

1 Doushantuo-type microfossils from latest Ediacaran
2 phosphorites of northern Mongolia

3 **Ross P. Anderson^{1*}, Francis A. Macdonald², David S. Jones³, Sean McMahon¹, and**
4 **Derek E.G. Briggs¹**

5 ¹*Department of Geology and Geophysics, Yale University, 210 Whitney Avenue, New*
6 *Haven, Connecticut 06511, USA*

7 ²*Department of Earth and Planetary Sciences, Harvard University, 20 Oxford Street,*
8 *Cambridge, Massachusetts 02138, USA*

9 ³*Geology Department, Amherst College, 11 Barrett Hill Road, Amherst, Massachusetts*
10 *01002, USA*

11 *E-mail: ross.anderson@yale.edu

12 **ABSTRACT**

13 Phosphorites of the latest Ediacaran upper Khesen Formation in the Khuvsgul
14 Group of northern Mongolia preserve a newly discovered, three-dimensionally
15 phosphatized Doushantuo-type microfossil assemblage. Eight genera include the second
16 occurrence of the putative multicellular fossil animal embryo *Megasphaera* outside South
17 China, the Doushantuo-Pertatataka-type acanthomorphic acritarchs *Appendisphaera*,
18 *Cavaspina*, and *Variomargosphaeridium*, and the possible alga *Archaeophycus*
19 *yunnanensis*. The assemblage occurs in the lowermost phosphorite horizon in foreland
20 basin deposits on the Khuvsgul terrane; lithostratigraphic and $\delta^{13}\text{C}$ correlation with the
21 Zavkhan terrane of southwestern Mongolia establishes a latest Ediacaran age for the
22 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 ca. 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 yr 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-long 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 ca. 800 Ma arc-volcanic rocks overlain by late Tonian rift-related strata, Cryogenian to 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, 2016b; Smith et al., 2016).

The Khesen Formation is divided into informal lower and upper members by a major unconformity (Figs. 1D–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 the GSA Data Repository¹ for occurrences), with five genera confined to just two samples (Yale Peabody Museum specimens 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

91 individuals of the possible oscillatoriacean cyanobacterium *Obruchevella* are also present
92 (Fig. 3F).

93 Most of the fossil diversity in the assemblage is made up of probable eukaryotes.

94 Simple leiosphaerid acritarchs are present in almost all fossiliferous samples.

95 *Archaeophycus yunnanensis* occurs as solitary cells, or dyad, triad, tetrad, and octad

96 clusters (Figs. 2A and 3A). The tetrad form of this fossil was previously compared (as

97 *Paratetrphycus giganteus*) to carposporangia of the modern bangialean alga *Porphyra*,

98 but convergent evolution among cyanobacteria and other algae cannot be ruled out (Xiao

99 et al., 1998, 2014a; Dong et al., 2009). In addition to these simple forms, the lower

100 phosphorites yield a variety of Doushantuo–Pertatataka–type acanthomorphic acritarchs,

101 most notably *Appendisphaera* (Fig. 2B), *Cavaspina* (Figs. 3B and 3C), and

102 *Variomargosphaeridium* (Figs. 2C–2F). *Appendisphaera* is characterized by a spheroidal

103 vesicle with densely spaced, long, hollow, unbranched processes (Moczyłowska et al.,

104 1993; Moczyłowska, 2005). Three species are identified in the Khesen phosphorites: *A.*

105 *grandis*, *A. fragilis*, and *A. tenuis*. An area of dense, dark organic matter can be present

106 between the processes (Fig. 2B). Several Khesen fossils are tentatively identified as

107 *Cavaspina*, which has conical processes that are commonly <10% of vesicle diameter

108 (Moczyłowska et al., 1993). The Khesen specimens have larger vesicle sizes (>250 μm)

109 than most reported examples of this genus, however, and the length of their processes,

110 while commonly <10% of vesicle diameter, can reach ~13%. They most closely resemble

111 *C. basiconica* from the Doushantuo Formation (cf. Xiao et al., 2014b, their figure 8, parts

112 1–4) in the number of processes and larger vesicle size. The most abundant

113 acanthomorph (tens of specimens) is assigned to *V. 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 that 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. Liu et al., 2014, their figure 103, parts 6, 7, and 18), 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 *Clonophycus 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; Fig. 1) 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 [[date?]]) 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, 2017; Xiao et al.,
2016). The similarity between the Khesen assemblage reported here and that of the older
Doushantuo Formation includes the presence of *A. grandis* and *A. tenuis*, *C. ?basiconica*,
Megasphaera, and *V. 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–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.




