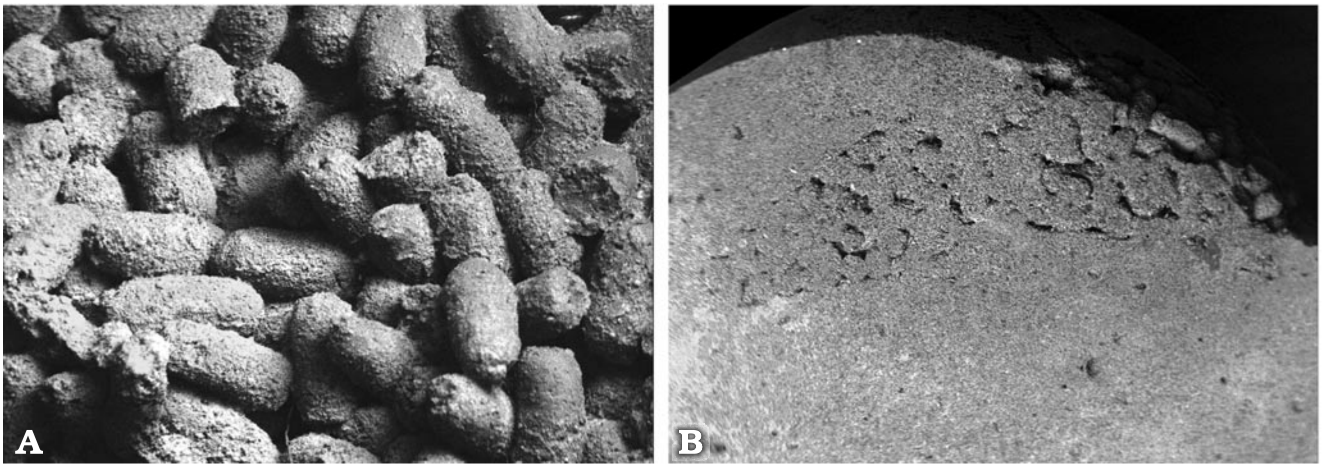

Fig. 4. SEM photographs of clusters of pellets. **A**. Detail of pellets in *Parabarrandia crassa* (Barrande, 1872), note that in the terminal parts of some pellets there are indications of central canals; NM L 16862, overall views of specimen are figured in Fig. 3C and F; × 21. **B**. Cross section through the cephalon of *Pricyclopyge binodosa* (Salter, 1859) showing arrangement of pellets inside the interior space of the glabella; NM L 35062, overall view of specimen is figured in Fig. 3A; orientation of the trilobite exoskeleton is dorsal side up, the cross section is oriented perpendicularly to the sagittal axis of the trilobite specimen; × 10.

have been observed among young trilobites *Placoparia cambriensis* Hicks, 1875.

NM L 33373. Locality Osek; Šárka Formation; siliceous nodule. Unusual specimen of trace fossil ?*Scolithos* ichnosp. in the infill of which are several tens of young holaspids of *Placoparia cambriensis* and several hundred minute pellets. The dimensions of the pellets are: 0.7 mm in length and 0.2 mm in diameter. This discovery was recently described by Mikuláš and Slavíčková (2002).

NM L 36486. Locality Díly; Šárka Formation; siliceous nodule. Longitudinal remnant of an ichnofossil preserved as a cavity with a "sponge-like" material thickening its wall. Inside the cavity there is a small cluster of at least ten pellets, 3.5 mm long and 1.1 mm in diameter.

D. Pellets associated with body fossils

Most studied accumulations of pellets are associated with body fossils of different animal groups. They usually fill (fully or partly) interiors or internal cavities of shells. Accumulations of pellets only rarely occur with exoskeletons of trilobite species. The pellets of approximately equal dimensions or smaller associated with trilobites have also been observed in the interiors of shells of several animal groups (for published data see Horný 1998a, b).

