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**A reassessment of the problematic Ediacaran genus *Orbisiana* Sokolov 1976**

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**Abstract**

The genus *Orbisiana* was established in 1976 by B.S. Sokolov based on a collection of seven specimens within core material from a borehole drilled through the Ediacaran-age Gavrilov Yam Formation of the Moscow Basin, Russia. Here we reassess the original material for the type species *Orbisiana simplex* Sokolov 1976, which was long considered to be lost; fix the holotype of the type species; and revise the original diagnosis of the genus and species. Pyritisation of the fossils, which are preserved in finely laminated shales, allows three-dimensional morphological characterisation of this taxon using X-ray microtomography ( $\mu$ CT). Morphological and taphonomic analyses of the type material and additional three-dimensionally preserved specimens from the Verkhovka Formation (Vendian of the White Sea area) suggest that *Orbisiana simplex* consisted of submillimetric to

millimetric globular chambers arranged in compact, grape-like clusters, or forming sinuous to linear aggregates. Occasionally, aggregates can bifurcate, with no appreciable change in chamber dimensions or shape. The phylogenetic affinity of *Orbisiana* remains uncertain, but its chambered construction, putative agglutinated structure of the chamber walls, and compact, occasionally branching chamber arrangement are shared with agglutinated tests of the Ediacaran genus *Palaeopascichnus*. Our reassessment and systematic study of the genus *Orbisiana* sheds new light on one of the least studied members of the late Ediacaran macroscopic biota.

**Key words:** *Orbisiana*, Ediacaran, East European Platform, Gavrilov Yam Formation, Moscow Basin, Verkhovka Formation, White Sea area, *Palaeopascichnus*, agglutination.

## 1. Introduction

The fossil taxon *Orbisiana simplex* was amongst the first taxa described by Sokolov (1976) to justify the establishment of the Vendian sedimentary sequence of the East European Platform. The type fossil material was collected from a drill-core recovered from the Soligalich 7 Borehole (Fig. 1), one of many that penetrated the subsurface within the Moscow Basin. The original taxonomic diagnosis was very brief, consisting only of a figure caption, with no information provided as to the whereabouts of the fossil material, the number of studied specimens, or their stratigraphic and geographic occurrence. Sokolov (1976) presented *Orbisiana* as a monospecific genus, and his published description would suggest that there was only one specimen in the original collection. The specimen figured in 1976 was subsequently refigured by Sokolov (1997, p. 120, pl. 11 fig. 6) and discussed as a holotype. The fossil *Orbisiana simplex* has since been found to be widely distributed across the East European Platform. In addition to the type locality, it occurs in the Southeast White Sea area (Fedonkin, 1981, 1985, 1990); the Kepina 775 Borehole in the Northeast White Sea area (collection of E.Yu. Golubkova); the middle reaches of the Onega River (Chistyakov et al., 1984; Ivantsov and Grazhdankin, 1997); the Kotlas Borehole in the south of Arkhangelsk Region (Grazhdankin et al., 2010); the Kunevichi 4 Borehole in the west of Leningrad Region (Jensen, 2003);

the Shotkusa 1 Borehole in the north-east of Leningrad Region (Golubkova et al., 2016, 2018; Kushim et al., 2016); and in the South Urals (Fig. 1). Despite this abundance of material, there have been no attempts to properly describe this taxon. The present reassessment of *Orbisiana simplex* was triggered by rediscovery of the original type material in collections in Novosibirsk, ~2500 km away from the type locality. The collections were handed over to the Trofimuk Institute of Petroleum Geology and Geophysics, Novosibirsk, by relatives of B.S. Sokolov, following his death in Moscow, September 2, 2013.

Most previous authors agree that *Orbisiana* had algal affinities (Sokolov, 1976, 1997; Xiao and Dong, 2006; Yuan et al., 2011), although morphologically similar albeit differently preserved fossils have been compared to faecal pellets (Fedonkin, 1977, 1980, 1981). Central to our study is a comparison drawn between *Orbisiana* and a palaeogeographically cosmopolitan late Ediacaran genus *Palaeopascichnus* (Gehling et al., 2000; Jensen, 2003; Jensen et al., 2006; Grazhdankin et al., 2010; Grazhdankin, 2014; Ivantsov, 2017). Recently, Wan et al. (2014) conducted taphonomic studies using X-ray micro-CT techniques of *Orbisiana*-like fossils from the middle Ediacaran Lantian Formation of South China. Those authors emended the original diagnosis of *Orbisiana*, erected a new species (*O. linearis*), and argued that *Orbisiana* consisted of uniserially arranged, tangentially-joined cylindrical units (Wan et al., 2014). Reassessment of the type material for *Orbisiana simplex* leads us to question the taxonomic assignment of the Lantian Formation specimens, and reveals novel insights into the palaeobiology and taxonomy of *Orbisiana*.

