



Chain organization of dimple-ended magnetite magnetosomes supports field-dependent cell linking in unicellular magnetotactic bacteria

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Magnetotactic bacteria (MTB) are generally thought to navigate as individual cells by using intracellular magnetosome chains that provide a stable magnetic moment for orientation along magnetic field lines. Whether nonclassical magnetosome geometries and particle-scale magnetic states can support robust chain-level magnetic function, and potentially mediate interactions between cells, remains unresolved. Here, to we report a unicellular magnetotactic bacterium, strain WYHV-1, that biomineralizes comparatively large prismatic magnetite magnetosomes with distinctive dimples at both crystal ends and organizes them into a single tightly packed intracellular chain. Off-axis electron holography reveals that individual dimple-ended particles commonly exhibit single-vortex behavior rather than a canonical uniformly magnetized single-domain (SD) state. Micromagnetic simulations indicate a size-dependent transition from SD to single-vortex behavior in dimple-ended particles and that tight intrachain coupling suppresses particle-scale nonuniformity, producing a predominantly SD-like magnetization within the chain and a strong chain-parallel remanent moment. Further simulations indicate that chain-generated stray fields concentrated at chain ends can generate intercellular magnetic attraction strong enough to promote head-to-tail linking between neighboring cells over subcellular distances. These results provide a physical explanation for field-dependent multicell-like assemblies observed in hanging-drop experiments and indicate that magnetic performance in WYHV-1 is governed primarily by chain-level organization rather than by the magnetic state of idealized isolated particles. Our findings expand the known structural and magnetic diversity of biogenic magnetite and reveal a cross-scale mechanism by which magnetosome chains support cellular orientation, and under field-aligned experimental conditions, mediate intercellular magnetic organization.

magnetotactic bacteria | magnetosome | biogenic magnetite | single-vortex state | biomineralization

Emergence of redox-stratified aquatic environments profoundly reshaped microbial evolution and elemental cycling on Earth (1). Oxidic–anoxic transition zones (OATZs) in sediments and stratified water columns are especially dynamic interfaces, where steep chemical gradients sustain diverse microorganisms adapted to locating and exploiting narrow metabolic niches (2, 3). Magnetotactic bacteria (MTB) are among the most distinctive inhabitants of such environments (4–6). They biomineralize membrane-enveloped magnetic nanocrystals within organelles known as magnetosomes, which are typically organized into one or more intracellular chains that impart a permanent magnetic dipole moment to the cell (7, 8). By aligning cells with geomagnetic field lines, these magnetosome chains enable MTB to reduce the search for favorable redox conditions from three dimensions to one, thereby increasing the efficiency of magneto-aero-chemotaxis (7, 9–12).

Current understanding of magnetosome function is largely framed by the canonical single-domain (SD) model, in which MTB optimize navigation by producing magnetosomal magnetite with regular morphologies and stable SD magnetic behavior (13–15). However, several observations suggest that this framework is incomplete. Some MTB produce unusually large magnetic particles (16), some organize magnetosomes nonlinearly or in partially disordered clusters (17–22), and some appear to synthesize more magnetic particles than required for navigation (5, 23–25). These observations raise two unresolved questions: whether nonuniform particle geometries and magnetic states can still support robust magnetic function, and whether magnetosome chains can contribute to cell organization beyond orienting individual cells.

Significance

Magnetotactic bacteria are widely viewed as single-celled “living compasses” whose magnetosome chains orient along geomagnetic field lines. We describe a bacterium that produces comparatively large, dimple-ended magnetite magnetosomes that commonly exhibit single-vortex magnetization at the particle scale. However, tight chain packing suppresses particle-scale nonuniformity and drives chain-embedded particles toward a predominantly single-domain-like state while maintaining a strong chain-parallel remanent moment. Micromagnetic simulations further indicate that chain-level stray fields can promote magnetic coupling and field-dependent linking between neighboring cells. These findings expand the known design space of magnetosome biomineralization, demonstrate how robust magnetic function can emerge from strong intrachain interactions, and reveal that magnetosome chains can mediate intercellular magnetic organization under field-aligned experimental conditions.

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Here we describe a unicellular MTB strain WYHV-1 from freshwater sediments of Weiyanghu Lake, China. WYHV-1 biomineralizes comparatively large, dimple-ended prismatic magnetosomes arranged in a single tightly packed intracellular chain. By combining electron microscopy, synchrotron spectromicroscopy, off-axis electron holography, and micromagnetic simulations, we show that individual WYHV-1 magnetosomes commonly adopt single-vortex (SV) states rather than canonical SD states, whereas tight chain organization suppresses particle-scale nonuniformity, drives chain-embedded particles toward a predominantly SD-like magnetization, and produces a strong chain-parallel magnetic moment. In hanging-drop preparations under applied magnetic fields, WYHV-1 cells can form head-to-tail multicell-like assemblies, and our simulations indicate that chain-end stray fields provide a physical mechanism for this field-dependent linking between neighboring cells. These findings expand the known design space of magnetosome biomineralization and reveal a cross-scale model of magnetic organization that links particle-scale magnetization, interaction-stabilized chain behavior, and field-dependent intercellular coupling in MTB.

Results

WYHV-1 Can Form Field-Dependent Multicell-Like Assemblies Through Head-to-Tail Linking. We identified a unicellular *magnetotactic vibrio*, tentatively designated as strain WYHV-1, in freshwater sediments from Weiyanghu Lake, Xi'an, China (SI Appendix). Based on 16S rRNA gene sequences, WYHV-1 belongs to the class *Alphaproteobacteria* within the phylum *Pseudomonadota*. Phylogenetic analysis shows that WYHV-1 forms a distinct monophyletic clade with MTB strains YQV-1 and XQGS-1 (22, 26), representing a putative novel genus within the *Alphaproteobacteria* (SI Appendix, Figs. S1 and S2). YQV-1 and XQGS-1 were detected previously from freshwater sediments of Yuqiao Lake, Tianjin, and Xingqinggong Lake, Xi'an, respectively. Both strains biomineralize cuboctahedral magnetite arranged in a single tightly packed intracellular chain (SI Appendix, Fig. S1 B and C). Magnetite in YQV-1 has mean crystal lengths and widths of 88.6 ± 13.0 nm and 82.0 ± 11.0 nm, respectively, whereas in XQGS-1 they have mean crystal lengths and widths of 88.3 ± 11.7 nm and 83.3 ± 11.0 nm, respectively (22, 26). Field-dependent head-to-tail linking has yet to be reported for either strain.

In hanging-drop experiments under applied magnetic fields (27), WYHV-1 cells usually behave as isolated motile bacteria, as expected for unicellular MTB (5, 7). However, when concentrated in hanging drops and exposed to ~ 0.1 to 1 mT applied magnetic fields, which are ~ 2 to 20 times stronger than the local geomagnetic field, cells frequently link end-to-end to form elongated multicell-like assemblies that reach ~ 20 to 50 μm or more in length (Fig. 1A and Movies S1–S3). These assemblies consistently align parallel to the external magnetic field. Unlike the directional swimming behavior characteristic of most MTB under comparable or stronger applied magnetic fields (28–30), and unlike isolated WYHV-1 cells themselves, the linked assemblies do not show clear evidence of active coordinated swimming. Instead, they commonly form near the edge of the hanging drop and appear to be organized predominantly by magnetic alignment and head-to-tail attraction. We, therefore, interpret this behavior as a field-dependent physical association between otherwise independent unicellular cells, rather than as evidence of obligate multicellularity or a developmentally fixed multicellular state.