Trilobites.—Five Ordovician trilobite specimens associated with pellets have been found. They come only from the Šárka and Dobrotivá formations (Llanvirnian) and belong to four species: *Parabarrandia crassa* (Barrande, 1872), *Pricyclopyge binodosa* (Salter, 1859), *Ormathops atavus* (Barrande, 1872). Pellets are predominantly placed in the visceral cavities of cephalic shields. The length of the pellets ranges from 1.0 to 2.0 mm. They occur in numbers of 10 to 100.

MR 529. Locality Osek; Šárka Formation; siliceous nodule (Fig. 3B). Internal mould of a complete specimen of *Ormathops atavus*, limonitized and covered by dense and minute *Arachnostega*-like ichnofossils. Some portions of the mould are broken off showing a porous, "sponge-like" infill of interior cavities. In the visceral cavity of the cephalon there are about seventeen pellets. They are relatively large, 2.0–2.3 mm long and 0.7 mm in diameter, and are arranged predominantly in row parallel to the sagittal line, below the left margin of the glabella. Most of the pellets in the row are oriented with their long axes parallel with the elongation of the row. The whole internal mould of trilobite including pellets is strongly weathered and limonitized.

NM L 36007. Locality Díly; Šárka Formation; siliceous nodule (Fig. 3D). The internal mould of the weathered and limonitized cephalic shield of *Ormathops atavus* is broken off anteriorly revealing about 25 strongly weathered pellets inside the porous, "sponge-like" matrix. They are medium sized, reaching 1.2 mm in length and 0.3 mm in diameter. The accumulation of pellets shows no prevailing arrangement.

MR 12779. Locality Těškov; Šárka Formation; siliceous nodule. The internal mould of a cephalon of *O. atavus*, is broken off anteriorly revealing 5 pellets in the porous "sponge-like" matrix. The pellets are approximately 1.3 mm long and 0.55 mm in diameter. The trilobite and pellets are strongly weathered and limonitized.

NM L 35062. Locality Praha-Šárka; Šárka Formation; siliceous nodule (Figs. 3A, 4B). The cluster is associated with an almost complete cephalon of *Pricyclopyge binodosa* with its first thoracic segment. Cephalon and especially eye are covered by minute *Arachnostega*-like ichnofossils. The cluster of pellets (about 40) is observable on the left part of the internal mould of the glabella, i.e., reaching the internal surface of the exoskeleton near the left eye. Most of the pellets lie parallel with the surface of the exoskeleton. The cross-section (Fig. 4B) of the glabella shows that pellets near the surface of the exoskeleton are only the terminal part of a larger

