Doushantuo-type microfossils from latest Ediacaran phosphorites of northern Mongolia

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Abstract:	Phosphorites of the latest Ediacaran upper Khesen Formation in the Khuvsgul Group of northern Mongolia preserve a newly discovered, three-dimensionally phosphatized Doushantuo-type microfossil assemblage. Eight genera include the second occurrence of the putative multicellular fossil animal embryo Megasphaera outside South China, the Doushantuo-Pertatataka-type acanthomorphic acritarchs Appendisphaera, Cavaspina, and Variomargosphaeridium, and the possible alga Archaeophycus yunnanensis. The assemblage occurs in the lowermost phosphorite horizon in foreland basin deposits on the Khuvsgul terrane; lithostratigraphic and 13C correlation with the Zavkhan terrane of southwestern Mongolia establish a latest Ediacaran age for the fossiliferous phosphorites. Thus, this is the youngest Doushantuo-type assemblage yet reported. It extends the range of Megasphaera, filling a gap in the record of phosphatized embryo-like forms between the ~600 Ma Doushantuo Weng'an Biota and Cambrian examples. The Khesen fossil assemblage emphasizes the potential of Mongolian phosphorites to provide new paleontological data on the Ediacaran-Cambrian transition, and to resolve the phylogenetic debate surrounding Megasphaera embryo-like taxa.
Response to Reviewers:	Response to reviewer's comments Line 116. I believe that the specimens in Fig. 3B and 3C represent Cavasipna acuminata. They have too short and small processes to be Tanarium. We have removed the reference to Tanarium. However, our fossils most closely resemble Cavaspina basiconica from the Doushantuo Formation (Xiao et al., 2014, J. Paleo.) which has larger numbers of more densely packed processes and can reach

larger sizes more similar to those of our specimens than to the type material of Cavaspina acuminata from Siberia. Please see lines 102–108 in the revised manuscript.

Line 137. Correct the citation: it is fig. 103 parts 6, 7, and 18 in Liu et al., 2014 (not fig. 117).

We have corrected the citation as suggested. Please see lines 126–127 in the revised manuscript.

Lines 162-164. The morphologically complex acanthomorphic microfossils of the Pertatataka-Doushantuo type are actually known from the late Ediacaran strata in Siberia and were reported by Moczydlowska and Nagovitsin (2012 in Precambrian Research 198-199, 1-24) and Moczydlowska (2015, Palynology online, and 2016 Palynology 40, 1, 83-121). The cited publication Golubkova et al., 2015, deals with the East European Platform, Baltica, record of microfossils.

In the text we note that Doushantuo-Pertatataka-type acanthomorphs are generally known from strata deposited prior to or synchronously with carbon isotope excursions interpreted to be equivalent to the Shuram carbon isotope excursion. The fossils reported in the publications of the reviewer come from the Ura and Chencha Formations in Siberia. The younger of these, the Chencha, was deposited synchronously with the Shuram isotope excursion (see Pokrovskii et al. 2006, Lithology and Mineral Resources for carbon isotope stratigraphy). In contrast the fossils of Golubkova et al. (2015) may be in the "high horizons of the Upper Vendian (Ediacaran)" presumably above the Shuram excursion. Xiao et al. (2016, Episodes), in their review of acanthomorph biostratigraphy for the Subcommission on Ediacaran Stratigraphy, detail this stratigraphic arrangement: "Doushantuo-Pertatataka-type acanthomorphs as a whole seem to be restricted to the lower Ediacaran System, below the Gaskiers-age Moelv diamictite in southern Norway and below negative 13C excursions in South China, South Australia, and Siberia that are interpreted as equivalent to the Shuram excursion. However, as mentioned above, recent reports of elements of Doushantuo- Pertatataka-type acanthomorphs in terminal Ediacaran rocks (Golubkova et al., 2015) need to be assessed critically."

We have altered the text to make clear that the Doushantuo-Pertatataka-type assemblage is "generally" found prior to "or synchronously with carbon isotope excursions interpreted to be equivalent to the Shuram carbon isotope excursion". Please see lines 157–160 in the revised manuscript.

We have also corrected the text by stating that the Golubkova et al. (2015) publication refers to the East European Platform rather than Siberia. Please see lines 154–156 in the revised manuscript.