Stronger external magnetic fields appear to promote formation of more and longer cell chains (Movies S1–S3), consistent with a

magnetic contribution to the linking process. We, therefore, refer to this behavior as field-dependent linking under experimental conditions, and do not infer from these observations alone that long multicell-like assemblies are common in situ. Both optical microscopy and transmission electron microscopy (TEM) indicate that WYHV-1 consists of intact single cells after magnetic enrichment and drying (Fig. 1 B–D), distinguishing it from obligately multicellular magnetotactic prokaryotes and from filamentous cable bacteria, whose multicellular organization is maintained by stable intercellular architecture rather than transient end-to-end association between otherwise independent cells (31–33).

Similar field-associated or collective chain-like arrangements have been noted in other MTB. For example, Lefèvre et al. reported collective swimming behavior in MTB containing large magnetosome numbers (34). Wu et al. described long magnetic nanochains assembled by unicellular MTB strain NMV-1 under directional magnetic fields, with chain length increasing under stronger fields (35). Together, these observations suggest that cell magnetic moment, local cell density, and external field strength can all influence collective assembly formation.

WYHV-1 Biomineralizes Comparatively Large, Dimple-Ended Magnetosomal Magnetite. TEM analyses indicate that strain WYHV-1 produces elongated prismatic magnetosomal magnetite arranged in a tightly packed chain along the cell long axis, with an exceptionally small interparticle gap of ~ 2 nm (Fig. 2 A–C). Relatively small particles commonly occur at both ends of the chain. WYHV-1 cells are ~ 1.3 to 2.9 μm long and ~ 0.5 to 1.0 μm wide, with mean dimensions of 2.0 ± 0.38 μm and 0.7 ± 0.08 μm , respectively ($n = 236$). Each cell contains 8 to 21 magnetosomes, with an average of 14 ± 3 particles ($n = 342$) (SI Appendix, Fig. S3).

Magnetosomal magnetite in WYHV-1 is notable for the combination of comparatively large size, prismatic morphology, terminal dimples, and tight chain packing. Measurement of 1,725 particles yields mean crystal dimensions of 105.3 ± 23.5 nm in length and 81.3 ± 19.9 nm in width, with more than 75% of particles falling between ~ 90 and 150 nm in length and between ~ 75 and 120 nm in width (Fig. 2D and SI Appendix, Fig. S3). These dimensions place WYHV-1 magnetosomes near the upper range reported for prismatic magnetic particles in many modern MTB (SI Appendix, Table S1), although comparably large particles have been described in some MTB and magnetofossil assemblages (14, 16, 22, 36, 37). While the size of magnetosomal magnetite in WYHV-1 has precedent, these particles are distinctive in combining comparatively large prismatic sizes with dimple-ended termini and exceptionally tight intracellular chain packing, a combination that provides the structural basis for the magnetic behavior examined below.

The size distribution of magnetosomal magnetite in WYHV-1 also overlaps with the range in which isolated magnetite particles are expected to develop nonuniform magnetic states rather than remaining uniformly magnetized in the SD state (13–15). This expectation is consistent with theoretical predictions that magnetostatic interactions in chains can drive particles that would be nonuniform when isolated toward more uniform, effectively SD-like magnetization when strongly coupled within a chain (SI Appendix, Fig. S4). WYHV-1, therefore, provides a useful biological system for testing how particle-scale nonuniform magnetization is modified by strong intrachain interactions within an intact magnetosome chain.

Unlike the smooth crystal ends commonly reported for magnetosomal magnetite in MTB (5, 22, 36), those in WYHV-1 have conspicuous dimples at both crystal ends (Fig. 2 E–I and Movies S4–S6).

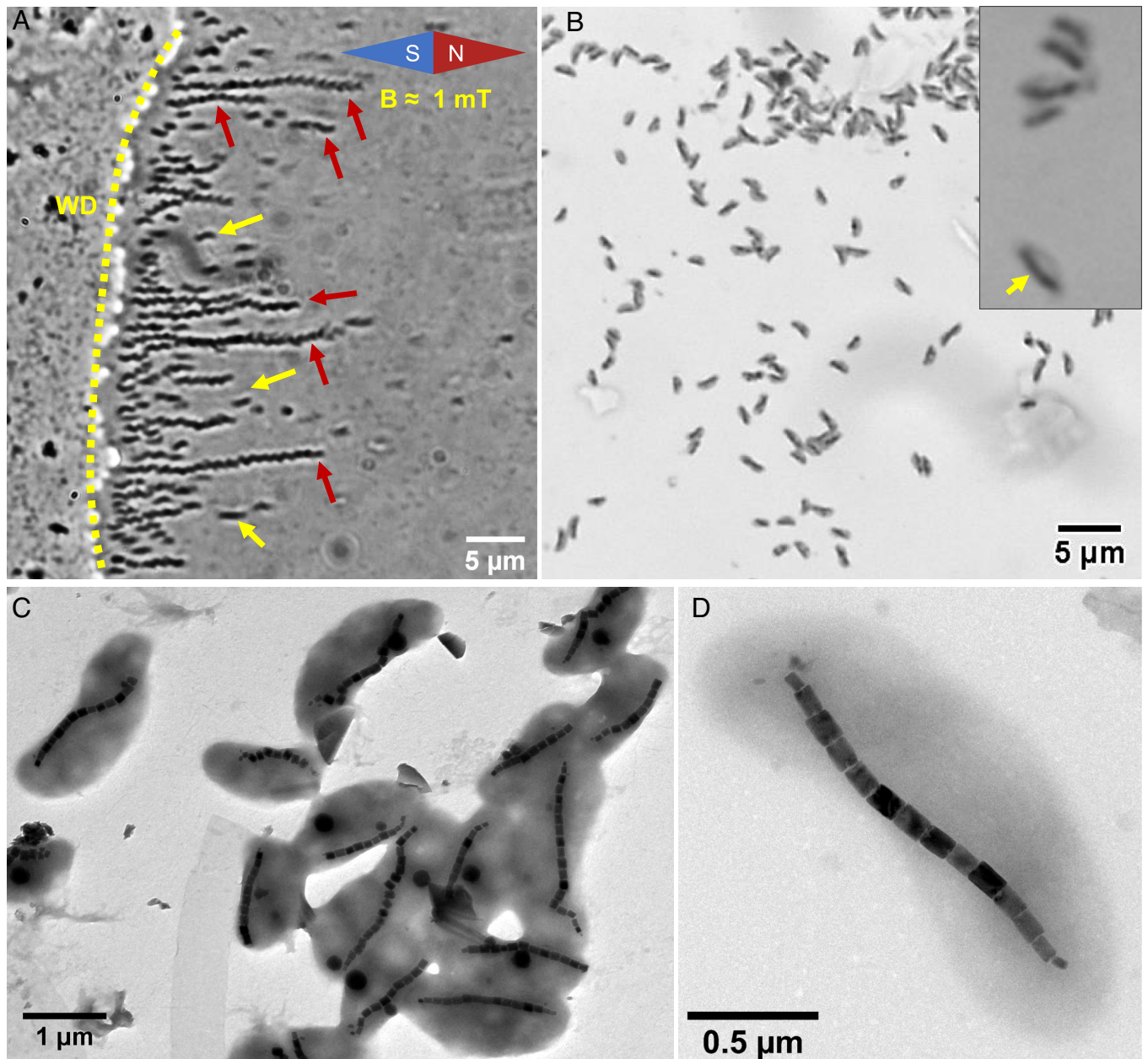


Fig. 1. Field-aligned chaining behavior and unicellular organization of strain WYHV-1. (A) Optical micrograph of living WYHV-1 cells in a hanging-drop preparation that reveals the end-to-end assembly of many cells into elongated cell chains (red arrows) under an applied magnetic field ($B \approx 1$ mT), whereas other cells remain isolated (yellow arrows). Cells are concentrated near the edge of the water droplet (WD, yellow dashed curve). (B) Optical micrograph of magnetically enriched WYHV-1 cells after crystal violet staining, with WYHV-1 consisting of individual unicellular cells. A faint dark intracellular line is visible in some cells (yellow arrow in inset), consistent with a magnetosome chain. (C) Bright-field TEM image of WYHV-1 cells with intact unicellular morphology and a single intracellular magnetosome chain within each cell. (D) Representative TEM image of a single WYHV-1 cell, with curved cell morphology and tightly packed magnetosome chain aligned along the cell long axis. See [Movies S1–S3](#) and [SI Appendix, Figs. S1 and S2](#) for additional analyses.

