Small faecal pellets in Ordovician shelly fossils from Estonia, Baltoscandia

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Abstract. Coprolites (fossil faeces) constitute a group of soft sediment trace fossils that provide useful palaeoecological and sedimentological information, but have generally low preservational potential. In this paper we report abundant occurrence and high diversity of small faecal pellets preserved inside different shelly fossils from Middle and Upper Ordovician carbonates of the Baltoscandian palaeobasin. The material contains ca 180 body fossils with faecal pellets from 40 localities, corresponding to a range of shallow-marine environments from cool-water carbonate ramp to tropical open shelf settings. Stratigraphically the finds range from the Volkhov to Pirgu regional stages (Dapingian to uppermost Katian). The pellets are elliptical or rod-shaped, 0.1–1.8 mm long and 0.08–0.75 mm in diameter, with the length/diameter ratio ranging from less than 2 to ca 6. They occur in shells of gastropods, bivalves, cephalopods, brachiopods, echinoderms and trilobites and represent two ichnospecies, *Coprulus oblongus* and *Coprulus bacilliformis*, and some intermediate forms belonging to the same ichnogenus. Additionally, two compound traces were identified: *Tubularina* (pellets inside small burrows with circular cross section) and *Alcyonidiopsis* (pellets inside ribbon-shaped burrows). The pellets were produced when the empty shells were located on the seafloor, or possibly during shallow burial in the oxic zone. The preservation of faecal pellets is due to an interaction of several factors, notably protection by the shells and rapid mineralization. The origin of trace makers remains speculative, but polychaete worms having compatible size and body plan and living representatives who produce similar faecal pellets are among the most likely groups. Possibly organisms with different feeding strategies were involved in producing the faecal pellets. Systematic examination of shelly fossils from selected localities showed that up to about half of the shells may contain pellets, which indicates great abundance and diversity of pellet-producing organisms in the Ordovician Baltoscandian basin. Our material also shows that the trace maker of *Arachnostega* was not related to the faecal pellets inside the shells.

Key words: micro-coprolites, faecal pellets, *Coprulus*, *Tubularina*, *Alcyonidiopsis*, shallow-marine carbonates, Ordovician, Estonia.

INTRODUCTION

Trace fossils are important environmental indicators and provide valuable knowledge of animal behaviour in the geological past (Seilacher 2007). Trace-fossil assemblages of the Ordovician of the Baltica craton are comparatively well studied (e.g. Dronov et al. 2002; Mikuláš & Dronov 2005; Knaust & Dronov 2013; Hanken et al. 2016), but only limited studies deal with material from Estonia (Männil 1966b; Vinn et al. 2014, 2015; Vinn & Toom 2016; Toom et al. 2019a, 2019b).

Coprolites (fossil faeces) represent a distinct category of trace fossils common since the early Palaeozoic – different morphotypes are known already from the Cambrian (e.g. Vizcaïno et al. 2004; Eriksson & Terfelt 2007; Shen et al. 2014; Kimming & Strotz 2017; Mángano et al. 2019). The term 'pellet' denotes grains of faecal origin according to Flügel (2004); however, some authors have used it without reference to their origin. The term is frequently used for small invertebrate excrements of millimetre scale, with simple elliptical or rod-shaped form. Like all soft-bodied organisms, coprolites have generally a low preservation potential. Their findings from Palaeozoic

siliciclastic sediments are mostly related to deeper-water settings with high sedimentation rates and specific preservation conditions. The occurrence of pellets in carbonate sediments is commonly related to tropical shallow-marine environments (Folk & Robles 1964; Shinn 1968; Wanless et al. 1981) and is widely reported from Mesozoic and Cenozoic strata. Rapid lithification has played an important role in their preservation in carbonates (Knaust et al. 2012). The majority of faecal pellet ichnotaxa in carbonates have characteristic inner structure and belong to the ichnofamily Favreinidae. Small faecal pellets with an ornamented outer surface are assigned to a number of different ichnogenera (e.g. Heer 1853; Elliott 1963; Gramann 1966; Gaździcki 1974; Gaillard 1978; Agarwal 1988; Živković & Bogner 2006), whereas isolated faecal pellets without internal structure and ornamentation are representing the ichnofamily Coprulidae (Knaust 2008).

Faecal pellets are common in the Ordovician rocks of Europe (Häntzschel 1962; Benton & Hiscock 1996). They were first mentioned from Bohemia by Barrande (1872) and are commonly related to the ichnogenus *Tomaculum* Groom, 1902 (e.g. Pickerill & Forbes 1979; Eiserhardt et al. 2001 and references therein; Mikuláš & Slavíčková 2001; Bruthansová & Kraft 2003; Neto de Carvalho & Farinha 2006; Podhalańska 2007; Martin et al. 2016; Neto de Carvalho et al. 2016; van Keulen & Rhebergen 2017). Groom (1902) left open the question of the origin of small pellets, but later authors have suggested a faecal origin for these particles (e.g. Frič 1908; Gutiérrez-Marco 1984; Mikuláš 1991; Eiserhardt et al. 2001; Bruthansová & Kraft 2003; Neto de Carvalho & Farinha 2006).

Faecal pellets may be associated with other trace fossils (e.g. Fürsich 1974; Seilacher 2007; Knaust 2008), constitute composite traces (Gaillard et al. 1994) or fill shells of molluscs and other invertebrates (e.g. Mayer 1955, 1958; Zhang et al. 2007; Mángano et al. 2019). From the Ordovician, faecal pellets in burrows have been described as *Syncoprulus* (=*Tomaculum*) (Richter & Richter 1939; Pickerill et al. 1987), *Alcyonidiopsis* (Chamberlain 1977; Pickerill 1980; Pickerill & Narbonne 1995; Orr 1996; Uchman et al. 2005), in branching burrows as *Quebecichnus* (Hofmann 1972) and in burrows with segmented fill as *Compaginatichnus* (Pickerill 1989). Gutiérrez-Marco (1984) described a cylindrical elongated cluster filled with small pellets inside a gastropod as *Cilindrotomaculum*.

The reports of pellets inside Ordovician shelly fossils are few and mostly come from siliciclastic basins (Gutiérrez-Marco 1984; Mikuláš 1992; Bruthansová & Kraft 2003). The occurrence of pellets in shells from carbonate settings has only been mentioned by Põlma (1982), more recently by Toom et al. (2017, 2019a, 2019b) and van Keulen & Rhebergen (2017). All these papers refer to the material from the Baltic region.

The aim of this study is to report the abundance of small faecal pellets inside various shelly fossils in the Ordovician shallow-marine carbonates of the Baltoscandian basin, describe their morphology and discuss the taxonomic, sedimentological and palaeobiological aspects.

GEOLOGICAL BACKGROUND

During the Ordovician, the study area was part of a shallow sea, which covered the western part of the Baltica craton. This epicontinental sea, the Baltoscandian basin, extended from Norway to the Volga area in western Russia, and from the Fennoscandian mainland in the north to the Sarmatian mainland in the south (Fig. 1; Nestor & Einasto 1997). The Ordovician outcrop area in northern Estonia, where most of the material of the present study derives from, was characterized by relatively shallow-water settings of the basin, whereas deeper shelf environments, the so-called Livonian basin, were located in the south (Fig. 1). Baltica drifted from high southern latitudes to the tropical area (Torsvik & Cocks 2013 and references therein), causing a gradual change in climate and depositional conditions. In Estonia, carbonate sedimentation commenced at the end of the Floian (latest Early Ordovician) in a relatively cool, flat-bottomed epicontinental basin (Dronov & Rozhnov 1997). In the Middle and early Late Ordovician, the basin was characterized by extremely low sedimentation rates and with little bathymetric differentiation (Jaanusson 1973). In the Late Ordovician, the climatic change resulted in an increase in carbonate production and sediment accumulation rates on the platform. The basin started to differentiate particularly in the early Katian (Nestor & Einasto 1997). At that time the first tropical carbonate buildups appeared in the region (Kröger et al. 2017 and references therein).

The total thickness of the Ordovician succession in Estonia reaches about 180 m (Nõlvak 1997). The Ordovician carbonate rocks in Estonia are rich in shelly fossils such as brachiopods, bryozoans, cephalopods, gastropods, echinoderms, trilobites, corals, etc. Trace fossils are also common and diverse (Toom et al. 2019a) and the degree of bioturbation is generally high (Harris et al. 2004). A significant feature of Palaeozoic rocks of Estonia and the entire eastern Baltic region is a very low burial temperature indicated by conodont colour alteration index (CAI) values around 1 (Männik 2017).

