Age of Neoproterozoic Bilatarian Body and Trace Fossils, White Sea, Russia: Implications for Metazoan Evolution

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A uranium-lead zircon age for a volcanic ash interstratified with fossil-bearing, shallow marine siliciclastic rocks in the Zimnie Gory section of the White Sea region indicates that a diverse assemblage of body and trace fossils occurred before 555.3 ± 0.3 million years ago. This age is a minimum for the oldest well-documented triploblastic bilaterian *Kimberella*. It also makes co-occurring trace fossils the oldest that are reliably dated. This determination of age implies that there is no simple relation between Ediacaran diversity and the carbon isotopic composition of Neoproterozoic seawater.

The terminal Neoproterozoic interval is characterized by a period of supercontinent amalgamation and dispersal (*1, 2*), low-latitude glaciations (*3, 4*), chemical perturbations of seawater (*5–7*), and the first appearance and subsequent diversification of metazoans. Construction of a terminal Neoproterozoic biostratigraphy has been hampered by preserva-

tional, paleoenvironmental, and biogeographic factors (*5, 8*). Global biostratigraphic correlations within the Neoproterozoic are tenuous and rely on sparse numerical chronology, inferred stratigraphic diversity trends, and chemostratigraphy (*8–13*). As a result, the position of many late Neoproterozoic soft-bodied organisms in metazoan phylogeny remains controversial. Fundamental to a solution of this problem is an understanding of the temporal relationship between fossil occurrences with Ediacaran-type preservation and other body fossils, small shelly fossils, and trace fossils of burrowing organisms.

Although Ediacaran biotas are globally distributed, their temporal distribution is poorly known. Simple annuli and discs pre-

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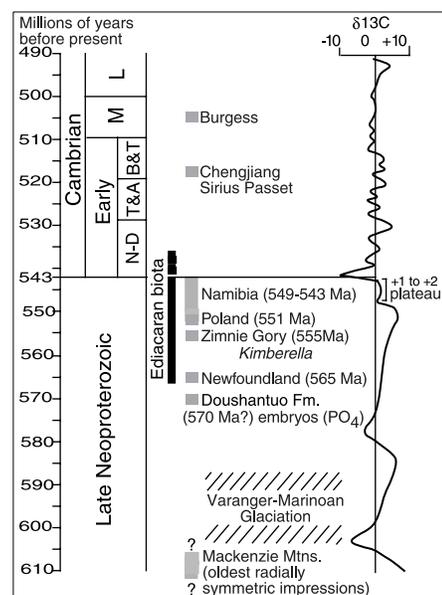
served below a glacial horizon in the Mackenzie Mountains of northwest Canada have been interpreted as possible metazoans and have been considered the oldest Ediacaran assemblage (*14*). Although their age is not constrained, they are commonly described as dating to 600 to 610 million years ago (Ma) (Fig. 1). The best-known diverse Ediacaran assemblages postdate the Varanger-Marinoan glaciation (*5, 8*). At Mistaken Point in eastern Newfoundland, fossils of soft-bodied organisms are dated at 565 ± 3 Ma (*15*). In the Ukraine, fossiliferous Upper Vendian strata of the Redkino Stage overlie volcanic rocks in Poland that are dated at 551 ± 4 Ma (*16, 17*). Ediacaran assemblages in the Nama Group in Namibia range from 548.8 ± 1 to 543.3 ± 1 Ma (*8*). Ediacaran-type fossils have been found together with *Treptichnus pedum* in what is described as Lower Cambrian sandstone of the Uratanna Formation in the Flinders Ranges, South Australia (*18*); in the Poleta Formation in the White-Inyo Mountains and Upper Wood Canyon Formation in the Death Valley region of California, USA (*19*); and in the Breivik Formation in arctic Norway (*20*). The two most abundant and diverse body and trace fossil assemblages—those from the Flinders Ranges (*10, 21*) in South Australia and White Sea coast in

Russia (*22*), which account for 60% of the well-described Ediacaran taxa (*23*)—have neither numerical age nor direct chemostratigraphic constraints. In this report, we summarize the biostratigraphy and age of the Zimnie Gory exposure along the White Sea in Russia, and place the spectacularly preserved trace and body fossils, including the triploblastic bilaterian *Kimberella* (*24*), into a global chronostratigraphic framework.

Many exposures in the White Sea region contain known Ediacaran biotas; however, the best fossil occurences are found along shoreline cliffs at Zimnie Gory (Fig. 2). These unmetamorphosed and nondeformed (except for present-day cliff-face slumping) siliciclastic rocks belong to the uppermost Ust-Pinega Formation and form the northern flank of the Mezen Basin along the southeast flank of the Baltic Shield. The section records three upward-coarsening sequences: A, B, and C (Fig. 2).