The dimples have an average depth of $\sim 11.0 \pm 1.7$ nm ($n = 82$). This morphology is observed consistently in multiple particles and viewing directions by high-angle annular dark-field scanning transmission electron microscopy (HAADF-STEM) (Fig. 2B and C and [SI Appendix, Fig. S3 B–E](#)), three-dimensional focused-ion-beam scanning electron microscopy (FIB-SEM) tomography (Fig. 2E and [Movie S6](#)), HAADF-STEM tomography (Fig. 2F and [Movies S4 and S5](#)), high-resolution TEM (HRTEM) (Fig. 2G–I and [SI Appendix, Fig. S5](#)), which indicate that the terminal depressions are intrinsic crystal features rather than artifacts of a single imaging or reconstruction method. HRTEM observations of particles viewed along different crystallographic orientations, combined with crystal modeling, indicate that the crystals can

be idealized as elongated hexagonal prisms bounded mainly by six $\{110\}$ side faces, with minor truncations by $\{100\}$ and $\{111\}$ faces. The dimpled termini appear to result from incomplete development of terminal $\{111\}$ faces (Fig. 2F–I and [SI Appendix, Fig. S5](#)).

Synchrotron-based scanning transmission X-ray microscopy coupled with X-ray magnetic circular dichroism (STXM-XMCD) confirms that the magnetic mineral is magnetite (38, 39) (Fig. 2J). Some cells also contain sulfur-rich, electron-dense granules (Fig. 2A and [SI Appendix, Fig. S6 A–G](#)), which STXM coupled with near-edge X-ray absorption fine structure (NEXAFS) spectroscopy identifies as zero-valent sulfur (12, 40) ([SI Appendix, Fig. S6 H–L](#)). These inclusions resemble sulfur globules reported

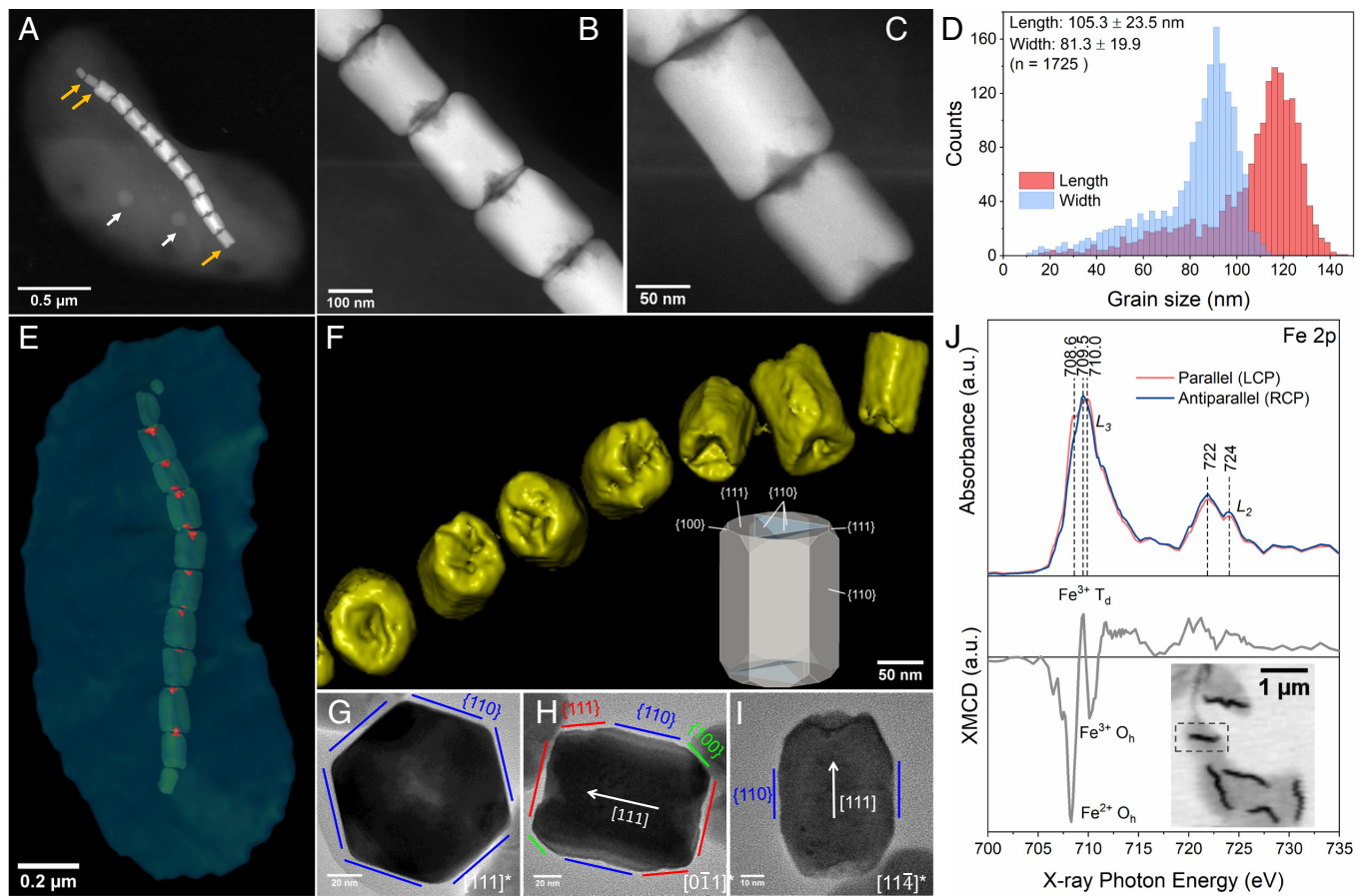


Fig. 2. Morphological and mineralogical features of magnetosomal magnetite in WYHV-1. (A) HAADF-STEM image of a WYHV-1 cell with a single magnetosome chain and two sulfur granules (white arrows), and smaller magnetite particles at the chain ends (yellow arrows). (B) Enlarged HAADF-STEM image of a tightly packed magnetosome chain. (C) Enlarged HAADF-STEM image of particles at the chain end. (D) Size distribution of WYHV-1 magnetosomal magnetite particles. (E) Three-dimensional FIB-SEM reconstruction of a WYHV-1 cell, with terminal dimples (red) on individual magnetosomal magnetite particles and their alignment along the magnetosome-chain axis. (F) Three-dimensional HAADF-STEM reconstruction of seven magnetic particles, highlighting the dimple-ended morphology. *Inset:* idealized crystal morphology; a disordered chain configuration is shown to better visualize the dimple-ended termini. (G–I) HRTEM images of individual particles viewed along the $[111]$ (G), $[011]$ (H), and $[114]$ (I) zone axes of magnetite. (J) Synchrotron-based STXM analysis of a magnetosome chain (dark dashed square). *Top*, Fe $L_{2,3}$ -edge X-ray absorption (XAS) spectra collected with parallel (red) and antiparallel (blue) polarization. *Bottom*, Fe $L_{2,3}$ -edge XMCD spectrum (gray) calculated as the difference between the two signals. See [Movies S4 and S5](#) and [SI Appendix, Figs. S3–S6](#) for additional analyses.

in other MTB and likely reflect sulfur metabolism rather than the magnetic properties of the magnetosome chain (12).