ACKNOWLEDGMENTS



S. Butts and J. Utrup managed the collections. U. Bold helped with logistics in Mongolia. This work was supported by a Geological Society of America ExxonMobil Student Grant, the NASA Astrobiology Institute ([grant](#) NNA13AA90A), a NASA Earth and Space Science Fellowship ([grant](#) NNX14AP10H), and the Yale Institute for

205 Biospheric Studies and the Peabody Museum. We thank Małgorzata Moczyłowska,
206 Shuhai Xiao, and an anonymous reviewer for helpful comments.

207 **REFERENCES CITED**

- 208 Bold, U., Crowley, J.L., Smith, E.F., Sambuu, O., and Macdonald, F.A., 2016a,
209 Neoproterozoic to early Paleozoic tectonic evolution of the Zavkhan terrane of
210 Mongolia: Implications for continental growth in the Central Asian orogenic belt:
211 Lithosphere, v. 8, p. 729–750, <https://doi.org/10.1130/L549.1>.
- 212 Bold, U., Smith, E.F., Rooney, A.D., Bowring, S.A., Buchwaldt, R., Dudás, F.Ö.,
213 Ramezani, J., Crowley, J.L., Schrag, D.P., and Macdonald, F.A., 2016b,
214 Neoproterozoic stratigraphy of the Zavkhan terrane of Mongolia: The backbone for
215 Cryogenian and early Ediacaran chemostratigraphic records: American Journal of
216 Science, v. 316, p. 1–63, <https://doi.org/10.2475/01.2016.01>.
- 217 Brasier, M.D., and Callow, R.H.T., 2007, Changes in the patterns of phosphatic
218 preservation across the Proterozoic-Cambrian transition: Memoirs of the Association
219 of Australasian Palaeontologists, v. 34, p. 377–389.
- 220 Cohen, P.A., and Macdonald, F.A., 2015, The Proterozoic record of eukaryotes:
221 Paleobiology, v. 41, p. 610–632, <https://doi.org/10.1017/pab.2015.25>.
- 222 Cunningham, J.A., Vargas, K., Yin, Z., Bengtson, S., and Donoghue, P.C.J., 2017, The
223 Weng'an Biota (Doushantuo Formation): An Ediacaran window on soft-bodied and
224 multicellular microorganisms: Journal of the Geological Society (London), v. 174, p.
225 793–802, <https://doi.org/10.1144/jgs2016-142>.
- 226 Dong, L., Xiao, S., Shen, B., Zhou, C., Li, G., and Yao, J., 2009, Basal Cambrian
227 microfossils from the Yangtze Gorges area (South China) and the Aksy area (Tarim

- 228 block, northwestern China): Journal of Paleontology, v. 83, p. 30–44,
229 <https://doi.org/10.1017/S0022336000058108>.
- 230 Donoghue, P.C.J., Kouchinsky, A., Waloszek, D., Bengtson, S., Dong, X., Val'kov, A.K.,
231 Cunningham, J.A., and Repetski, J.E., 2006, Fossilized embryos are widespread but
232 the record is temporally and taxonomically biased: Evolution & Development, v. 8,
233 p. 232–238, <https://doi.org/10.1111/j.1525-142X.2006.00093.x>.
- 234  Donovan, N.A., Edemsky, H.B., and Ilyin, A.V., 1967, Cambrian phosphorites of Mongolia
235 Popular Republic: Sovetskaya Geologia, v. 3, p. 55–60.
- 236 Golubkova, E.Y., Zaitseva, T.S., Kuznetsov, A.B., Dovzhikova, E.G., and Maslov, A.V.,
237 2015, Microfossils and Rb-Sr age of glauconite in the key section of the Upper
238 Proterozoic of the northeastern part of the Russian plate (Keltmen-1 borehole):
239 Doklady Earth Sciences, v. 462, p. 547–551,
240 <https://doi.org/10.1134/S1028334X15060045>.
- 241  **[[In Russian? Check page information]]** Ilyin, A.V., 1973, Khubsugul phosphorite-
242 bearing basin: Moscow, Geolicheskiy Institut, Doklady Akademiiy Nauk SSSR, p.
243 167.
- 244 Ilyin, A.V., 2004, The Khubsugul phosphate-bearing basin: New data and concepts:
245 Lithology and Mineral Resources, v. 39, p. 454–467,
246 <https://doi.org/10.1023/B:LIMI.0000040735.76025.80>.
- 247  Ilyin, A.V., and Zhuravleva, I.T., 1968, On the boundary between the Cambrian and the
248 Precambrian at Prikhubsugulie (Mongolian PR): Doklady Akademii Nauk SSSR,
249 v. 182, p. 1164–1166.

