New Ediacaran fossils from the Ukraine, some with a putative tunicate relationship

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Abstract

Sack-like body fossils *Finkoella ukrainica* gen. et sp. nov. and *F. oblonga* sp. nov., and reticulate fossil *Pharyngomorpha reticulata* gen. et sp. nov. are described from the upper Ediacaran shallow-marine deposits of Ukraine, which are no younger than 557 Ma. The first two resemble the flattened bodies of tunicates showing mainly the outline of tunica, while the third is considered as a fragment of the pharyngeal basket of a tunicate. *F. ukrainica* is represented by smaller individuals interpreted as juveniles, which may occur in clusters together with less numerous larger individuals. The larger forms are interpreted as adults, some of which show the preserved oral/atrial syphons and possible traces of internal organs bulging through the tunica. Moreover, *Burykhia* sp. from the uppermost Ediacaran of the same region is presented. This is the second and younger occurrence of the genus *Burykhia*, which is preserved as a possible fragment of the pharyngeal basket. All the fossils are preserved as the “death masks” between microbial mats, and their appearance depends partly on the relation to the parting surface on which they are observed. The presented new taxa along with the literature data reinforce the possibility that tunicates originated already in late Ediacaran.

Keywords Vendian · Precambrian · Tunicata · Ascidiacea · East European Platform

Introduction

In the recent marine environments, the Ascidiacean tunicates (Tunicata: Ascidiacea) are world-widespread and diverse (2815 species) filter-feeding, mostly sessile, colonial or solitary invertebrates having sack-like body and two syphons. They are important link in the phylogenetic tree because they are regarded as the ancestors of chordates (Lambert 2005; Shenkar and Swalla 2011; Holland 2016). Their unquestionable fossils are dated back to the early Cambrian, as exemplified by *Shankouclava shankouense* Chen et al., 2003 from

China. However, three taxa considered as ascidiaceans are known from the upper Ediacaran, i.e. *Ausia fenestrata* Hahn and Pflug, 1985 from the Kuibis Quartzite (549–543 Ma) of the Nama Group in Namibia, poorly preserved *Yarnemia acidiformis* Nessov in Chistyakov et al., 1984 from the Ediacaran in the middle reaches of the Onega river (lower part of the Erginskaya Formation (550–552 Ma; see Grazhdankin 2011; Grazhdankin and Maslov 2015), and *Burykhia huntii* Fedonkin et al., 2012 from the Ediacaran beds (Verkhovka Formation, 555 Ma), both in the White Sea coast region in the north-western Russia. *Ausia* is known from one specimen, and *Burykhia* from two specimens.

In this paper, four new fossil taxa which could be ascidiacean tunicates are presented from the Ediacaran of Podolia in Ukraine (Fig. 1). One of them is represented by several specimens. These fossils add a new information to the discussion on the still poorly recognized early evolution of the class Ascidiacea. The rocks bearing them are no younger than 557 Ma. Therefore, the fossils are potentially the possible oldest representatives of tunicates if their systematic position is so. The Ediacaran of Podolia provided several taxa of macrofossils belonging to diverse taxonomic groups (e.g., Palić 1976; Fedonkin 1985; Velikanov 1985; Fedonkin

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Fig. 1 Location maps. **a** Location of the study region. **b** Study region with indication of the studied sections. **c** Location of the upper Ediacaran section (star) near the Dniester hydroelectric dam (DPHS);

based on Google Maps. **d** Location of the uppermost Ediacaran section (star) of the Stenitsa Formation at Kitajgorod; based on Google Maps

and Vickers-Rich 2007; Martyshyn 2012; Gozhik 2013; Ivantsov et al. 2015; Dzik and Martyshyn 2015, 2017; Neseterovsky et al. 2018; Soldatenko et al. 2019). Moreover, some ichnotaxa are described from these deposits (e.g., Palij 1974, 1976; Gureev 1983, 1984, 1986; Ivantsov et al. 2015; Grytsenko 2020; Uchman and Martyshyn 2020).

Geological setting

The study area stretches on the southwest flank of the Ukrainian Shield, which is called the Volyn-Podillya-Moldavia Basin. During the Ediacaran Period, the basin

developed as a rifted, passive continental margin in the tectonic extension regime (Poprawa et al. 2018). The Ediacaran deposits belong to the Volyn (Volhynia), Mogilev-Podolsky (Mohyliv-Podilsky) and the Kanilovka (Kanyliv) groups. The Mogilev-Podolsky Group contains the Mogilev Formation (Mogilev Series in the Russian literature) in the lower part. Almost all the studied fossils derive from the Mogilev Formation, except for *Burykhia* sp., which derives from the Studenitsa Formation at the top of the Kanilovka Group (Fig. 2).