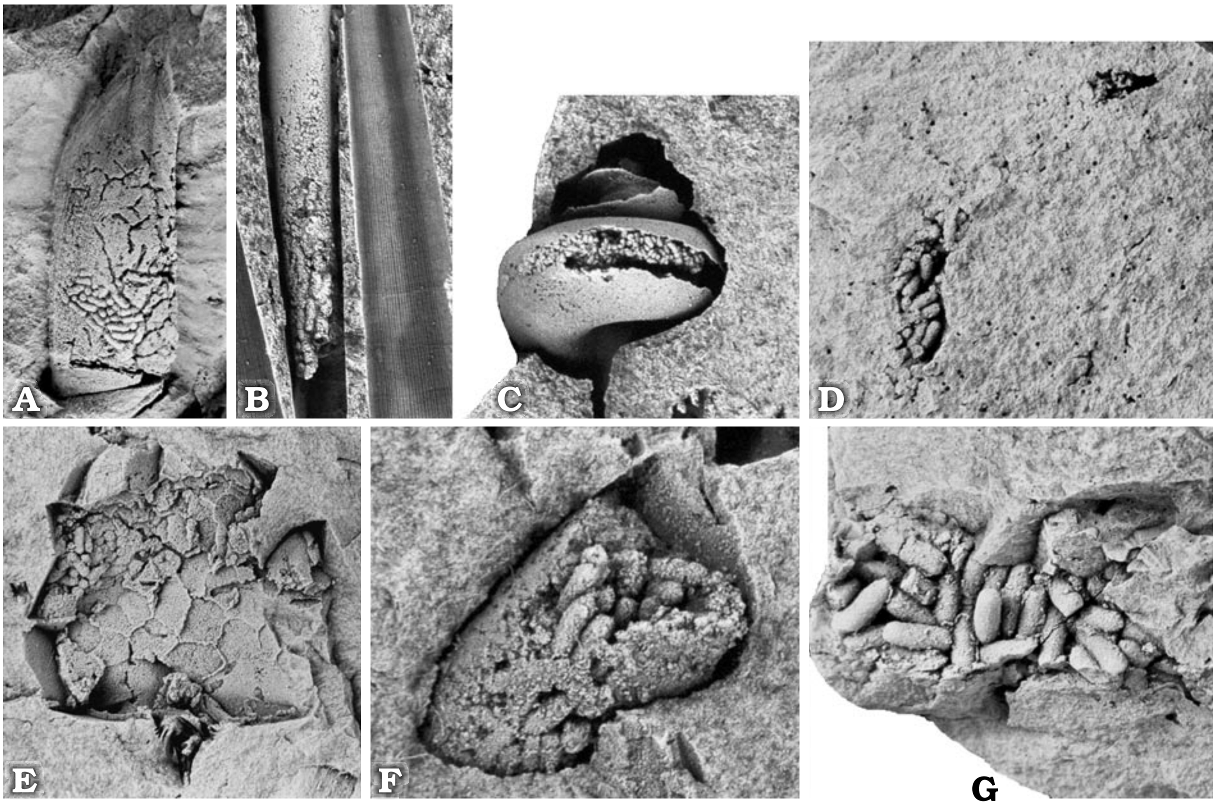

Fig. 5. Clusters of pellets associated with echinoderms (**A**, **E**), hyolithids (**B**, **F**), gastropods (**C**), and independent of body fossils (**D**, **G**). **A**. *Sagittacystis prima* (Barrande, 1887); specimen with pellets in the posterior part of the plastron; NM L 36008; Osek; Šárka Formation; × 2.5. **B**. *Bactrotheca teres* (Barrande, 1867); specimen with several pellets in the adapertural portion of the shell; NM L 36137; Praha-Šárka (pole u vily); Dobrotivá Formation; × 5.4. **C**. *Trochonema excavatum* Barrande *in* Perner, 1903; shell with one convolution filled by thousands of pellets; NM L 36502; Dubeč; Zahořany Formation; × 10.3. **D**. *Tomaculum problematicum* Groom, 1902; row with several tens of pellets; MR 9615; Díly; Šárka Formation; × 3.3. **E**. *Mitrocystites mitra* Barrande, 1887; specimen with cluster of pellets in the antero-lateral part of theca; CGU JH 1199; Díly; Šárka Formation; × 2.7. **F**. *Elegantilites elegans* (Barrande, 1847); specimen with several pellets; MR 22454; Díly; Šárka Formation; × 10. **G**. *Tomaculum problematicum* Groom, 1902; row with several tens of pellets; MR 9614; Rokycany; Šárka Formation; × 3. All specimens from the Ordovician of the Prague Basin, Czech Republic.

elongated cluster running latero-ventrally obliquely to the right. The whole accumulation consists of more than a hundred chaotically arranged pellets, 0.9 mm long and 0.4 mm in diameter. Microprobe analysis of the pellets shows only a high degree of silicification.

NM L 16862. Locality Svata Dobrotivá; Dobrotivá Formation; black shale (Figs. 3C, F, 4A). This specimen was described and figured by Barrande (1872: pl. 11: 6, 11). In the anterior part of the almost complete cephalothorax of *Parabarrandia crassa*, a bubble-like structure containing hundreds of minute pellets is present. The pellets are 0.95–1.0 mm long and 0.3–0.4 mm in diameter. They show no pattern of arrangement or prevailing orientation except anteriorly where is an orientation with long axes perpendicular to the exoskeleton surface. It seems that pellets in this cluster are not of uniform size; they seem to be smaller in the posterior part of this "swelling" where only a few pellets are partially visible. The pellets are smooth and densely arranged, overlying each other.

Microprobe analysis of pellets shows a predominance of SiO_2 and in comparison with surrounding rock, a more than ten-fold increase in P_2O_5 and a three- to ten-fold decrease in Al_2O_3.