## 2. Material and methods

The type collection consists of seven specimens preserved as pyritised compressions on parting surfaces in grey, finely laminated shales, within a 42 mm-diameter drill-core. The type specimens were compared with slightly younger material collected by us in the Southeast White Sea area in 2016–2018 (comprising 34 specimens). The studied material was imaged using a Canon EOS 6D digital single-lens reflex camera with a Canon 100mm f/2.8 USM Macro lens mounted on a Canon



Extension Tube (EF 25 II). Additional images were obtained from a Leica DFC295 Camera attached to a Leica M295C optical microscope. Selected fossils, including the holotype fixed herein, were scanned using a Nikon XTH-225  $\mu$ CT scanner in the Life Sciences Building, University of Bristol, U.K. X-rays were generated using a tungsten target, with a current of 80  $\mu$ A, a voltage of 215 kV, and no filtration. Three-dimensional morphological reconstruction of fossils was undertaken using SPIERS (Sutton et al., 2012). A black-and-white negative film sheet with an image of the holotype of *Orbisiana simplex* was found in Sokolov's archive collection housed in the Trofimuk Institute of Petroleum Geology and Geophysics (Novosibirsk). The film was scanned using an Epson V750 professional photo scanner in the LighthouseFilmLab, an analogue photographic laboratory in Novosibirsk. The original  $\mu$ CT scan data, as well as digital photographs of the holotype, are available upon request from the corresponding author.

### 3. Stratigraphic settings

The holotype of *Orbisiana simplex* Sokolov 1976 originates from the Soligalich 7 Borehole, drilled in the 1960s in the north Kostroma Region (Fig. 1). We could not acquire the original description of the Soligalich 7 Borehole section. A note found together with the type material (handwritten by B.S. Sokolov) suggests that the fossil material is confined to the Nelidovo beds, and that it was collected by V.V. Kirsanov, who erected the Nelidovo Beds (Kirsanov, 1970), which were the stratigraphic precursor to the Nelidovo Formation (Kirsanov, 1974). Both the Nelidovo beds and the Nelidovo Formation are currently treated by the Russian Interdepartmental Stratigraphic Committee as junior synonyms of the Gavrilov Yam Formation, and have been eliminated from the Stratigraphic Correlation Chart of the Moscow Basin (Kuzmenko and Burzin, 1996) (Fig. 1).

The Gavrilov Yam Formation (maximum thickness 124 m) constitutes pale grey, poorly sorted sandstones at its base, followed by a coarsening-upward succession of dark grey, greenish grey, and reddish grey finely laminated shales with thin volcanic tuff interbeds (Lower Member), and packages of greenish grey sandstones interstratified with dark grey shales, and greenish grey intervals of

alternating siltstone and shale interbeds (Upper Member; Fig. 1; Kuzmenko and Burzin, 1996). The underlying Pletenevka Formation (maximum thickness 66 m) comprises pale grey, poorly sorted, pebbly sandstones, which fine upwards into dark-to-reddish grey siltstones. The overlying Nepeitsino Formation (maximum thickness 156 m) can be divided into two members. The Lower Member consists of pale grey sandstones (which are genetically related to the Gavrilov Yam parasequence) and overlying greenish-to-dark grey shales with volcanic tuff interbeds. The Upper Member comprises a package of interstratified greenish grey sandstones, siltstones and dark grey shales, overlain by a thick interval of dark grey and greyish green shales (Fig. 1; Kuzmenko and Burzin, 1996). The Gavrilov Yam Formation and Lower Member of the Nepeitsino Formation constitute a highstand systems tract formed as a result of shoreface progradation onto a low energy inner shelf (Maslov et al., 2008). Correlation with the Soligalich 7 Borehole suggests that the type material of *Orbisiana simplex* originates from the middle part of the Lower Member of the Gavrilov Yam Formation, representing a low energy inner shelf depositional system (Fig. 1). In addition to *Orbisiana simplex*, the Gavrilov Yam Formation has yielded the carbonaceous compression microfossils *Eoholynia mosquensis*, *Caudina cauda*, *Striatella coriacea*, *Palaeolyngbya* sp., *Zinkovioides inclusis*, and *Taenitrichoides* sp. (Kuzmenko and Burzin, 1996).

Ongoing advances in the Vendian stratigraphy of the East European Platform allow a reliable correlation to be made between the Moscow Basin and sections in the Southeast White Sea area (Maslov et al., 2008; Marusin et al., 2011; Grazhdankin, 2014; Grazhdankin and Maslov, 2015). The Gavrilov Yam Formation is a part of the Redkinian Regional Stage, and is coeval with the lower part of the Lyamtsa Formation of the Southeast White Sea area. Volcanic tuff interbeds at the base of the overlying Verkhovka Formation yielded a U–Pb zircon date of  $558 \pm 1$  Ma (Grazhdankin, 2003, 2004, 2014). The type material for *Orbisiana simplex*, therefore, is considered to be older than 558 Ma. The studied material of *Orbisiana simplex* from the Southeast White Sea area was collected in the Verkhovka Formation, cropping out along the right bank of Syuzma River (Onega Peninsula). These fossils are slightly younger than  $558 \pm 1$  Ma, but older than a U–Pb zircon date of  $552.85 \pm 0.77$  Ma

(Schmitz, 2012, recalculated from Martin et al., 2000), from volcanic tuffs at the base of the overlying Zimnegory Formation (Fig. 1).

