The Habitat of Primitive Vertebrates: The Need for Sedimentary Geology in Paleontology

Steven M. Holland
Department of Geology, The University of Georgia, Athens, GA 30602-2501

Jessica Allen
Department of Geology and Geophysics, The University of Utah, Salt Lake City, UT 84112-0111

ABSTRACT

The habitat in which early fish originated and diversified has long been controversial, with arguments spanning everything from marine to fresh-water. A recent sequence stratigraphic analysis of the Ordovician Harding Formation of central Colorado demonstrates that the primitive fish first described by Charles Walcott did indeed live in a shallow marine environment, as he argued. This study underscores the need for analyses of the depositional environment and sequence architecture of fossiliferous deposits to guide paleobiological and biostratigraphic inferences.

INTRODUCTION

For many years, the habitat of primitive vertebrates has been debated, with interpretations ranging from marine to fresh-water, and everything in between. That such a basic interpretation for such an important group of fossils could be unresolved highlights the much broader need for a sedimentological and stratigraphic understanding of the fossil record.

THE CONTROVERSY

In December of 1890, Charles Walcott traveled by train and wagon to Cañon City, Colorado to investigate fish fossils reported from the Ordovician Harding Sandstone by Timothy W. Stanton. The significance of these fossils was immediately apparent to Walcott, as they were substantially older than the oldest accepted fish, which were late Silurian. The Cañon City fossils pushed the origin of vertebrates much earlier, and for over eighty years, they would be the oldest known vertebrates.

Walcott reported the fish to the Biological Society of Washington in 1891 and returned to Cañon City with his wife Helena in May of 1892 for more study. He presented his results to the Geological Society of America in 1892, and in the Bulletin, he named two fish, *Astraspis desiderata* and *Eriptychius americanus*, based on disarticulated plates and an incomplete head. Both are now regarded as pteraspidomorph agnathans, primitive jawless fish that look like scaly tadpoles with armored heads (see cover illustration of a reconstructed *Astraspis desiderata*). Walcott also argued that the Harding Sandstone was a marine deposit, based on the presence of mollusks, abundant burrows, and abraded fish plates (Fig. 1). That these were fish fossils was immediately controversial, with paleontological giants E.D. Cope and E.W. Claypole voicing doubts.

The controversy over habitat soon followed. By 1935, a fresh-water or possibly estuarine environment for early fish was generally preferred, but essentially in disregard for the sedimentology of the Harding (Romer and Grove, 1935). Devonian fish were abundant in fresh-water strata and the lack of fish in demonstrably marine Ordovician strata supported a fresh-water origin. The abrasion of dermal plates in the Harding was considered proof that the fish were transported from a fresh-water habitat to their burial in a littoral environment. The fresh-water interpretation quickly led to paleobiological inference, as armored heads were thought to be a defense against eurypterids living in fresh-water habitats. Paleobiological inference also drove the fresh-water interpretation, with biologists arguing that the physiology of kidneys necessitated a fresh-water origin for fish.

Despite an ongoing debate over the habitat, little new evidence was presented until Fischer (1978) reported an unusual trace and body fossil assemblage in the Harding and, based on the sedimentology, interpreted the depositional environment as a fluvial point bar in an estuarine system. The next year, Nils Spjeldnaes (1979) argued for an intertidal to shallow subtidal setting within a lagoon, estuary, or delta, subject to changing salinity and a warm climate. He based his interpretation on scarce sedimentary structures, quartz grain morphology, boron content in illite, trace fossils, and invertebrate fossils. Graffin (1992) described a new locality of the Harding Sandstone west of Cañon City and interpreted it as fluvial based on the presence of conglomerate, channelized deposits, and lateral accretion surfaces. Reconciling the evidence was difficult. The key was the assumption in all of these studies that the Harding was homogenous. All of these studies interpreted the Harding as a single unit or as a pair of units, but did not consider the numerous internal facies changes. In addition, each of these studies based their interpretation on a single exposure of the Harding, rather than taking a regional perspective.