Fossils from the Mogilev Formation were collected from the Novodnistrovs'k Quarry (Fig. 1c), which was monitored since 20 years by the senior author (Martyshyn 2012). At the bottom of the quarry, Lower Proterozoic granites and migmatites of the Ukrainian Shield are exposed. They are blanked by thin (up to a metre), discontinuous layer of basal conglomerates, which underlie the Lomozov (Lomoziv) Member of the Mogilev Formation. This member is dominated by mudstones and siltstones, which represent the second sedimentary cycle in the Podolia Ediacaran (Korenchuk and Ishchenko 1981). Some specimens of *Finkoella oblonga*, *Pharyngomorpha reticulata* and *F. ukrainica* derive from this unit. The Lomozov Member contains rare dickinsoniids (Dzik and Martyshyn 2015) and relatively common disc-like representatives of the Petalonamae group (Dzik and Martyshyn 2017). A higher position is occupied by the Yampol (Yampil) Member, which is composed of thick and very thick, partly cross-bedded sandstones (up to 9 m thick) and a package of thin sandstone and siltstone beds (up to 3 m thick) at the top. The holotype and paratype of *Finkoella ukrainica* presented in this paper derive from the top part of the Yampol Member. The overlying Lyadova (Lyadov) Member crowns the Mogilev Formation. It consists up to 2 m-thick siltstone at the base followed by up to 14 m-thick mudstone with intercalations of thin siltstone or sandstone beds.

The base of the overlying Yaryshev (Yarishiv) Formation was previously dated to 553 Ma by Grazhdankin et al. (2011) and Grazhdankin (2014) but newer dating of bentonite layers from the Yampol Member top package (layer B1, c. 1 m above the thick-bedded sandstones) points to 556.78 ± 0.18 Ma (Soldatenko et al. 2019). The presented fossils from the upper part of the Yampol Member are below the bentonite. Therefore, all the presented fossils are no younger than roughly 557 Ma.

Burykhia was found in a small abandoned quarry in the Ternava river gorge near Kitaygorod in the Khmelnytsky region (Fig. 1d), where the Komarovo Member forms the uppermost part of the Studenitsa Formation (60 m thick) which is located in the uppermost part top of the Kanilovka Group. The Komarovo Member is composed of rhythmic intercalations of laminated mudstones and siltstones, which are intercalated with occasional sandstone

beds. This formation transits up to the lower part of the Okunets Formation of the Baltic Group, which is already considered as the lower Cambrian (Cambrian Series 1) containing the trace fossil *Treptichnus pedum* (Seilacher, 1955) (see Ivantsov et al. 2015). Beside this and other trace fossils, the Studenitsa Formation contains body fossils of algae, including *Tyrasotaenia podolica* Gnilovskaya, 1971, *Vendotaenia antiqua* Gnilovskaya, 1971 (Ivantsov et al. 2015), *Tymkivia stuzhuki* Martyshyn in Nesterovsky et al., 2018, the protozoan or alga *Harlaniella vermiformis* Martyshyn in Nesterovsky et al., 2018, and the protozoan *Palaeopascichnus delicatus* Palij, 1976 (Nesterovsky et al. 2018).

Materials

The presented specimens are collected by (1) A. Martyshyn in collaboration with a research group during 20 years of the field work and monitoring of the quarry near the Dniester hydroelectric dam (DPHS) and other outcrops (Fig. 1), and by (2) S. Finko who provided the holotype of *F. ukrainica* and the large sandstone slab with the paratype of *F. ukrainica* material for research. Specimens of the described taxa are in the collection of the Institute of Geology of the Taras Shevchenko National University of Kyiv. They have the institutional abbreviation IGKNU.

Systematic description

Subphylum **Tunicata** Lamarck, 1816

Class **Asciidiacea** de Blainville, 1824

Remarks. Classification of the fossil Asciidiacea is based on (1) their pouch-like structure, which is similar to recent representatives of this class, (2) the presence of traces of siphons, and (3) imprints of internal organs on the surface of semi-decomposed remains, which are similar to the tunic, pharyngeal basket mantle (branchial sac), atrium, stomach, and the atrial/oral siphons of the present-day tunicates. These morphological features are typical of the family Asciidiidae Herdman, 1882 (Herdman 1882; Fedonkin et al. 2012) and cannot be misled for other group of organisms.