#### 4. Taphonomy and morphology

The holotype of *Orbisiana simplex* is preserved as a sinuous aggregate of pyritised, ring-shaped units on a parting surface in greenish-grey thin laminated shale (Fig. 2A–B). Only a fragment of the specimen has been previously illustrated. The complete length of the aggregate reaches 20 mm. In addition, the aggregate appears to bifurcate at one end (Fig. 2A, C–D). The width of the specimen varies between 0.5 and 1.25 mm. The aggregate consists of over 80 ring-shaped units of variable size (0.25–0.5 mm in diameter). There is a tendency towards a biserial arrangement of alternating units throughout the entire length of the holotype, although this regularity does not seem to be consistent (Fig. 2A). The six paratypes are preserved as sinuous, rectilinear (Fig. 2E–F) or irregularly clustered (Fig. 2G–J) aggregates of pyritised ring-shaped units of variable size (0.25–1.0 mm in diameter). In some instances, individual units appear as globular or hemispherical structures (Fig. 2E–F). Branching of the aggregates has been observed on several occasions (Fig. 2G, 2I, 3A). The width of paratype aggregates varies between 0.5 and 2 mm. The largest aggregate reaches 20 mm in length and comprises 150 ring-shaped units.

Additional observations of the type material using X-ray  $\mu$ CT confirm the aggregate-like arrangement of pyritised ring-shaped units (Figs 2C–D, 3B). Furthermore, the interior of the holotype-hosting core sample appears to host additional specimens and fragments of *Orbisiana* at separate levels. All the linear aggregates within the core are broadly aligned along the same axis, but the X-ray  $\mu$ CT data suggest a slight deviation from planar geometry in the arrangement of the units, with the pyritised ring-shaped units forming compact grape-like clusters.

*Orbisiana simplex* in the White Sea area is often preserved as aggregates of globular sandstone units, 0.5–2 mm in diameter, on erosional lower bedding surfaces of thin-laminated, fine-grained sandstone

(Fig. 4). Individual aggregates may comprise over 150 globular units, can be curved or rectilinear, reach 70 mm in length, and have variable width between 1.5 and 5 mm. Occasionally the aggregates diverge, with no appreciable change in either diameter or shape of the units, into two branches that are similar in appearance (Fig. 4B). We therefore suggest that divergence resulted from addition of new globular units in two directions. In contrast to the pyritised ring-shaped units in the holotype, not only are units in the White Sea specimens globular, but occasionally their units are preserved as sandstone hemispheres (Fig. 4B). We suggest that the aggregates originally comprised globular chambers, with the rings and hemispheres being taphonomic departures resulting from compaction. As in the type material, the aggregates from the White Sea area represent compact grape-like clusters (Fig. 4).

We could not determine unambiguously whether the chambers were agglutinated, organic-walled or biomineralised in life; however, preservation of some chambers as hollow hemispheres lined with sand grains and appearing concave on the lower bedding surface of sandstones in the White Sea area points towards an agglutinated structure for their walls. Low-relief negative imprints of *Orbisiana simplex* can be seen on erosional lower bedding surfaces of several sandstones from the White Sea area (Fig. 4C). Some specimens are fossilised in part as an aggregate of globular sandstone units, with associated negative ‘counterpart’ impressions on the adjacent bedding surface (Fig. 4C). Such ‘complementary’ preservation could be a product of weathering: the slab CSGM 2079-46 (Fig. 4C) was collected from float, and prolonged exposure to modern weathering processes could be responsible for the destruction of all but a few aggregates. Alternatively, the aggregates could be agglutinated, with chamber walls comprising clay particles ‘glued’ together with an organic cement rather than sand grains (as in modern foraminifera inhabiting muddy substrates; Gooday et al., 2008; Schieber, 2012). Aggregates of *Orbisiana simplex* consisting of agglutinated clay particles would theoretically collapse and flatten after burial leaving only low-relief negative impressions on bedding surfaces (Fig. 4C).

The type material of *Orbisiana simplex* is preserved in laminated shale (Figs 2, 3) and therefore it could have originally consisted of agglutinated clay particles cemented by organic material. The latter

could then become selectively pyritised as a result of sulfate reduction by bacteria (e.g. Briggs et al., 1991, 1996; Farrell and Briggs, 2007; Hegna et al., 2017). We consider pyritisation to have been preceded by flattening of the globular chambers, concurrent with sediment compaction after burial. Organic matter would presumably attain the highest concentration in the vertical sides of the globular chambers, since they would be expected to thicken during compaction and become accentuated by subsequent pyrite formation. This would explain the observed ring-shaped appearance of the pyritised flattened chambers (Figs 2, 3), as well as the occasional preservation of pyritised units as globular or hemispherical structures (Fig. 2E–F).

Despite the difference in preservation, there is little doubt that specimens collected in the White Sea area are identical to the type material from the Moscow Basin: both consist of globular chambers arranged in compact grape-like clusters and forming sinuous to linear aggregates. We assume that each aggregate originally consisted of similar-sized chambers, with the observed minor variation in size of the units in the fossils being a taphonomic artefact of flattening.