WALCOTT WAS RIGHT

Allulee and Holland (2005) took a fresh look at the Harding and conducted a facies and sequence stratigraphic analysis across its exposure belt in central Colorado. Their analysis included all of the localities examined by Walcott (1892), Fischer (1978), Spjeldnaes

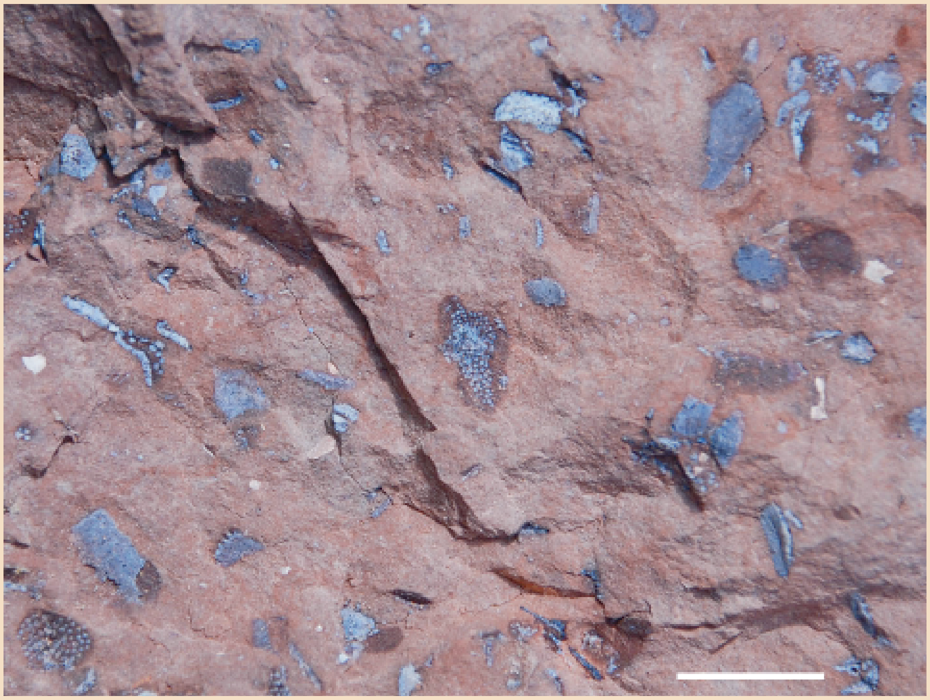

Figure 1. Disarticulated dermal plates of pteraspidomorph agnathan fish from the Upper Ordovician Harding Formation at Cañon City, Colorado. Most fish from the Harding are now disarticulated plates, although four partially to fully articulated specimens have been found. Scale bar is 1 cm.

(1979), and Graffin (1992), as well as several additional localities.

It became clear that the Harding did not represent a single depositional environment, but a spectrum of coastal and shallow marine environments. The Harding also contained numerous flooding surfaces as well as a sequence boundary that divided it, removing the possibility of a strictly Waltherian interpretation. Furthermore, fish plates were not evenly distributed through the Harding, but were concentrated along particular surfaces and facies.

Harding environments

Facies in the Harding comprise two broad associations, one deposited in a shallow-marine setting and the other in an estuarine setting (Fig. 2). Bioturbation is pervasive in the shallow-marine sandstones, with a diverse array of trace fossils from a mixed *Cruziana-Skolithos* ichnofacies. Lingulid brachiopods are the only common invertebrates, but bivalves, gastropods, nautiloids, and even crinoid columnals are present. The shallow-marine facies display upward coarsening and bed thickening on the scale of a few meters, as well as a transition from primarily physical sedimentary structures to mostly biogenic structures. The lower portions of these parasequences contain common wave-ripple lamination, planar lamination, and rare hummocky cross-lamination. The upper portions of these units are more intensely bioturbated, but have small pockets of planar and wave-ripple lamination.

These shallow marine sandstones record an environment in which waves were the primary depositional agent, but one in which wave energy was so weak that burrowing organisms could destroy most laminae, resulting in pervasively bioturbated sandstone. The lower thin-bedded units are interpreted as lower shoreface, with the upper thick-bedded bioturbated units interpreted as low-energy upper shoreface. Among possible modern analogs, the microtidal, low wave-energy coasts of Texas and the Florida panhandle bear a strong similarity. In both of these settings, coarsening-upward parasequences are developed, wave-generated structures are dominant, and the shoreface is intensely bioturbated.