Gastropods.—All investigated specimens come from the Caradoc. Pellets display no prevailing orientation in accumulations. They are small in size, their length varies between 0.2–0.9 mm and they occur in numbers varying from single specimens up to thousands.

NM L 36502. Locality Dubeč; Zahořany Formation; nodule (Fig. 5C). The internal mould of *Trochonema excavatum* Barrande in Perner, 1903 shows thousands of minute pellets in the fill of the preserved whorl, reaching 0.2–0.3 mm in length and 0.1–0.15 mm in diameter.

NM L 36503. Locality Dubeč; Zahořany Formation; nodule. The internal mould of the single preserved whorl of *Trochonema excavatum* contains at least several tens of minute pellets in the porous, "sponge-like" matrix. The pellets are of two different sizes. The longer pellets are up to 0.7 mm long and 0.2 mm in diameter, the shorter ones 0.4 mm long and 0.2 mm in diameter.

NM L 36504. Locality Dubeč; Zahořany Formation; nodule. The internal mould of *Trochonema excavatum* displays at least 6 oval pellets in the porous, "sponge-like" infill of the preserved whorls. The pellets are 0.9 mm long and 0.3 mm in diameter.

Hyolithids.—Pellets occur in clusters situated in different parts of the shells. They are medium sized, their length varies between 0.8–1.2 mm and they occur exclusively in numbers of in the tens range.

MR 22454. Locality Díly; Šárka Formation; siliceous nodule (Fig. 5F). Inside the shell of *Elegantilites elegans* (Barrande, 1847) about 10 pellets are observable. They are predominantely oriented with the long axis parallel with the walls of the shell. The pellets are covered by limonite and are 0.8 mm long and 0.3 mm in diameter.

MR 12750. Locality Těškov; Šárka Formation; siliceous nodule. Some 20 pellets, 1.0–1.2 mm long and 0.3 mm in diameter, are observable in the anterior, i.e., adapertural part of the shell of ?*Elegantilites elegans*. The specimen was figured by Horný (1998b: pl. 1: 6).

NM L 32733. Locality Praha—Šárka (pole u vily); Dobrotivá Formation (Fig. 5B); siliceous nodule. In the internal mould of *Bactrotheca teres* (Barrande, 1867) some 10 pellets, all parallel with the walls of the shell, occur in the posterior, i.e., adapical portion of the shell. The specimen was described and figured by Horný (1998b: pl. 1: 5).

Echinoderms.—Pellets found inside echinoderm thecae form small clusters containing a maximum of a few tens of specimens. They are of large size ranging between 1.1–1.5 mm and have only been found in the Šárka Formation.

NM L 36008. Locality Osek; Šárka Formation; siliceous nodule (Fig. 5A). Pellets occur in the internal mould of the theca of *Sagittacystis prima* (Barrande, 1887) with several minute *Arachnostega*-like ichnofossils. The cluster of pellets is situated in the posterior part of plastron. Most of the pellets are orientated parallel with the surface of the plastron with long axis oblique to the axis of body. There are about 30 pellets which are some 1.1–1.2 mm long and 0.3–0.4 mm in diameter.

CGU JH 1199. Locality Díly; Šárka Formation; siliceous nodule (Fig. 5E). On the internal surface of the ventral side of a theca of *Mitrocystites mitra* Barrande, 1887 there is a cluster of some 15 pellets situated anterolaterally. The pellets are chaotically arranged and are approximately 1.5 mm in length and 0.4–0.5 mm in diameter.

Discussion

Vaughan (1924), etc. described ellipsoidal objects and interpreted them as the coprolites of mud-eating organisms. In contrast, others such as Bureau (1900) considered them to be eggs of indeterminable origin. However, invertebrate eggs are mostly circular in outline (Van Waveren and Marcus 1993, Fortey and Owens 1997) and a cylindrical shape is unusual.

Dana (1932) defined coprolites as being "impure calcium phosphate". But coprolites may be silicified or carbonatized as noted by Amstutz (1958). Our material displays high SiO_2 content, increased content of P_2O_5 and low content of Al_2O_3. It shows the low content of clay minerals. Silicification and phosphatization (it is not clear if primary or secondary) of pellets took place during early diagenesis conserving the 3-D shape of pellets.