The stratigraphic framework and time-correlations in the region are based on Baltic regional stages and high-resolution biostratigraphy, notably trilobite, conodont, chitinozoan and graptolite zones (Nõlvak et al. 2006). We refer to both regional as well as global stages and series in the present study (Fig. 2).
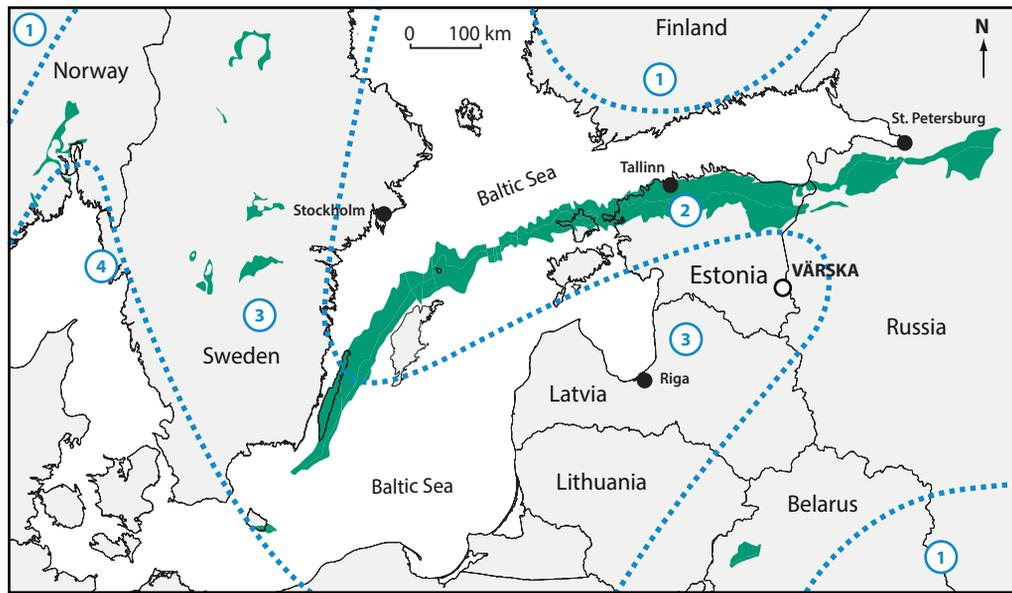
Fig. 1. Locality map showing the outcrop area of Ordovician rocks in the Baltic region (green) and schematic configuration of the Baltoscandian basin (after Männil 1966a and Nestor & Einasto 1997). 1, main land areas; 2, shallow-water Estonian shelf; 3, deeper-water Livonian basin and Central Baltoscandian facies belt; 4, deep shelf of the Scanian facies belt (modified after Toom et al. 2019a).
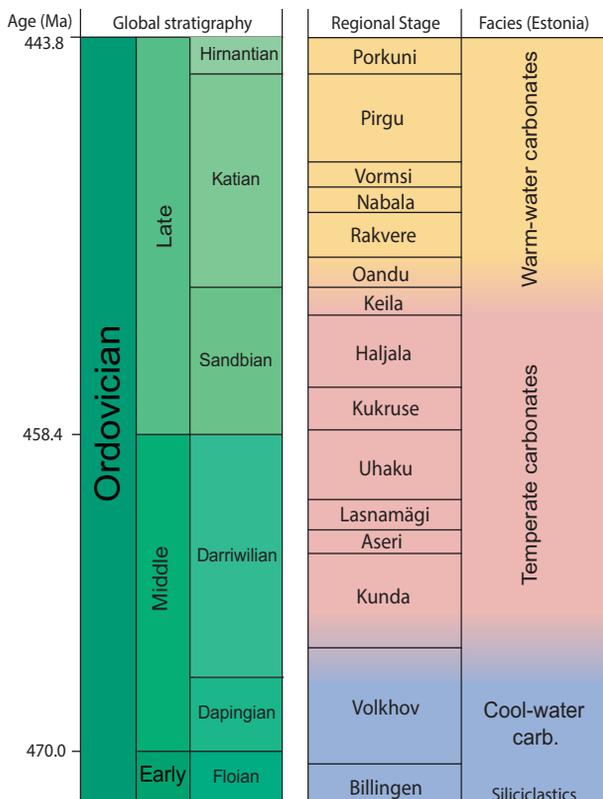
Fig. 2. Regional and international stratigraphy of the studied interval, showing transition from cool-water to warm-water carbonate deposits (modified after Toom et al. 2019a).

MATERIAL AND METHODS

Large palaeontological collections of Ordovician fossils from Estonia, housed at the Department of Geology, Tallinn University of Technology (indicated by the prefix GIT) and the Natural History Museum, University of Tartu (prefix TUG), were searched for shelly fossils containing small coprolites. In addition, the extensive lithological collection of eastern Baltic Ordovician rocks by Lembit Põlma (prefix GIT) was examined in order to reveal similar pellets dispersed in carbonate matrix.

The main method to identify the pellets was non-destructive observation of steinkerns, broken shelly fossils and rock samples already cut during previous studies. Better-preserved specimens were studied on steinkern surfaces only; the less valuable material was sectioned and polished for the determination and measurements of pellets. Only the specimens containing a large number of individual pellets on sectioned shells or steinkerns were used for measurements.

Additionally, a selection of shelly fossils from two localities were sectioned and examined in order to assess the relative abundance and distribution of pellet-filled shells. In this way, 30 gastropods and 30 brachiopods from the Aluvere quarry (Haljala Stage, Sandbian) and 30 gastropods from the Mõnuste quarry (Vormsi Stage, Katian) were studied.

Specimens were photographed with a Canon EOS 5DS R digital camera and a Leica Z16 APO zoom microscope system at the Department of Geology,

Tallinn University of Technology. Measurements were taken from calibrated digital photos using Fiji image analysis software (https://imagej.net/Fiji). Selected specimens were additionally studied under a scanning electron microscope and analysed for chemical composition with EDS (TESCAN VEGA II XMU SEM with an X-Ray Energy Dispersive INCA ENERGY 450 microanalysis system at the A. A. Borissiak Paleontological Institute, Moscow). Data of individual specimens and related pellets (including images and localities) are deposited in the database of Estonian geocollections, which is accessible online at https://geocollections.info.

RESULTS AND DISCUSSION

Characterization of faecal pellets and host shells

Small pellets have been identified inside about 180 shelly fossils coming from 40 localities across the Ordovician outcrop area in Estonia and representing normal shallow-marine settings of the Estonian shelf (Table 1). So far only one specimen has been recovered from the deeper-shelf Livonian basin (Fig. 1). Stratigraphically the pellets in shells are known from the Volkhov (Dapingian) to Pirgu regional stages (Upper Katian); however, the majority comes from temperate and tropical carbonates (Table 1), with only a single record from cool-water limestone of the Volkhov Stage. The host rocks of shelly fossils with pellets are varied, ranging from wackestones and packstones to pure carbonate mudstones. Notably, so far, loose pellets have not been found from the host rocks.

Host shells containing faecal pellets belong to common Palaeozoic fossil groups: gastropods, bivalves, cephalopods, brachiopods, echinoderms and trilobites (Table 1). In general, the host dimensions range from ca 10 to 45 mm; for cephalopods the diameter of the body chamber is less than 25 mm. The size of pellets is very variable, ranging from 0.1 to 1.8 mm in length, and 0.08 to 0.5 mm in diameter. Within a single host shell, however, pellets are principally similar in their dimensions. The pellets are elongated, mostly elliptical or rod-shaped and always with circular cross section. Their length/diameter ratio is mostly less than 2 (Figs 3A, D, 4F–H, 5J, K) or 2–3 (Figs 3I, 4A, B, D, I, 5C). Only few specimens show more elongated pellets, with the length/diameter ratio between 4 and 6 (Figs 3F, 5B). All pellets are devoid of the internal structure, and no constructional wall or lining has been observed. The EDS chemical analysis suggested a similar carbonate composition for pellets and rock matrix, while only a single specimen from the Haljala Stage (Sandbian) showed traces of silicification.