## 5. Discussion

The chambered construction, putative agglutinated structure of the chamber walls, and compact linear, occasionally branching arrangement of the chambers in *Orbisiana simplex* corroborate earlier suggestions regarding close affinities between this taxon and representatives of the genus *Palaeopascichnus* (Seilacher et al., 2003, 2005; Jensen, 2003; Jensen et al., 2006; Seilacher, 2007; Seilacher and Mrinjek, 2011; Grazhdankin, 2014; Seilacher and Gishlick, 2015; Kolesnikov et al., 2015; Ivantsov, 2017). The fossil *Palaeopascichnus* has been reconstructed as an agglutinated, elongated, curved or rectilinear, occasionally branching shell consisting of a single series of globular, ellipsoidal or sausage-shaped chambers (Kolesnikov et al., 2018) that occasionally may diverge dichotomously. Chambers in *Palaeopascichnus* gradually increase in size distally within a series until divergence of the series occurs, at which point the width of the chambers at the beginning of each new branch is two to three times smaller than the size of the chambers at the point of divergence. The

superficially similar modular ‘palaeopascichnid’ fossil *Curviacus ediacaranus* from the Shibantan Member, Dengying Formation, South China (Shen et al., 2017), is not considered by us to represent a palaeopascichnid organism (Kolesnikov et al., 2018).

*Orbisiana* nevertheless differs from *Palaeopascichnus* in possessing chambers that are always globular regardless of their size (chambers in *Palaeopascichnus* can be globular in some varieties, but are mostly ellipsoidal or sausage-shaped). Furthermore, the chamber size in *Orbisiana* is always consistent within each individual, whereas in *Palaeopascichnus* there often appears to be a trend of systematic and directional increase in chamber width along the series. The two genera also differ in gross morphology: in *Orbisiana* the chambers can form a compact grape-like cluster, whereas in *Palaeopascichnus* the chambers are always arranged in a series (Kolesnikov et al., 2018). Finally, unlike in *Palaeopascichnus*, where branching of the series is accompanied by a reduction in width of the chambers, branching of the *Orbisiana* aggregates is accompanied by no appreciable change in chamber dimensions or shape.

The fossils from the Lantian Formation of South China described as *Orbisiana linearis* by Chen et al. (1994) have a greater similarity to *Palaeopascichnus* than to any specimen of *Orbisiana simplex* from the type collection. Indeed, *Orbisiana linearis* is preserved as flattened cylindrical structures (circular or elliptical in plan view) arranged in ‘uniseriate chains’ that can be straight or sinuous, and occasionally branch dichotomously (Wan et al., 2014). In many specimens of *Orbisiana linearis* there seems to be a gradual increase in cylinder diameter and height from one end of the series to the other (Wan et al., 2014). The flattened cylindrical shape of the units in *Orbisiana linearis* is more akin to the chamber preservation in *Palaeopascichnus*, specifically that observed in carbonate-hosted specimens from the Khatyspyt Formation of Siberia (Nagovitsin et al., 2015; Kolesnikov et al., 2018). We therefore suggest exclusion of the species *Orbisiana linearis* Chen from the genus *Orbisiana* Sokolov. Furthermore, we restore the original ‘diagnosis’ of the genus *Orbisiana* Sokolov (1976), and revise it to take into account new observations of the type material and of coeval three-dimensionally preserved material from the Southeast White Sea area. Now that we have identified and fixed the type

material, the genus *Orbisiana* Sokolov can no longer be regarded as nomen nudum (cf. Hofmann, 1994).

*Palaeopascichnus* has been variously interpreted as trace fossils (Glaessner, 1969; Palij, 1976; Palij et al., 1979; Fedonkin, 1981; Narbonne et al., 1987; Becker, 2013), macrophytes (Haines, 2000), or protists (Seilacher et al., 2003, 2005; Seilacher, Mrinjek, 2011; Antcliffe et al., 2011; Kolesnikov et al., 2018). Gehling and Droser (2009) regarded *Palaeopascichnus* as an encrusting benthic organism and even compared it to other so-called ‘textured organic surfaces [that] commonly do not have a defined shape or size that might enable taxonomic description’. Although a possibility for these fossils to be faecal pellets could be ruled out, more work is needed before any firm conclusion can be made on phylogenetic affinities of *Orbisiana simplex*.

## 6. Conclusion

*Orbisiana simplex* Sokolov (1976) is a valid taxon with an uncertain phylogenetic position. It shares a chambered construction and agglutinated structure with the coeval chambered taxon *Palaeopascichnus*. The reassessment of the genus *Orbisiana* made herein is central to the identification of possible homologies between *Orbisiana* and *Palaeopascichnus*, and should provide a robust framework for future classification of Ediacaran chambered organisms and reconstruction of their phylogenies.

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## Appendix

### *Systematic palaeontology*

Genus *Orbisiana* Sokolov 1976, emend.

#### Synonyms

1976\* *Orbisiana* – Sokolov, p. 138, text-fig.