Genus ***Finkoella*** gen. nov. Martyshyn

Etymology. After S.V. Finko, an amateur palaeontologist, who provided the holotype and paratype of the type species.

Type species. *Finkoella ukrainica* sp. nov. Martyshyn.

Diagnosis. A convex or concave, ovate, oval, or rarely oblong, cucumber-shaped, lenticular structure on the lower or upper surface of sandstone/siltstone/mudstone layers. In most specimens, one end is more elongated, and the opposite one is more rounded or almost even. One of the ends may show a protruded, short neck and/or a shallow sinus. A low/shallow circular protrusion/depression can be present in the convex or concave structure, respectively. The protrusion/depression is usually located eccentrically towards one of the ends. Moreover, some shallow/low concavities/convexities may occur on the surface. The edges are usually slightly elevated in convex specimens or depressed in concave forms.

Species. *Finkoella ukrainica* and *F. oblonga* described in this paper.

Comparison. No analogues among the Ediacaran and younger fossils.

Distribution. Lomozov and Yampol members, Mogilev Formation, Mogilev-Podolsky Group, upper Ediacaran.

***Finkoella ukrainica* sp. nov.** Martyshyn

Figures 3a–d, 4a–b, 5a–i, 6a–f, 7

v 2018 problematic organism, probably Tunicata.—Nesterovsky et al.: fig. 4c.

Etymology. After the country Ukraine.

Diagnosis. *Finkoella* showing oval to elliptical, rarely oblong shape, which may show a protruded, short neck and/or a shallow sinus. A low/shallow circular protrusion/depression can be present in the convex or concave structure, respectively. Smaller specimens can be without neck and protrusions/depressions.

Holotype. One of two larger structures (Figs. 3a, b) on the lower surface of the slab IGKNU17p170, i.e. the specimen IGKNU17p170/1 (Fig. 3c). The slab is built of muddy, very fine-grained sandstone and derives from the upper part of the Yampol Member of the Mogilev Formation,

Fig. 3 Types of *Finkoella ukrainica* Martyshyn sp. nov. from the Yampol Member of the Mogilev Formation (upper Ediacaran) in the quarry near the DHPS, *bg* bulge, *ee* elevated edge, *dmr* double marginal ridge. **a, b** Lower surface of slab IGKNU17p170 showing the holotype (IGKNU17p170/1), specimen IGKNU17p170/2),

and a group of smaller specimens between them considered as juveniles. Very fine grained muddy sandstone, Yampol Member of the Mogilev Formation. **c** Close view of the holotype. **d** The paratype IGKNU17p201/1, upper surface of sandstone slab, Yampol Member of the Mogilev Formation

Fig. 4 Upper surface of a large fine-grained sandstone slab IGKNU17p202 from the Yampol Member of the Mogilev Formation in the quarry near the DHPS. **a** General view showing several specimens *Finkoella ukrainica*, including the paratype. **b** Schematic drawing of **a**. Rosette in the right lower corner shows orientation of the longer axis in 31 specimens on the slab

Mogilev-Podolsky Group, in the quarry near the DHPS at Bernashivka village, Vinnytsia region.

Other materials. (1) paratype IG KNU17p201/1 (Figs. 3d, 4a, b) and all other (at least 46) specimens on the upper surface of sandstone slab from the upper part of the Yampol Member (Figs. 4a, b, 5); moreover (2) two specimens in slabs IGKNU17p204 (Fig. 7a), IGKNU17p210 (Fig. 7f), IGKNU17p2011 (Fig. 7g), and IGKNU 17p214 (Fig. 7j), and single specimens in slabs IGKNU17p205 (Fig. 7d), IGKNU17p207 (Fig. 7e), IGKNU17p209 (Fig. 7b), IGKNU17p208 (Fig. 7c), and IGKNU17p213 (Fig. 7i), all from the Lomozov Member of the Mogilev Formation in the quarry near the DHPS at Bernashivka village, Vinnytsia region.