Pellets inside shells are organized in two different modes: the majority is represented by massive accumulations (Figs 3A–I, 4A–I, 5A–F), and in fewer cases (15 specimens), pellets are associated with small burrows (Fig. 5F–K). Massive accumulations consist of randomly oriented pellets which are not mixed with the sediment. The boundary between the sediment and pellets may be distinct (Fig. 3A) or transitional (Fig. 3G). The degree of preservation of pellets is variable, especially for the sets of massive accumulations. The decomposition process may affect an entire set (Fig. 3C) or only the periphery of an accumulation (Fig. 3G–I). The sediment inside the shells probably consists of decomposed pellets, especially if it does not contain bioclastic material. Some specimens contain pellets of two different sizes, located in separate sets (Figs 3E, 4I). The number of pellets in accumulations varies widely: for large pellets, less than hundred pieces make up an accumulation, but for the smallest pellets a set may contain more than a thousand pellets (Fig. 3A).

Sinuous, branching small burrows (diameter about 1–3 mm, traceable length less than 10 mm) may contain micritic, randomly oriented isolated elliptical pellets with the length/diameter ratio around 2 (Fig. 5F–J). Such pellets are well preserved, randomly oriented and loose. The burrows have sharp outline, circular cross section, which is mostly constant in diameter, and lack ornamentation or lining. In most cases the burrows with pellets are found within gastropods, but few are known inside brachiopods and bivalves. These burrows are oriented in different directions, but their total length and general configuration are difficult to establish as the pellets are mostly visible in cross section (Fig. 5G, H). A massive accumulation of pellets and burrows with pellets may occur together inside the same shell (Fig. 5I, J). However, the pellets inside the burrows are not coming from massive accumulations as they are different in size and preservation, and are thus likely made by the producers of the burrows. Additionally, a few trilobite specimens demonstrate specific ribbon-shaped, pellet-filled burrows with varying diameter (Fig. 5K).

The majority of pellet-filled fossils (a total of 112 specimens) are molluscs, especially gastropods (Figs 3E, F–I, 4A–D, 5D, E, I, J). All common Ordovician gastropod genera are represented, but most finds are related to oblong and conical forms such as *Subulites*, *Murchisonia*, *Hormotoma*, *Lophospira*, *Holopea*, *Liospira* and *Deaechospira*. Fewer specimens come from depressed gastropod shells (the diameter is much larger than the height) like *Pachystrophia*, *Lesueurilla*, *Cymbularia*, *Bucanella*, *Megalomphala* and *Salpingostoma*. The gastropods vary in size, with the smallest measured specimen being 10.1 mm high and 16.4 mm wide, and the largest 102.1 mm high and 53.8 mm wide. Massive clusters of pellets are typically

Table 1. Stratigraphic distribution of shelly fossils with pellets inside the Ordovician carbonate succession of Estonia. The basin margin and type of sediments after Dronov & Rozhnov (1997). The numbers after the plus sign denote finds from 30 randomly selected sliced shells. Note that pellets have not been recorded in the topmost Ordovician Porkuni Stage so far

Regional Stage	Age	Basin type	Type of carbonate sediment	Type of pellets	Trace fossil	Gastropoda	Cephalopoda	Bivalvia	Brachiopoda	Echinodermata	Trilobita	Total	Length (mm)	Width (mm)
Porkuni	Hirnantian	Rimmed shelf	Tropical	–	–	–	–	–	–	–	–	0		
Pirgu	Katian	Rimmed shelf	Tropical	Elliptical; L/D ratio ≤2, 2–3	*Coprulus, Tubularina*, unidentified burrow	2	2	–	–	–	–	4	0.23–0.34	0.09–0.23
Vormsi	Katian	Rimmed shelf	Tropical	Elliptical; L/D ratio ≤2, 2–3	*Coprulus*	4 + 11	1	–	–	–	–	16	0.46–0.95	0.19–0.45
Nabala	Katian	Rimmed shelf	Tropical	Elliptical; L/D ratio ≤2, 2–3	*Coprulus*	3	–	–	–	–	–	3	0.6–1.2	0.3–0.5
Rakvere	Katian	Rimmed shelf	Tropical	Elliptical, elongated elliptical, rod-shaped; L/D ratio ≤2, 2–3, 5–6	*Coprulus, Tubularina*	38	–	9	3	–	–	50	0.2–1.8	0.1–0.75
Oandu	Katian	Rimmed shelf	Tropical	Elliptical, elongated elliptical; L/D ratio 2–3, 5	*Coprulus, Tubularina*, unidentified burrow	1	–	2	12	–	–	15	0.3–0.7	0.1–0.3
Keila	Katian	Rimmed shelf	Tropical	Elliptical; L/D ratio ≤2	*Coprulus, Tubularina, Alcyonidiopsis*, unidentified burrow	3	–	1	4	–	1	9	0.26–0.38	0.15–0.2
Haljala	Sandbian	Carbonate ramp	Temperate	Elliptical, rod-shaped; L/D ratio ≤2, 2–3, 4–5?	*Coprulus, Tubularina, Alcyonidiopsis*	28 + 15	5	2	0 + 12	1	1	64	≤0.1–0.8	0.08–0.4
Kukruse	Sandbian	Carbonate ramp	Temperate	Elliptical; L/D ratio ≤2	*Coprulus*	2	–	1	–	1	–	4	0.17–0.3	0.09–0.15
Uhaku	Darriwilian	Carbonate ramp	Temperate	Elliptical; L/D ratio ≤2, 2–3	*Coprulus*	5	–	–	–	–	–	5	0.4–0.6	0.11–0.3
Lasnamägi	Darriwilian	Carbonate ramp	Temperate	Elliptical; L/D ratio ≤2	*Coprulus*	–	3	–	–	–	–	3	0.13–0.14	0.25
Aseri	Darriwilian	Carbonate ramp	Temperate	Elliptical; L/D ratio ≤2	*Coprulus*	–	1	–	–	–	–	1	0.24	0.12
Kunda	Darriwilian	Carbonate ramp	Temperate	Elliptical; L/D ratio ≤2, 2–3	*Coprulus*	–	4	–	–	–	–	4	0.3–0.5	0.15–0.2
Volkhov	Dapingian	Carbonate ramp	Cool	Elliptical; L/D ratio 2–3	*Coprulus*	–	–	–	1	–	–	1	0.45	0.2
					Total:	112	16	15	32	2	2	179		