Electron Holography Reveals a Particle-Scale Vortex-Like Magnetization and a Dominant Chain-Parallel Magnetic Response. To determine how the comparatively large dimple-ended magnetosomes behave magnetically within intact chains, we examined WYHV-1 magnetosomes by off-axis electron holography (EH) (41). In intact intracellular chains, dominant magnetic phase contours are oriented approximately parallel to the chain axis, indicating a strong chain-parallel uniaxial magnetic response (Fig. 3 A and B). The magnetic moment of each chain is sufficiently strong that chains in neighboring head-to-tail aligned cells can interact magnetostatically, even when chains are separated by intact cell bodies in neighboring cells (Fig. 3 A and B and [SI Appendix, Fig. S7](#)).

Although the chain-level magnetic field is dominated by the chain-parallel component, closer inspection nevertheless reveals weak but systematic nonuniformity at the individual particle scale. In the cell shown in Fig. 3 A–D, the dominant projected magnetic component is parallel to the chain axis (B_x), whereas a much weaker chain-perpendicular component (B_y) occurs mainly near particle margins (Fig. 3 C and D). Quantitative profiles extracted from the magnetic phase-gradient maps indicate that the chain-perpendicular signal is approximately an order of magnitude

weaker than the chain-parallel signal. This indicates that local particle-scale nonuniformity is present but remains subordinate to the dominant chain-parallel magnetic signal.

The particle-scale nonuniformity is clearest in end-of-chain or locally collapsed chains, in which individual magnetic particles are less constrained by neighboring particles (Fig. 3 E–H). In these particles, EH resolves vortex-like magnetic structures characterized by closed magnetic-flux patterns and narrow central cores approximately 15 nm wide. These observations indicate that individual WYHV-1 magnetosomes are not uniformly magnetized ideal SD particles when considered in isolation or at chain ends. Instead, they commonly show SV-like magnetic configurations while remaining magnetically coupled within a chain whose net magnetic response is predominantly chain-parallel.

Micromagnetic Simulations Reveal a Size-Dependent SD-SV Transition and Interaction-Stabilized Chain-Level Response. To clarify the magnetic consequences of particle size, dimple-ended morphology, and chain organization, we performed micromagnetic simulations constrained by measured magnetosomal magnetite dimensions and chain geometry in WYHV-1 ([SI Appendix](#)). We first simulated individual dimple-ended particles over the observed size range. The simulations reveal a size-dependent transition in which smaller particles (e.g., 40 to 85 nm long) are exclusively in

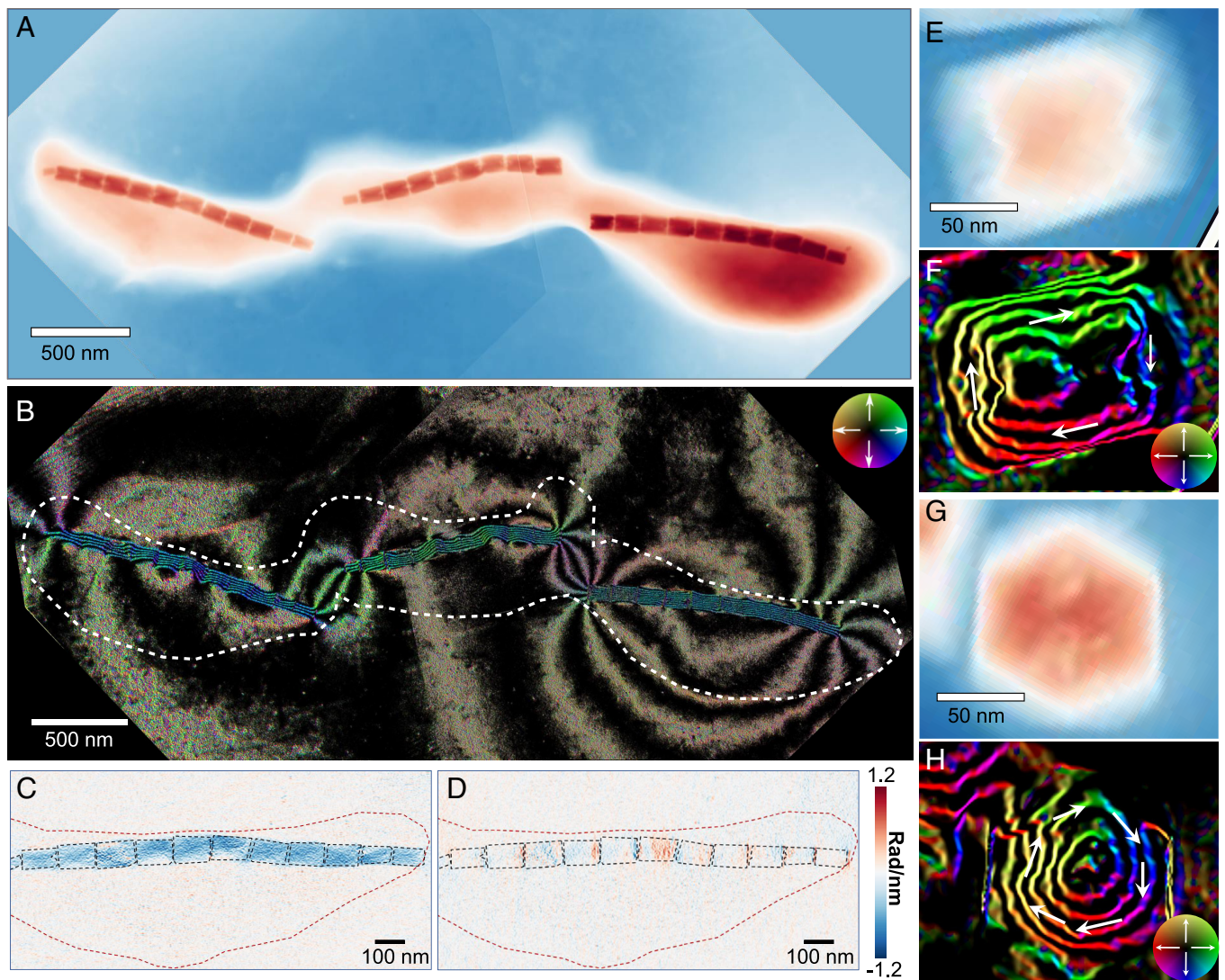


Fig. 3. Magnetic field distribution of WYHV-1 magnetosomal magnetite revealed by off-axis electron holography. (A) Mean inner potential image for well-ordered magnetite magnetosome chains in three cells connected in series. (B) Projected magnetic field B in the remanent state, with approximately uniform magnetic flux parallel to the chain axis and strong magnetic interaction between head-to-tail connected cells. The color wheel indicates the magnetic field direction, and contour density represents magnetic field magnitude. (C and D) Calculated magnetic field components from the WYHV-1 cell on the Left in A: (C) B_x , parallel to the magnetosome chain, and (D) B_y , perpendicular to the chain. These maps indicate a largely uniform B_x component and a weakly nonuniform B_y component. The estimated average B_x value is ~ 0.45 rad/nm, whereas the maximum B_y value is ~ 0.04 rad/nm. (E–H) Mean inner potential images (E and G) and magnetic field distribution maps (F and H) of two end-of-chain magnetosomes that are less constrained by intrachain interactions because of chain collapses. These particles have a clear magnetic vortex structure when viewed from the magnetosome side (E and F) and tip (G and H). Magnetic phase contour spacing is $\pi/5$ radians, which corresponds to 4.14×10^{-15} T m^2 .

the SD state, whereas larger particles (e.g., 90 to 150 nm length) mostly occur in the SV state with a vortex core aligned along the particle long axis (LSV state). Remaining particles in this large size range occur in the SD state (~ 90 nm long) or in the SV state with vortex core aligned with the particle short axis (SSV state; ≥ 110 nm) (Fig. 4A and SI Appendix, Fig. S8). These results are consistent with the expectation that isolated magnetite particles in this size range can develop nonuniform magnetic configurations rather than remain uniformly magnetized SD grains.