The estuarine facies association is dominated by a thick chocolate-brown mudstone deposited in a lagoonal setting, based on its geographic distribution and facies relationships, along with two sandy facies found in association. Isolated beds of bioturbated sandstone are common within the lagoon facies, particularly near its upper and lower contacts with marine facies, and are interpreted as washover fan deposits and possibly flood-tidal deltas. Also common near the base of the lagoon facies are coarsening-upward sandy facies dominated by current-ripple lamination and interpreted to represent small bayhead deltas. Many beds within the bayhead delta facies have numerous burrows and trackways, including the unusual association described by Fischer (1978), with traces attributed to horseshoe crabs, eurypterids, scorpions, and crustaceans. One trace was also attributed to fish, but without direct evidence and is no longer accepted.

The association of lagoonal facies, common washover fan deposits, and bayhead deltas suggests the presence of microtidal wave-dominated estuaries (Fig. 3). Such estuaries fit well with the analog of the Texas coast and Florida panhandle.

The habitat of the fish

Fish plates are present at many horizons in the Harding, but are especially common in the shoreface facies and on flooding surfaces of the upper Harding sequence (Fig. 2). Their remains are also common near the top of the estuarine complex, but are consistently associated with washover-fan facies, suggesting that these remains may be transported. As Walcott had argued, the fish are found in marine strata.

Fish remains are conspicuously absent from bayhead delta facies and from most of the lagoon deposits. Their absence makes it unlikely that they lived in the brackish to fresh-water conditions of the estuary or the rivers and streams feeding the bayhead deltas. Their absence from the bayhead delta facies also makes it unlikely that their remains were transported from rivers into a marine setting. Romer and Grove (1935) argued for this transport, but the absence of fish in bayhead deltas would require that post-mortem transport effectively removed all remains from the life habitat. The simplest interpretation is that the fish are most abundant where they actually lived, in shallow-marine settings.

More recent work has confirmed and enriched this picture. Davies et al. (2007) found that the Gondwanan Ordovician pteraspidomorph fish *Sacabambaspis* was restricted to sandy shoreface environments, like its relatives in the Harding. More recently, Ivan Sansom and coworkers have found additional vertebrates in the Harding,