– no finds.
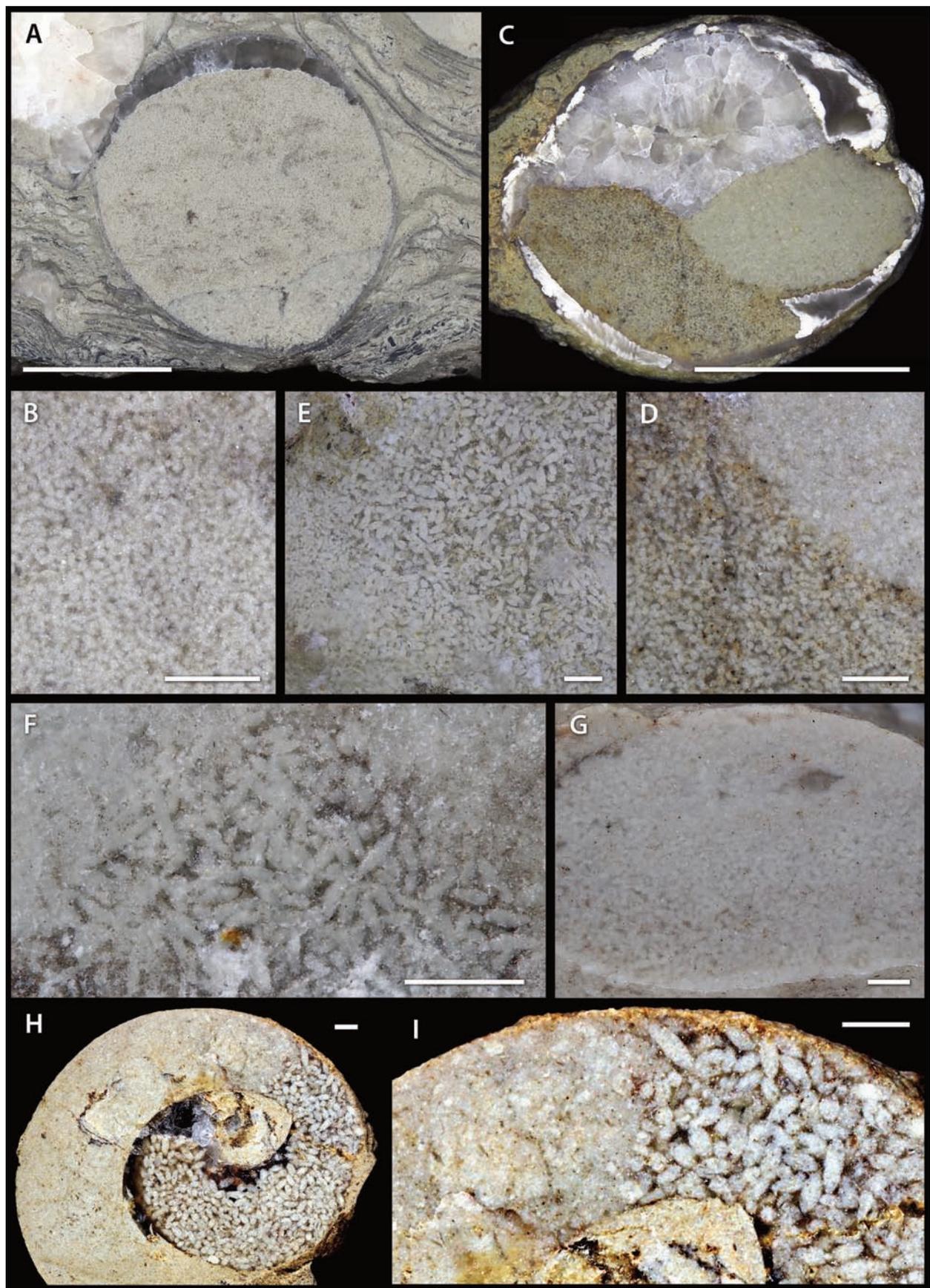
located in the apical parts of gastropod shells (Fig. 3H, I). For smaller shells, the entire whorl may be filled with pellets. In larger specimens, like *Hormotoma insignis* from the Rakvere Stage, the pellets may be accumulated in one side of the shell and the occurrence of pellets may be observed also in body whorl (Fig. 4C). Clusters, clusters together with burrows (Fig. 5I, J) and only burrows filled with pellets are observed in gastropod shells, however, the last case is rather exceptional. Stratigraphically the pellet-filled gastropods have been recorded from the Uhaku (late Darriwilian) to Pirgu stages (late Katian), with a higher number of finds from two levels: the Haljala (Sandbian) and Rakvere stages (Katian). The pellets inside gastropods show the highest variability in size and shape, including the largest pellets recovered during this study (Fig. 4A). Elliptical and rod-shaped pellets with a length of 0.23–1.8 mm, diameter 0.09–0.75 mm and various length/diameter ratios (≤2, 2–3 and 4–5) are known. Notably, there is no correlation between the size of the shells and the size of the pellets they contain. The large open aperture of gastropods probably made them easy to inhabit and may have controlled the occurrence and variability of pellets. However, the higher variability of pellets in gastropod shells may also result from the largest number of specimens studied. The trace fossil *Arachnostega* is observed on the surface of some gastropod steinkerns (Fig. 4C, D).

Sixteen specimens of cephalopods contain pellets. Infills have been found in the body chamber, phragmocone between septae (Fig. 4E), as well as siphuncle (Fig. 4F). Frequently only one chamber between septae is filled (Fig. 4E) and bioturbation is common. Finds of pellets in cephalopods are mostly related to coiled and medium-size specimens with a diameter of aperture less than 25 mm. Stratigraphically the occurrences range from the Kunda to Lasnamägi stages (Darriwilian), the Haljala Stage (Sandbian) and from the Vormsi to Nabala stages (Upper Katian). Most of the pellets are poorly preserved and relatively small in size (length 0.23–0.5 mm, diameter 0.09–0.2 mm), with the length/diameter ratio below 2 or 2–3. Most finds come from temperate-water carbonates, which may be the cause of a relatively small size of pellets in cephalopod shells. In addition, due to small holes in damaged phragmocones the shells could be inhabited by only small animals with a slender body plan. The small number of cephalopod specimens with pellets may be biased due to insufficient study, although, a recent thorough examination of a large number of lower Katian cephalopods by Kröger & Aubrechtová (2018) did not reveal any finds with pellets.

Fifteen specimens of bivalves representing the genera *Modiolopsis*, *Aristerella* and *Cypricardinia* contain pellets (Fig. 5A–C, F–H). Shells with a length of 28–61 mm, height 16–44 mm and width 23–44 mm are partially filled with irregular clusters. Only the largest *Cypricardinia* contain several small burrows filled with pellets (Fig. 5F). Bivalves filled with pellets are recorded from the Kukruse to Rakvere stages (Sandbian to Katian). The pellets are elliptical (length 0.26–0.76 mm, diameter 0.18–0.43 mm), elongated elliptical (length 0.61 mm, diameter 0.16 mm) or rod-shaped (length 1.19 mm, diameter 0.22 mm), with the length/diameter ratio of ≤2, 2–3 or 4–6. A relatively small number of finds exhibit surprisingly high variability of the shape of pellets. Few bivalve steinkerns show the presence of *Arachnostega*.

Thirty-two specimens of brachiopods contain pellets (examples in Figs 3C, D, 4G–I). Shell sections may be filled only with pellets (Fig. 3C), or more commonly, the irregular accumulations of pellets occur in some parts of the shell sections examined, like the spondylium (Fig. 4G). The smallest brachiopod with pellets is *Platystrophia* with a height of 9.4 mm and a width of 21.6 mm, the largest is *Porambonites wesenbergensis* with a height of 45.4 mm and a width of 33.9 mm. Bioturbation and multiple accumulations with different sizes of pellets are related to larger specimens (Fig. 4I). A single occurrence has been recorded from the Volkhov Stage, other finds come from the Haljala to Rakvere stages (Sandbian to Katian). Only elliptical pellets are observed, with a length of 0.2–1.1 mm, diameter 0.1–0.5 mm and the length/diameter ratio ≤2 or 2–3. Commonly large pellets occur inside large brachiopods, which may be related to the size of the pedicle opening. Few specimens of brachiopods also show the presence of *Arachnostega*.

Two echinoderm specimens belonging to *Echinosphaerites* and *Sphaeronites* contain irregular accumulations of small, elliptical pellets with a length of 0.1–0.4 mm, diameter 0.08–0.24 and the length/diameter

