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Chemosynthetic microbial communities formed wrinkle structures in ancient turbidites

Rowan C. Martindale[1,*], Sinjini Sinha[1], Travis N. Stone[1], Tanner Fonville[1], Stéphane Bodin[2], François-Nicolas Krencker[3], Peter Girguis[4], Crispin T.S. Little[5], and Lahcen Kabiri[6]

[1]Department of Earth and Planetary Sciences, The University of Texas at Austin, 2275 Speedway Stop C9000, 78712 Austin, Texas, USA
[2]Department of Geoscience, Aarhus University, Høegh-Guldbergs Gade 2, 8000 Aarhus C, Denmark
[3]Geology, Institute of Earth System Sciences, Leibniz University Hannover, Hannover 30167, Germany
[4]Department of Organismic and Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts 02138, USA
[5]School of Earth and Environment, University of Leeds, Woodhouse Lane, Leeds LS2 9JT, UK
[6]Department of Geoscience, Faculty of Science and Technology of Errachidia, Moulay Ismail University, BP 509, Boutalamine-Errachidia, RDT, Morocco

ABSTRACT

Wrinkle structures are often interpreted to be formed by photosynthetic microbial mats. They are rare in Phanerozoic marine subtidal environments because animal activity typically destroys mats or biofilms before lithification. We report wrinkle structures in lower Toarcian (Lower Jurassic) turbidites from the Tagoudite Formation in Morocco. These wrinkles are consistent with those from shallower deposits; however, given their paleodepth (~200 m), it is unlikely they were formed by photoautotrophic communities. Modern turbidites are known to host chemosynthetic communities, often with extensive microbial mat formation. We propose the Tagoudite Formation wrinkles were formed by chemosynthetic communities, and the sedimentological, geochemical, and hydrographical conditions of the turbidites excluded grazers, allowing wrinkle structure lithification. Wrinkle structures occur in Cambrian, Silurian, Devonian, and Jurassic turbidites, and we posit that chemosynthetic mats growing on turbidity deposits represent a previously dismissed, underappreciated, or unrecognized mode of preservation. The chemosynthetic mat–induced wrinkle paradigm has significant implications; this taphonomic window for wrinkle preservation in turbidites expands the range of environments where these microbially induced sedimentary structures form and the communities that made them. Wrinkles in turbidites also represent new possibilities for the study of chemosynthetic ecosystems in deep time.

INTRODUCTION

Wrinkle Structures

Wrinkle structures (runzelmarken) are irregular, millimeter- to centimeter-scale ridges or pits recognizable with the naked eye. This term is applied to numerous textures in ancient and modern environments, with both abiotic and biotic origins (Porada and Bouougri, 2007; Davies et al., 2016; Wignall et al., 2025). Biotic wrinkles found on the tops of sandy bedding planes are attributed to algal and microbial communities that form mats or aggregates (e.g., Hagadorn and Bottjer, 1997; Noffke et al., 2001; Mata and Bottjer, 2009; Mariotti et al., 2014).

Structures interpreted as microbially induced wrinkles include elongate crests, rounded ridges and troughs with sharp or flattened crests (e.g., "Kinneyia"), "elephant skin," and other forms (Hagadorn and Bottjer, 1997; Bottjer and Hagadorn, 2007). They are common in Precambrian and Cambrian marine strata and are important for their connection with early life (e.g., Hagadorn and Bottjer, 1997; Noffke et al., 2001; Mata and Bottjer, 2009). Equivalent structures occur in modern intertidal and supratidal settings but are rarely observed in other environments as animal activity destroys mats before lithification (e.g., Fenchel, 1998). Thus, wrinkles are rare in fully marine facies younger than the Cambrian (Mata and Bottjer, 2009). Wrinkle structures also occur after mass extinctions that were so severe they eliminated grazing animals, thus preserving wrinkles (e.g., Pruss et al., 2004). Wrinkles are typically observed in the offshore transition (between fair-weather and storm wave base) and shallow lagoonal to intertidal settings, where light is sufficient for photosynthesis and interbedded sands and muds preserve wrinkles (Mata and Bottjer, 2009). Wrinkles and "transverse wrinkles" have been reported from deeper-water settings but are often interpreted as density contrasts and flow-induced interfacial deformation (i.e., abiotic wrinkles) (e.g., Dżułyński and Sanders, 1962; Dżułyński and Simpson, 1966; Peakall et al., 2024).