Lines 165-166. I would rather say "predate the Shuram excursion" not the end of the excursion. The "end of the Shuram excursion" means that the successions of the EN3/Shuram excursion intervals contain the microfossils. In fact only the terminal Ediacaran member IV of the Doushantuo Formation is devoid insofar of the Doushantuo type microfossils in China. In Siberia and the EEP, and now in Mongolia, this type of microfossils occurs in the terminal Ediacaran strata. I agree that the record in Mongolia may be the youngest.

We have reworded this sentence to read: "Elsewhere in the world Doushantuo-Pertatataka-type acanthomorphs occur generally in rocks that predate or are synchronous with carbon isotope excursions interpreted to be equivalent to the Shuram carbon isotope excursion (Zhou et al., 2007; Xiao et al., 2016; Zhou et al., 2017)" for the reasons detailed in our response to the comment on lines 162-164 above. Please see lines 157–160 in the revised manuscript.

Line 166. I would add the recent reference to Zhou et al, 2017, Precambrian Research

	288, 23-38. We have added the reference as suggested. Please see lines 160 and 335–339 in the revised manuscript. Lines 171-173. Absolutely, in Siberia and EEP, and now in Mongolia at the latest Ediacaran. Please see our responses above to the reviewer's comments on lines 162–164 and 165–166. Line 272. Incorrect reference. The paper by Liu et al., 2014 is published in Palaeontology Memoir 72, 1-133. We have corrected the reference as suggested. Please see lines 261–264 in the revised manuscript.

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Doushantuo-type microfossils from latest Ediacaran phosphorites of northern Mongolia

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ABSTRACT

Phosphorites of the latest Ediacaran upper Khesen Formation in the Khuvsgul Group of northern Mongolia preserve a newly discovered, three-dimensionally phosphatized Doushantuo-type microfossil assemblage. Eight genera include the second occurrence of the putative multicellular fossil animal embryo *Megasphaera* outside South China, the Doushantuo-Pertatataka-type acanthomorphic acritarchs *Appendisphaera*, *Cavaspina*, and *Variomargosphaeridium*, and the possible alga *Archaeophycus yunnanensis*. The assemblage occurs in the lowermost phosphorite horizon in foreland basin deposits on the Khuvsgul terrane; lithostratigraphic and $\delta^{13}C$ correlation with the Zavkhan terrane of southwestern Mongolia establish a latest Ediacaran age for the fossiliferous phosphorites. Thus, this is the youngest Doushantuo-type assemblage yet

reported. It extends the range of *Megasphaera*, filling a gap in the record of phosphatized embryo-like forms between the ~600 Ma Doushantuo Weng'an Biota and Cambrian examples. The Khesen fossil assemblage emphasizes the potential of Mongolian phosphorites to provide new paleontological data on the Ediacaran–Cambrian transition, and to resolve the phylogenetic debate surrounding *Megasphaera* embryo-like taxa.

INTRODUCTION

The Ediacaran Period represents a critical juncture in Earth's history with the emergence of macroscopic eukaryotic communities with animal components (e.g., Xiao et al., 2016). Ornamented spheroidal microfossils, known as Doushantuo-Pertatataka-type acanthomorphic acritarchs, are found in Ediacaran successions globally (see Cohen and Macdonald, 2015, and references therein). The discovery of similar fossils preserved in phosphorites of the Doushantuo Formation at Weng'an in South China has yielded critical insights into Ediacaran paleobiology (e.g., Xiao et al., 2014a). Some of the Doushantuo fossils may be the oldest fossil animals, resembling embryonic forms, although their phylogenetic affinities, even after ~20 years of study, remain controversial—none of the characters used to marshal the evidence for an animal affinity are unequivocally diagnostic (Cunningham et al., 2017). Similar phosphatized fossils have been recovered recently elsewhere in South China (Zhang and Zhang, 2017). However, despite the importance of Doushantuo-type preservation to studies of Ediacaran diversity and animal evolution, few phosphatized fossils have been reported from other global Ediacaran successions with the exception of the Biskopås Formation, Norway and the Chambaghat Formation, India. Although the Biskopås Formation has yielded a variety of acanthomorphs, embryo-like forms have not been discovered (see

Vidal, 1990, and references therein), and possible embryo-like forms reported from the Chambaghat Formation (Shome et al., 2014) are not preserved with the same fidelity as those of the Doushantuo Formation. Here we report new Ediacaran phosphatized microfossils, which include Doushantuo-Pertatataka-type acanthomorphs and most notably multicellular embryo-like forms, from the upper Khesen Formation, Mongolia.