Fig. 3. Faecal pellets inside Ordovician shelly fossils from Estonia. Scale bars: 1 cm for A, C, H; 1 mm for B, E, D, F, G, I. **A**, echinoderm *Sphaeronites*, massive accumulation of pellets, vertical section, GIT 156-1066, Värska 6 drill core, 381.8 m, Haljala Stage, Sandbian. **B**, detail of GIT 156-1066, *C. oblongus*. **C**, brachiopod *Porambonites*, two sets of pellets inside, boundary between sets is distinct, one of the sets is almost completely decomposed, GIT 399-1961, Aluvere quarry, Haljala Stage, Sandbian. **D**, detail of GIT 399-1961, *C. oblongus*. **E**, gastropod *Hormotoma insignis*, surface of steinkern, two different sizes of *Coprulus* (L/W ratio 2.7), TUG 80-484, Piilse, Rakvere Stage, Katian. **F**, bivalve *Aristerella*, detail of surface, *Coprulus* (L/W ratio 4), GIT 694-93, Kullaaru ditch, Oandu Stage, Katian. **G**, gastropod *Subulites wesenbergensis*, horizontal section through the apical part of steinkern, boundary between the accumulation of pellets and sediment is transitional, decomposition of pellets is almost finished, GIT 404-639, Mõnuste quarry Harjumaa, Vormsi Stage, Katian. **H**, gastropod *Lesueurilla*, horizontal section through the apical part, *Coprulus* (L/W ratio 2.3), GIT 720-1, Aluvere quarry, Haljala Stage, Sandbian. **I**, detail of GIT 720-1, on the left side of the image are decomposed pellets.
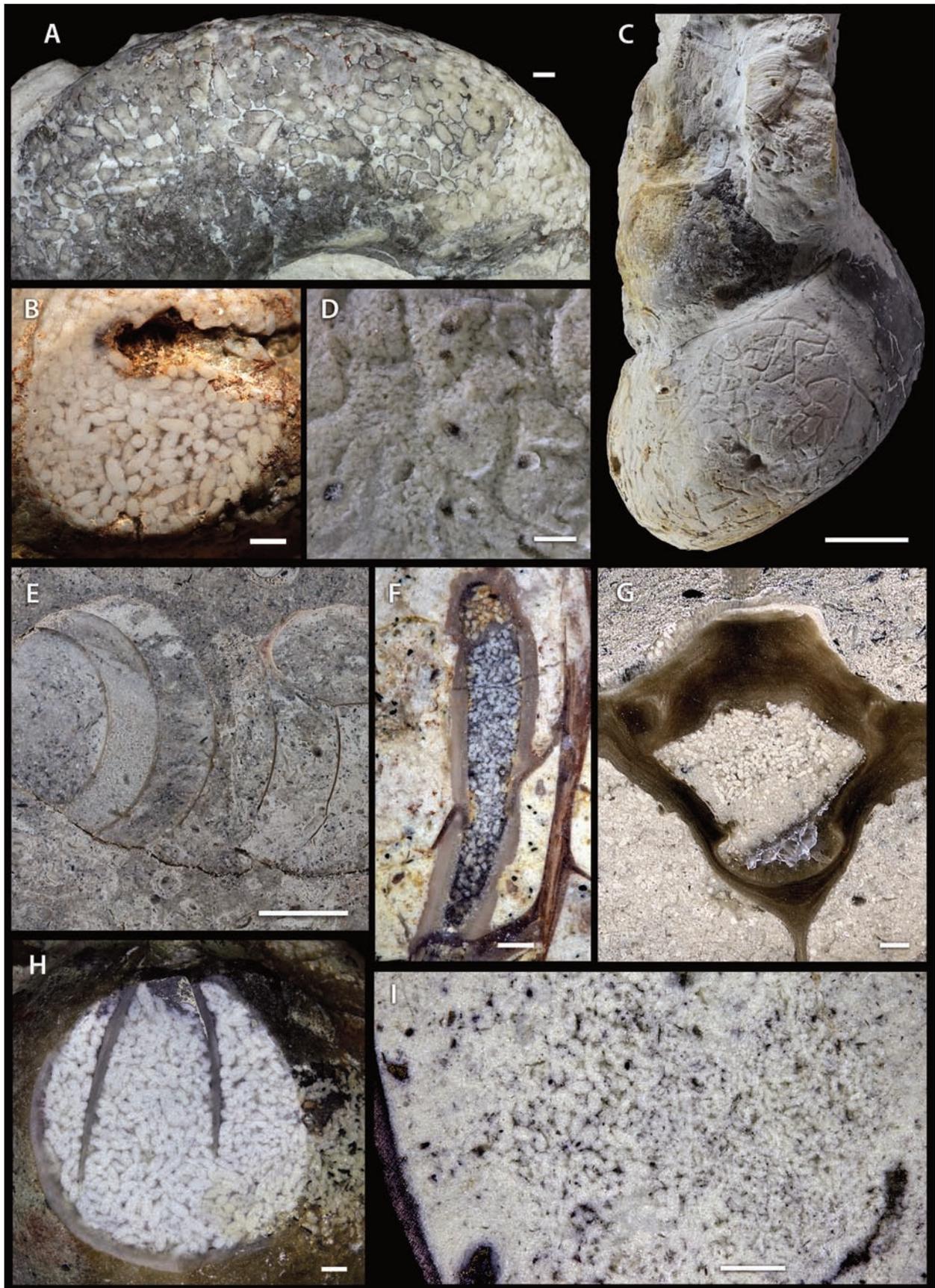
ratio below 2. The *Sphaeronites* shell is so far the only specimen characterizing the deeper shelf environments. It is noteworthy that the pellets it contains are the smallest among those recorded during the present study (Fig. 3A). The two specimens come from the Kukruse and Haljala stages (Sandbian).

Two trilobites have ribbon-shaped burrows on the dorsal surface of sediment infill of the cephalon of *Oculichasmops* and the pygidium of an asaphid trilobite (Fig. 5K). Stratigraphically the finds come from the Haljala and Keila stages (Sandbian and lower Katian). The pellets inside trilobites are elliptical in shape, with a length of 0.13–0.19 mm, diameter 0.32–0.36 mm and the length/diameter ratio below 2 or 2–3.

To some extent the data on pellet occurrences presented in Table 1 are biased by the different detection and study methods and the number of previous studies on different fossil groups. Pellets can rarely be observed on natural break surfaces due to the similar colour of pellets and matrix. However, the sectioning and polishing of surfaces reveals the pellets inside shells. The number of finds also depends on the degree of preservation of the shelly fossils. For instance, brachiopods have commonly well-preserved shells and pellet finds are related only to damaged specimens or material which was sectioned for other purposes. The prevalence of molluscs, and especially gastropods, can be explained by the conditions of 'calcite sea', where aragonitic shells dissolved rapidly (Palmer et al. 1988; Palmer & Wilson 2004) and therefore the internal moulds with pellets became visible. Pellets were particularly well observable on the steinkerns of gastropods and bivalves derived from pure tropical lime-mudstones of the Rakvere and Nabala stages (Katian). These specimens were redeposited on the sediment surface before complete lithification of steinkerns but after the dissolution of shells. Steinkerns are deformed, with crush marks (Fig. 5D), containing small cracks (Fig. 5E), overgrown by trepostome bryozoans (Fig. 5D, E) and covered by pyrite threads (Fig. 5A). It can easily be identified on which side a gastropod or bivalve was lying on the sea floor after redeposition, as selective erosion by dissolution has made the pellets more distinct

(Fig. 5D, E). The dominance of gastropods among pellet substrates can also be explained by a more favourable microenvironment inside empty gastropod shells for pellet producers. An appropriate shape and size of shells may have contributed to better preservation. In addition, the open apertures of gastropod shells made them easily habitable, which is supported by a high variability in the size and shape of pellets.

The present collection is probably too small and taxonomically biased to fully assess the distribution of pellet-containing shells, including differences between fossil groups. However, the 90 randomly examined gastropod and brachiopod shells from two localities provide useful insights into these questions. Shelly fossils with pelletoidal infill were especially common in the Haljala and Rakvere stages (middle Sandbian and middle Katian; Table 1). Thirty random gastropods and 30 brachiopods from the fossil collection of the Aluvere quarry (Haljala Stage, Sandbian), without external indications of pellet occurrence, were sectioned and examined. The previous data from the same locality had shown high abundance of pellets inside gastropods and their absence inside brachiopods. From the selected 60 shells, 15 gastropods and 12 brachiopods yielded pellets, suggesting that nearly half of the shells contained pellets in both fossil groups. For comparison, 30 gastropods from the Mõnuste quarry (Vormsi Stage, upper Katian) were sectioned. Only few previous finds of shelly fossils with pellets were known from this stratigraphical interval. However, the study of 30 gastropod steinkerns revealed pellets in 11 cases, that is, in every third shell. This approach clearly shows that the pelletoidal infill is a very common phenomenon related to different shelly fossil groups and stratigraphical intervals within the Middle and Upper Ordovician carbonate succession of Estonia.

Ichnogenus *Coprulus* – pellets in massive accumulations and inside burrows

Richter & Richter (1939) proposed the term *Coprulus* as an informal name. The formal ichnogenus *Coprulus* was erected by Mayer (1952) for isolated small pellets. Two

Fig. 4. Faecal pellets inside Ordovician shelly fossils from Estonia. Scale bars: 1 mm for A, B, D, F–I; 1 cm for C, E. **A**, gastropod *Liospira wesenbergense,* weathered steinkern, largest *Coprulus* (L/W ratio 2.5), TUG 1780-380, Rägavere quarry, Rakvere Stage, Katian. **B**, gastropod *Hormotoma insignis*, polished surface of steinkern, *Coprulus* (L/W ratio 2.4), TUG 76-63, Rägavere quarry, Rakvere Stage, Katian. **C**, gastropod *Hormotoma insignis,* steinkern surface with pellets and trace fossil *Arachnostega*, TUG 2-393, Rakvere, Rakvere Stage, Katian. **D**, detail of TUG 2-393, *Coprulus* (L/W ratio 3), *Arachnostega* and openings of small burrows filled with sparry calcite. **E**, section through the cephalopod phragmocone, only one chamber is filled with pellets, GIT 362-740, Viki drill core, 360.9 m, Kunda Stage, Darriwilian. **F**, section of cephalopod *Estonioceras*, detail from siphuncle filled with *C. oblongus*, GIT 146-7, Valkla outcrop, Kunda Stage, Darriwilian. **G**, section of brachiopod *Clinambon anomalus*, detail of spondylium filled with *C. oblongus*, GIT 543-1367, Saku 1098 drill core, 10.3 m, Keila Stage, Katian. **H**, brachiopod *Porambonites*, polished surface, *C. oblongus* (L/W ratio 2), GIT 619-85, Oandu River outcrops, Rakvere Stage, Katian. **I**, brachiopod *Porambonites wesenbergensis*, detail of sectioned surface, bioturbated pellets different in shape and size, TUG 1766-141, Oandu, Oandu Stage, Katian.