We document the first Toarcian wrinkle structures formed in turbidites at ~200 m depth. We describe their morphology and composition and propose a model for deep-water biotic wrinkle structures.

Geological Setting

In the earliest Toarcian, the Dadès Valley area (Central High Atlas Mountains, Morocco) experienced a shift from an arid to a humid climate, which increased sediment supply to the basin (Krencker et al., 2020, 2022; Andrieu et al., 2022). Near Boumrdoul (31.619°N, 5.8531°W), the offshore marl/limestone-dominated Ouchbis Formation transitions to the lower Toarcian terrigenous prodeltaic Tagoudite Formation (Ettaki and Chellaï, 2005; Krencker et al., 2020). The minimum reconstructed paleodepth is ~200 m based on the integration of quantitative calculations (Andrieu et al., 2022) and stratigraphic cor-

Rowan C. Martindale https://orcid.org/0000-0003-2681-083X
*Martindale@jsg.utexas.edu

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relations (Krencker et al., 2022) (see Geological Settings and Sedimentological Description in the Supplemental Material[1]).

METHODS

A lithostratigraphic log (Fig. 1) was created for Boumrdoul (31.618472°N, 5.852694°W); wrinkles were photographed, and representative samples collected, cut, polished, and thin sections prepared. Thin sections were examined with light microscopy and scanning electron microscopy (SEM), and energy dispersive X-Ray spectroscopy (EDS) maps were collected to determine elemental compositions. Samples are reposited at the University of Texas at Austin (USA) (samples NPL00090497–NPL00090502) (see the Supplemental Material for details about the methods and curation).

RESULTS

Wrinkle structures occur at the top of thin-bedded, low-density siliciclastic turbidites in the lower Tagoudite Formation (Figs. 1 and 2; see the Supplemental Material). Turbidites are dominated by siltstones and fine sandstones with Bouma sequences (Ta–Te layers), where the Tc–Te layers dominate (Ettaki and Chellaï, 2005). Burrows are common on the bottoms of sandy beds (hypichnial traces). The ~150 m of prodeltaic turbidites were deposited in <300 k.y. (calculated from Kemp et al., 2024). The depth and frequency of turbidity currents limited light penetration, suggesting wrinkles occurred below the effective photic zone.

The best-preserved wrinkles are found atop the bedding plane of a ~1-m-thick sandy turbidite (74 m, Tc layer; Fig. 1), overlain by greenish silty claystones. Wrinkles (Figs. 2 and 3) are reticulate rounded ridges of sandstone and sinuous troughs, typically 1 mm to 1 cm in size, and are circular to elongated oval (e.g., Figs. 2D–2G). They are extensive and well defined in some exposures (Figs. 1 and 2) but faint in others (laterally variable). Wrinkles are most distinct and abundant in deep ripple troughs, but often extend over ripple crests (linguoid to straight ripples) (Figs. 2A–2H).

In cross section, wrinkles are only apparent in the uppermost 2 mm of rippled surfaces. In EDS maps (Fig. 3), particulate carbon is concentrated below the wrinkled surface (250-μm to 750-μm-thick interval with high carbon and low calcium). Host sediments contain pervasive aluminum, silicon, iron, and sulfur, and grains high in titanium and barium (Fig. 3).

[1]Supplemental Material. Details about the geological setting, paleodepth, lithological description, analytical methods, and images of modern chemosynthesizing mats, microbially induced sedimentary structures, and flow-induced interfacial deformation structures. Please visit https://doi.org/10.1130/GEOL.S.30651329 to access the supplemental material; contact editing@geosociety.org with any questions.

INTERPRETATIONS AND DISCUSSION

Biotic Origin of Tagoudite Formation Wrinkles

Tagoudite Formation wrinkles are interpreted as microbially induced sedimentary structures. The textures (Fig. 2) are indistinguishable from Archean, Proterozoic, Cambrian, and Lower Triassic wrinkle structures (e.g., Hagadorn and Bottjer, 1997; Noffke et al., 2001; Mata and Bottjer, 2009), all of which are interpreted as photosynthetic mat-sediment interactions. Microbially induced wrinkles can be distinguished from wind- or load-induced wrinkles by their cross section (Porada and Bouougri, 2007; Wignall et al., 2025; see the Supplemental Material); Tagoudite Formation wrinkles occur on bed tops and are rounded crests of sandstone (Figs. 3A and 3C), denoting a biotic origin. Moreover, elevated carbon concentrations immediately below wrinkled surfaces (Fig. 3) indicate a concentration of organic matter, which could be the material that fed a microbial community, the remnants of a community itself, or both. Well-developed rounded wrinkle ridges and troughs (e.g., Fig. 2E) likely formed from movements of microbial aggregates or mat fragments on the seafloor (e.g., Mariotti et al., 2014). In areas lacking wrinkles, thicker, more cohesive mats may have stabilized sediment, or a local absence of mats resulted in strata controlled by physical forces (e.g., erosion; Fig. 2D).