GEOLOGICAL SETTING

The Khesen Formation of the Khuvsgul Group (Fig. 1) is exposed discontinuously along a 250 km north-south belt on the western margin of Lake Khuvsgul in northern Mongolia (Macdonald and Jones, 2011). During Neoproterozoic and Cambrian time, the Khuvsgul and Zavkhan terranes formed one contiguous margin (Fig. 1A). Both terranes are characterized by ~800 Ma arc-volcanic rocks overlain by late Tonian rift-related strata, Cryogenian–early Ediacaran carbonate platforms interrupted by two Snowball Earth intervals, and latest Ediacaran to early Cambrian foreland basin successions (Macdonald et al., 2009; Kuzmichev and Larionov, 2011; Macdonald and Jones, 2011; Bold et al., 2016a; Bold et al., 2016b; Smith et al., 2016).

The Khesen Formation is divided into informal lower and upper members by a major unconformity (Fig. 1D, 1E, and 1F) that separates Marinoan glacial deposits and a basal Ediacaran cap carbonate succession from latest Ediacaran to early Cambrian carbonate, shale, and phosphorite deposits (Donov et al., 1967; Ilyin, 1973; Ilyin et al., 1986; Osokin and Tyzhinov, 1998; Macdonald and Jones, 2011). An equivalent unconformity is present on the Zavkhan terrane (Fig. 1C), separating early Ediacaran carbonates of the Ol and Shuurgat formations from latest Ediacaran phosphorite and carbonate of the terminal Ediacaran Zuun-Arts Formation (Bold et al., 2016b; Smith et al., 2016). Latest Ediacaran–Terreneuvian phosphorite-bearing foreland basins formed on the Khuvsgul and Zavkhan terranes as the result of the collision of the Khantaishir-Agradag arc (Bold et al., 2016a; Smith et al., 2016). On both terranes, two phosphorite-rich successions bracket the Proterozoic–Phanerozoic boundary and additional phosphorite is present in overlying early Cambrian strata (Ilyin, 2004; Smith et al., 2016). The sediment-starved carbonate succession of the upper Khesen Formation preserves reworked granular phosphorite grainstone beds and massive replacive phosphate beds (Fig. 1). A minimum age constraint for the upper Khesen Formation is provided by Cambrian archaeocyathids and trilobites in the overlying Erkhelnur Formation (Ilyin and Zhuraveleva, 1968; Korobov, 1980).

A NEW FOSSIL ASSEMBLAGE

Eight genera of phosphatized microfossils (Figs. 2 and 3) were recovered from the lowermost phosphorite horizon of the upper Khesen Formation (see supplementary information for occurrences) with 5 genera confined to just two samples (Yale Peabody Museum YPM 536747 and 536748) from granular phosphorites along the ridgeline east of Urandush Uul (at 21 and 22 m, Fig. 1F). Probable cyanobacteria are found in most fossiliferous samples. Filaments of *Siphonophycus* occur as clusters of a few individuals, patchworks of hundreds of criss-crossing individuals, and clasts of microbial mat several hundred micrometers in maximum dimension. A few individuals of the possible oscillatoriacean cyanobacterium *Obruchevella* are also present (Fig. 3F).

