A valuable aspect of the study by Liu *et al.* is that they documented the process of establishment and displacement as it occurred over time in different areas within China and Australia. Rarely has this approach been possible or undertaken: Invasions and displacements often are not detected or studied until they are widespread and complete. Consequently, much of our information on these historical events is derived from retrospective studies, which can be confounded by rapid evolutionary changes in both invading and indigenous populations (12).

In turn, these displacements should not be regarded as total victory for the invaders. Some authors argue that invasive competitors may cause local extinctions of indigenous species but are unlikely to cause the complete extinction of indigenous species (13). Further, some invasive populations have undergone seemingly unexplained crashes, which open opportunities for additional changes in invaded communities (14, 15). It remains to be seen whether remnant populations of the indigenous biotypes exist and may respond evolutionarily to the invasive biotype B.

Liu et al. conclude that invasions bring about intense interactions between previously geographically isolated species. In such asymmetric interactions, the B biotype is competitively superior and indigenous biotypes suffer more from interactions with the B biotype than the B biotype suffers from interactions with the indigenous types. It still would be of interest to compare invasive populations of biotype B with populations in its indigenous habitats of the Middle East and Asia Minor to determine whether biotype B inherently has invasive characteristics, or whether populations have been selected for through previous invasions. Such questions of how invasive populations compare with their original source populations are among the most pertinent in invasion biology today (16).

Maintaining a long-term perspective is important, as the results of Liu *et al.* show. Brief snapshots of the event may not have led to the same conclusions as did their longer-term study. Clearly, invasions provide opportunities for dramatic ecological and evolutionary experimentation. Unfortunately, invasions

come at tremendous environmental and economic costs, yet understanding interactions between invaders and residents will continue to be necessary for more effective control of invasive species (9).

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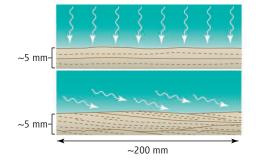
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**GEOLOGY** 

## On the Accumulation of Mud

## Joe H. S. Macquaker and Kevin M. Bohacs

n page 1760 of this issue, Schieber et al. (1) document a mechanism for depositing mud that is at odds with perceived wisdom. Geoscientists tend to assume that most mud accumulates directly from suspension in the water column, that mud deposition requires quiet bottom-water conditions, and that mudstones containing closely spaced, parallel laminae represent continuous deposition (see the first figure, top panel). In contrast, the authors show that mud can accumulate as current ripples composed of grain aggregates under currents that can transport very fine sand (see the first figure, bottom panel). Thus, a layer of muddy sediment can be eroded and transported laterally without showing obvious signs of such disturbance and may record surface-water conditions elsewhere in the basin. The results call for critical reappraisal of all mudstones previously interpreted as having been continuously



deposited under still waters. Such rocks are widely used to infer past climates, ocean conditions, and orbital variations.

Fine-grained sedimentary rocks such as shales or mudstones—with an average grain size of less than 62.5  $\mu m$ —are by far the most common sedimentary rocks preserved close to Earth's surface. Most were deposited on lake or ocean floors, where they provide a record of Earth's history. These rocks also play an important part in the global carbon budget, groundwater flow, and landfill containment and contribute important resources such as oil, shale gas, minerals, and metals.

Mudstones typically consist of various materials, including clays, quartz, organic

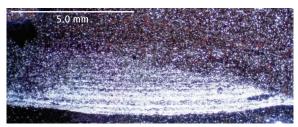
Mudstones can be deposited under more energetic conditions than widely assumed, requiring a reappraisal of many geologic records.

**Not so simple.** Mud deposition via suspension settling (wavy vertical arrows) (**top**) and the advective sediment transport processes close to the sediment-water interface (wavy close-to-horizontal arrows) identified by Schieber *et al.* (**bottom**). Bedding planes are indicated by solid lines, laminae by dotted lines. The vertical scale is exaggerated relative to the horizontal scale. In mudstone successions, the expression of these two very different physical processes can only be distinguished by detailed inspection of the textures present.

matter, remains of organisms, and chemical precipitates formed when the sediment was buried. Because of their very fine grain size, they appear homogeneous in hand specimens; moreover, their high clay content makes them very susceptible to weathering. Thus, they do not reward casual inspection and are poorly understood relative to other rock types. Researchers typically resort to analysis of attributes such as fossil content, chemical composition, and electromagnetic characteristics to deduce the conditions under which the mudstone was deposited.