Description. The holotype (Fig. 3a–c) is a convex oval structure on the lower surface of a thin bed of micaceous, clayey, very fine-grained sandstone. It is 95 mm long and up to 55 mm wide. A round protrusion, 5 mm in diameter, is located slightly eccentrically towards one of the ends. One of the ends is more elongated, and the opposite one is more rounded. The more rounded end shows a protruded short neck, which is wider at its termination. The termination is unevenly lobate. The margins are sharp and even. The surface of the structure is generally smooth, except for local grain-size corrugations, thin and short grooves and a longer, narrow, shallow groove which runs obliquely through three quarters of the width close to the wider end.

The second fossil is located on the same side of the slab bearing the holotype (Fig. 3a, b). This is a concave, smooth structure in the shape of a simple cucumber. One end of the structure shows a sinus, which is 4 mm deep and 7 mm wide. The opposite end is broken on the edge of the slab and therefore not available. The preserved margins are sharp and locally elevated.

The paratype (Figs. 3d, 4a, b) is a concave, elongate oval structure on the upper surface of a sandstone slab. It is 56 mm long and up to 25 mm wide. The wider end is tapered and the opposite, narrower end shows a short, indistinct neck. The surface is covered with local bulges of oval outline and irregular, gentle depressions. The structure is mostly sharply bounded along its margin, but locally the boundary is less distinct. From one side, the margin is elevated and locally marked by a double ridge, which is 2 mm

wide (Fig. 3d). The ridge is separated by an uneven narrow groove.

Other specimens (Figs. 4, 5, 6) are usually oval, convex or concave structures; some are obtuse from one end. They show variable sizes, with length ranging from 5 to 110 mm and width from 5 to 55 mm. The width versus length of all specimens show strong positive correlation ($r=0.84$; Fig. 8). Most of the smaller specimens are usually smooth, without any neck and protrusions, but some of them show slightly elevated/depressed edges and or bulges interpreted as atrial siphon. Only some of them show a short neck (Fig. 7c) interpreted as oral siphon and knob-like protrusions/depressions. One of them shows a narrow side neck, which can be atrial syphon (Fig. 7i).

The described structures may occur in clusters (Figs. 3a, b, 4a, b). Individuals in the cluster may show different size. Longer axis of the fossil shows distinct orientation (rosette in Fig. 4b).

Remarks. The small specimens, which are less than 25 mm wide (see Fig. 8), are considered as representing juvenile organisms (see “Discussion”). The holotype was selected from specimens representing large, fully developed and most completely preserved organism (Fig. 9).

Finkoella oblonga sp. nov.

Figures 10

Etymology. After oblongus (Latin)—elongate, in correspondence to the overall shape.

Diagnosis. Elongated *Finkoella* showing winding margins and longitudinal furrows/ridges, which tend to run parallel to the margin.

Holotype. Split slab of horizontally to wavy laminated siltstone showing positive, i.e. convex fossil (IGKNU17p202/1) and is counterpart showing negative, i.e. concave part (IGKNU17p202/2). This is the only specimens of the species. It derives from the Lomozov Member of the Mogilev Formation, Mogilev-Podolsky Group, in the quarry near the DHPS at Bernashivka village, Vinnytsia region.

Other material. A split slab with specimen IGKNU17p215 and its counterpart IGKNU17p215/1, Yampol Member (Fig. 10b). Moreover, IGKNU17p216, Lomozov Member (determined as *Finkoella* cf. *oblonga*).

Description. The holotype (Fig. 10a) is an elongate, cucumber-like structure, 120 mm long and up to 42 mm wide, which is visible as a positive (convex) part and its negative (concave) counterpart in a horizontally split slab. It shows six longitudinal, low grooves and ridges, which show gentle

Fig. 5 Details of the large slab from Fig. 4

slopes and are 3–4 mm wide. They run parallel to the margin of the structure and turn accordingly at the terminations, so they tend to form concentric rings. They are more continuous on one side than on the other side, where only their

fragments are visible. Moreover, the structure shows small corrugations, but without any pattern. Edges of the structure are distinctly elevated/depressed and locally show a double ridge or groove, which is 1.5–3 mm wide.

Fig. 6 Other details (a–d) of the large slab from Fig. 4, *as* atrial syphon, *dmr* double marginal ridge

The specimen KSU17p215 and KSU17p215/1 (Fig. 10b) shows the same shape as the holotype. It is 95 mm long, up to 40 mm wide. Six, more or less complete and an additional one incomplete ridges/grooves are visible. Their course is the same as in the holotype. The edges are sharp and locally elevated. One of the termination is narrower. It forms a dome-like protrusion. The other end is obtuse and seems to partly broken.