Most of the fossil diversity in the assemblage is made up of probable eukaryotes. Simple leiosphaerid acritarchs are present in almost all fossiliferous samples. *Archaeophycus yunnanensis* occurs as solitary cells, or dyad, triad, tetrad, and octad clusters (Figs. 2A and 3A). The tetrad form of this fossil was previously compared (as *Paratetraphycus giganteus*) to carposporangia of the modern bangialean alga *Porphyra* but convergent evolution among cyanobacteria and other algae cannot be ruled out (Xiao et al., 1998; Dong et al., 2009; Xiao et al., 2014a). In addition to these simple forms, the lower phosphorites yield a variety of Doushantuo-Pertatataka-type acanthomorphic acritarchs, most notably *Appendisphaera* (Fig. 2B), *Cavaspina* (Figs. 3B and 3C), and *Variomargosphaeridium* (Figs. 2C, 2D, 2E, and 2F). *Appendisphaera* is characterized by a spheroidal vesicle with densely spaced, long, hollow, unbranched processes (Moczydlowska et al., 1993; Moczydlowska, 2005). Three species are identified in the Khesen phosphorites: *A. grandis*, *A. fragilis*, and *A. tenuis*. An area of dense, dark organic matter can be present between the processes (Fig. 2B). Several Khesen fossils are tentatively identified as *Cavaspina*, which has conical processes that are commonly <10% of vesicle diameter (Moczydlowska et al., 1993). The Khesen specimens have larger vesicle sizes (>250 μm) than most reported examples of this genus, however, and the length of their processes, while commonly <10% of vesicle diameter, can reach ~13%. They most closely resemble *C. basiconica* from the Doushantuo Formation (cf. Fig. 8 parts 1–4 in Xiao et al., 2014b) in the number of processes and larger vesicle size. The most abundant acanthomorph (tens of specimens) is assigned to *Variomargosphaeridium gracile*. *Variomargosphaeridium* is characterized by heteromorphic, hollow, multi-branched processes (e.g., Fig. 2E); *V. gracile* is small (vesicle 30–150 μm in maximum diameter) with thin processes (9–21 μm in length). Some of the Khesen specimens contain numerous cell-like structures (Fig. 2C) allowing *V. gracile* to be added to a growing list of Ediacaran acanthomorphs which display possible multicellular features (Xiao et al., 2014b). A number of specimens (<10 individuals) with branching processes that are <10% of the vesicle diameter may represent a new species of *Variomargosphaeridium* (Fig. 2F).

Most notably, the assemblage includes the second reported occurrences (~50 specimens of which <10 are well-preserved) of the multicellular fossil *Megasphaera* outside South China, where it occurs in the Doushantuo and Denying phosphorites (Xiao et al., 2014b; Zhang and Zhang, 2017). The Khesen fossils (Figs. 2G, 2H, 2I, 3D, and 3E) are readily accommodated by the emended diagnosis of *Megasphaera* (Xiao et al., 2014b), which calls for a large vesicle without long processes and enclosing one or more internal cells. However, the Khesen specimens also bear morphological similarities to leiosphaerid acritarchs from the upper Khesen Formation, to "leiospheres with cellular inclusions" from cherts of the Doushantuo Formation (cf. Fig. 103 parts 6, 7, and 18 in Liu et al., 2014), and to *Clonophycus* from other cherts of Ediacaran and Cambrian age in South China (Nantuo and Taozichong formations) (Oehler, 1977, 1978; Luo et al., 1982). They differ from *Leiosphaeridia* in the upper Khesen Formation in the presence of internal structures, are intermediate in size between species of *Megasphaera* found elsewhere and Doushantuo leiospheres with cellular inclusions, and are significantly larger than *C. guizhouensis*, the largest species of *Clonophycus*. The thick vesicle wall (Fig. 3D and 3E) supports our identification of these fossils as *Megasphaera*.

THE AGE OF THE KHESEN ASSEMBLAGE

Macdonald and Jones (2011) interpreted the age of the fossil-bearing lowermost phosphorite unit of the upper Khesen Formation as latest Ediacaran based on lithostratigraphic correlation with the Zuun-Arts Formation of southwestern Mongolia, which preserves the Proterozoic–Phanerozoic boundary (Smith et al., 2016), and with the Zabit Formation of Siberia, which yields the latest Ediacaran fossil *Cloudina* (Kherzaskova and Samygin, 1992). The stratigraphy of the upper Khesen Formation is remarkably similar to that of the Zuun-Arts Formation and the basal Bayangol Formation (also southwestern Mongolia), comprising fossiliferous lower granular phosphorite beds, limestone, and upper bedded phosphorites (Macdonald and Jones, 2011; Smith et al., 2016). This correlation implies that the carbon isotope excursion between the phosphorite-rich successions in the upper Khesen Formation (Ilyin, 2004; Vishnevskaya and Letnikova, 2013, and Figure 1 herein) represents the Proterozoic–Phanerozoic boundary as it does in the Zuun-Arts Formation (Smith et al., 2016; Fig. 1). Such a correlation is consistent with the geodynamics of foreland basin development (Sinclair and Naylor, 2012) in which the migration of loads can create diachronous deposition over a few million years but not over tens of millions of years, as would be required for an early Ediacaran (i.e., older than the Shuram carbon isotope excursion) age for the Khesen fossils. Thus, geological evidence, as well as chemostratigraphic data, suggest that the Khesen fossil assemblage lies immediately below the Proterozoic–Phanerozoic boundary. This inference is consistent with recent reports of Doushantuo-Pertatataka-type acanthomorphs from possible late Ediacaran strata on the East European Platform (Golubkova et al., 2015).