- 250 Ilyin, A.V., Zaitsev, N.S., and Bjamba, Z., 1986, Proterozoic and Cambrian phosphorites
251 deposits: Khubsugul, Mongolian People's Republic, *in* Cook, P.J., and Shergold,
252 J.H., eds., *Phosphate Deposits of the World, Volume 1: Proterozoic and Cambrian*
253 *Phosphorites*: Cambridge, UK, Cambridge University Press, p. 162–174.
- 254 Kherzaskova, T.N., and Samygin, S.G., 1992, Tectonic conditions in the East Sayan
255 Vendian–Middle Cambrian terrigenous carbonate association: *Geotectonics*, v. 26,
256 p. 445–458.
- 257  Korobov, M.N., 1980, Lower Cambrian biostratigraphy and miomeroid trilobites of the
258 Lower Cambrian of Mongolia, *in* Menner, V.V., and Meyen, S.V., eds., *Lower*
259 *Cambrian and Carboniferous Biostratigraphy of Mongolia*, Volume 26: Moscow,
260 *Trudy Sovmestnou Sovetskogo-Mongol-skoy Paleontologicheskoy Ekspeditsii*, p. 5–
261 108.
- 262 Kuzmichev, A.B., and Larionov, A.N., 2011, The Sarkhoi Group in East Sayan:
263 Neoproterozoic (~770–800 Ma) volcanic belt of the Andean type: *Russian Geology*
264 *and Geophysics*, v. 52, p. 685–700, <https://doi.org/10.1016/j.rgg.2011.06.001>.
- 265 Liu, P., Xiao, S., Yin, C., Chen, S., Zhou, C., and Li, M., 2014, Ediacaran
266 acanthomorphic acritarchs and other microfossils from chert nodules of the Upper
267 Doushantuo Formation in the Yangtze Gorges area, South China: *Paleontology*
268 *Memoir*, v. 72, p. 1–139, <https://doi.org/10.1666/13-009>.  [\[\[DOI points to Journal of](#)
269 [Paleontology, v. 88 \(perhaps Special Issue 72\) – please check journal name and](#)
270 [volume\]\]](#)
- 271 Luo, Q., Wang, F., and Wang, Y., 1982, Uppermost Sinian–lowest Cambrian age
272 microfossils from Qingzhen-Zhijin County, Guizhou Province: *Bulletin of the*

- 273 Tianjin Institute of Geology and Mineral Resources, Chinese Academy of Sciences,
274 v. 6, p. 23–41.
- 275 Macdonald, F.A., and Jones, D.S., 2011, The Khubsugul Group, northern Mongolia, *in*
276 Arnaud, E., et al., eds., The Geological Record of Neoproterozoic Glaciations:
277 Geological Society of London Memoir 36, p. 339–345,
278 <https://doi.org/10.1144/M36.30>.
- 279 Macdonald, F.A., Jones, D.S., and Schrag, D.P., 2009, Stratigraphic and tectonic
280 implications of a newly discovered glacial diamictite–cap carbonate couplet in
281 southwestern Mongolia: *Geology*, v. 37, p. 123–126,
282 <https://doi.org/10.1130/G24797A.1>.
- 283 Moczyłowska, M., 2005, Taxonomic review of some Ediacaran acritarchs from the
284 Siberian Platform: *Precambrian Research*, v. 136, p. 283–307,
285 <https://doi.org/10.1016/j.precamres.2004.12.001>.
- 286 Moczyłowska, M., Vidal, G., and Rudavskaya, V.A., 1993, Neoproterozoic (Vendian)
287 phytoplankton from the Siberian Platform, Yakutia: *Palaeontology*, v. 36, p. 495–
288 521.
- 289 Muscente, A.D., Hawkins, A.D., and Xiao, S., 2015, Fossil preservation through
290 phosphatization and silicification in the Ediacaran Doushantuo Formation (South
291 China): A comparative synthesis: *Palaeogeography, Palaeoclimatology,*
292 *Palaeoecology*, v. 434, p. 46–62, <https://doi.org/10.1016/j.palaeo.2014.10.013>.
- 293 Oehler, D.Z., 1977, Microflora of the H.Y.C. Pyrite Shale Member of the Barney Creek
294 Formation (McArthur Group), middle Proterozoic of northern Australia: *Alcheringa*,
295 v. 1, p. 315–349, <https://doi.org/10.1080/03115517708527768>.