The specimen IGKNU17p216 (Fig. 10c, d) is ovate, 38 mm long, up to 21 mm wide. It becomes gradually narrower toward its semi-circular distal. The opposite end is obtuse and uneven. The perimeter is located in one third of the length from the obtuse end. Six low ridges and grooves run parallel to the lateral margins of the structure. They

disappear toward the ends. A curved tail of small corrugations emerges from the obtuse end (rm in Fig. 10c). Its margins are diffused. Similar corrugations cover larger part of the fossil body.

Remarks. In the holotype, both terminations of the structure touch the edge of the slab, so a possible neck-like protrusion is not visible, if it was present at all. The neck is also not obvious in KSU17p215. The specimen IGKNU17p216 is determined as *Finkoella* cf. *oblonga* because its ovate shape differs from the elliptical, cucumber-like shape of the holotype. It is also distinctly smaller than the holotype.

Fig. 7 Other specimens of *Finkoella ukrainica* from the Lomozov Member of the Mogilev Formation in the quarry near the DHPS, convex hyporeliefs. **a** Two specimens on slab IGKNU17p204. **b** IGKNU17p209, *ee* elevated edge. **c** IGKNU17p208, elevated edge, *os* oral syphon. **d** IGKNU17p205. **e** Two specimens on

slab IGKNU17p207. **f** Slab IGKNU17p205. **f** Two specimens on slab IGKNU17p210. **g** IGKNU17p211. **h** IGKNU17p212. **i** IGKNU17p213; not the neck-like protrusion (*np*) on the right side, which is interpreted as the atrial syphon. **j** Two specimens on slab IGKNU17p214, *ee* elevated edge

Genus *Pharyngomorpha* gen. nov.

Etymology. After the pharyngeal basket, the characteristic anatomic part of tunicates, which is probably preserved in the type species of this genus, and after *morpha*—in relation to morphology the pharyngeal basket.

Type species: *Pharyngomorpha reticulata* sp. nov.

Diagnosis. Basket-like structures showing ribs and/or grooves arranged in a rectangular net.

Species. Only *Pharyngomorpha reticulata*—monotypic genus.

Fig. 8 Plot of width versus length for *Finkoella ukrainica*

Comparison. No analogues among the Ediacaran and younger fossils.

Distribution. Lomozov Member, Mogilev Formation, Mogilev-Podolsky Group, Upper Ediacaran. Also the lower part of the Nagoryany Formation (Dzhurzhevka Member) in Moldova, dated roughly to 555–551 Ma (Francovschi et al. 2021).

***Pharyngomorpha reticulata* sp. nov.**

Figure 11a–c

2021 ?*Ausia/Gibbavasis* sponge-like organism—Francovschi et al.: fig. 14E

Etymology. After reticulum (Latin)—net, in correspondence to the morphology.

Fig. 9 Reconstruction of *Finkoella ukrainica* (drawn by S.S. Solodkyi)

Diagnosis. Elongated *Finkoella* showing winding margins and longitudinal furrows/ridges, which tend to run parallel to the margins.

Holotype. One specimen in the slab IGKNU17p203 (Fig. 11), i.e. IGKNU17p203/1 (Fig. 11b, c) from the Lomozov Member of the Mogilev Formation, Mogilev-Podolsky Group, in the quarry near the DHPS at Bernashivka village, Vinnytsia region.

Description. The holotype is 37 mm long and up to 19 mm wide. It contains about ten, straight, perpendicular, densely packed parallel ribs separated by narrow furrows. There is 4 ribs per 10 mm. The furrows are less than 1 mm wide. The ribs are crossed by five longitudinal furrows (running along the structure) which are perpendicular to the ribs. The longitudinal furrows are c. 1 mm wide. The ribs in the place of intersection with the longitudinal furrows are still visible but they are much lower than in the inter-ribs stretches. The inter-ribs stretches form rectangles (5.0 × 2.5 mm), which are perpendicularly oriented to the structure, so they show the net-like pattern. The structure is elevated in the marginal part. In the narrower part, short bars occur on the margins.

The smaller specimen IGKNU17p203/1 is located c. 20 mm from the holotype. It is 14 mm long and 12 mm wide and composed of five ribs separated by narrow furrows, which are similar to these in the holotype.