Elsewhere in the world Doushantuo-Pertatataka-type acanthomorphs occur generally in rocks that predate or are synchronous with carbon isotope excursions interpreted to be equivalent to the Shuram excursion (Zhou et al., 2007; Xiao et al., 2016; Zhou et al., 2017). The similarity between the Khesen assemblage reported here and that

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of the older Doushantuo Formation includes the presence of *Appendisphaera grandis* and *A. tenuis*, *Cavaspina* ?*basiconica*, *Megasphaera*, and *Variomargosphaeridium gracile* (Xiao et al., 2014b). Such similarities can be accounted for by conditions favoring similar preservation in phosphate rather than coeval deposition, and imply longer ranges than previously recorded for some taxa. Thus, the Khesen fossils suggest that Doushantuo-Pertatataka-type acanthomorphs are not confined to pre-Shuram strata, but extend into latest Ediacaran time.

DISCUSSION AND CONCLUSIONS

The fossils of the upper Khesen Formation represent a new discovery of embryo-like forms (e.g., *Megasphaera*) in Ediacaran phosphorites, adding to those of the Doushantuo and Denying Formations, South China (Xiao et al., 2014b; Zhang and Zhang, 2017) and the Chambaghat Formation, India (Shome et al., 2014). *Megasphaera* is >200 μm in diameter in China and India (Shome et al., 2014; Xiao et al., 2014b; Zhang and Zhang, 2017). The Khesen fossils (Figs. 2G, 2H, 2I, 3D, and 3E) include specimens with a maximum diameter as low as 80 μm and probably represent a new species. The spheroidal cellular inclusions are rarely in contact, presumably due to some degradation and shrinkage. The number in each vesicle ranges from 20 to 106 but thin sections do not reveal them all. Although this new material does not settle the question of whether or not *Megasphaera* represents the earliest animal fossils, the exceptional preservation, diversity of form, and age range provide new constraints on the paleobiology of this iconic taxon.

The discovery of possible fossil embryos in latest Ediacaran strata fills the gap in exceptional phosphatic preservation between the older South China occurrences (and possible equivalents in India) and unequivocal embryos in Cambrian successions (e.g., Donoghue et al., 2006; Brasier and Callow, 2007; Muscente et al., 2015). Doushantuo-type preservation involves the concentration of phosphate and organic matter through siliciclastic sediment starvation and the Doushantuo Formation at Weng'an comprises phosphatic grainstones resulting from reworking and winnowing (Xiao et al., 1998; Xiao and Knoll, 1999; Muscente et al., 2015). The Khesen assemblage is preserved in similar facies, with both massive replacive and granular phosphorites preserved within a condensed sediment-starved carbonate succession. The preservation of the Khesen fossils rivals that in the Doushantuo Formation: cell-division is evident in extracted specimens of *Archaeophycus yunnanensis* (Fig. 3A), and processes on other acanthomorphs are preserved with exceptional fidelity (Figs. 2C, 2D, 3B, and 3C). This similarity emphasizes the potential of Mongolian phosphorites to provide new paleontological data on the Ediacaran–Cambrian transition, and to resolve the phylogenetic debate surrounding *Megasphaera* embryo-like taxa.

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FIGURE CAPTIONS

Figure 1. Geological setting of the Khesen fossil assemblage. A: Map showing the extent of the Khuvsgul (Khuv.) and Zavkhan (Zav.) terranes. B: Geological map of the western margin of Lake Khuvsgul. C: Simplified stratigraphy of the Tsagaan Olom Group of the Zavkhan Basin (MU = Maikhan-Uul, BG = Bayangol). D: Simplified stratigraphy of the Khuvsgul Group (phos. = phosphorite). E: Khesen Formation at Ongoluk Gol with carbon isotope record. F: Khesen Formation stratigraphy from the ridgeline east of Urandush Uul.