Fortey and Owens (1997) described several examples of trilobites possessing a bubble-like profile of an inflated cephalic lobe. They concluded that some of them might have had enlarged stomach cavities. Fortey and Hughes (1998) continued the study of these structures and suggested that they may have been brood pouches for retaining and protecting larvae. They compared them with Recent ostracods (see Jaanusson 1985) and limuloids that possess a spherical, anterior, brood chamber that develops on the last instar of the female. Fortey and Hughes (1998) suggested that pairs of bubble-headed and non bubble-headed trilobites occurring in the same fossil sites might represent the female and male of single species. The specimen of *Parabarrandia crassa* (Fig. 3C, F) described herein looks as if it might be an example of a bubble-headed trilobite in its reproductive period as an only slightly vaulted glabella, typical for *P. crassa*. However, the unusual vaulting of the anterior of the glabella was most probably formed secondarily during diagenesis when that part of the cephalon filled by hundreds of pellets was less flattened and deformed than the remaining exoskeleton.

The size of the pellets is not directly related to the length of an animal but to a combination of body weight and the quantity of food eaten at any one time (Edwards 1974). The size also depends on some attributes of producers such as diameter of the rectum (or anus) and peristaltic movement. In addition, such cylindrical faecal pellets of relatively uniform shape can be produced by members of different invertebrate groups (e.g., molluscs, arthropods, echinoderms). Faecal pellets of modern invertebrates are very often of cylindrical shape and reach 0.1 to 10 mm in length. They often possess ridges on their surface and different outer and inner canals (Frankenberg et al. 1967, Johanes and Satomi 1966). Similar objects are to be expected in the fossil record. Some data on fossil pellets were summarized by Amstutz (1958), Brönnimann and Norton (1960) and Scott (1977).

The studied pellets are of various sizes and lack any distinctive features. There are some indications of channels in pellets from *Parabarrandia crassa* (Fig. 4A). But this could be caused by diagenetic processes.

It is impossible to decide if the investigated pellets were produced by different invertebrates. However, in one chronofacies it is more probable that they come from different growth stages of a limited number of taxa.

A similar occurrence of pellets to those described above was published by Horný (1998a) who described pellets of very small dimensions, reaching tenths of millimetres in the silicified gut contents of the mollusc *Cyrtodiscus nitidus* (Barrande in Perner, 1903) from the Bohemian Llanvirnian (Šárka Formation). He observed, interpreted and figured several different kinds of adapertural shell fillings (Horný 1998a: fig. 3), including a type with the matrix containing the faecal pellets of infaunal inhabitants of an empty shell (Horný 1998a: fig. 3a). These pellets are of very small dimensions. Horný (1998b) also published a paper describing the intestinal filling of the hyolith *Gomphonites cinctus* (Barrande, 1867). He showed (*ibid*. fig. 6) one specimen partly filled by faecal pellets of an undetermined organism probably dwelling within the adapertural part of the empty shell.

Those pellet clusters and *Tomaculum* in general (Eiserhardt et al. 2001) are stratigraphically restricted to the Ordovician. There could be several reasons for their pre-Silurian disappearance, e.g., extinction of producers, appearance of organisms (consumers) using a new trophic strategy of feeding on the pellet clusters (personal communication R. Mikuláš).

Conclusions

The studied pellets occur in isolated clusters (real *Tomaculum* in the sense of Eiserhardt et al. 2001) or associated with fossils of different invertebrates (*Tomaculum* s. l.). The former are arranged in lenticular clusters or in rows. The latter have been observed in the interiors of only a few trilobite species from the Bohemian Ordovician: *Ormathops atavus*, *Parabarrandia crassa*, and *Pricyclopyge binodosa*. Tens to hundreds of pellets are situated inside their cephalic shields and similar pellets were observed in echinoderm thecae and the shells of bellerophontids and hyolithids. The systematic classification of such clusters as *Tomaculum* is questionable because it is uncertain whether they originated on or below the sediment surface.