Although most wrinkle structures are attributed to the euphotic zone (Mata and Bottjer, 2009), the Toarcian wrinkles formed in deeper water (minimum of ~200 m) (Krencker et al., 2020, 2022; Andrieu et al., 2022). The depth and turbidity make it improbable that light reaching those depths was sufficient to support photosynthetic mats (i.e., below the euphotic zone; see the Supplemental Material).

Instead, we suggest the wrinkles were induced by chemosynthesizing microbial communities. We define chemosynthesizing microbial communities as the assemblage of bacteria and archaea largely dependent on chemolithoautotrophic primary production, that form macroscopic, expansive multilayered assemblages, and thrive at interfaces where reduced and oxidized compounds are present (e.g., marine and freshwater sediments). Chemosynthesizing mat bacteria are typically Beggiatoaceae, *Thioploca* spp., and other phenotypically similar Gammaproteobacteria. These sulfur-oxidizing microbes thrive in the absence of sunlight and, like cyanobacteria, the filamentous bacteria trap and bind sediments, forming large mats and potentially wrinkle structures (Bailey et al., 2009; Flood et al., 2014). In the modern ocean, chemosynthesizing mats are widespread, occurring at depths between 150 m and 5 km (see the Supplemental Material). These communities thrive where there is sufficient organic load in the sediment to produce sulfide and other chemically reduced compounds (Paull et al., 2005, 2010), such as on continental shelves (e.g., the Peruvian and Chilean coasts [Schulz et al., 1996] and the Congo River deep sea fan [Olu et al., 2017]), in sediments beneath oxygen minimum zones (Marlow et al., 2021), and around hydrocarbon seeps or hydrothermal vents (Lloyd et al., 2010). Chemosynthesizing mats often occur where surface productivity and organic matter export rates are high; they thrive in waters of varying oxygen concentrations, from well-oxygenated to euxinic or anoxic waters (Lloyd et al., 2010; Yousavich et al., 2024). Modern continental shelves with frequent turbidity currents and chemosynthesizing mat communities are useful analogs for the Tagoudite Formation and the mats that formed the wrinkle structures.

We propose that rapid deposition and burial of organic material in turbidites encouraged the presence of chemosynthetic communities. Organic matter respiration typically leads to sulfate reduction to sulfide, anaerobic sulfur oxidation, or methanogenesis within the sediment pore water (Maltby et al., 2016). Decomposition of woody detritus, abundant in the Tagoudite Formation, is known to be a source of hydrogen sulfide for modern chemosynthetic communities (Paull et al., 2005, 2010; Olu et al., 2017). Byproducts of these chemical reactions either remain in the sediment or percolate up to the sediment-water interface. During turbidity currents or slumps, buried sediments and chemical compounds are exposed and remobilized, stimulating the production of hydrogen sulfide by microbial anaerobic oxidation of methane (e.g., Paull et al., 2005, 2010). Aerobic or anaerobic respiration can produce byproducts (e.g., sulfides) toxic to many animals. Sufficiently high amounts of sulfide are known to severely limit or exclude animals that consume microbial aggregates and perturb sediments (Rabalais et al., 2014), thus "opening" the taphonomic window for wrinkle structure preservation.

Similar wrinkles have been found in gravity deposits from the Cambrian (Buatois and Mángano, 2003), Silurian–Devonian (Pazos et al., 2015), and Middle Jurassic (Rodriguez et al., 2024) of Argentina, as well as from the Middle Devonian of the Czech Republic (Vodrážková et al., 2019). These deposits could not have been in the euphotic zone, but many are associated with additional environmental stresses, such as anoxia or extinctions (e.g., Rodriguez et al., 2024), which may promote preservation of turbidite wrinkles by decreasing metazoan activity. Alternatively, Paull et al. (2010) suggested that disturbances are necessary to sustain chemosynthetic communities, so fluctuating conditions, seismicity, or other perturbations may promote their growth in turbidites.