Patterns of change in these proxy data are typically attributed to variations in ocean circulation, water chemistry, plankton growth,

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**Beyond suspension settling.** Thin-section scan of a mudstone collected from the Kimmeridge Clay Formation (Upper Jurassic). The sample is mainly composed of silt and clay and contains a ripple. The existence of this ripple indicates that the sediment was not simply delivered by suspension settling, but rather was deposited from traction currents operating close to the sediment-water interface.

climate, or Earth-Sun distance. It is commonly assumed—but not always explicitly stated—that fine-grained sediment was delivered more or less continuously from buoyant plumes produced by storms and river floods, zones of high primary productivity, or turbidity currents before settling out of suspension as individual grains in still waters.

This paradigm appears to fit available proxy data and is consistent with the few sedimentary structures that are readily visible. It is, however, at odds with observations in modern oceans and lakes (2), where environments and water-column chemistries can change rapidly and a variety of sediment transport processes have been observed. Fine-grained sediment is seldom deposited as individual grains but commonly organized into grain aggregates. Doubts about the validity of the paradigm have also emerged from imaging studies of ancient fine-grained rocks (3), which have revealed the presence of millimeter-scale sedimentary structures, including localized erosion, progressively fine-grained beds, and low-angle ripple laminae (see the second figure).

The laboratory investigations reported by Schieber *et al.* now provide direct evidence of advective sediment transport of mud-sized material, using apparatus designed to maintain the integrity of the floccules. In the experiments, clay aggregates formed migrating ripples that deposited sediment under much higher current velocities than previously assumed. These floccule ripples have low crests (2 to 20 mm) and very long spacings (300 to 400 mm); they deposit nonparallel inclined laminae that could be easily misinterpreted as parallel-laminated.

Together, these studies indicate that many of our preconceptions about fine-grained rocks are naïve. First, mud accumulation can occur in higher-energy conditions than most researchers had assumed. Second, Schieber *et al.* suggest that advective traction currents commonly erode, transport, and deposit substantial volumes of fine-grained sediment; as a

result, fine-grained successions in the sedimentary record are much less complete than commonly assumed. Third, most researchers did not consider it important that floccules can be stable under traction transport, although some, including coastal engineers, have recognized the vital role that floccules probably play (4). Most models of mudstone deposition do not incorporate any of these factors. Geologists will have to revisit these rocks and generate much subtler

models to explain their variability.

These results come at a time when mudstone science is poised for a paradigm shift. Observations accumulated over the past 30 years (3, 5–9) indicate that deposition and burial of mud is as dynamic and complex as that of sand or limestone—or possibly even more so, because of myriad processes—including grain-size changes due to aggregate growth and decay, presence of biofilms, reworking, and cement precipitation—that occur in mudstones to control their variability. We can now

recognize traces of bottom currents in very fine-grained rocks, supported by laboratory, modern mud, and ancient rock studies.

The study by Schieber *et al.* enables us to critically reexamine existing databases and to extract maximal information from new ones. Such studies will reward us with deeper insights into the inner workings of the dominant sediment type on Earth.

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**TRANSCRIPTION** 

# **Seven Ups the Code**

Jeffry L. Corden

Patterns of phosphorylation in a region of RNA polymerase II may constitute a code that controls the recruitment of regulatory factors to control gene expression.

**¬** ukaryotic RNA polymerase II, the enzyme that converts DNA informa-✓ tion into RNA, couples this transcriptional activity to both modifying the DNA template (chromatin) and to processing nascent RNA transcripts into mature forms. Proteins that carry out the latter two functions are tethered to the catalytic core of polymerase II by a flexible carboxyl-terminal domain (CTD) that harbors tandem repeats of the consensus amino acid sequence Tyr<sup>1</sup>-Ser<sup>2</sup>-Pro<sup>3</sup>-Thr<sup>4</sup>-Ser<sup>5</sup>-Pro<sup>6</sup>-Ser<sup>7</sup> (1–3). Actively transcribing polymerase II is phosphorylated on different sites within this heptapeptide sequence, and the pattern of phosphorylation has been proposed as a code that controls the binding of different regulatory factors to the enzyme (4). Two papers in this issue, by

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Chapman *et al.* on page 1780 (5) and by Egloff *et al.* on page 1777 (6), provide evidence that expands the number of potential CTD phosphorylation states, supporting the notion of a CTD code. Together, the papers show that CTD phosphorylation is more complicated than previously thought and link, for the first time, expression of specific genes with a distinct CTD phosphorylation pattern.

CTD heptapeptides are tandemly repeated from 17 to 52 times in different eukaryotes and these sequences are modified by phosphorylation, glycosylation, and proline isomerization (2, 3). In principle, CTD modification could dictate many aspects of polymerase II function including assembly of the multisubunit enzyme, its transport to the nucleus, its localization either on the DNA template or within subnuclear domains, and its eventual destruction.

Most work to date has focused on the role of CTD phosphorylation during transcription. The pattern of phosphorylation is established