Figure 2. Paleontology of the Khesen Formation in thin-sections. A: *Archeophycus yunnanensis*, YPM 536754. B: *Appendisphaera grandis*, YPM 536755. C: *Variomargosphaeridium gracile* with possible internal structures, YPM 536772. D: *V. gracile*, YPM 536800. E: *V. gracile* showing distal end of processes to the upper left, YPM 536802. F: *V*. sp., YPM 536787. G–I: *Megasphaera* sp.. G: YPM 536794. H: YPM 536784. I: YPM 536766. Scale bars 50 μm.

Figure 3. Paleontology of the Khesen Formation revealed by 20% acetic acid maceration. A: *Archaeophycus yunnanensis* showing T cell-division, YPM 538070. B–C: *Cavaspina* ?*basiconica*. B: YPM 538071 C: YPM 538072. D–E: *Megasphaera* sp.. D: YPM 538073. E: YPM 538074. F: *Obruchevella magna*, YPM 538075. Scale bars 100 μm.

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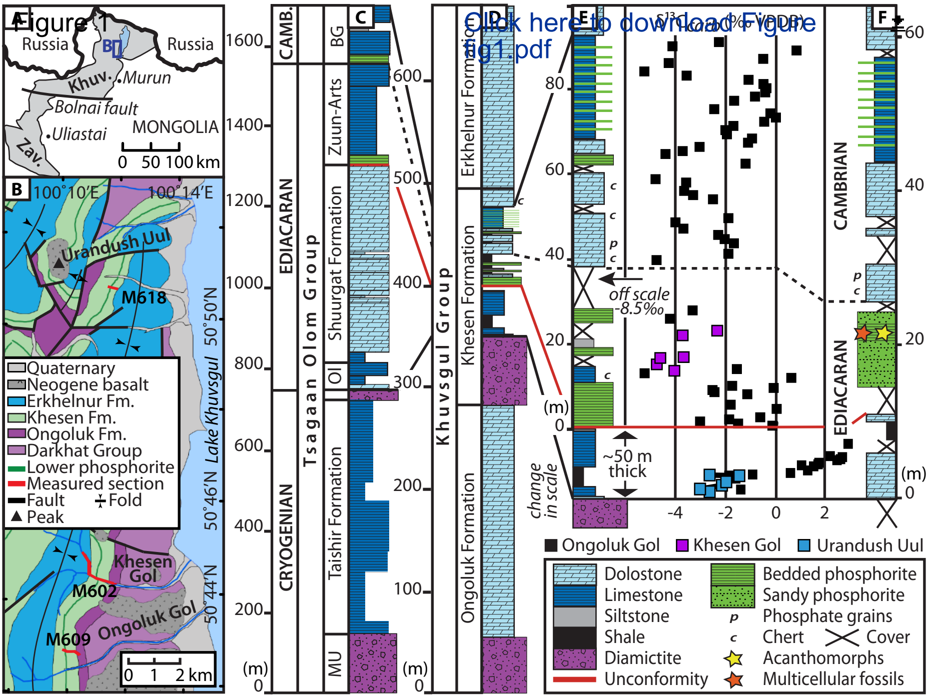
Figure 1



A
Russia
Russia
B
Khuv.
Murun
Bolnai fault
Uliastai
MONGOLIA
Zav.
0 50 100 km
B
100˚10'E
100˚14'E
Urandush Uul
M618
50˚50'N
Lake Khuvsgul
50˚46'N
50˚44'N
Khesen Gol
M602
M609
Ongoluk Gol
0 1 2 km
Quaternary
Neogene basalt
Erkhelnur Fm.
Khesen Fm.
Ongoluk Fm.
Darkhat Group
Lower phosphorite
Measured section
Fault
Fold
Peak
CAMB.
EDIACARAN
CRYOGENIAN
Tsagaan Olom Group
BG
Zuun-Arts
Shuurgat Formation
Ol
Taishir Formation
MU
C
D
Khuvsgul Group
Erkhelnur Formation
Khesen Formation
Ongoluk Formation
E
δ13Ccarb ‰ (VPDB)
off scale -8.5‰
~50 m thick
change in scale
F
CAMBRIAN
EDIACARAN
Ongoluk Gol
Khesen Gol
Urandush Uul
Dolostone
Limestone
Siltstone
Shale
Diamictite
Unconformity
Bedded phosphorite
Sandy phosphorite
Phosphate grains
Chert
Cover
Acanthomorphs
Multicellular fossils