A New Paradigm for Deep Sea Wrinkle Formation

Turbidites should be considered a taphonomic window for wrinkle structure preserva-

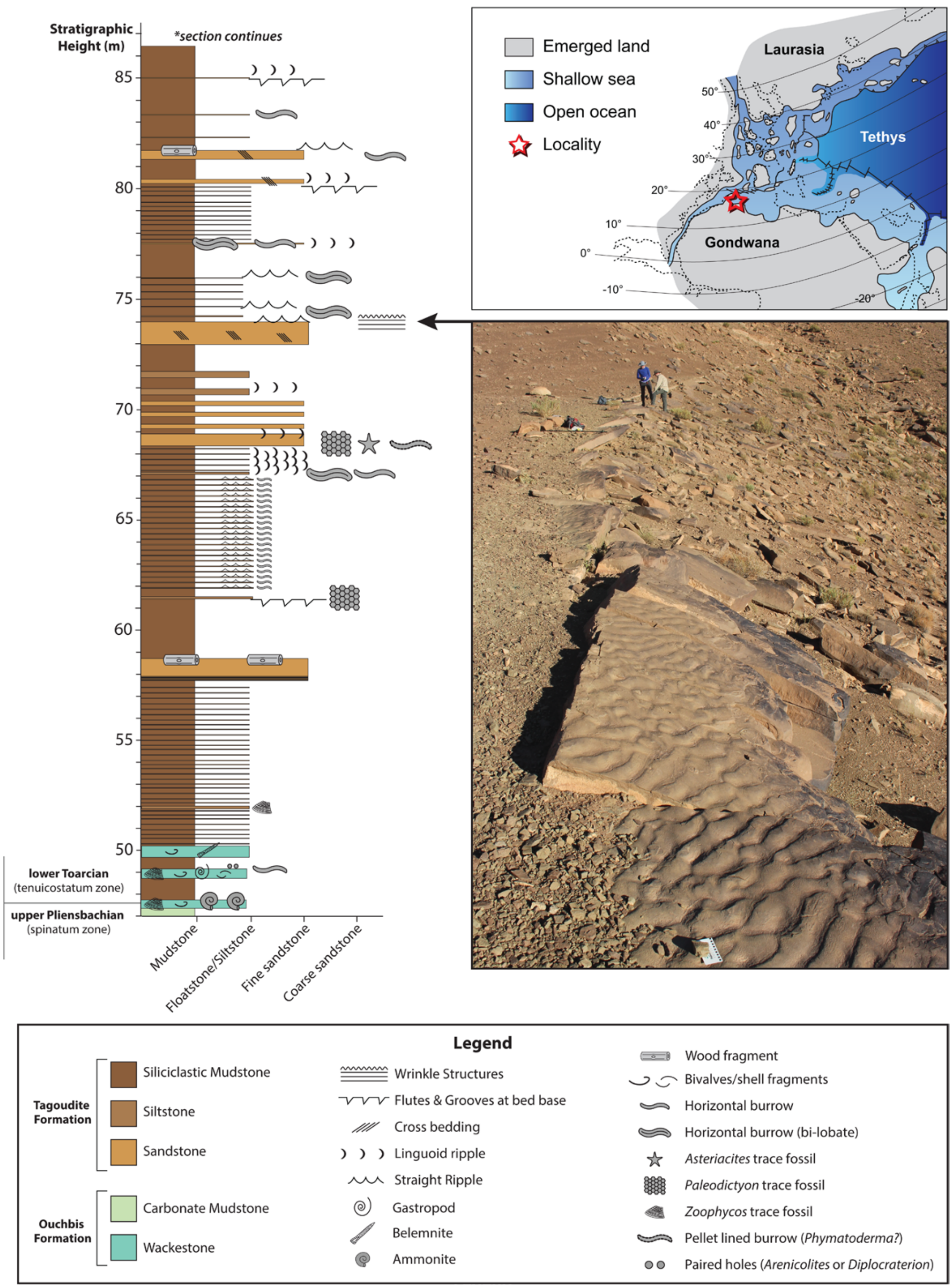

Figure 1. Lithological log of the Tagoudite Formation in the Central High Atlas Mountains, Morocco. Inset map shows the Toarcian paleoenvironmental reconstruction of the western Tethys Ocean (modified from Bodin et al., 2016, and references therein) and the location of the study area. Photograph of the wrinkle structure outcrop shows the top of the rippled bed at ~74 m. The section continues below (Ouchbis Formation) and above (Tagoudite and Tafraout Formations) the log.