**Type species:** *Orbisiana simplex* Sokolov 1976.

**Original description** (translated from Russian): Integral aggregates of large (up to 2–3 mm) cells forming elongated and irregular clusters; cell walls are often pyritised (Sokolov, 1976, p. 138).

**Emended diagnosis:** Compact elongate grape-like clusters and irregular aggregates of globular chambers (0.25–2 mm in diameter). Chamber size tends to be uniform within each cluster or aggregate, but varies among individuals.

**Remarks:** Wan et al. (2014) synonymised the genus *Seirisphaera* Chen in Chen et al. (1994) within the genus *Orbisiana* Sokolov (1976) and accordingly emended the original diagnosis of the latter to accommodate characters such as ‘serially arranged elements’ and ‘elongated chains’ that are



diagnostic of the closely related genus *Palaeopascichnus* Palij (1976). *Seirisphaera lineare* Chen in Chen et al. (1994), the type species of *Seirisphaera* Chen in Chen et al. (1994), has been regarded as a junior synonym of *Palaeopascichnus linearis* Fedonkin in Kolesnikov et al. (2018). We therefore reject the genus *Seirisphaera* Chen in Chen et al. (1994) as a junior synonym of the genus *Orbisiana* Sokolov (1976), and restore the original ‘diagnosis’ of the genus *Orbisiana* Sokolov (1976), revising it based on our reassessment of the type material and of the coeval three-dimensionally preserved material from the Southeast White Sea area.

*Orbisiana simplex* Sokolov 1976, emend.

(Figs 2–4)

#### Synonyms

1976\* *Orbisiana simplex* Sokolov. – Sokolov, p. 138, text-fig.

1994 *Seirisphaera zhangii* Chen. – Chen et al., p. 259–260, pl. 1, fig. 1.

1997 *Orbisiana simplex* Sokolov. – Sokolov, p. 120, pl. 11, fig. 6.

2003 *Orbisiana simplex* Sokolov. – Jensen, p. 223, figs. 5c, 5d.

2006 *Seirisphaera zhangii* Chen. – Xiao and Dong, fig. 1e.

2010 *Orbisiana* [sic] – Grazhdankin et al., p. 225, fig. 113c.

2016 *Orbisiana simplex* Sokolov. – Golubkova et al., p. 56, text-pl., fig. 2.

2016 *Orbisiana simplex* Sokolov. – Kushim et al., p. 21, text-pl., fig. 2.

2018 *Orbisiana simplex* Sokolov. – Golubkova et al., p. 302, fig. 2d.

2018 *Orbisiana* af. *O. simplex* Sokolov [sic] – Golubkova et al., p. 302, figs 2e, 2f.

**Holotype:** CSGM No. 2076-001 (Fig. 2A, B).

**Paratypes:** CSGM Nos. 2076-002 (Fig. 2E), 2076-003 (Fig. 2F), 2076-004 (Fig. 2G), 2076-005 (Fig. 2H), 2076-007 (Figs 2I, 3A), 2076-008 (Fig. 2J).

**Type locality:** Soligalich 7 Borehole (depths 2153–2114 m) drilled ca. 10–15 km from the town of Soligalich, Kostroma Region, Russia; middle part of the Lower Member of the Gavrilov Yam Formation (Upper Vendian).

**Diagnosis:** Globular chambers arranged in compact grape-like clusters and constituting sinuous linear aggregates, the longest measured at 70 mm and comprising over 150 chambers. The width of the aggregates varies between 0.5 and 5.0 mm. Aggregates can diverge, with no appreciable change in chamber dimensions or shape, into two branches that are similar in appearance.

**Material:** Type collection; 32 specimens from the Verkhovka Formation (Upper Vendian), Syuzma River, Southeast White Sea area.

**Occurrence:** All the occurrences of *Orbisiana simplex* are correlated to rocks of Ediacaran age. (1) Piyuncun, Lantian Country, South China, Member 2 of the Lantian Formation (Chen et al., 1994; Xiao and Dong, 2006; Yuan et al., 2011; Wan et al., 2014); (2) Soligalich 7 Borehole (depths 2153–2114 m), Kostroma Region, Russia, Lower Member of the Gavrilov Yam Formation (Sokolov, 1976); (3) Shotkusa 1 Borehole (depths 225.7–218.5 m), Leningrad Region, Russia, Staraya Russa Formation (Golubkova et al., 2016, 2018; Kushim et al., 2016); (4) Kunevichi 4 Borehole (depth 558–557 m), Leningrad Region, Russia, Staraya Russa Formation (Jensen, 2003); (5) Kepina 775 Borehole, Arkhangelsk Region, Russia, Lyamtsa Formation (collection of E.Yu. Golubkova); (6) Onega River near Yarnema Village, Arkhangelsk Region, Russia, Erga Formation (Chistyakov et al., 1984; Ivantsov and Grazhdankin, 1997); (7) Onega Ranges near Lyamtsa Village, Arkhangelsk Region, Russia, Lyamtsa Formation; (8) Solza River, Arkhangelsk Region, Russia, Verkhovka Formation; (9) Syuzma River, Arkhangelsk Region, Russia, Verkhovka Formation (Fedonkin, 1976, 1977, 1981); (10) Winter Mountains, White Sea Winter Coast, Arkhangelsk Region, Russia, Erga Formation (Grazhdankin and Ivantsov, 1996); (11) Kotlas Borehole (depths 1827.85–1822.05), Arkhangelsk Region, Russia, Erga Formation (Grazhdankin et al., 2010); (12) Tramshak River,

Republic of Bashkortostan, Russia, Basa Formation (Kolesnikov et al., 2015); (13) Inzer River, Republic of Bashkortostan, Russia, Basa Formation (Kolesnikov et al., 2015).