Figure 2

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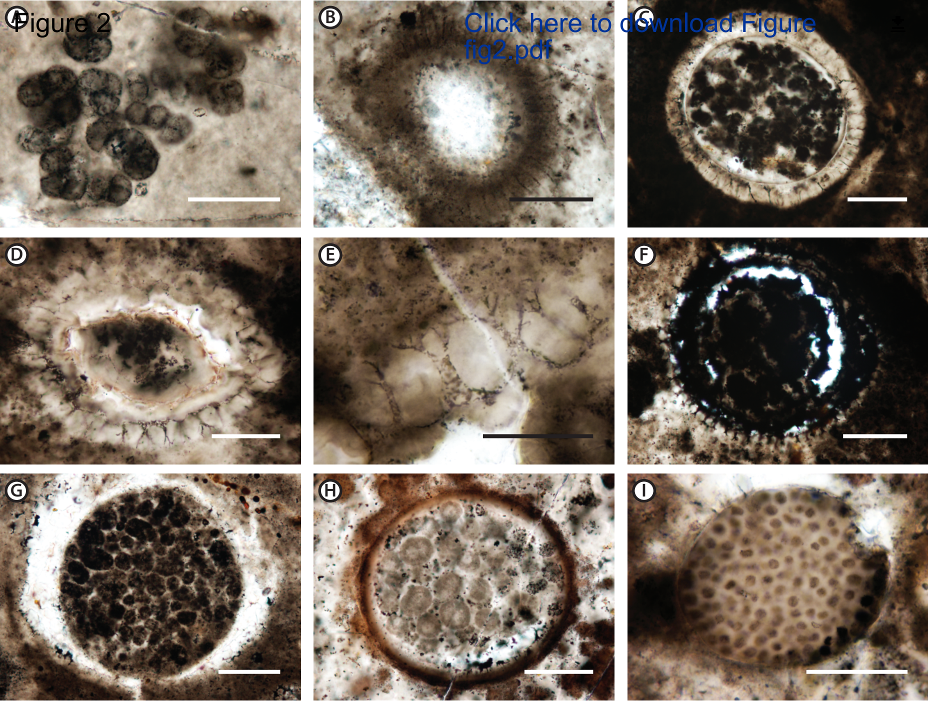

Figure 3

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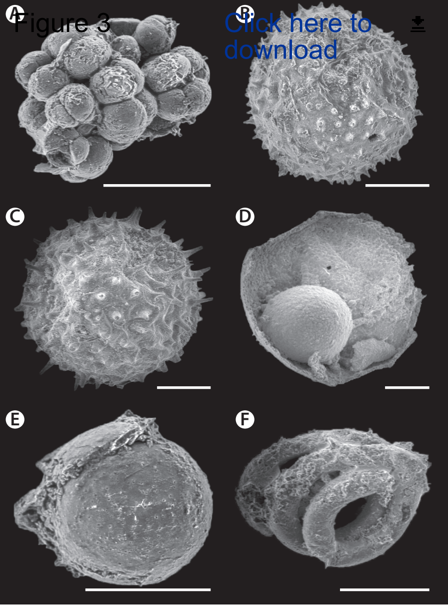

Supplementary Information

Doushantuo-type microfossils from latest Ediacaran phosphorites of northern Mongolia

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Methods

The Khesen fossils were examined in thin-section and by scanning electron microscopy following 20% acetic acid maceration. All materials are deposited in the Yale Peabody Museum of Natural History (YPM). Carbon isotope ratios of micro-drilled carbonate powders were measured following methods described in Macdonald et al. (2009).

Biostratigraphy

Khesen Gol
YPM 536746 and 536748 are at 0 and 3 m respectively in Fig. 1E.

Urandush Uul
YPM 536747 and 536748 are at 21 and 22 m respectively in Fig. 1F.

	Khesen Gol		**Urandush Uul**	
	YPM 536746	YPM 536749	YPM 536747	YPM 536748
Cyanobacteria				
Obruchevella delicata	R			
Obruchevella magna			R	R
Obruchevella parvissima				R
Obruchevella sp.				R
Siphonophycus spp.	C	C	C	C
?Algae				
Archaeophycus yunnanensis			R	
Acritarchs				
Appendisphaera grandis			R	
Appendisphaera fragilis		R		R
Appendisphaera tenuis			R	
Cavaspina ?*basiconica*			R	
Leiosphaeridia spp.	R	R	C	C
Megasphaera sp.			C	C
Variomargosphaeridium gracile			C	C
Variomargosphaeridium sp.				R

Table S1: Biostratigraphy of the upper Khesen Formation showing reported taxa from the four most diverse samples and their relative abundance within the assemblage. R = rare (isolated individuals, only a few specimens). C = common (10s of individuals). In the case of *Megasphaera* 10s of individuals are reported but only a few are preserved with enough fidelity to confidently interpret internal structures. YPM sample numbers are given for reference.