Sequence A is 10 m thick and consists of planar- to wavy-laminated interbedded siltstone and claystone with fine- to medium-grained, cross-stratified sandstone. The sharp transition to maroon and variegated claystone of sequence B is marked by an unconformity that drapes an erosional undulatory relief on the top of sequence A. The lowest part of this

Fig. 1. Time scale showing temporal distribution of dated Ediacaran assemblages and several well-known Cambrian fossil assemblages (gray squares) and glaciations and carbon-isotopic curve. The ¹³C isotopic curve is adopted from Knoll and Carroll (*35*). Phosphatized embryos that are similar to modern arthropods in the Doushantuo Formation of China are commonly cited as dated to 570 Ma (*31, 36*); however, there are no precise chronological constraints on this speculation of their age. Regional Siberian stage names are as follows: N-D, Nemakit-Daldynian; T&A, Tommotian and Atdabanian; and B&T, Botomian and Toyonia; M, Middle; L, Late.
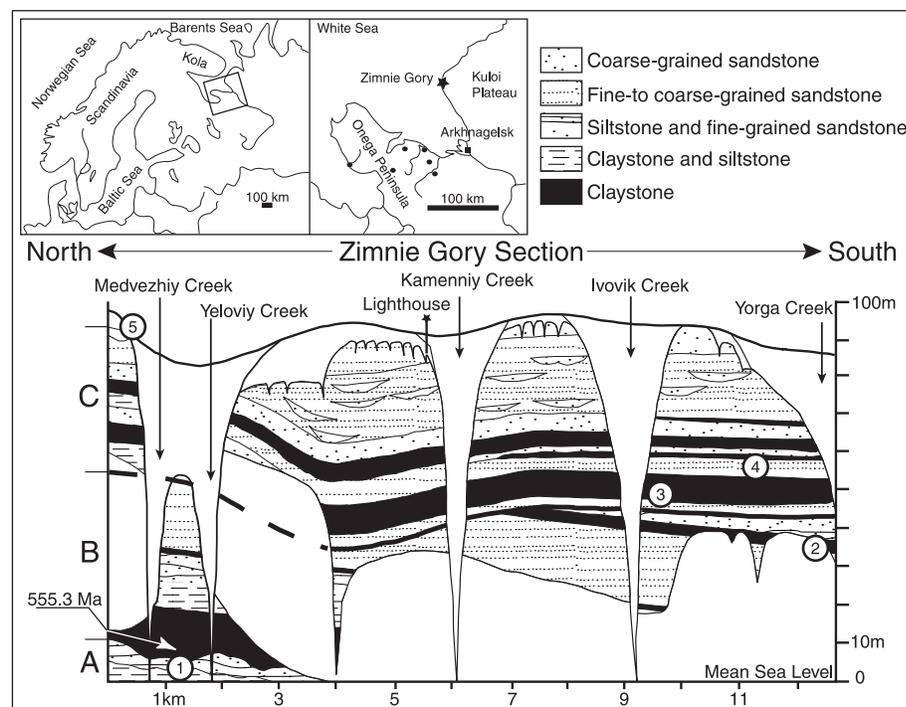

Fig. 2. Location map of the White Sea region in Russia and composite stratigraphic section of the Zimnie Gory section. Black dots on the inset map of the Onega Peninsula mark locations of known late Neoproterozoic fossils. Numbers on the stratigraphic section mark the positions of known fossils as follows: (**1**) *Charnia*, *Tribrachidium*, *Dickinsonia*, *Kimberella*, and *Eoporpita*; (**2**) *Charnia*; (**3**) *Dickinsonia*, *Kimberella*, *Parvancorina*, *Eoporpita*, and *Ovatoscutum*; (**4**) *Tribrachidium*, *Dickinsonia*, *Kimberella*, *Parvancorina*, *Eoporpita*, *Yorgia*, *Mawsonites*, and *Vendia*; and (**5**) *Tribrachidium*, *Dickinsonia*, *Kimberella*, and *Parvancorina*. Table 1 is a complete list of body and trace fossils from each sequence. Dated volcanic ash was collected between Medvezhiy and Yeloviy creeks near the base of sequence B.

claystone horizon contains a laterally discontinuous, pale-green volcanic ash that is 1 to 10 cm thick. The claystone passes upward into interbedded siltstone and claystone, which are overlain by channel and sheet siltstone and sandstone. The maximum thickness of sequence B is about 55 m. The top of sequence B is marked by an erosional unconformity that locally has cut 20 m of relief. Sequence C, locally attaining a thickness of 55 m, is composed of a basal thin horizon of flat-pebble to cobble conglomerate that is locally imbricated, which is overlain by interbedded sandstone, siltstone, and claystone. Grain size and sedimentary structures associated with sequences A, B, and C indicate a shallow, siliciclastic marine-dominated environment.