ichnospecies, *C. oblongus* and *C. sphaeroideus*, were described and later *C. bacilliformis* was added (Mayer 1955). Knaust (2008) revised the diagnoses for the ichnogenus *Coprulus* and ichnospecies *C. oblongus* and brought out an important diagnostic feature for small pellets – the length/diameter ratio. *Coprulus sphaeroideus*

and the ichnogenus *Tibiokia* Hatai et al., 1970 were regarded as junior synonyms of *C. oblongus*; thus, the ichnogenus *Coprulus* includes two ichnospecies, *C. oblongus* and *C. bacilliformis* (Knaust 2008). The pellets of *C. oblongus* are isolated pills with a smooth surface, cylindrical to oval in shape and having a length/diameter ratio commonly between 1.5 and 2.0 (Knaust 2008). The pellets of *C. bacilliformis* have the length/diameter ratio around 6 and are rod-shaped (Mayer 1955).

It should be noted that diagnoses of *C. oblongus* by Mayer (1952) and Knaust (2008) are based on material where pellets are partly or completely washed in different burrows. According to Mayer (1952), *C. oblongus* has 'long-oval' shape, but Knaust (2008) refers to 'cylindrical to oval' shape. The pellets that were possibly washed in, instead of being formed *in situ*, may represent composite traces (structures made by combined activity of two or more species) and, according to Bertling et al. (2006), have no ichnotaxonomic standing. Arakawa (1970) introduced a detailed morphological classification of bivalve faeces. The faeces were divided into several types according to the structure and form. Three basic types were distinguished: oval, rod-shaped and ribbon-like pellets, and a large number of subtypes (pellet-types by Arakawa). According to Knaust (2008), *C. oblongus* includes pellets from oval to cylindrical shape, thus from two different basic types of Arakawa (1970). It has to be noted that for poorly preserved very small pellets with small length/diameter ratio values, differentiating between elliptical and rod-shaped forms may be complicated (see Fig. 3B).

Estonian faecal pellets in accumulations are mostly elliptical in shape, with the length/diameter ratio below 2 or 2–3 (Table 1). In few specimens with two different outlines, elliptical (Fig. 4F) and rod-shaped (Fig. 5B), this value is between 4 and 6. Only half of shelly fossils in the Estonian material contained faecal pellets with an average length/diameter ratio around 2, and these can be confidently identified as *C. oblongus*. A small number of rod-shaped faecal pellets have the length/diameter ratio about 4–6, and these can be named as *C. bacilliformis*. However, a large number of pellets are elliptical with the length/diameter ratio over 2; these cannot be named at present without erecting a new species or emending the diagnoses of the existing species (Figs 3E, F, H, 4A, B,

D, 5C). Péneau (1941) described this type of pellets as *Tomaculum*. The Estonian material suggests that it is reasonable to include the elliptical pellets with the length/diameter ratio of 2–3 in the ichnospecies *C. oblongus*. However, it is questionable that there is a good basis to assign the oblong elliptical pellets with length/diameter values over 4 to *C. bacilliformis*. As far as the original material of *C. oblongus* and *C. bacilliformis* described and figured by Mayer (1952, 1955) is not available for re-examination, we identify the elongated elliptical pellets with the length/diameter ratio over 2 only at the genus level.

Compound trace *Tubularina* – pellets in small burrows

Compound traces consist of combined individual traces with different morphologies that would be named differently if they were preserved in isolation (Miller 2003). Compound traces can only be named if all structures have been produced simultaneously (Bertling et al. 2006). For simple burrows filled with pellets, two compound trace-fossil genera *Alcyonidiopsis* Massalongo, 1856 and *Tomaculum* Groom, 1902 are most commonly identified and discussed from Palaeozoic strata. From Jurassic lagoonal limestones, *Tubularina* Gaillard et al. 1994, a small (diameter up to 2 mm) firmground burrow filled with sparry calcite and loose pellets has been described. The walls of *Tubularina* are smooth, without ornamentation, and branching is observed. *Tubularina* is penetrating the sediment sinuously in very different directions. Burrows inside shelly fossils from the Haljala to Oandu stages (Sandbian and lower Katian) are very similar to the Jurassic material. Skeletal debris displaced concentrically around the burrows, and also the sharp contours and circular cross section of the burrow indicate that the traces were made into a coherent substrate.

Ichnogenus *Alcyonidiopsis* – ribbon-shaped burrows with pellets inside trilobites

Two specimens of trilobites from the Haljala and Keila stages contain curved ribbon-shaped burrows inside, filled with sparry calcite and pellets (Fig. 5K). No

Fig. 5. Faecal pellets inside Ordovician shelly fossils from Estonia. Scale bars: 1 cm for A, D, F, I; 1 mm for B, C, E, J, G, H, K. **A**, bivalve *Modiolopsis*, weathered steinkern covered by pyrite threads, TUG 1779-477, Rakvere, Rakvere Stage, Katian. **B**, detail of TUG 1779-477, rod-shaped pellets *C. bacilliformis*. **C**, bivalve *Modiolopsis*, detail of strongly weathered steinkern surface, *Coprulus* (L/W ratio 3), TUG 1779-439, Estonia, Rakvere Stage, Katian. **D**, gastropod *Hormotoma insignis*, redeposited steinkern with crush mark, cracks, overgrown by trepostome bryozoans, TUG 76-62, Rägavere quarry, Rakvere Stage, Katian. **E**, detail of TUG 76-62, steinkern surface with pellets and small bryozoan colony. **F**, bivalve *Cypricardinia,* vertical section, bioturbated sediments and composite trace fossil *Tubularina*, GIT 156-1079, Oandu, Keila Stage, Katian. **G**, **H**, detail of GIT 156-1079, *Tubularina* filled with *C. oblongus*, cross sections at different angles. **I**, gastropod *Subulites amphora*, vertical section, bioturbated accumulations of pellets and trace fossil *Tubularina* filled with *C. oblongus*, GIT 399-999, Aluvere quarry, Haljala Stage, Sandbian. **J**, detail of GIT 399-999. **K**, pygidium of asaphid trilobite, *Alcyonidiopsis* filled with *C. oblongus*, GIT 362-726, Vasalemma quarry, Keila Stage, Katian.

constructional wall or lining is observed; the boundary of the structure is marked by calcite. The burrows are located on the dorsal surface of the sediment infill, one on the cephalon and the other on the pygidium. The burrows are 1.7–2.9 mm and 1.1 mm wide, of somewhat variable width. The pellets are elliptical in shape and represent the ichnogenus *Coprulus*. These burrows are different from *Tubularina*, which has a circular cross section (Gaillard et al. 1994), and from *Phymatoderma*, which is a subhorizontally branching burrow system filled with pellets (Izumi 2012). The location of burrows on steinkerns is similar to that of *Arachnostega*, but the traces do not demonstrate the network characteristic of the latter; besides, the pelletoidal infill is unknown in *Arachnostega*. Bruthansová & Kraft (2003) described pellets arranged in rows inside Ordovician trilobites as *Tomaculum*. However, a number of authors have considered that *Alcyonidiopsis* is the proper name for tubular burrows filled with faecal pellets (Chamberlain 1977; Pickerill 1980; Pickerill & Narbonne 1995; Uchman 1995, 1999; Orr 1996; Uchman et al. 2005, 2013; Buatois at al. 2017; Mángano et al. 2019). *Tomaculum* consists of tightly packed pellets on bedding planes and is indicative of deep-water settings (e.g. Benton & Trewin 1978; Zagora 1997; Podhalańska 2007). The trace is rare in Palaeozoic carbonates (Chamberlain 1977) but is also known from non-marine settings (Metz 2015). Mángano et al. (2019) described small burrows with pellets inside Cambrian bivalved arthropods as *Alcyonidiopsis*. The Estonian ribbon-shaped small burrows inside trilobites are most similar to *Alcyonidiopsis*. Additionally, a few shelly fossils with pellets inside demonstrate poorly preserved burrows with unclear shape and cross section (Table 1), which cannot be named at present.