- 296 Oehler, D.Z., 1978, Microflora of the middle Proterozoic Balbrini Dolomite (McArthur
297 Group) of Australia: *Alcheringa*, v. 2, p. 269–309,
298 <https://doi.org/10.1080/03115517808527785>.
- 299 Osokin, P.V., and Tyzhinov, A.V., 1998, Precambrian tilloids of the Oka-Khubsugul
300 phosphorite-bearing basin (Eastern Sayan, Northwestern Mongolia): *Lithology and*
301 *Mineral Resources*, v. 33, p. 142–154.
- 302 Shome, S., Mathur, V.K., Nath, S., Xiao, S., and Broce, J., 2014, Occurrence of
303 Neoproterozoic animal embryos in the Chambaghat Formation of Himachal Lesser
304 Himalaya, India: *Current Science*, v. 106, p. 813–815.
- 305 Sinclair, H., and Naylor, M., 2012, Foreland basin subsidence driven by topographic
306 growth versus plate subduction: *Geological Society of America Bulletin*, v. 124,
307 p. 368–379, <https://doi.org/10.1130/B30383.1>.
- 308 Smith, E.F., Macdonald, F.A., Petach, T.A., Bold, U., and Schrag, D.P., 2016, Integrated
309 stratigraphic, geochemical, and paleontological late Ediacaran to early Cambrian
310 records from southwestern Mongolia: *Geological Society of America Bulletin*,
311 v. 128, p. 442–468, <https://doi.org/10.1130/B31248.1>.
- 312 Vidal, G., 1990, Giant acanthomorph acritarchs from the upper Proterozoic in southern
313 Norway: *Palaeontology*, v. 33, p. 287–298.
- 314 Vishnevskaya, I.A., and Letnikova, E.F., 2013, Chemostratigraphy of the Vendian–
315 Cambrian carbonate sedimentary cover of the Tuva-Mongolian microcontinent:
316 *Russian Geology and Geophysics*, v. 54, p. 567–586,
317 <https://doi.org/10.1016/j.rgg.2013.04.008>.

- 318 Xiao, S., and Knoll, A.H., 1999, Fossil preservation in the Neoproterozoic Doushantuo
319 phosphorite Lagerstätte, South China: *Lethaia*, v. 32, p. 219–238,
320 <https://doi.org/10.1111/j.1502-3931.1999.tb00541.x>.
- 321 Xiao, S., Zhang, Y., and Knoll, A.H., 1998, Three-dimensional preservation of algae and
322 animal embryos in a Neoproterozoic phosphorite: *Nature*, v. 391, p. 553–558,
323 <https://doi.org/10.1038/35318>.
- 324 Xiao, S., Muscente, A.D., Chen, L., Zhou, C.-M., Schiffbauer, J.D., Wood, A.D., Polys,
325 N.F., and Yuan, X.-L., 2014a, The Weng'an biota and the Ediacaran radiation of
326 multicellular eukaryotes: *National Science Review*, v. 1, p. 498–520,
327 <https://doi.org/10.1093/nsr/nwu061>.
- 328 Xiao, S., Zhou, C., Liu, P., Wang, D., and Yuan, X., 2014b, Phosphatized
329 acanthomorphic acritarchs and related microfossils from the Ediacaran Doushantuo
330 Formation at Weng'an (South China) and their implications for biostratigraphic
331 correlation: *Journal of Paleontology*, v. 88, p. 1–67, <https://doi.org/10.1666/12-157R>.
- 332 Xiao, S., Narbonne, G.M., Zhou, C.-M., Laflamme, M., Grazhdankin, D.V.,
333 Moczydlowska-Vidal, M., and Cui, H., 2016, Towards an Ediacaran time scale:
334 Problems, protocols, and prospects: *Episodes*, v. 39, p. 540–555,
335 <https://doi.org/10.18814/epiiugs/2016/v39i4/103886>.
- 336 Zhang, Y., and Zhang, X., 2017, New *Megasphaera*-like microfossils reveal their
337 reproductive strategies: *Precambrian Research*, v. 300, p. 141–150,
338 <https://doi.org/10.1016/j.precamres.2017.08.006>.
- 339 Zhou, C., Xie, G., McFadden, K.A., Xiao, S., and Yuan, X., 2007, The diversification
340 and extinction of Doushantuo-Pertatataka acritarchs in South China: Causes and