Table 1 lists body and trace fossils found in sequences A, B, and C. Body fossil diversities in sequences A and C are similar at the genus level; however, the assemblage of sequence C is noteworthy for its much greater diversity at the species level and for greater number of fossils. The trace fossils of sequence C appear to be more advanced forms than those found in sequence A. It is unclear whether these differences are real or are a function of limited exposure and sample bias in sequence A. Therefore, diversity as a means of comparing fossil assemblages in sequence A and C cannot be evaluated appropriately. Given their proposed distant paleogeographic positions at this time (2), the body and trace fossil assemblage of sequence C at Zimnie Gory compares well with that of the type-Ediacaran section in the Flinders Ranges, Australia, in terms of preservation style and composition at the level of genera and species (10, 25, 26). The remarkable similarity of these two assemblages could imply that they have closer paleogeographic affinities (27) not suggested by current paleogeographic reconstructions (1, 2).

We dated zircons from the volcanic ash in the lower part of the 15-m-thick claystone unit in the lower part of sequence B between Medvezhiy and Yeloviy creeks (Fig. 2). Zircons separated from this sample are euhedral, doubly terminated prisms up to 275 μm long, with aspect ratios ranging from 2:1 to 7:1; many are rich in inclusions. Four multigrain and 15 single-grain analyses are reported (Fig. 3) (28). With the exception of one multigrain analysis (three zircons), which we interpret to contain an older inherited component, the analyses yield a normally discordant array ($^{207}Pb/^{206}Pb > ^{207}Pb/^{235}U > ^{206}Pb/^{238}U$) anchored by one concordant analysis. A linear regression through these 18 data sets yields an upper intercept age of 555.4 ± 1.6 Ma [mean squared weighted deviation (MSWD) = 0.10] and a lower intercept indistinguishable from 0 Ma, suggesting that normal discordancy is a function of recent Pb loss. The 13 most precise analyses (% error in both of

the Pb/U ratios ≤0.26) (Table 1) yield an upper intercept of 555.4 ± 1.7 Ma. Because the lower intercept in either case is indistinguishable from zero, the weighted mean of all the $^{207}Pb/^{206}Pb$ dates is interpreted as the best estimate for the age of the ash bed, 555.3 ± 0.3 Ma (MSWD = 0.10). The weighted mean of the 13 most precise $^{207}Pb/^{206}Pb$ dates is identical, at 555.3 ± 0.3 Ma (MSWD = 0.14).

This provides a minimum age for the oldest definitive triploblastic bilaterian, *Kimberella*, and the oldest well-developed trace fossils; and it documents that spectacularly diverse and preserved Ediacaran fossils formed more than 12 million years before the base of the Cambrian (Fig. 1). The oldest known bilaterian fossil, *Kimberella* (24), is only known from South Australia and the White Sea. *Kimberella* is an oval- to pear-
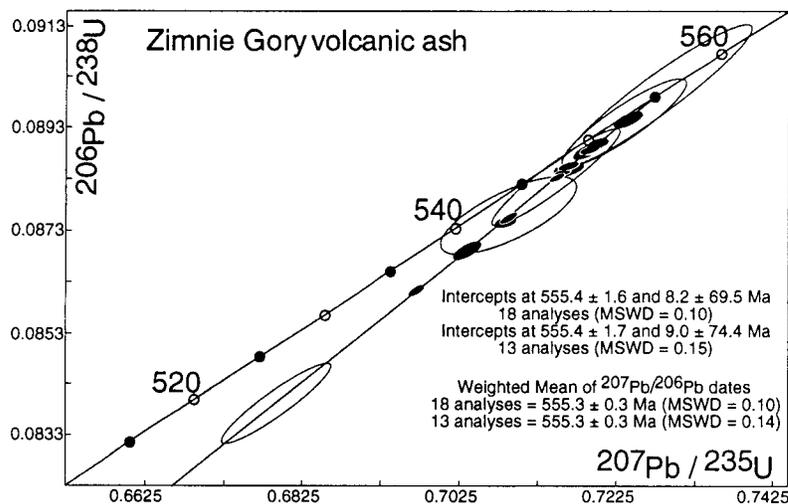

Fig. 3. U-Pb concordia diagram for Zimnie Gory volcanic ash.