We next simulated magnetosome chains using experimentally constrained particle dimensions and interparticle spacing (Fig. 4B). Strong intrachain magnetostatic interactions substantially suppress the nonuniform magnetization of larger particles once they are assembled into a tightly packed chain, driving most chain-embedded particles toward a nearly uniform, effectively SD-like state. Accordingly, the intact chain has a strong remanent moment parallel to the chain axis, although subtle local nonuniformity persists within some particles, particularly near chain ends

(Fig. 4B). This simulated behavior is consistent with the EH observations, which indicate dominant chain-parallel magnetic contours in intact WYHV-1 magnetosome chains (Fig. 3B).

This behavior is consistent with micromagnetic predictions that particles that are too large to remain uniformly magnetized in isolation can adopt a more uniform, effectively SD-like state when strongly coupled within magnetosome chains (14). Thus, the particle size of magnetosomal magnetite in WYHV-1 alone does not imply a magnetic function failure. Rather, WYHV-1 provides a clear biological example in which particle-scale SV behavior in isolated or weakly constrained particles coexists with interaction-stabilized, predominantly SD-like magnetization within an intact magnetosome chain.

Sensitivity simulations using simplified nondimpled prismatic particles with the same dimensions and interparticle spacing indicate that removal of terminal dimples does not substantially change the overall chain-parallel remanent state (SI Appendix, Fig. S9). Because we did not directly compare chain-end stray

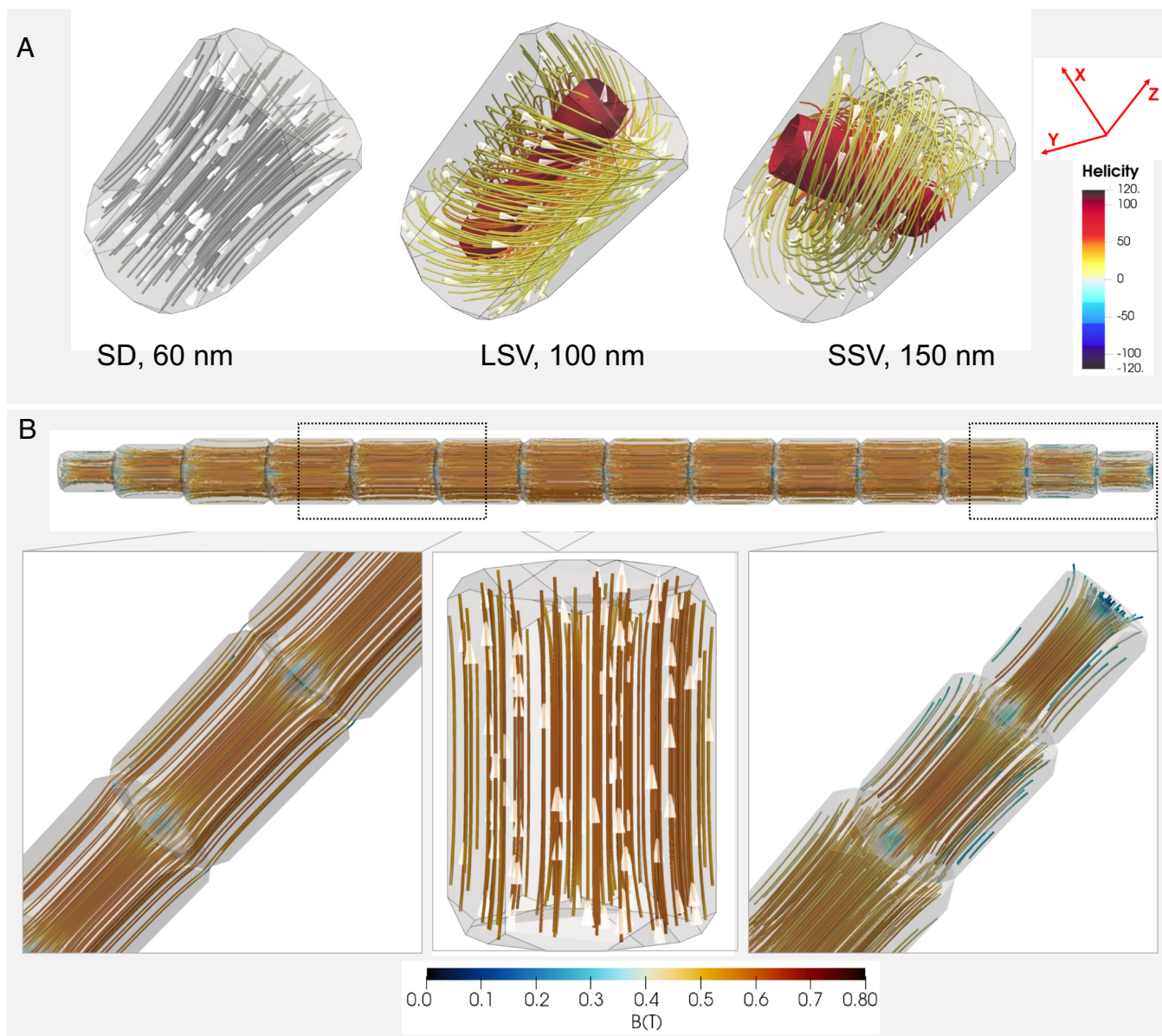


Fig. 4. Micromagnetic simulations of WYHV-1 magnetosomal magnetite particles. (A) Micromagnetic structures of three representative dimple-ended magnetite particles with different lengths (L), with stable SD and single-vortex (SV) states. The 60 nm particle is in the SD state; the 100 nm particle is in a SV state with the vortex core parallel to the particle long axis (LSV); and the 150 nm particle is in a SV state with the vortex core parallel to the particle short axis (SSV). The color scale indicates magnetic induction helicity after z component removal. (B) Remanent magnetic state of a WYHV-1 magnetosome chain. Insets are enlarged views of selected particles within the chain and at the chain end; the *Lower Middle* inset indicates the micromagnetic structure of a single particle within the chain. Strong intrachain coupling drives most chain-embedded particles toward a predominantly SD-like magnetization and produces a strong chain-parallel remanent moment, while local nonuniformity persists particularly near particle and chain ends. The color bar B (T) denotes magnetic induction, where $B = \mu_0(M + H_d)$, μ_0 is the vacuum permeability, M is the magnetization vector, and H_d is the demagnetizing field.

fields or intercellular coupling energies between matched dimpled and nondimpled models, we do not assign a specific magnetic function to the dimples. They are, therefore, treated here as a distinctive biomineral morphology rather than as a demonstrated determinant of magnetic linking.

Together, EH and micromagnetic simulations indicate that magnetic performance in WYHV-1 is governed primarily by the coupled magnetosome chain rather than by the idealized magnetic state of isolated particles. Strong intrachain coupling suppresses particle-scale nonuniformity and supports a robust chain-parallel cellular magnetic moment, while the magnetosome chain as a whole provides the physical basis for strong stray fields at chain ends.

Strong Chain-End Fields Promote Field-Dependent Magnetic Linking Between Adjacent Cells.