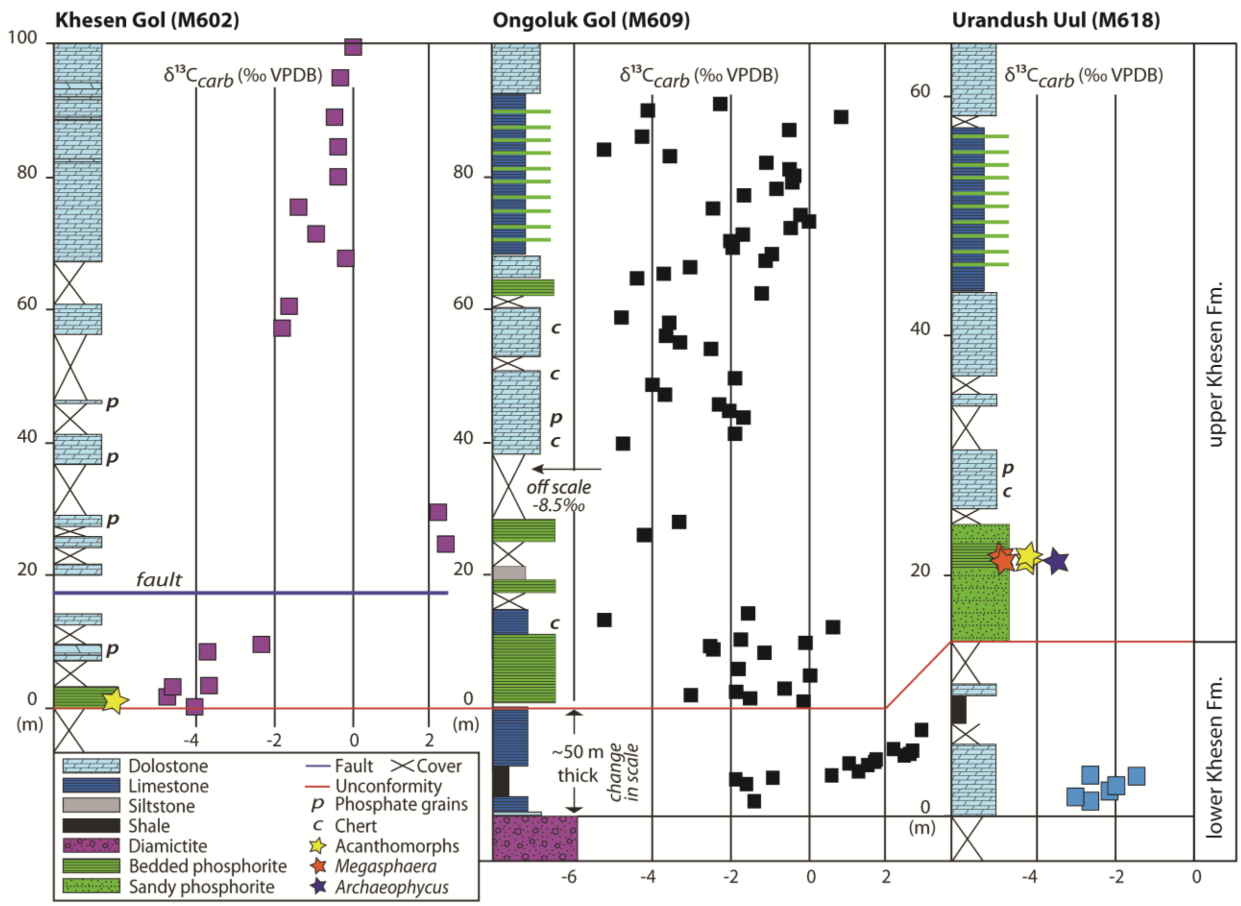

Figure S1: Expanded stratigraphy showing relationships between Khesen, Ongoluk, and Urandush Uul localities. See Figure 1 for locality information.

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