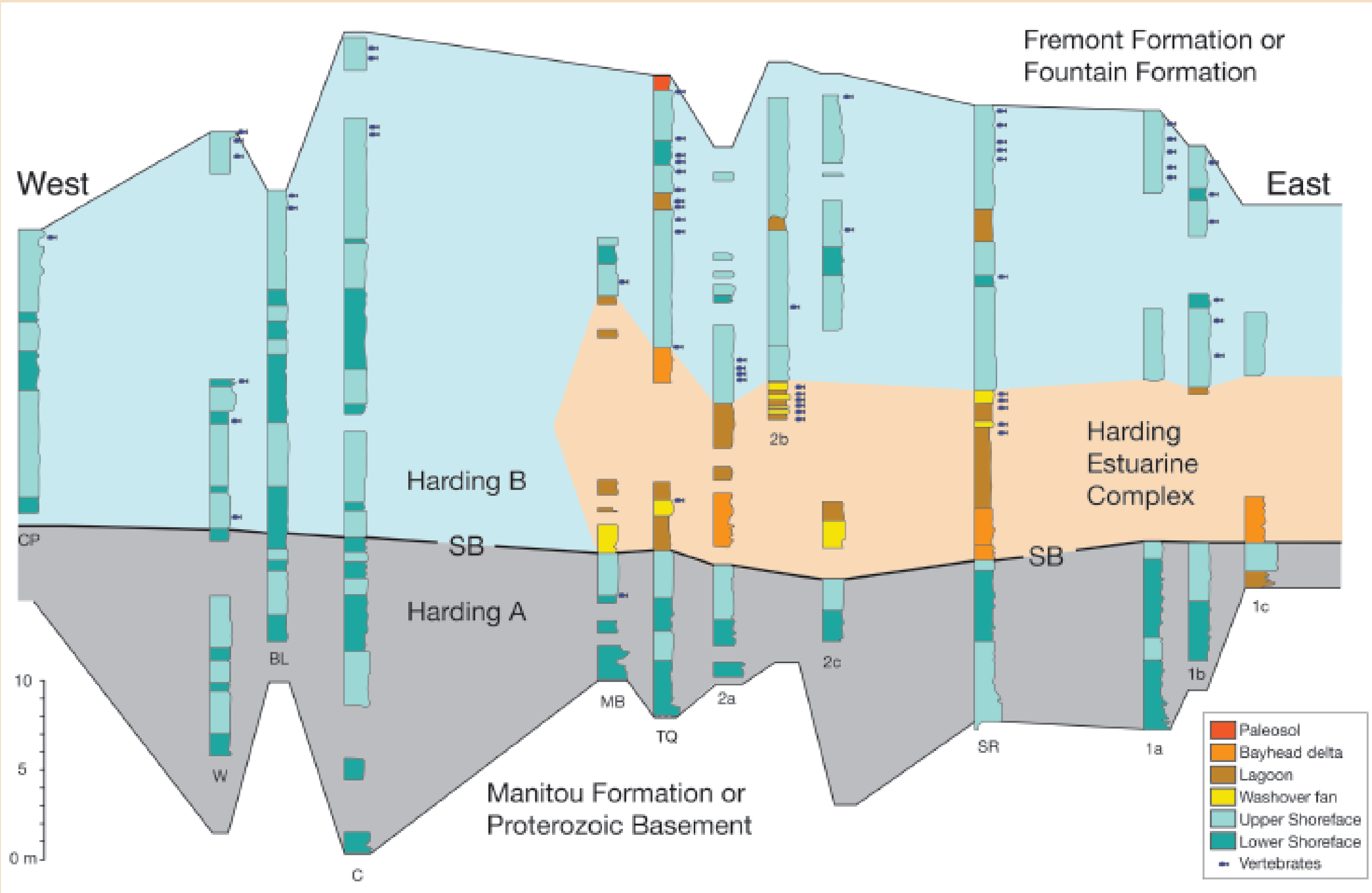

Figure 2. Cross-section of the Harding Formation in central Colorado, showing depositional environments and the occurrence of fish fossils. Sections are arrayed from west to east as in Figure 3, but their lateral spacing is not to scale, owing to the many sections along strike.

beyond the two species that Walcott described. Interestingly, these vertebrates are each found most commonly in a different habitat in the Harding, showing that these shallow Ordovician seas contained a far more diverse and environmentally differentiated vertebrate fauna than previously thought (Sansom, pers. comm.). Collectively, these discoveries enrich our understanding of the origin and diversification of primitive vertebrates.

OPPORTUNITIES ABOUND

The Harding is just one example of how sequence stratigraphy promotes paleobiological interpretation. In the past decade, impressive advances have been made on the depositional setting of many paleontologically significant deposits, especially cases of exceptional preservation (e.g., Gaines et al., 2004; Jiang and Sha, 2007). Knowing the sedimentary environment of such lagerstätte is doubly important, not just because it constrains their paleobiological interpretation, but also because it can lead to the discovery of new deposits (e.g., Hook and Ferm, 1985; Babcock et al., 2001). Solid environmental interpretations are also establishing the framework for biologically critical transitions, such as terrestrialization in the Devonian (e.g., Wehrmann et al., 2005). PALAIOS showcases some of the best of this work on the depositional setting of paleontologically significant strata.

More recently, the sequence stratigraphic context of significant fossiliferous deposits has played an increasing role in paleobiology and biostratigraphy (e.g.,, Rogers and Kidwell, 2000; Brett et al., 2007; Egenhoff and Maletz, 2007). Here again, PALAIOS is at the forefront of this research, having recently hosted a special issue on sea-level change and the structure of marine ecosystems. Sequence stratigraphy has gained new value for understanding how changes in sea level shape the composition and diversity of ecological communities (e.g.,, Dominici and Kowalke, 2007, Scarponi and Kowalewski, 2007).

Despite this research, ample opportunities abound, not just for spectacular deposits, but also for deposits more typical of the fossil record. For example, half of the 53,000 marine invertebrate collections in the Paleobiology Database (paleodb.org) have no environment recorded or are listed simply as marine, coastal, or carbonate. For some collections, the paleontological report may not specify a depositional environment, even if known to sedimentologists. In other cases, the environment may never have been established, or not established with modern methods. In short, there are ample opportunities for fruitful collaborations between sedimentologists, stratigraphers, and paleontologists. These collaborations will undoubtedly enrich our understanding of the history of life on Earth.