We next tested whether the main functional significance of the WYHV-1 magnetosome architecture emerges at the level of intercellular interactions. To evaluate this possibility, we constructed single-chain and head-to-tail double-chain models based on experimentally constrained particle-size configurations and calculated their magnetic induction intensity and magnetostatic interaction energy (Fig. 5 and *SI Appendix*, Figs. S10 and S11). The magnetic contribution of a neighboring chain was estimated from differences between corresponding single- and double-chain models. For all model types, magnetic induction intensity decreases monotonically with increasing distance from the chain end but remains above the local geomagnetic field strength

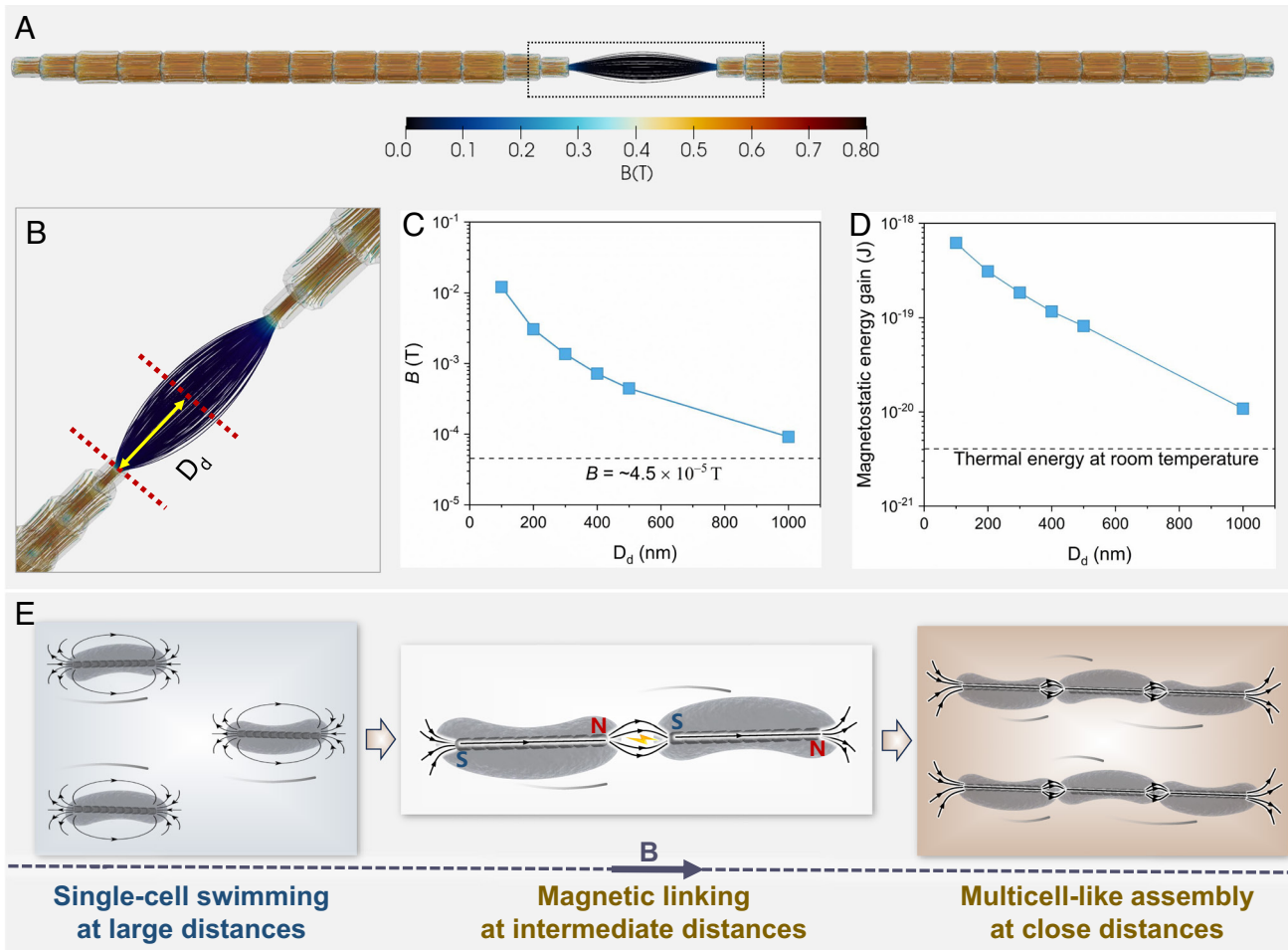


Fig. 5. Micromagnetic simulations and magnetic coupling of two head-to-tail aligned magnetosome chains. (A) Remanent-state micromagnetic simulation of two head-to-tail aligned SV-particle chains. (B) Micromagnetic structure in the region between the two chains separated by a 400-nm gap (black dashed box in A), with magnetic coupling between them. The slicing plane is located midway between the two chains. (C) Maximum magnetic induction, B , at the midpoint of the double-chain system as a function of half interchain spacing (D_d). The dashed line marks local geomagnetic field strength ($\sim 4.5 \times 10^{-5}$ T). (D) Magnetostatic coupling gain of the double-chain system as a function of D_d , which is defined as the magnetostatic interaction energy increase relative to an isolated single chain. The dashed line marks thermal energy at room temperature. (E) Schematic illustration of magnetic linking between WYHV-1 cells after alignment within an external magnetic field B .

($\sim 4.5 \times 10^{-5}$ T) over the simulated 100 to 1,000 nm range (Fig. 5C and SI Appendix, Fig. S12). Likewise, the magnetostatic energy gain of double-chain systems exceeds thermal energy at room temperature ($k_B T$, $\sim 4.047 \times 10^{-21}$ J) across the modeled range (Fig. 5D and SI Appendix, Fig. S12). These results indicate that, once neighboring cells are brought into close proximity and approximately aligned in a head-to-tail geometry, interchain magnetic interactions are strong enough to promote magnetic linking and relinking.

The strength and distance dependence of coupling vary among chain configurations. In particular, chains composed of larger SV particles maintain stronger intermediate-range magnetic coupling than those composed entirely of small SD particles (SI Appendix, Fig. S12). Taken together, these calculations suggest that two living WYHV-1 cells can remain magnetically coupled over distances up to $\sim 2,000$ nm, approximately the length of a single cell, despite continual Brownian perturbation in freshwater. This inference is consistent with EH observations and provides a direct physical explanation for the head-to-tail linking behavior observed in hanging-drop experiments (Figs. 1A and 3 and SI Appendix, Fig. S7).

Once cells are aligned approximately by an external magnetic field, stray fields concentrated at chain ends can promote end-to-end attraction, linking, and stabilization of elongated multicell-like

assemblies (Fig. 5E). Thus, under field-aligned experimental conditions, the WYHV-1 magnetosome chain can act not only as an intracellular compass but also as an intercellular physical actuator that mediates magnetic interactions between neighboring cells.

Discussion

Our results reveal an unusual mode of magnetosome biomineralization and magnetic organization in a unicellular MTB. WYHV-1 produces comparatively large, dimple-ended prismatic magnetosomal magnetite arranged in an exceptionally tight intracellular chain. Individual particles commonly have nonuniform, SV-like magnetization, yet the intact chain retains a strong chain-parallel magnetic response. Under hanging-drop conditions and applied magnetic fields, WYHV-1 cells can also undergo head-to-tail linking to form elongated, field-aligned multicell-like assemblies. Together, these observations identify a cross-scale magnetic mechanism that links particle-scale magnetization, chain-level magnetic organization, and field-dependent intercellular coupling.

A first key finding is that WYHV-1 biomineralizes dimple-ended prismatic magnetosomes, a morphology that differs from the smoother and more regular crystal habits commonly described in many MTB (5, 22, 36). Dimple-ended magnetosomal magnetite

is unusual, but it does not appear to be unique to WYHV-1. In addition to the closely related strains YQV-1 and XQGS-1, which produce large cuboctahedral magnetosomal magnetite with dimples at one end (22, 26), the gammaproteobacterial strain NS-1 from a brackish lagoon in Brazil also produces elongated prismatic magnetite with dimples at both ends (*SI Appendix, Fig. S1*) (42). These comparisons suggest that dimple-ended magnetite may have arisen in multiple MTB lineages. We, therefore, interpret this morphology as a recurrent but uncommon biomineralization feature rather than a purely idiosyncratic irregularity of WYHV-1. The genetic and molecular basis of this morphology remains unknown and should be tested in future through comparative genomics, targeted mutagenesis, and biomimetic mineralization experiments (22, 43, 44).