tion. Turbidity flows provide appropriate sedimentological and hydrographic conditions for wrinkle formation: (1) interbedded sands and muds, and (2) water movement to destabilize a mat or oscillate microbial aggregates at the sediment-water interface. Chemosynthesizing mats (e.g., Fig. S6 in the Supplemental Material) form at interfaces of reductants (e.g., sulfide) and oxidants [e.g., oxygen, nitrate, Fe(III), or sulfate]. Turbidites rapidly deliver and bury abundant organic matter, leading to anoxic conditions in the sediment, which allows for numerous microbial pathways (e.g., Nunoura et al., 2009; Olu et al., 2017), often producing sulfide and other reduced compounds. When sufficiently high, sulfide excludes grazers locally, allowing wrinkle lithification. Furthermore, gravity flows remobilize organic material, methane, and sulfide for heterotrophic or chemosynthetic communities (Paull et al., 2005, 2010; Yousavich et al., 2024). Chemosynthesizing microbes can colonize modern turbidites within weeks to months (Paull et al., 2010) and persist until the next turbidity flow. Turbidites satisfy all the conditions required for wrinkle structure formation by chemosynthesizing communities (i.e., sandy and muddy sediments, water movement, mat or aggregate formation, and exclusion of mat destroyers).

Further research may identify unique attributes of turbidite wrinkles resulting from che-