Notes on the preservation of pellets

For all sectioned specimens, the taphonomic evidence suggests that the large accumulations of pellets were formed *in situ*, inside the shells. This is also proved by the specimens containing only pellets inside (Fig. 3C). Massive accumulations of pellets are not evenly mixed with the sediment, which also indicates that the pellets were not washed into the shells together with the sediment. Random placement of skeletal grains around the sets of pellets suggests that the sediment was not affected by the formation of pellets and proves that the pellets were not made in shells filled with sediment. In the case of shells with large apertures, like in gastropods, it is more likely that pellets were produced when the empty shell was lying on the sea floor and was afterwards filled with sediment. However, it is also possible that the dead body closed the aperture of the gastropods and pellets were formed when the shell was shallowly buried. More likely, shells with small openings,

like brachiopods or echinoderms, could also be colonized by meiofauna and small macrofauna after shallow burial and the pellets were produced by infauna. According to Wilson & Palmer (1992), the cementation is fastest just below the water–sediment interface. Rapid lithification is important for the formation and preservation of trace fossils in carbonates (Knaust et al. 2012). Eriksson et al. (2011) expressed the same opinion for the preservation of coprolites. Rapid lithification was likely favoured by small dimensions of the pellets examined in our study. Cementation by calcite resulting from aragonite dissolution may be confined to the areas immediately adjacent to dissolving bioclasts (Wilson & Palmer 1992). This may be the explanation for the large number of finds related to the different mollusc shells.

In the Ordovician sediments of Estonia, pellets are found in cool-water to tropical carbonates (Table 1). Two stratigraphical levels, tropical carbonates of the Rakvere Stage (Katian) and temperate-water carbonates of the Haljala Stage (Sandbian), demonstrate a higher occurrence and better preservation of pellets. According to Flügel (2004), carbonate pellets can be preserved in warm-water environments with low energy and reduced sedimentation rates. The fossilization of the originally soft particles requires bacterial decomposition of organic mucus and intra-granular cementation by Mg-calcite. The higher number of findings and large scale in the shape and size of pellets are related to the Upper Ordovician, possibly due to the better preservation conditions in warm waters.

The increased number of shells with pellets in the Haljala Stage could be caused by the beginning of climate warming and supported by silicification of sediments. Extremely well-preserved pellets inside shelly fossils from Bohemia also showed a high degree of silicification (Bruthansová & Kraft 2003). Tarhan et al. (2016) and Liu et al. (2019) have discussed rapid silicification for the preservation of soft-bodied fossils. Slightly silicified rocks have a wide distribution in Estonian shallow-water carbonate rocks, especially in the Haljala Stage. The source of silica is supposed to be organic, in particular siliceous sponges, and/or volcanic (Jürgenson 1958; Siir et al. 2015).

Environmental conditions, such as low oxygen levels in the sediment and/or fast burial, related to increase in sedimentation rates, may have contributed to the preservation of pellets. Anoxic conditions slowed down or stopped the decomposition of pellets. The processes occurring at the oxic/anoxic boundaries are controlled by the temperature, supply of organic matter, light, water currents and bioturbation (Kristensen 2000). The bioturbation inside a large number of steinkerns and on their surfaces indicates the existence of oxic environmental conditions inside the shells after the burial and before lithification. In addition, the activities of

infaunal benthos stimulate microbial activity (Aller & Aller 1982) and may in turn accelerate the decomposition of pellets. The physical mixing of sediments lowered the carbonate cementation (Wright & Cherns 2016) and may have supported the degradation of pellets. The best-preserved pellets were found inside the shells where bioturbation was not recorded. The tropical pure carbonates of the Rakvere Stage are, in general, characterized by a relatively low bioturbation rate and a small number of soft-sediment traces (Toom et al. 2019a).

High-energy environments with enhanced oxygen exposure are generally characterized by a very low burial efficiency of organic matter (Arndt et al. 2013). Microenvironment inside the shells was probably less affected, the oxygen diffusion into the sediment was decreased and the degradation of pellets was slowed down. The shells also shielded pellets and pellet-filled burrows with pellets from compaction and allowed an early cementation to occur as suggested by Mángano et al. (2019). This may explain the absence of pellets in the host rocks. However, water circulation in the uppermost sediment column favoured the lithification (Coimbra et al. 2009), and the shells may have acted as traps for calcium ions and promoted early cementation of small pellets. Supposedly, the microenvironment inside the protective shell was an important factor for the preservation of pellets in cool- and temperate-water environments of the Ordovician of Estonia.

Microbial communities are important in the decomposition of organic matter (Solan & Wigham 2005; Morata & Seuthe 2014). Microbes on pellets could originate from the water or sediment, or the gut of pellet producers being ingested with the food. The accumulations of fresh pellets, which contained less microorganisms, had a better preservation potential (Hargrave 1976). The decomposition process, which started from the outer edge of the set, did not reach the end of the set inside an elongated and narrow whorl (Fig. 3H). This may be the reason for a large number of finds of pellets in the apical parts of gastropod steinkerns. The organic matter may have played a major role in inhibiting precipitation of sedimentary carbonates (Morse et al. 2007).

In conclusion, it is difficult to identify one main reason for the observed preservation of pellets. Most likely it is due to the interaction of several factors including sea water and pore water chemistry, temperature, rapid lithification of small particles, favourable microenvironment inside the shells and the composition of pellets and microbial communities.

The trace makers

Flügel (2004) summarized a modern view on trace makers of small pellets: the assignment of pellets to specific pellet-producing animals is difficult because the pellets of most invertebrates lack specific morphological features. However, there are many publications dealing with excrements of different recent aquatic invertebrate groups (e.g. Moore 1931a, 1931b, 1939; Moore & Kruse 1956; Manning & Kumpf 1959; Kornicker 1962; Arakawa 1970, 1971; Kraeuter & Haven 1970; Pryor 1975; Martens 1978; Ladle & Griffiths 1980; Wotton & Malmqvist 2001; Kulkarni & Panchang 2015). In addition to detailed descriptions and classifications of pellets, a wide range of problems have been discussed. Moore (1939) concluded that in general carnivorous animals tend to produce faeces of loose consistency, and faeces of deposit feeders are the most resistant of all. Arakawa (1970) noted that variations in pellets are related to feeding habits and mode of life, and that the pellets of carnivores are very soft and irregular in shape. Excrements of loose consistency cannot be preserved as fossils (Kornicker 1962). The nature and form of faecal pellets are related to the structure and function of the digestive organs (Stamhuis et al. 1998). Unsculptured faecal rods are formed as mid-gut is very simple and circular (Arakawa 1970). The exact shape of pellets may vary; for instance, the excrements of a stressed or starved animal may be thinner and irregular in shape (Arakawa 1971).

Similar pellets inside different shells are described and discussed by Bruthansová & Kraft (2003). These authors demonstrated that the pellets were not related to the animals that originally inhabited the shells. Our observations on the Ordovician material from Estonia confirm this conclusion – the pellets located on the ventral muscle scar of a brachiopod shell and in cephalopod phragmocone could not be produced by a brachiopod and cephalopod, respectively.

It is possible that some pellets were made by scavengers feeding on soft parts after the death of the animal with the shell (Bruthansová & Kraft 2003) or on microbial halo formed around the decaying soft body. Deposit feeders appear to be limited largely to worms longer than 1 cm. In general, juveniles and small worms are restricted to ingest highly digestible organic matter and rich food items (Jumars et al. 2015) and may be the trace makers, especially in the case of complete brachiopod shells, where a slender body shape was needed to enter the shell. Priapulids and arthropods, trilobites included, with mobile epifaunal lifestyle, are discussed as crayon feeders (Hu 2005). In addition, nematodes could feed on bacteria, fungi, algae and protozoans (Sun et al. 2014). Predators and scavengers have high assimilation efficiencies and produce small numbers of faecal pellets (Wotton & Malmqvist 2001). The accumulations with a relatively small number of pellets (much less than 100 pellets per cm^2 according to Wotton & Malmqvist 2001) can be made by scavengers. However, in some cases the

pellets were located in parts of the shell which did not contain a soft body, like between septae in the phragmocone. Other animals than scavengers should have been producing these clusters. Estonian pellets, composed of the same material as the host sediment, suggest that deposit feeders or suspension feeders were trace makers rather than predators and scavengers.