Remarks. It is not excluded that the smaller specimen is a disarticulated part of the holotype. In the vicinity of the holotype, poorly outlined ribs can be visible, which may also derive from fragmentation of the organisms represented by the holotype or other individuals. Both specimens

Fig. 10 *Finkoella oblonga* sp. nov. from the Mogilev Formation in the quarry near the DHPS. **a** The holotype IGKNU17p202 from the Lomozov Member, *dmg* double marginal groove, *dmr* double marginal ridge, *ee* elevated edge. **b**. IGKNU17p215, Yampol Member. **c**

Finkoella cf. *oblonga*, IGKNU17p216, Lomozov Member, *rm* realised material (from the body interior). **d** Close view of the specimen in **c**

co-occur with *Finkoella ukrainica* on the same surfaces. ?*Ausia/Gibbavasis* sponge-like organism (Francovschi et al. 2021: fig. 14E) is so far the best preserved specimen ascribed to *Pharyngomorpha reticulata*.

Genus *Burykhia* Fedonkin et al., 2012

Burykhia sp.

Figure 12a, b

Material. One specimen IGKNU17p191a, b (positive and negative) in a thin (3–8 mm) mudstone slab from village Kitaygorod in the Khmelnytsky region. Uppermost

Ediacaran, Kanilov (Kanyliv) Group, Studenitsa Formation (Komarovo Member), 7 m below the boundary with the Okunets Formation, ca. 12 m below the Precambrian–Cambrian Boundary. The slab contains *Harlaniella* on the reverse side.

Description. An incomplete (broken) convex structure having its concave counterpart and an outline of incomplete ellipse, up to 45 mm wide and at least 42 mm long (probably twice longer when would be complete). It shows diagonal, straight, narrow furrows, which are about 0.5 mm wide and 5–8 mm apart. The furrows show slit-like widenings, up to 4 mm long and up to 2 mm wide, 4–5 m apart, which are deeper than the remaining parts of the furrow. In some

Fig. 11 *Pharyngomorpha reticulata* sp. nov. from the Lomozov Member of the Mogilev Formation in the quarry near the DHPS. **a** Two specimens of *Pharyngomorpha* on the right and *Finkoella ukrainica* (Fu) on the left, IGKNU17p209. **b, c** Close views of specimen IGKNU17p209/1

inter-furrow areas, small, oval depressions, 1–2 mm wide may occur. They have a concave counterpart. They are located in the middle between the furrows, in a line parallel to them.

Remarks. *Burykhia hunti* Fedonkin et al., 2012 (Fig. 11c, d), the only known species of *Burykhia* is also known from fragments of the pharyngeal basket. However, the pattern of the furrows and depressions and their counterpart is different: it does not show the slit-like depressions along the furrows, and the structures in *Burykhia* sp. are arranged diagonally, while in *B. hunti* they are transverse and longitudinal.

Discussion

The morphological features of the described fossils point to animals, which are similar to these of the class Ascidiacea (tunicates). The overall shape of *Finkoella* resembles sack-like soft body. The neck or sinus at the end of *F. ukrainica* can be interpreted as the oral (branchial, inhalant, incurrent) syphon, while the more regular, circular bulges can be the atrial (exhalant, excurrent) syphon. The elevated edge and the double marginal ridge/groove which are present in some specimens are an evidence of a compressed, elastic sack, which can be interpreted as the tunic. Other irregularities (bulges) on the surface can be manifestations of some internal anatomic elements (heart, stomach, gonads) of the tunicate bulging through the tunic (Fig. 13). Preservation of the syphons may depend on the position of the body during burial. If the syphons are underside the body, they can be

Fig. 12 *Burykhia*. **a** *Burykhia* sp. in mudstone from the Studenitsa Formation at Kitaygorod, IGKNU17p191a (left, upper surface) and **b** (right, lower surface). **b** Drawing of **a**. **c**, **d** *Burykhia hunti*, the type

material (PIN, no. 3992/5048, The Orlov Paleontological Museum of the Paleontological Institute of the Russian Academy of Sciences, Moscow) from the Verkhovka Formation, White Sea coast region

visible only as bulges on the opposite of the body and cannot be clearly recognized.