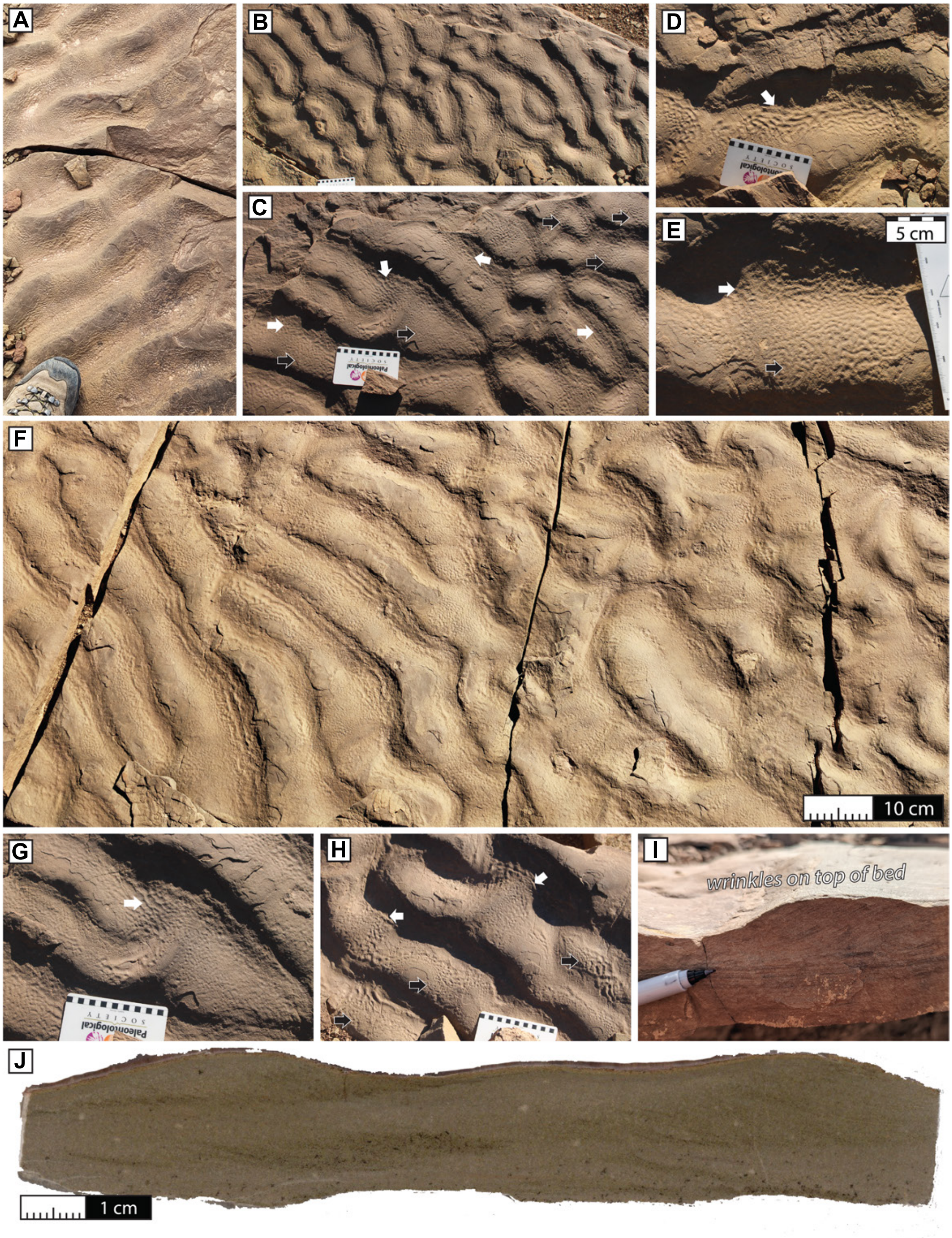

Figure 2. Photographs of wrinkle structures in the Tagoudite Formation of the Central High Atlas Mountains, Morocco. Black arrows point to wrinkles on ripple crests; white arrows point to wrinkles in ripple troughs. (A) Straight rippled bedding plane with wrinkles. (B) Complex ripples with wrinkles (scale bar squares are 5 × 5 mm). (C) Close-up of wrinkles in ripple troughs and crests from panel B. (D) Wrinkles in ripple troughs. Note the lack of wrinkles on the crest. (E) Well-developed wrinkles in the trough and crest of ripples. (F–H) Variations in size, shape, and texture of wrinkles as they interact with ripples on the bedding plane at ~74 m in the stratigraphic log. (I) Cross section of rippled unit (pen diameter is 9 mm at widest point). (J) Polished cross section through wrinkle structure sample (NPL00090497). Samples are reposited at the University of Texas at Austin (USA).

mosynthetic communities (e.g., different binding properties or textures) and water movement. Due to the erosive nature of turbidites, as well as the heterogeneous and ephemeral nature of chemosynthetic communities (Paull et al., 2005, 2010), turbidite wrinkles are likely not as commonly preserved nor as extensive as shallow-water wrinkles. The boundaries of modern chemosynthetic mats are often sharp (Bailey et al., 2009; Fig. S6), so small outcrops may not provide sufficient exposure to find well-preserved wrinkles. Care should be taken when interpreting the biogenicity of wrinkle structures in turbidites, because "wrinkly" structures can be produced by physical forces (Wignall et al., 2025; see the Supplemental Material). Moreover, the vague and variable definitions of "wrinkle structures" likely confounds identification and interpretation of these features (Davies et al., 2016). Nevertheless, we suggest biotic wrinkle structures may be a regular feature in turbidites.

CONCLUSIONS

Lower Toarcian wrinkle structures are millimeter- to centimeter-scale rounded ridges and troughs that occur on the tops of rippled bedding surfaces of turbidites in the Tagoudite Formation, Morocco. Despite their similarity to shallow-water wrinkles, their ~200 m paleodepth confirms they were not formed by photoautotrophic communities. We propose these, and other turbidite wrinkle structures, were created by chemosynthetic mat-forming