The interpretation of the pellets as coprolites rather than eggs is more probable because of their different sizes inside a single cluster and indications of central canals.

It is apparent that the pellets are not related to the animals that secreted the shells. For example hundreds of pellets in the whorls of gastropods, pellets infilling adapertural parts of hyolithid shells and/or row of pellets obliquely crossing the visceral cavity of a trilobite cephalon indicate a secondary infill. The producers of pellets only used the empty shells as hiding places. They could also be carcass-feeders feeding on soft parts inside shells and/or using shells as protection. The occurrence of pellets in trilobites, restricted to the anterior part of the cephala, suggests that the producer of the pellets preferred the most vaulted part of the exoskeleton. The accumulations of pellets, which in some cases fill up the essential space available in cavities show that the producers used those places only temporarily.

In several specimens pellets are associated with an *Arachnostega*-like ichnofossil. This ichnofossil is interpreted as broken tunnels on the internal surface of a shell. The pellets could be the faeces of the unknown producers of *Arachnostega*.

The increased content of P_2O_5 and low content of Al_2O_3 in analysed pellets indicate a low content of clay minerals suggesting that the producer was not a mud-feeder (substrate-feeder). The huge accumulations, such as in *Parabarrandia crassa* (Fig. 3C, F) show that the producer remained in one place for a longer time. This is also incompatible with the mode of life of mud-feeders.

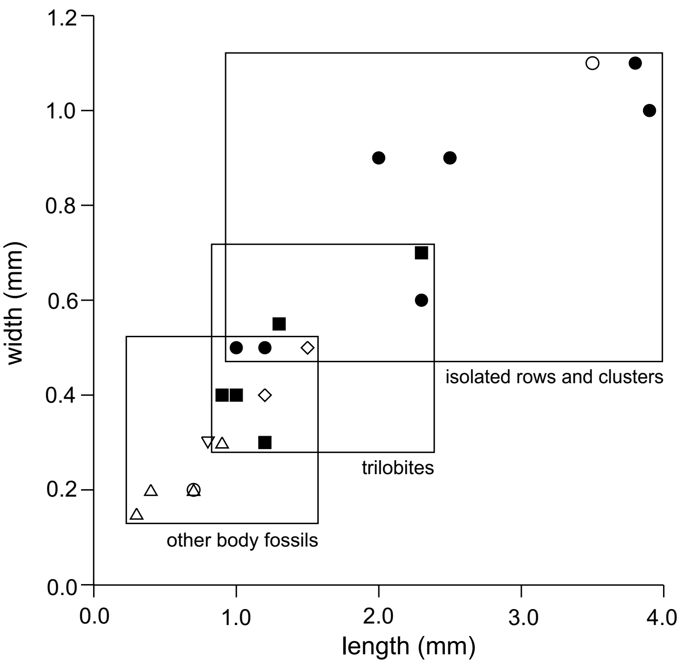

Fig. 6. Graph of length/width ratios of studied pellets. Filled circle, pellets in isolated rows and clusters; empty circle, pellets inside ichnofosssils; filled quadrangle, pellets associated with trilobites; empty triangle, pellets associated with gastropods; empty triangle inverted, pellets associated with hyolithids; empty diamond, pellets associated with echinoderms.

The pellets are not uniform in size and shape. Some are slender, others thicker, with different length/wide ratio. This suggests that they come from different producers or, at least, from producers of different growth stages. The size of the pellets depends on where they occur (Fig. 6). In this respect pellets can be divided into three groups. The largest pellets occur in isolated clusters and rows (A and B); the smaller ones are associated with trilobites (C), echinoderms and hyolithids; the smallest ones occur inside bellerophontid shells (D). Even it may not always be the case (as mentioned above) it seems that size of the pellets roughly reflects the body size of the producers. It may be that producers preferred spaces in shells corresponding to their body dimensions and therefore selected different shells as their body size increased. After their body grew beyond some size limit they could become independent of the passive protection of shell remains. This interpretation can explain the existence of isolated clusters and rows but only within a single group of producers. Another interpretation is that size groups of pellets were produced by invertebrates of different taxa. No cluster of pellets was found related to any apparent producer; therefore the producers remain enigmatic.