**Remarks:** Sokolov (1976) illustrated just one specimen from the available collection when he described the species *Orbisiana simplex*. Six other specimens, all originating from the same interval in the Soligalich 7 Borehole, were known to B.S. Sokolov and recognised by him as *Orbisiana simplex* when the nominal species was established. No holotype was fixed in the original publication (Sokolov, 1976); however, Sokolov treated the illustrated specimen as a holotype specimen. In a later publication, Sokolov (1997, p. 120) clearly indicated that a figured specimen identical to that figured in the original publication is the holotype. Following Recommendation 72.4.1.1 of the International Code of Zoological Nomenclature (ICZN), we consider that the only illustrated specimen (Sokolov, 1976, p. 138) is the holotype. Thus, all the seven specimens in collection are regarded as the type series of *Orbisiana simplex*, with the remaining six specimens being properly described as paratypes (ICZN, Article 72.4.5). Following the ICZN (Recommendation 73D), we here designate these remaining specimens in the type collection as paratypes of the taxon *Orbisiana simplex*.

Specimens of *Orbisiana simplex* preserved on the lower bedding surfaces in sandstones were initially identified as trace fossils *Neonereites biserialis* Seilacher (Fedonkin, 1977, p. 189, pl. 1, fig. d; Palij et al., 1979, p. 207, fig. 2; Fedonkin, 1980, p. 215, pl. 2, fig. 8; Fedonkin, 1981, p. 81, pl. 14, figs 2, 5; Fedonkin, 1985, p. 207, pl. 28, figs 4, 5; Fedonkin, 1990; p. 274, pl. 28, figs 4, 5; Fedonkin and Runnegar, 1992, p. 393, fig. 7.6.3g; Fedonkin, 1994, p. 372, fig. 6a; Sokolov, 1997, p. 146–147, pl. 24, fig. 6; McCall, 2006, p. 75, figs 53-4, 53-5; Becker, 2013, p. 60, pl. 2, fig. 17) or, on rare occasions, as *Neonereites multiseriatis* Pickerill et Harland (Becker, 2013, p. 60, pl. 2, fig. 17). The identification of these fossils as faecal pellets was not borne out by subsequent studies (Seilacher et al., 2003, 2005; Jensen, 2003; Seilacher, 2007; Seilacher and Mrinjek, 2011; Seilacher and Gishlick, 2015; Kolesnikov et al., 2015). The Russian palaeontologist L.A. Nessonov from Leningrad (Saint Petersburg) State University was the first to note that ‘multiple branching of these structures had cast certain doubts on their interpretation as coprolites’ (Chistyakov et al., 1984, p. 17).

There is a striking similarity between pyritised *Orbisiana simplex* Sokolov (1976) and ‘biserial chains’ of circular units described as *Seirisphaera zhangii* Chen (Chen et al., 1994) from the Lantian Formation, South China (Xiao and Dong, 2006). If confirmed by future studies, this would be the only occurrence of *Orbisiana simplex* outside the East European Platform. Of the published identifications of *Orbisiana*, two appear to be misplaced in the genus: one from the Suket Shale of the Semri Group (Lower Vindhyan), central India is a filamentous carbonaceous compression (Azmi et al., 2008), and another from the Gavrillov Yam Formation in the Dorogobuzh Borehole (depths 881–873 m), Smolensk Region, Russia, is an elongated aggregate of optically dense circular structures on a carbonaceous film (Gnilovskaya, 1985, 1990).