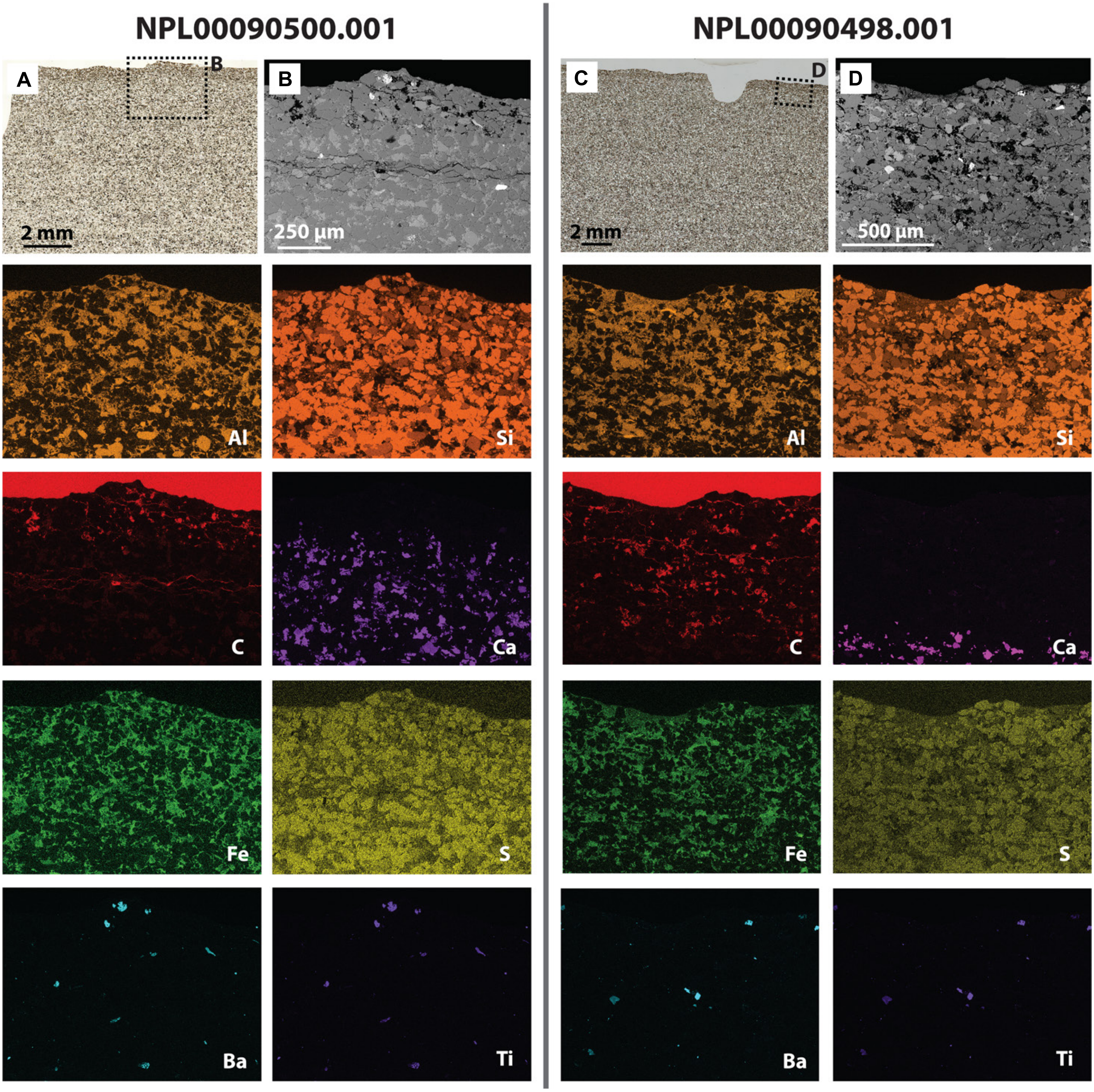

Figure 3. Cross sections of wrinkle structures from the Tagoudite Formation of the Central High Atlas Mountains, Morocco. Thin sections are perpendicular to the bedding plane (wrinkles at top). (A) Photomicrograph (plane polarized light [PPL]) of thin section NPL00090500.001. (B) Backscattered electron–scanning electron microscopy (BSE-SEM) image of dashed box in panel A. Images below panels A and B are energy dispersive X-Ray spectroscopy (EDS) maps of the BSE-SEM image in panel B (same scale). (C) Photomicrograph (PPL) of thin section NPL00090498.001. (D) BSE-SEM image of dashed box in panel C. Images below panels C and D are EDS maps of the BSE-SEM image in panel D (same scale). Elements are noted in the bottom right corner of the EDS maps; epoxy (top of the thin section) is black in most maps but red in the carbon map.

communities, like those in modern turbidites. Physical conditions during turbidity flows, or toxic byproducts of organic matter reduction, excluded grazers, allowing the preservation of wrinkles. Wrinkle structures have been observed in turbidites throughout the Phanerozoic; therefore, these features may be common but frequently overlooked or misinterpreted. Turbidites represent a key taphonomic window for the preservation of microbially induced sedimentary structures, and our criteria for interpreting the depositional depth or biogenicity of wrinkles must accommodate this paradigm. Turbidite-hosted wrinkles are also an underexplored record of ancient chemosynthetic communities.

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