It was observed that isolated lenticular clusters (A) and isolated rows (B) are never related to any ichnofossil and the ends of such clusters do not pass into any trace indicating other activities. Thus, typical *Tomaculum* deposited on the bottom surface is apparently a result of time-limited defecation and can be considered to be a coprolite composed of pellets.

Acknowledgements

We thank Dr. Jiří Frýda for chemical analyses, SEM photos and valuable discussions, Dr. Radvan Horný for valuable comments and Dr. Radek Mikuláš for ichnological discussions. We are grateful to Dr. Alan Owen, Prof. Euan Clarkson and Prof. Art Boucot for their help with the English and valuable comments and reviews. This contribution was presented at the Third International Conference in Trilobites and their Relatives in Oxford (2001) with the support of the Sepkoski Research Grant Program and Foundation Nadání J.M.Z. Hlávkových, Český výbor ICOM. Petr Kraft's contribution was supported by a Grant of the Ministry of Education MSM 113100006 and includes data obtained during a research fellowship supported by the Alexander von Humboldt Foundation. This is a contribution to IGCP 410.

References

Amstutz, G.C. 1958. Coprolites: A review of the literature and a study of specimens from southern Washington. *Journal of Sedimentary Petrology* 28: 498–508.

Barrande, J. 1872. *Systęme silurien du centre de la Bohème. Vol. I, Suppl. I.* 647 pp. J. Barrande, Prague.

Brönnimann, P. and Norton, P. 1960. On the classification of fossil fecal pellets and description of new forms from Cuba, Guatemala and Libya. *Schweizerische Palaeontologische Gesellschaft* 53 (2): 832–842.

Bureau, L. 1900. *Notice sur la Géologie de la Loire-Inférieure*. 181 pp. E. Grimaud, Nantes. (*non vidi*)

Couto, H., Brenchley, P.J., and McDougall, N.D. 1986. New information concerning the age of the beds immediately overlying the Armorican Quartzite in Central Portugal. *Geobios* 19 (4): 421–433.

Dana, E.S 1932. *A Textbook of Mineralogy* (4th ed.). 851 pp. Revised and enlarged by W.E. Ford. John Wiley & Sons, Inc., New York. (*non vidi*)

Eiserhardt, K.-H., Koch, L., and Eiserhardt, W.L. 2001. Revision des Ichnotaxon *Tomaculum* Groom, 1902. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 221 (3): 325–358.

Edwards, C.A. 1974. Macroarthropods. *In*: C.H. Dickinson and G.J.F. Pugh (eds.), *Biology of Plant Litter Decomposition*, vol. 2, 533–554. Academic Press, London. (*non vidi*)

Fortey, R.A. and Owens, R.M. 1997. Bubble-headed trilobites, and a new olenid example. *Palaeontology* 40 (2): 451–459.

Fortey, R.A. and Hughes, N.C. 1998. Brood pouches in trilobites. *Journal of Paleontology* 72 (4): 638–649.

Frankenberg, D., Coles, S.L., and Johanes, R.E. 1967. The potential trophic significance of *Callianassa major* fecal pellets. *Limnology and Oceanography* 12: 113–120.

Frič, A. 1908. *Problematica Silurica. Système silurien du centre de la Bohème:* 3–28. A. Frič, Prague.

Groom, T. 1902. The sequence of the Cambrian and associated beds of the Malvern Hills. *Quarterly Journal of the Geological Society of London* 58: 89–149.

Gutiérrez-Marco, J.C. 1984. Una interesante deñal de actividad biológica en el Ordovícico de los montes de Toledo. *COL-PA* 39: 17–25.

Gutiérrez-Marco, J.C., Albani, R., Aramburu, C., Arbizu, M., Babin, C., García-Ramos, J.C., Méndez-Bedia, I., Rábano, I., Truyols, J., Vannier, J., and Villas, E. 1996. Bioestratigrafía de la Formación Pizarras del Sueve (Ordovícico Medio) en el sector septentrional de la escama de Laviana-Sueve (Zona Cantábrica, Norte de España. *Revista Española de Paleontología* 11 (1): 48–74.