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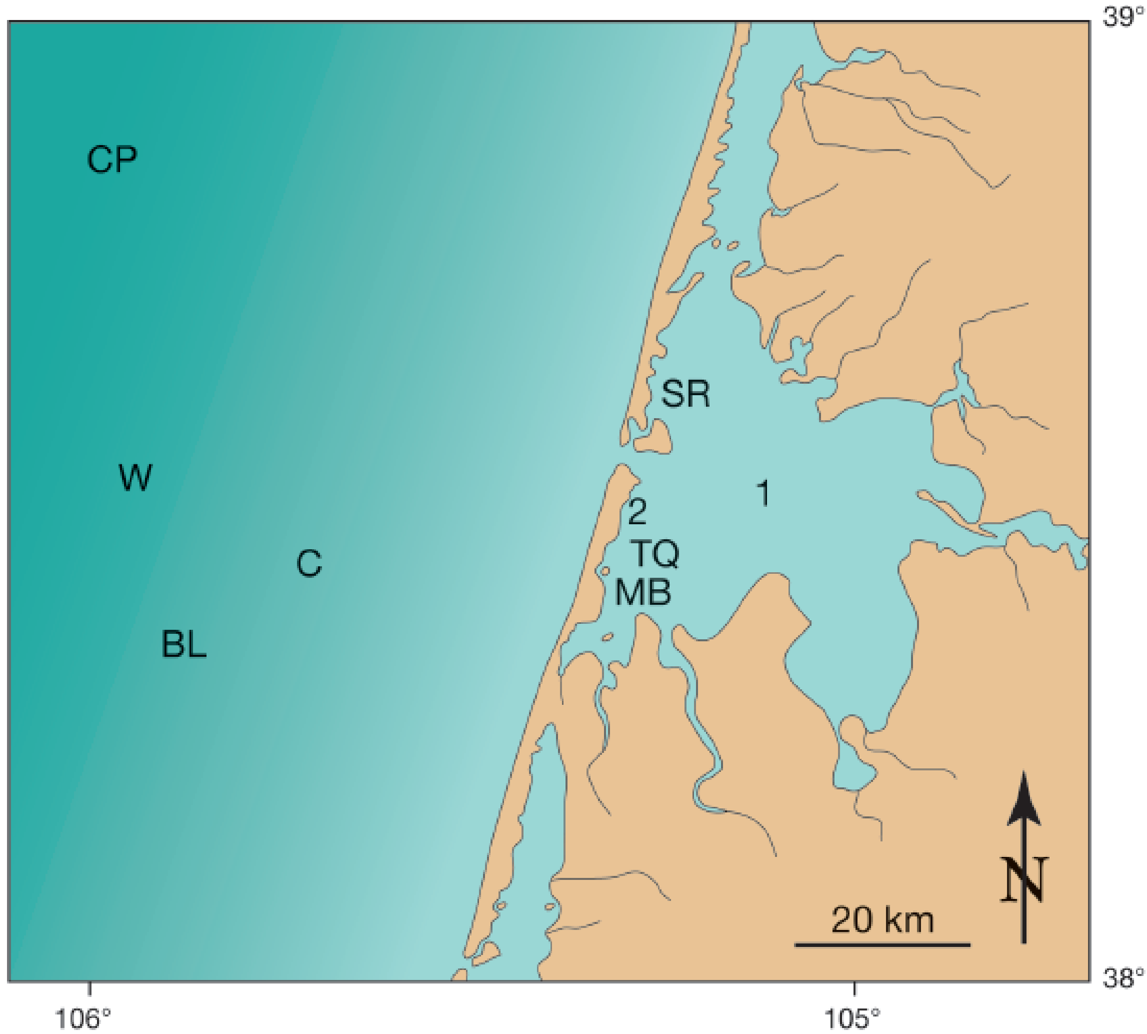

Figure 3. Hypothesized reconstruction of depositional environments in the transgressive systems tract of Harding sequence B. Abbreviations indicate locations of measured sections in figure 2. Numbers 1 and 2 each correspond to a cluster of three localities (1a-c and 2a-c) that are too closely spaced to plot separately.

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