Table 1. List of body and trace fossils present in sequences A, B, and C.

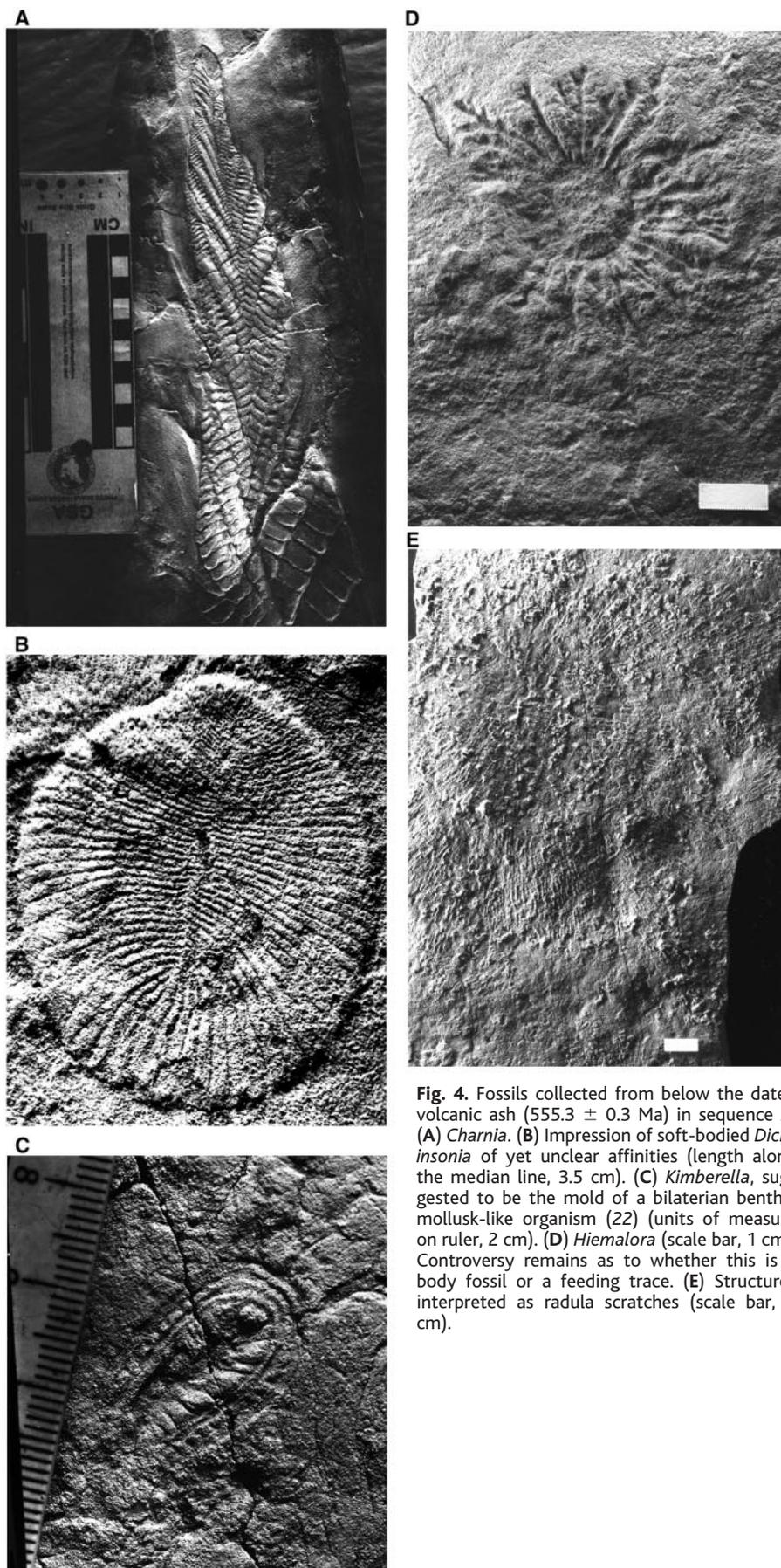| Sequence A	Sequence B	Sequence C
	Body fossils	
Anfesta	*Charnia*	*Anfesta*
Beltanelloides-like structures	*Ovatoscutum*	*Brachina*
Bonata	*Staurinidia*	*Cyclomedusa*
Charnia (Fig. 4A)	Molds of soft tubular structures; simple circular impressions	*Dickinsonia*
Cyclomedusa		*Ediacaria*
Dickinsonia (Fig. 4B)		*Eoporpita*
Ediacaria		*Inaria*
Eoporpita		*Irridinitus*
Hiemalora		*Kimberella*
Inaria		*Mawsonites*
Irridinitus		*Nemiana*
Kaisalia		*Parvancorina*
Kimberella (Fig. 4C)		*Ovatoscutum*
Nimbia		*Tribrachidium*
Protodipleurosoma		*Vendia*
Tribrachidium		*Yorgia*
Three-dimensional molds of tubular structures and others		Others, including numerous new forms
	Trace fossils	
Simple radial feeding burrows (Fig. 4D); backfilled burrows with circular path behavior; traces of crawling mollusk-like organism; fan-shaped sets of scratch marks (Fig. 4E)	Vertical burrows	Diverse radial feeding burrows; traces of crawling mollusk-like organism; fan-shaped sets of scratch marks; diverse vertical burrows; simple tunnels
	Enigmatic biological structures	
Yelovichnus		*Yelovichnus*
Palaeopascichnus		*Palaeopascichnus*
Intrites		*Intrites*