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**Figure captions**

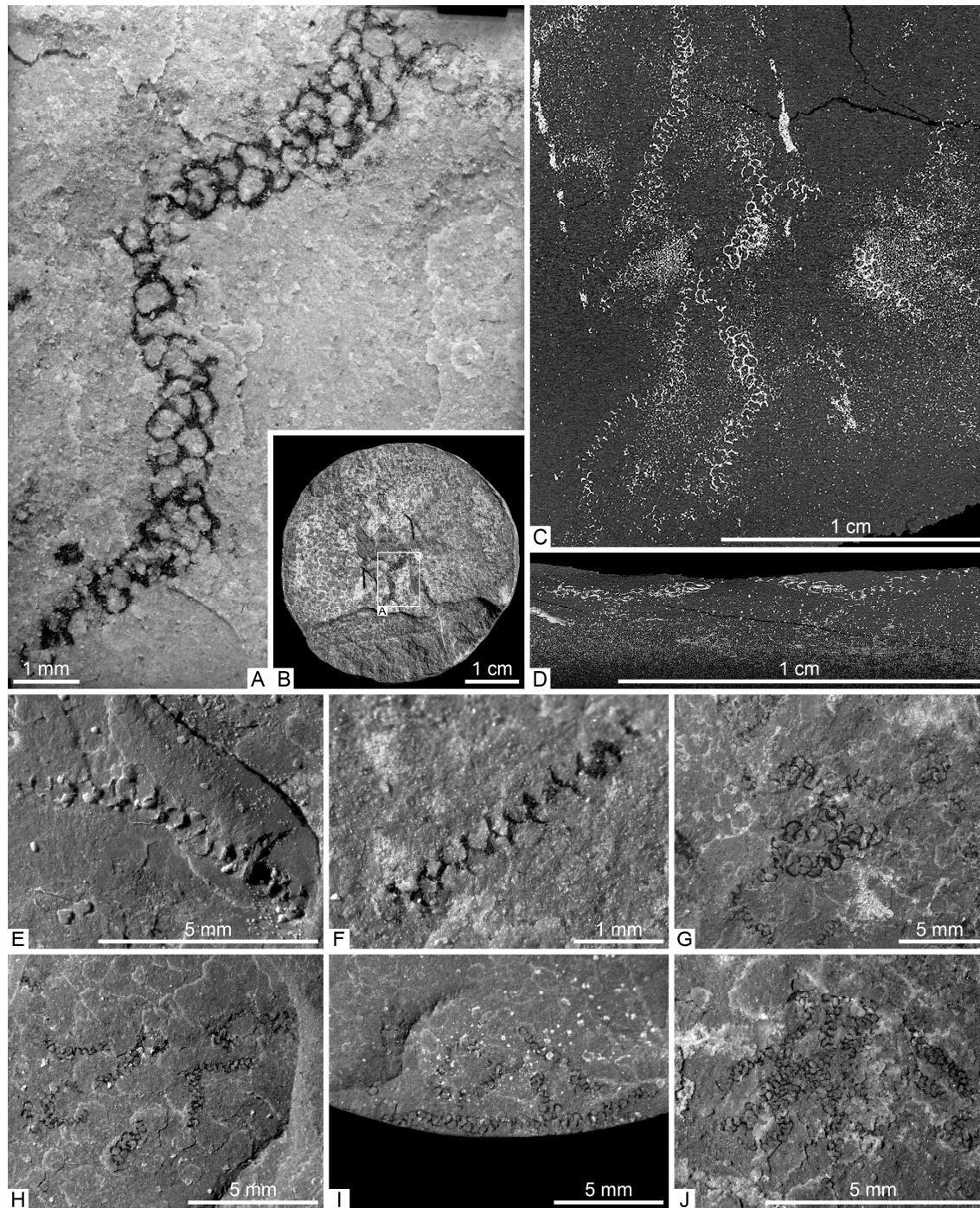
**Figure 1.** Locations of the 13 sites known to contain *Orbisiana simplex* Sokolov (1976). Stratigraphic position of the type material (Soligalich R-1 Borehole section) and sequence stratigraphic correlation with a composite section of the White Sea area, show the position of the studied material, available U–Pb zircon dates, and the first appearance of *Dickinsonia*.

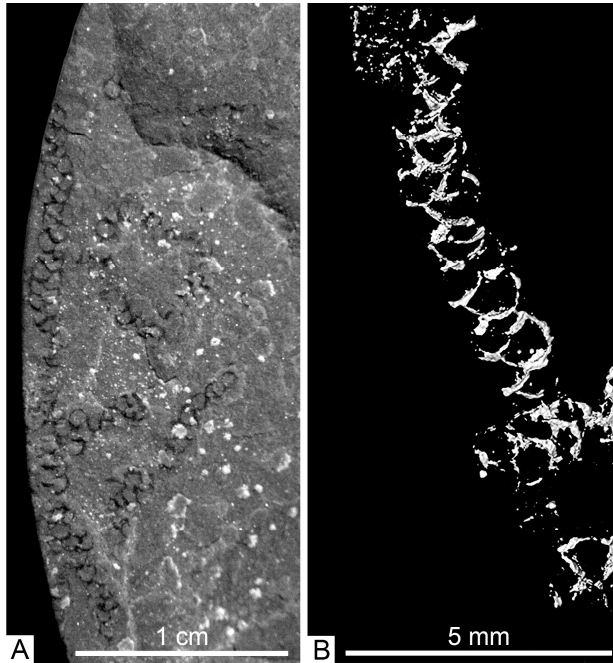
**Figure 2.** The type collection of *Orbisiana simplex* Sokolov (1976) from the Soligalich 7 Borehole, Gavrillov Yam Formation, Moscow Basin. (A) Holotype CSGM 2076-001, digital scan of the original black-and-white negative film sheet. Arrows mark the limits of the previously illustrated fragment. (B) Drill core sample with position of the holotype CSGM 2076-001. (C, D) X-ray  $\mu$ CT images of the paratypes (including associated specimens that are not visible on the parting surface of the drill core). Arrows mark the limits of the previously illustrated fragment. (E–J) Paratypes: (E) CSGM 2076-002, (F) CSGM 2076-003, (G) CSGM 2076-004, (H) CSGM 2076-005, (I) CSGM 2076-007, (J) CSGM 2076-008.