Hermite, H. 1878. Étude préliminaire du terrain silurien des environs d'Angers. *Bulletin de la Société Géologique de France* 6 (3): 531–543.

Hofmann, H.J. 1972. Systematically branching burrows from the Lower Ordovician (Quebec Group) near Quebec, Canada. *Paläontologische Zeitschrift* 46 (3/4): 186–198.

Horný, R.J. 1998a. Fossilized intestinal contents in the Lower Ordovician *Cyrtodiscus nitidus* (Mollusca, Tergomya) from the Barrandian Area (Bohemia). *Věstník Českého geologického ústavu* 73 (3): 211–216.

Horný, R.J. 1998b. Lower Ordovician *Nephrotheca sarkaensis* (Orthothecida, Hyolitha) with fossilized intestinal contents *in situ* (Šárka Formation, Bohemia). *Časopis Národního muzea, Řada přírodovědná* 167 (1–4): 95–98.

Jaanusson, V. 1985. Functional morphology of the shell in platycope ostracodes—a study of arrested evolution. *Lethaia* 18: 73–84.

Johannes, R.E. and Satomi, M. 1966. Composition and nutritive value of fecal pellets of a marine crustacean. *Limnology and Oceanography* 11: 191–197.

Koch, L. 1999. Die Familie Cyclopygidiae (Trilobita) im Ordovizium des Ebbe- und Remscheider Sattels (Rheinisches Schiefergebirge, Deutschland). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 213 (3): 375–431.

Mikuláš, R. 1991. Trace fossils from siliceous concretions in the Šárka and Dobrotivá Formations (Ordovician, central Bohemia). *Časopis pro mineralogii a geologii* 36 (1): 29–38.

Mikuláš, R. and Slavíčková, J. 2002: Trilobites and minute ovoid pellets in a burrow (Ordovician, Llanvirnian, Czech Republic). *Ichnos* 8:243–249.

Péneau, J. 1941. Die Anwesenheit von *Tomaculum problematicum* im Ordovicium West-Frankreichs. *Senckenbergiana* 23: 127–132.

Radig, F. 1964. Die Lebensspur *Tomaculum problematicum* Groom 1902 im Llandeilo der Iberischen Halbinsel. *Neue Jahrbuch für Geologie und Paläontologie, Abhandlungen* 119 (1): 12–18.

Richter, R. and Richter, E. 1939a. Die Kot-Schnur *Tomaculum* Groom (= *Syncoprulus* Rud. & E. Richter), ähnliche Scheitel-Platten und beider stratigraphische Bedeutung. *Senckenbergiana* 21: 278–291.

Richter, R. and Richter, E. 1939b. Eine Lebens-Spur (*Syncoprolus pharmaceus*), gemeinsam dem rheinischen und böhmischen Ordovicium. *Senckenbergiana* 21: 152–167.

Richter, R. and Richter, E. 1941. Das stratigraphische Verhalten von *Tomaculum* als Beispiel für die Bedeutung von Lebensspuren. *Senckenbergiana* 23: 133–135.

Scott, A.C. 1977. Coprolites containing plant material from the Carboniferous of Britain. *Palaeontology* 20: 59–68.

Thoral, M. 1935. *Contribution l'Etude Paléontologique de l'Ordovicien inférieur de la Montagne Noire*. 362 pp. Imprimerie de la Charité, Montpellier.

Van Waveren, I.M. and Marcus, N.H. 1993. Morphology of recent copepod egg envelopes from Turkey Point, Gulf of Mexico, and their implications for acritarch affinity. *Special Papers in Palaeontology* 48: 111–124.

Vaughan, T.W. 1924. Oceanography in its relation to other Earth sciences. *Journal Washington Academy of Sciences* 14: 307–333. (*non vidi*)

Volk, M. 1941. Die Lebensspur *Tomaculum problematicum* Groom auch im Griffelschiefer des Thüringer Ordoviciums. *Senckenbergiana* 23: 123–126.

Walcott, C.D. 1879. Note upon the eggs of the trilobite. *New York State Museum Annual Report* 31: 66–67.