Fig. 4. Fossils collected from below the dated volcanic ash (555.3 ± 0.3 Ma) in sequence A. (**A**) *Charnia*. (**B**) Impression of soft-bodied *Dickinsonia* of yet unclear affinities (length along the median line, 3.5 cm). (**C**) *Kimberella*, suggested to be the mold of a bilaterian benthic mollusk-like organism (*22*) (units of measure on ruler, 2 cm). (**D**) *Hiemalora* (scale bar, 1 cm). Controversy remains as to whether this is a body fossil or a feeding trace. (**E**) Structures interpreted as radula scratches (scale bar, 1 cm).

shaped bilaterally symmetric fossil that ranges from 0.3 to 14 cm long and has several zones arranged concentrically with both soft and firm body parts (*24*) (Fig. 4C). Fedonkin and Waggoner (*24*) interpreted *Kimberella* as being more complex than a flatworm and having possible molluscan synapomorphies, such as a broad muscular foot. Seilacher (*29*) proposed that the radula scratches found in rocks of similar antiquity and lithology in South Australia (*30*) were made by a bilaterian (possibly *Kimberella*) during pendulum grazing, which is also a molluscan feature. Radula scratches (Fig. 3E) now found with *Kimberella* below the dated ash at Zimnie Gory support this interpretation. However, whether *Kimberella* at 555 Ma indicates that the protostome-deuterostome split is even older is not yet resolvable (*31*). Finally, our age determination places such characteristic late Neoproterozoic guide genera as *Charnia*, *Dickinsonia*, *Tribrachidium*, and *Kimberella* at least 6 million years before the Namibian assemblage (549 to 543 Ma) (*8, 13*).

In addition to the radula scratches, complex trace fossils found below and above the dated ash (Fig. 4D) establish that metazoans capable of active crawling and burrowing were present by that time. These trace fossils probably require an animal with a morphologic grade more complex than cnidarians or flatworms (*31*).

This age also implies that there is no clear relationship between Ediacaran diversity and the terminal Neoproterozoic ^{13}C +1 to +2 plateau. (Fig. 1), in contrast to that suggested by Grotzinger *et al.* (*8*). Biostratigraphic correlation between Ediacaran localities is difficult because many localities contain limited numbers of specimens and few taxa. Biostratigraphic zonations, based on taxa diversity and carbon-isotope chemostratigraphy, have suggested (*8, 10, 13, 21, 25, 32*) that the sections in the Flinders Ranges and the White Sea are correlatives. Grotzinger *et al.* (*8*) noted that "very" diverse Ediacaran assemblages worldwide occur within the +1 to +2 ^{13}C interval, the so-called "+2 plateau" (Fig. 1), and demonstrated that the oldest part of this assemblage in Namibia was about 6 million years older than the Proterozoic-Cambrian boundary.

Detailed comparisons of taxa between Zimnie Gory and the type-Ediacaran in the Flinders Ranges suggest that they are coeval with our new age of 555.3 Ma. However, juxtaposition of the type-Ediacaran section with a composite carbon-isotopic curve (*10*) derived from correlative sections lacking Ediacaran fossils in southern and central Australia (*33*) suggests that it has chemostratigraphic affinity to the +1 to +2 ^{13}C interval dated at 549 to 543 Ma in southern Namibia (*8*) (Fig. 1). This observation requires that either the biostratigraphic correlation spans a