In shallow-marine environments, a cryptic environment inside shells provides shelter and food to different encrusters (Vinn et al. 2018). Our unpublished material of steinkerns brought up new data showing that the encrusting community is widespread and consists of different bryozoans, cornulitids and inarticulate brachiopods. It confirms that the empty shells provided suitable living environments in shallow-marine conditions. However, co-occurrence of pellets and different encrusters has not been observed. Considering the large number of pellets that the suspension feeders produce (Pryor 1975; Wotton & Malmqvist 2001, and references therein), different cavities inside the shells were used as temporary hiding places rather than permanent domicile. Mobile trilobites used empty cephalopod shells for hiding (Davis et al. 2001). Bruthansová & Kraft (2003) suggested that producers selected the shells according to their body dimensions. Our material supports this idea – pellets have not been observed inside the largest shells. In addition, the apertures/holes in shells that controlled the inhabiting community of shells were important.

García-Ramos et al. (2014) discussed a situation where pellets were stored to be used as a bacteria-enriched resource. Gardeners have low turbative activity, inhabiting relatively simple and almost permanent burrows with storage rooms (Stamhuis et al. 1998), and pellets may be stored inside the shells by gardeners. Invertebrates may live in a mixture of faecal pellets and fine particles (Levinton 2017).

Mayer (1952, 1958) originally interpreted *Coprulus* as faecal pellets of annelids. Recent excrements similar to *Coprulus* are commonly produced by polychaetes (Bałuk & Radwański 1979; Gaillard et al. 1994; Knaust 2008; Kulkarni & Panchang 2015). Kraeuter & Haven (1970) investigated pellets of six modern shallow-marine phyla represented by 70 species and described thoroughly several characteristics. The elliptical or rod-like shape was common, but faecal pellets of polychaetes were of rod-like or ellipsoidal shape, with circular cross section, lacking sculpture and having mostly solid consistency. Various mud-dwelling and suspension-feeding polychaetes form solid and resistant pellets of very constant shape (Moore 1931b; Pryor 1975). *Alcyonidiopsis* and *Tubularina*, burrows actively filled with pellets, were interpreted as a feeding structure of polychaetes (Chamberlain 1977; Gaillard et al. 1994; Uchman et al. 2005; Mángano et al. 2019). Recently, palaeoscolecidans were discussed as

potential trace makers (see Martin et al. 2016 and references therein). Based on evidence of scolecodonts, polychaetes were abundant and diverse in the Ordovician of Baltoscandia, especially starting from the Darriwilian (Hints 2000; Hints & Eriksson 2007; Eriksson et al. 2013), and might have been responsible for various trace fossils, including the pellets reported herein. However, in ichnology the identity of trace makers mostly remains speculative. We may have the case of unknown feeding strategies and the animals that made the pellets may have no close living representatives.

Bruthansová & Kraft (2003) described several *Coprulus* (as *Tomaculum*) specimens inside shells associated with *Arachnostega*-like traces. They suggested that pellets could be the faeces of the cryptic producers of *Arachnostega* which is a feeding trace inside the body fossils found at the contact of sediment filling and the inner surface of body fossils. *Arachnostega* is common also in the Ordovician of Estonia (Vinn et al. 2014). We recorded the co-occurrence of faecal pellets and *Arachnostega* in only few specimens, indicating that the trace maker of *Arachnostega* was probably not the producer of pellets inside the shells. Moreover, *Arachnostega* and *Tubularina* were made within coherent sediment, whereas faecal pellets were put into empty shells. Thus, the two traces could not be created simultaneously.

Bruthansová & Kraft (2003) concluded that the producers of pellets inside shells come from different growth stages of a limited number of non-deposit-feeding taxa. The Estonian material inside shells is similar to the Bohemian pellets; they were made by trace makers with similar feeding strategies. Most likely filter feeders and scavengers looking for shelter were the producers of the pellets described herein. However, the large variation in size, shape and the number of pellets in accumulations and burrows suggest a wide spectrum of potential trace makers.

CONCLUSIONS

- Small faecal pellets are common inside shelly fossils (gastropods, bivalves, cephalopods, brachiopods, echinoderms and trilobites) in the Ordovician carbonate succession of Estonia. They may fill up half of the fossil shells.
- The faecal pellets are representing the ichnogenus *Coprulus* Mayer, 1952 and ichnospecies *C. oblongus* Mayer, 1952 *sensu* Knaust 2008, *C. bacilliformis* Mayer, 1955 and transitional unidentified forms.
- Compound traces consisting of small burrows with circular cross section and filled with faecal pellets inside various shelly fossils are representing the ichnogenus *Tubularina* Gaillard et al., 1994. Ribbon-shaped burrows with faecal pellets inside trilobites are

representing the ichnogenus *Alcyonidiopsis* Massalongo, 1856.

- Stratigraphically, faecal pellets occur in the Volkhov to Pirgu regional stages (Dapingian to upper Katian), thus they can be preserved in cool, temperate and warm-water shallow-marine conditions. The highest number of finds and largest morphological diversity, however, are encountered in the Upper Ordovician sediments.
- The size and shape of host shells control the occurrence of pellets in two ways: shells with large apertures were easier to inhabit by animals with different size and body plan, while in narrow and elongated shells, the process of decomposition was slowed down.
- The preservation of pellets has been due to interaction of several factors: chemical and physical processes that affect rapid lithification, factors that disturb mechanical and biological decomposition and the composition of pellets. In some cases, silicification may have supported the preservation of pellets in carbonates.
- Fauna inhabiting various empty shells was diverse through the Middle and Late Ordovician in Estonia. It consisted of mobile trace makers with different feeding strategies.
- The trace maker of *Arachnostega* was most probably not the producer of the faecal pellets inside shells.

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Mikrokoproliidid Eesti Ordoviitsiumi makrofossiilides

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Fossiilsed ekskremendid ehk koproliidid on halvasti säilivad jäljekivistised, mis kannavad olulist paleoökoloogilist ja sedimentoloogilist teavet. Artiklis on kirjeldatud Eesti Kesk- ja Ülem-Ordoviitsiumist (Baltoskandia paleobassein) makrofossiilide kodade sisemuses säilinud mikrokoproliite ning nende levikut ja mitmekesisust. Uuritud materjal sisaldab üle 180 koproliite sisaldava makrofossiili, mis on kogutud enam kui 40 leiukohast ja esindavad mitmesuguseid madalaveelisi keskkondi alates jahedaveelisest karbonaatsest platvormist troopilise avašelfini. Stratigraafiliselt pärinevad mikrokoproliitide leiud Volhovi lademest kuni Pirgu lademeni (Dapingi kuni Kati globaallade). Mikrokoproliidid on ovaalsed või pulkjad, 0,1–1,8 mm pikkused ja 0,08–0,75 mm läbimõõduga; pikkuse/läbimõõdu suhe ulatub 6-ni. Mikrokoproliidid esinevad tigude, karpide, peajalgsete, käsijalgsete, okasnahksete ja trilobiitide kodades ning kuuluvad valdavalt liikidesse *Coprulus oblongus* ja *Coprulus bacilliformis*. Lisaks tuvastati kaks kompleks-jäljekivistist: *Tubularina* (koproliidid ümmarguse ristlõikega käikudes) ja *Alcyonidiopsis* (koproliidid lintjates käikudes). Mikrokoproliidid tekitati siis, kui organismide tühjad kojad asusid merepõhjas või olid veidi settesse mattunud. Koproliidid säilisid tõenäoliselt tänu kodade mehaanilisele kaitsele ja kiirele mineraliseerumisele. Mikrokoproliitide tekitajate bioloogiline päritolu jääb spekulatiivseks, kuid tõenäolisemate rühmade hulka kuuluvad polüheedid, kellel on sobiv suurus ja kehakuju ning kelle tänapäevased esindajad tekitavad ühesuguseid fekaale. Võimalik, et mikrokoproliitide tekitamisel osalesid erineva toitumisstrateegiaga organismid. Valitud leiukohtade makrofossiilide süstemaatiline uuring näitas, et kuni pooltes kodades esineb mikrokoproliite. See näitab koproliite tootvate organismide suurt arvukust ja mitmekesisust Baltoskandia Ordoviitsiumi basseinis. Meie materjal näitas ka, et *Arachnostega* jäljekivististe tekitaja ei olnud tõenäoliselt mikrokoproliitidega seotud.