A second major finding is that magnetosomal magnetite in WYHV-1 does not conform to an idealized uniformly magnetized SD particle model when considered individually. EH results and micromagnetic simulations indicate that many magnetite particles, especially those in the larger size range or at chain ends, commonly adopt SV-like magnetic configurations. Within the tightly packed chain, however, micromagnetic simulations indicate that strong intrachain interactions suppress much of this nonuniformity and drive chain-embedded particles toward a more uniform, effectively SD-like magnetization, while EH indicates that the net chain field remains strongly chain-parallel. Thus, WYHV-1 does not overturn the established importance of chain interactions in MTB magnetism; rather, it provides a clear natural example of how particle-scale vortex behavior can be modified by intrachain coupling to produce a robust cellular magnetic moment. This distinction refines how magnetic performance in WYHV-1 should be interpreted. In many discussions of MTB, magnetic function is framed in terms of particle sizes and shapes that favor stable SD behavior and maximize the magnetic moment of individual cells (8, 13, 15). WYHV-1 points to a complementary perspective: The relevant magnetic unit can be the strongly coupled magnetosome chain rather than the isolated particle. We, thus, use chain-level magnetic organization, rather than optimization of isolated particles, as the most appropriate framework for interpreting WYHV-1 magnetism (19, 21, 45, 46).

The dimple-ended morphology is a distinctive biomineralization feature, but its magnetic function remains unresolved. Our nondimpled control simulations indicate that removing terminal dimples does not substantially alter the overall chain-parallel remanent state. We, therefore, attribute the observed and simulated intercellular coupling to strong chain-end fields generated by the tightly packed magnetosome chain as a whole, while treating the dimples as a morphological feature whose specific magnetic role, if any, remains to be established.

The most unexpected implication of this architecture emerges at the cellular level. Electron holography, micromagnetic simulations, and hanging-drop observations consistently support the interpretation that magnetosome chains in WYHV-1 can magnetically couple neighboring cells once they are brought into close proximity and approximately aligned by an external field. This behavior differs from obligately multicellular magnetotactic prokaryotes and magnetotactic holobionts, in which multicellular or consortium-level organization is an intrinsic life-history trait (32, 33, 47, 48). WYHV-1 instead appears to generate multicell-like assemblies through reversible magnetic association between otherwise independent unicellular cells. Under the experimental conditions examined here, the magnetosome chain can act not only as an intracellular compass but also as an intercellular physical actuator that mediates magnetic coupling between neighboring cells. At the same time, this field-dependent

linking behavior should be interpreted with caution. WYHV-1 cells usually behave as isolated motile bacteria, whereas long multicell-like assemblies formed most clearly in hanging-drop preparations under applied magnetic fields and at locally high cell density, especially near droplet edges. The experimental applied fields used are stronger than the local geomagnetic field. We, therefore, do not infer that long multicell-like WYHV-1 assemblies are common in situ. Rather, our data establish the physical plausibility and mechanism of intercellular magnetic coupling under field-aligned experimental conditions.

Several factors may limit the occurrence of long cell chains in natural environments. First, the in situ WYHV-1 abundance in the original sediment remains unknown; if the population density is low, close cell-cell encounters would be rare. Second, cells occupying the same redox-gradient layer may often be oriented approximately parallel to one another rather than positioned in head-to-tail configurations. Third, natural hydrodynamic conditions, sediment pore geometry, and local chemical gradients may disrupt or prevent stable end-to-end association. Finally, the applied magnetic fields used during hanging-drop observation may enhance aggregation events that would otherwise be rare under geomagnetic-field conditions. Direct observations in low-field microcosms and measurements of WYHV-1 abundance in natural sediments will be required to evaluate the ecological frequency of this behavior.

The mechanism described here may also not be unique to WYHV-1. Other MTB that produce high cellular magnetic moments could, in principle, also undergo field-dependent intercellular magnetic attraction under suitable conditions. Candidate systems include strains with large prismatic magnetic particles, exceptionally tight interparticle gaps, multiple magnetosome chains, or unusually high particle numbers, such as Itaipu-1 and related high-moment MTB (16, 24, 34, 35). Reports of collective or chain-like arrangements in MTB, including collective swimming behavior and field-enhanced nanochain formation, are consistent with the idea that cell magnetic moment, local cell density, and applied field strength can all influence collective assembly (34, 35). WYHV-1 provides a particularly clear case because its dimple-ended large prismatic particles, tight chain organization, particle-scale vortex-like magnetization, and field-dependent linking can be examined together within a single mechanistic framework.

The significance of WYHV-1, thus, does not depend solely on whether long cell chains occur frequently in natural sediments. Rather, WYHV-1 reveals a cross-scale magnetic mechanism in which nonuniform particle-scale magnetization, strong chain-level magnetic organization, and intercellular magnetic coupling are integrated within a single bacterial system. This mechanism extends the potential functional scope of magnetosome chains from intracellular orientation to physical interactions between cells under suitable field-aligned conditions.

The possible ecological or physiological significance of field-dependent magnetic cell linking remains unresolved. MTB are typically most abundant at or just below OATZs, where magneto-aerotaxis helps them to localize within favorable redox niches (7, 49). Magnetotaxis has also been proposed to facilitate repeated shuttling across OATZs, thereby coupling oxidative and reductive half-reactions in sulfur cycling (12). If transient linking occurs under natural conditions, it could potentially influence cell alignment, local retention, or stability in structured sediment microenvironments. For example, a longer magnetic unit would experience a larger magnetic torque and could, in principle, stabilize field-parallel orientation after local disturbance. Transient association might also increase residence time near favorable redox interfaces or alter interactions with sediment particles, biofilms, or predators; larger aggregates may also be less susceptible to

grazing by protists or other bacterivores. In a more speculative sense, the elongated WYHV-1 assemblies raise a conceptual comparison with cable bacteria, whose multicellular filaments span distinct chemical environments, and couple spatially separated redox reactions (50, 51). However, whether transient WYHV-1 assemblies could provide any analogous spatial coupling remains unknown, and the broader ecological and physiological significance of field-dependent magnetic cell linking under natural conditions remains unresolved. Future low-field microcosm experiments, in situ abundance measurements, and physiological tests are needed to determine whether field-dependent linking occurs under natural conditions and whether it provides any selective advantage in redox-stratified environments.

Dimple-ended prismatic magnetosomal magnetite may also have implications for magnetofossil interpretation. Similar dimple-ended prismatic magnetic particles have occasionally been observed in magnetofossil-bearing marine sediments, but their biological origin and source organisms have been difficult to assess (52). WYHV-1 provides a modern biological analog where such particles are demonstrated to be produced intracellularly by MTB. However, a dimple-ended morphology alone should not be used as a diagnostic criterion for biogenicity. Instead, crystal morphology, size distribution, chain arrangement, magnetic properties, and sedimentary context should be evaluated together when assessing the origin of similar particles in the geological record (15, 53).

In conclusion, evidence from WYHV-1 broadens the known range of magnetic architectures in MTB. Rather than relying exclusively on smooth, uniformly magnetized SD particles, some MTB lineages may combine unusual crystal geometries, nonuniform particle-scale magnetic states, and strong chain-level interactions to achieve robust magnetic behavior. WYHV-1 expands the conceptual framework of magnetosome biology in three ways: first, by revealing a distinctive dimple-ended biomineral morphology; second, by showing that vortex-like magnetization in isolated or weakly constrained particles can be suppressed toward predominantly SD-like states by strong intrachain coupling, yielding a robust chain-parallel magnetic moment; and third, by demonstrating that chain-generated magnetic fields can mediate field-dependent linking between neighboring unicellular bacteria. Future work should determine how widespread this strategy is among MTB, how dimple-ended magnetosomal magnetic particles are produced genetically and mechanistically, whether the dimples have a specific magnetic function, and whether field-dependent multicell-like assemblies occur in natural redox-stratified environments and, if so, whether they provide any selective advantage or ecosystem function.