biostratigraphic significance: Geological Journal, v. 42, p. 229–262,

<https://doi.org/10.1002/gj.1062>.

Zhou, C., Xiao, S., Wang, W., Guan, C., Ouyang, Q., and Chen, Z., 2017, The stratigraphic complexity of the middle Ediacaran carbon isotope record in the Yangtze Gorges area, South China, and its implications for the age and chemostratigraphic significance of the Shuram excursion: Precambrian Research, v. 288, p. 23–38, <https://doi.org/10.1016/j.precamres.2016.11.007>.

FIGURE CAPTIONS

Figure 1. Geological setting of Khesen fossil assemblage (northern Mongolia). A: Map showing extent of Khuvsgul (Khuv.) and Zavkhan (Zav.) terranes. B: Geological map of western margin of Lake Khuvsgul. **[[Explain the “M618”, “M602”, and “M609” labels]]** C: Simplified stratigraphy of Tsagaan Olom Group of Zavkhan Basin (MU—Maikhan-Uul; BG—Bayangol). D: Simplified stratigraphy of Khuvsgul Group. E: Khesen Formation at Ongoluk Gol with carbon isotope record (**carb—carbonate; VPDB—Vienna Peedee belemnite**). F: Khesen Formation stratigraphy from ridgeline east of Urandush Uul.

Figure 2. Paleontology of Khesen Formation (northern Mongolia) in thin sections. A: *Archaeophycus yunnanensis*, **Yale Peabody Museum (YPM) specimen** 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 upper left, YPM 536802. F: *Variomargosphaeridium*

363 sp., YPM 536787. G–I: *Megasphaera* sp. G: YPM 536794. H: YPM 536784. I: YPM
364 536766. Scale bars 50 µm.