The smaller specimens of *Finkoella ukrainica* probably represent juvenile individuals (less than 25 mm wide by convention; Fig. 8). They prevail in number. Their occurrence in clusters in association with larger, well developed individuals suggest colonial style of life. Such style of life

may result from the asexual reproduction by budding known from some recent ascidians (Holland 2016). This explains the occurrence of numerous juveniles close to small number of adults. However, accumulation by weak currents is not excluded. Distinct orientation of *F. ukrainica* (Fig. 4b) can result from such currents, which are related to tides, as the

Fig. 13 Preservational mode of preservation of *Finkoella*. **a** Formation of “death masks” in between microbial mats with indication of splitting surface. **b** Appearance on splitting surfaces. **c** Some morpho-

logical features of *Finkoella*. The bulge can be formed over an internal organ of the tunicate

intertidal environment is proposed for the rocks bearing the fossils (Uchman and Martyshyn 2020).

Most of the modern tunicates have the standing life position, with their bag-shaped body attached to various hard substrates. However, some tunicates are passively lying on the bottom (Bonnet et al. 2013). It is possible that *Finkoella* was a tunicate of such type, which is adapted to soft substrates (Fig. 9). This is inferred from the fact that there are no sediment elements that would be hard and no evidence a part of the body which would be attached to such elements or would be anchored in the sediment. Similar mode of life is interpreted to the Ediacaran *Yarnemia*, which is also tentatively ascribed to tunicates (Chistyakov et al. 1984).

The net-like structure in *Pharyngomorpha* strongly suggests that it is an imprint or mold of the pharyngeal basket, which is partly similar to the other ascidian *Burykhia huntii* Fedonkin et al., 2012 from the late Ediacaran deposits

(555 Ma) on the White Sea coast region (Fedonkin et al. 2012). The pharyngeal basket is a characteristic and unique anatomical element of tunicates, where the food particles are trapped in mucus and supplied into the stomach. It shows a sac-like morphology, which may occupy a large part of the body. Its wall is perforated with gill slits and reinforced with ribs. Morphological detail of the basket (arrangements and shape of the gill slits, ribs) may differ among taxa and develop through ontogenetic stages (Lambert 2005; Shenkar and Swalla 2011; Holland 2016). The pharyngeal basket is present in *Shankouclava*, the oldest reliable tunicate (Chen et al. 2003). Nevertheless, the reticulate anatomical elements, which may resemble the pharyngeal basket can occur in some Ediacaran fossils which ascidian affinity remains controversial, e.g. in *Ausia* (Hahn and Pflug 1985). *Burykhia* belongs also to them. The arrangement of slits and ribs in *Burykhia* points to a

more complex morphology than simple reticulate form in *Pharyngomorpha*.

The described *Burykhia* isp. represents the second occurrence of this genus, which extends its stratigraphic range by about 15 Myr to the latest Ediacaran. *Finkoella* preserved mostly external part of the body, i.e. tunica, while *Burykhia* and *Pharyngomorpha* are probably preserved fragments of the pharyngeal basket. Therefore, *Finkoella* can be considered as a more completely preserved body of a tunicate.

The changeability of morphology in *Finkoella* demonstrates dependence on taphonomic factors. These fossils are preserved as probable “death masks” (Gehling 1999) formed by microbes between microbial mats which enveloped the organism after its death (Fig. 13a). Local ferruginization of the surface of the fossils (Figs. 3d, 4a) can be derived from the weathered pyrite, which mineralize the body and is common in this type of preservation. Surfaces of the mats and bedding surfaces are the parting surfaces on which the fossils are observed. The concave or convex appearance depends on whether the parting surface propagated below or above to the fossil (Fig. 13b). Therefore, both, convex or concave structures may occur on the same surface as e.g., in the case of slab bearing the holotype (Fig. 3a, b), with their counterparts on the opposite surface, including external molds if the surface runs on the surface of the fossil and the body of the fossil remains on the counterpart surface. If the surface runs through the fossil, its parts can be preserved on both sides. Such cases show that the broken fossil contains at least two layers (Figs. 6a, b, 7b), accordingly to the sack-like morphology.

The presented new taxa along with these which are described so far from the Ediacaran (*Ausia*, *Yarnemia*, *Burykhia*) reinforces the possibility that tunicates originated already in late Ediacaran. As *Ausia* is no older than 549 Ma, *Yarnemia* than 552 Ma and *Burykhia* than 555 Ma, *Finkoella* and *Pharyngomorpha* with their age no younger than 557 Ma can be regarded as the possible oldest representatives of tunicates. In this way, deep roots of vertebrates seem to be more and more probable.

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