Materials and Methods

Field Sampling, MTB Collection, and Sample Preparation. Surface sediments were sampled from Weiyanghu (WYH) Lake, Xi'an, northwest China, and were incubated in the laboratory to establish a simulated OATZ microcosm (54). Living MTB were examined periodically using the hanging-drop method (27) with an Olympus BX51 microscope equipped with phase-contrast and fluorescence optics and a DP70 digital camera system (Olympus Corp., Tokyo, Japan). During observations, an externally applied magnetic field was generated using a pair of Helmholtz coils. The magnetic field intensity at the center of the water droplet ranged from ~0.1 to ~1 mT, stronger than the local geomagnetic field. Thus, these observations represent field-aligned experimental conditions rather than direct in situ behavior.

Living WYHV-1 cells were extracted magnetically from ~200 mL of sediment microcosm material using a homemade magnetic separation apparatus under an external magnetic field of ~1 mT for ~2 h (24). Harvested MTB cells were washed three times with Milli-Q water and resuspended in ~200 μ L of Milli-Q

water for microscopic analyses, including TEM and synchrotron-based STXM, 16S rRNA gene sequencing, and correlative fluorescence in situ hybridization and scanning electron microscopy (FISH-SEM) experiments (55). Samples prepared for TEM and synchrotron-based STXM were stored under pure nitrogen at -20°C before analysis.

Magnetic cell linking was defined as a reversible head-to-tail association between two or more morphologically independent WYHV-1 cells aligned with the applied magnetic field. Side-by-side contacts, nonspecific aggregation, and crowding near the droplet edge are not classified as linking unless individual cells are aligned end-to-end and remain associated during field alignment or reorientation. These observations were made directly from laboratory microcosms before magnetic enrichment and under applied magnetic fields, rather than in undisturbed sediments, so they were not used to estimate the natural abundance of WYHV-1 or the in situ frequency of cell linking. Detailed descriptions of field sampling, laboratory incubation, hanging-drop observations, applied magnetic-field conditions, and living-cell behavior analyses are provided in the *SI Appendix*.

TEM. Conventional TEM observations were performed using a JEM-2100 microscope (JEOL Ltd., Tokyo, Japan) at 200 kV at the Electron Microscopy Laboratory, Institute of Geology and Geophysics, Chinese Academy of Sciences (IGGCAS), Beijing, China. HRTEM, HAADF-STEM, and STEM energy-dispersive X-ray spectroscopy (STEM-EDXS) mapping were carried out with a JEM-2100F microscope (JEOL) at 200 kV at the Institut de Minéralogie, Physique des Matériaux et Cosmochimie (IMPMC), Paris, France.

Cell length was measured along the cell long axis, and cell width perpendicular to it. Magnetic particle lengths were measured along the crystal long axis, and width perpendicular to it. Interparticle spacing was measured as the shortest edge-to-edge distance between adjacent particles in well-resolved chain segments. Dimple depth was measured as the distance between the inferred terminal crystal face and the deepest point of the terminal depression. Values are reported as mean $\pm$ SD unless otherwise stated.

HAADF-STEM and FIB-SEM Tomography. HAADF-STEM tomography was performed using an FEI Tecnai F20 microscope at 200 kV at the Institut de Chimie et des Matériaux de Paris Est (ICMPE), Thiais, France. Tomographic tilt series were acquired at 1° increments over an angular range of $\pm 70^{\circ}$ using the STEM tomography module in DigitalMicrograph (Gatan). Tilt-series alignment, three-dimensional reconstruction, and visualization were carried out using Dragonfly Pro software.

FIB-SEM tomography was performed using a ZEISS Crossbeam 550 Ga-source FIB-SEM at IGGCAS, with voxel sizes of $2\text{ nm} \times 2\text{ nm} \times 4\text{ nm}$ in the x, y, and z directions, respectively. Slice-series alignment, three-dimensional reconstruction, and visualization were carried out using the Dragonfly Pro software.

HAADF-STEM tomography provides high-contrast, projection-based three-dimensional reconstructions of electron-dense magnetite particles at high spatial resolution, whereas FIB-SEM tomography uses serial ion-beam milling and SEM imaging to provide site-specific three-dimensional volume information over a larger cellular region; the two approaches, therefore, offer complementary constraints on magnetosome morphology and the authenticity of terminal dimples (56, 57).

Terminal depressions are observed consistently by conventional TEM, HRTEM, HAADF-STEM, HAADF-STEM tomography, and 3D FIB-SEM tomography. They are, therefore, interpreted as intrinsic crystal features rather than as artifacts of a single imaging or reconstruction method.

Off-Axis Electron Holography. Off-axis electron holograms were acquired under magnetic-field-free conditions using an image-aberration-corrected FEI Titan 80-300 TEM at the Ernst Ruska-Centre for Microscopy and Spectroscopy with Electrons, Jülich, Germany. This microscope was equipped with a high brightness field-emission gun, two electron biprisms, and a direct electron counting camera (Gatan K2 IS). Phase images were reconstructed using the HoloWorks 5 software. Reconstructed phase images contain both magnetic and electrostatic contributions, so these components were separated by recording a second hologram after turning the specimen over and calculating one-half of the difference and one-half of the sum of the two reconstructed phase images.

Synchrotron-Based STXM. Synchrotron-based STXM experiments were performed at the 10ID-1 Soft X-ray Spectromicroscopy beamline of the Canadian Light Source (CLS) (58). After sample insertion, the microscope chamber was

evacuated to 100 mTorr and then backfilled with helium. Monochromated X-rays were focused to an approximately 30-nm spot using a Fresnel zone plate. Images were acquired by raster-scanning the sample in the *x-y* plane while recording transmitted X-ray intensity. Image stacks covering the S 2*p* (158 to 180 eV) and Fe 2*p* (700 to 735 eV) energy ranges were collected to determine the spatial distribution and chemical state of sulfur and iron in WYHV-1 cells.

For Fe L_{2,3}-edge X-ray magnetic circular dichroism (XMCD) (39), a whole WYHV-1 cell was deposited horizontally onto a TEM grid and was selected and tilted approximately 30° out of plane to improve alignment between the magnetosome-chain magnetic moment and the incident X-ray beam. Image stacks were then collected under left circular polarization (LCP; parallel) and right circular polarization (RCP; antiparallel), yielding one X-ray absorption spectrum (XAS) for each polarization. The XMCD spectrum was calculated as the difference between the two polarized XAS spectra. STXM data were analyzed using the aXis2000 software (59).

Molecular and Correlative FISH-SEM. 16S rRNA gene sequencing was performed as described by Li et al. (55). Correlative phylogenetic and structural identification of WYHV-1 at the single cell level was carried out following the protocol of Li et al. (55). Detailed phylogenetic analysis is provided in the [SI Appendix](#).

Micromagnetic Simulation. Micromagnetic simulations were carried out using the finite element micromagnetic modeling package MERRILL version 1.8.6 (60) and simulation results were visualized using ParaView 5.11.1 (61). Detailed descriptions of the micromagnetic procedure are provided in the [SI Appendix](#).

Data, Materials, and Software Availability. The 16S rRNA gene sequence of WYHV-1 has been deposited in GenBank under accession no. PP905258 (62). All other study data are included in the article and/or [supporting information](#).

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