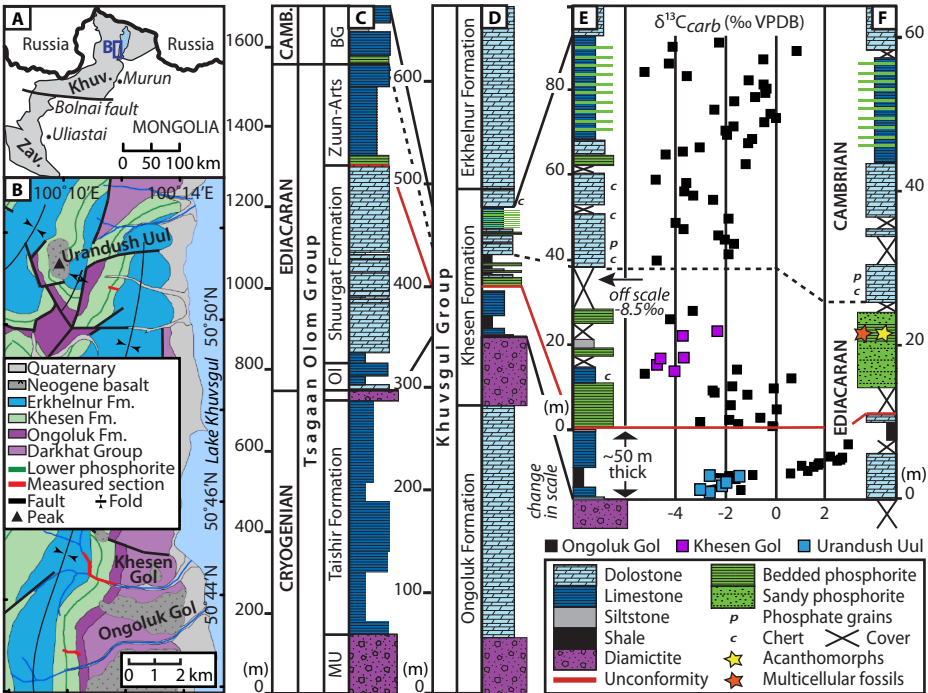
365

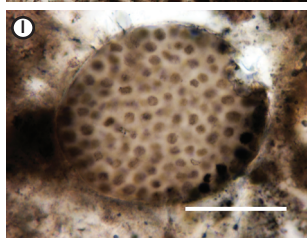
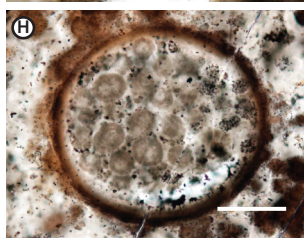
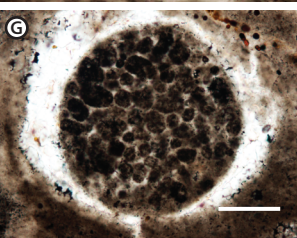
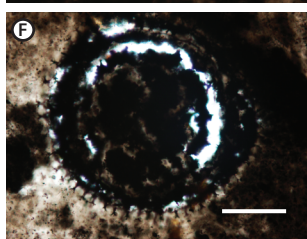
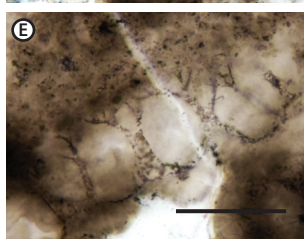
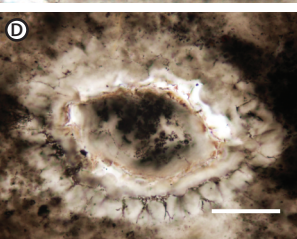
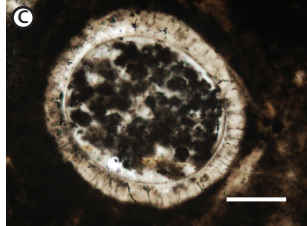
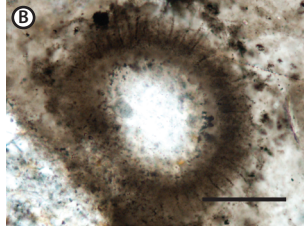
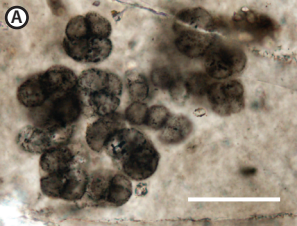
366 Figure 3. Paleontology of Khesen Formation (northern Mongolia) revealed by 20% acetic
367 acid maceration. A: *Archaeophycus yunnanensis* showing T cell division, **Yale Peabody**
368 **Museum (YPM) specimen** 538070. B–C: *Cavaspina ?basiconica*. B: YPM 538071. C:
369 YPM 538072. D–E: *Megasphaera* sp. D: YPM 538073. E: YPM 538074. F:
370 *Obruchevella magna*, YPM 538075. Scale bars 100 µm.

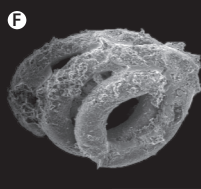
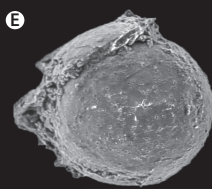
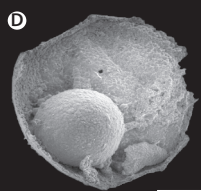
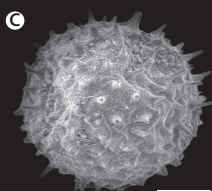
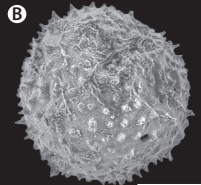
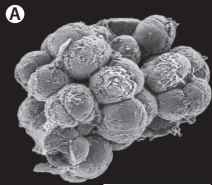
371



372 ¹GSA Data Repository item 2017xxx, **[[Please provide DR item name(s) and brief**
373 **descriptions here]]**, is available online at
374 <http://www.geosociety.org/datarepository/2017/> or on request from
375 editing@geosociety.org.







Supplementary Information

Doushantuo-type microfossils from latest Ediacaran phosphorites of northern Mongolia

Ross P. Anderson, Francis A. Macdonald, David S. Jones, Sean McMahon, Derek E.G. Briggs

Email: ross.anderson@yale.edu

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 536749 are at 0 and 3 m respectively in Fig. S1.