**Figure 3.** Paratype CSGM 2076-007 (A) and a rendered 3D image of the same specimen constructed from X-ray  $\mu$ CT data (B); Soligalich 7 Borehole, Gavrillov Yam Formation, Moscow Basin.

**Figure 4.** *Orbisiana simplex* Sokolov (1976) from Verkhovka Formation, Suzma River, White Sea area. (A, B) CSGM 2079-80, preserved on the erosional sole of a sandstone bed. Camera lucida drawing shows preservation of globular chambers as sandstone hemispheres. (C) Lower bedding surface of the slab CSGM 2079-46 with numerous specimens preserved either as an aggregate of globular sandstone units, or as negative ‘counterpart’ impressions.

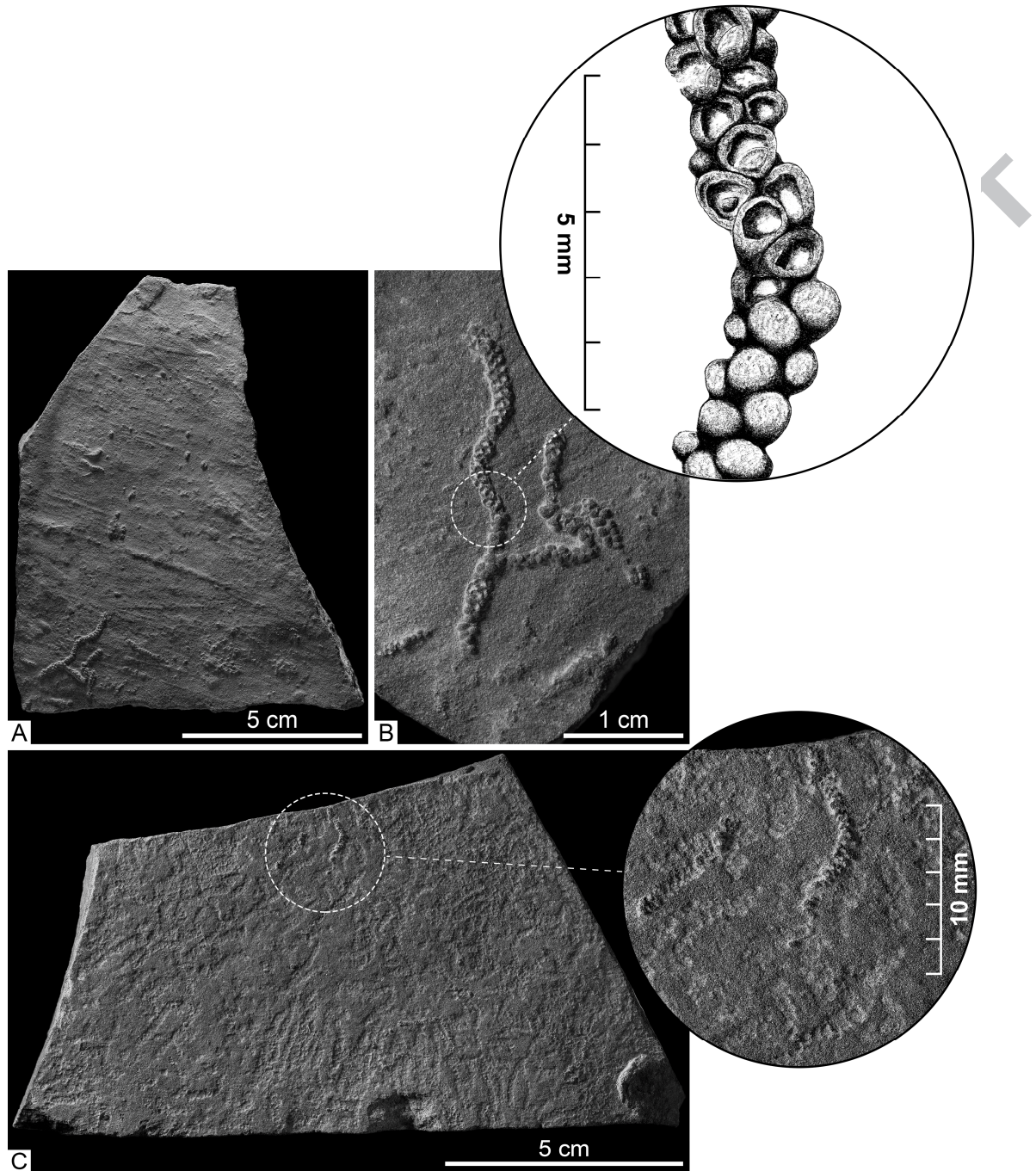






ACCEPTED MANUSCRIPT







- Ediacaran macroscopic skeletal organism
- Taxonomy of *Orbisiana*
- Ecological success of organisms

ACCEPTED MANUSCRIPT