Urandush Uul

YPM 536747 and 536748 are at 21 and 22 m respectively in Fig. S1.

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

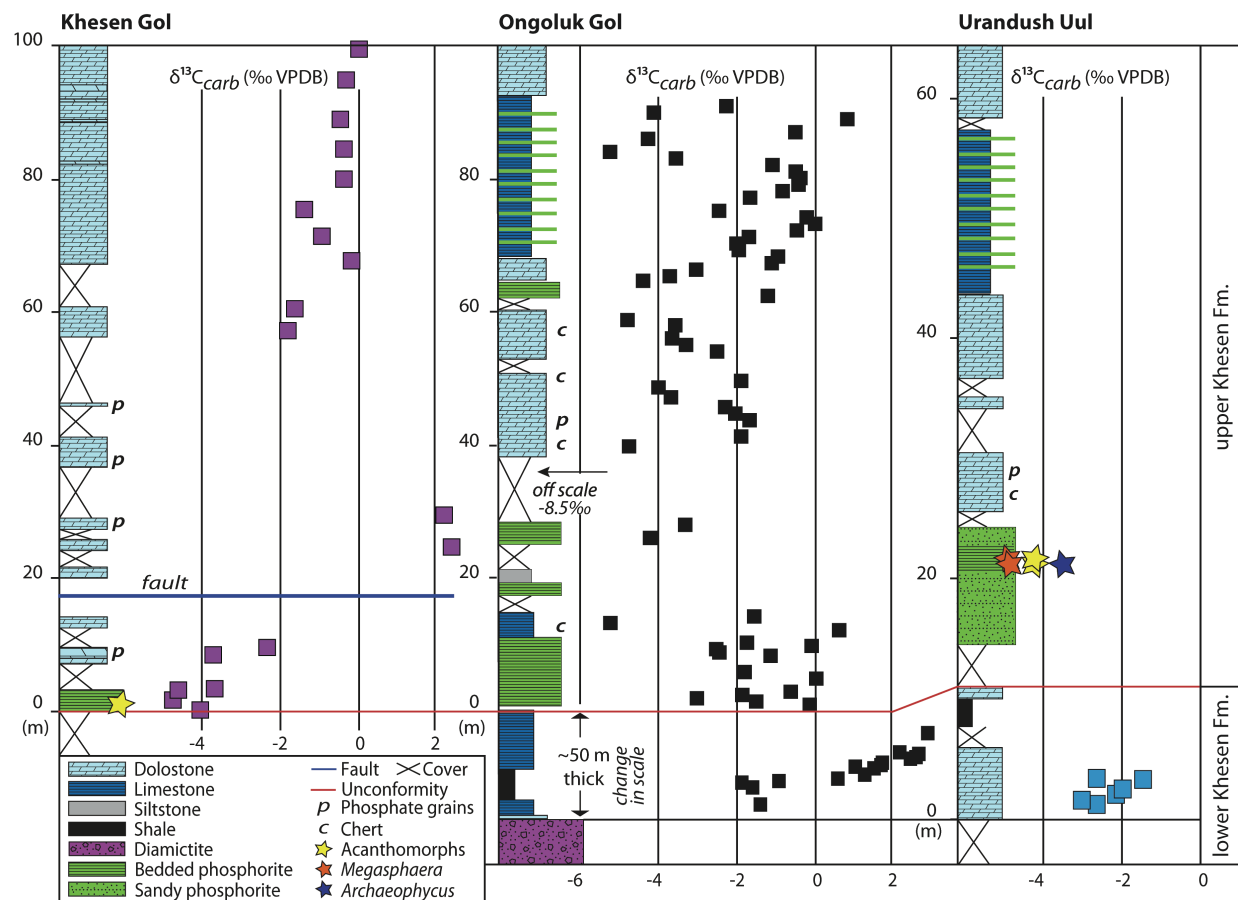


Figure S1: Expanded stratigraphy showing relationships between Khesen Gol, Ongoluk Gol, and Urandush Uul localities. See Figure 1 for locality information.

References

Macdonald, F.A., Jones, D.S., and Schrag, D.P., 2009. Stratigraphic and tectonic implications of a newly discovered glacial diamictite-cap carbonate couplet in southwestern Mongolia: *Geology*, v. 37, p. 123–126, <https://doi.org/10.1130/G24797A.1>.