PALAIOS
Emphasizing the impact of life on Earth's history

PALAIOS, 2016, v. 31, 327–338
Research Article
DOI: http://dx.doi.org/10.2110/palo.2016.013

MACROSCOPIC STRUCTURES IN THE 1.1 Ga CONTINENTAL COPPER HARBOR FORMATION: CONCRETIONS OR FOSSILS?

ROSS P. ANDERSON,[1] LIDYA G. TARHAN,[1] KATHERINE E. CUMMINGS,[2] NOAH J. PLANAVSKY,[1] AND MARCIA BJØRNERUD[3]
[1]*Department of Geology and Geophysics, Yale University, 210 Whitney Avenue, New Haven, Connecticut 06511, USA*
[2]*Department of Natural History, University of Florida, Gainesville, Florida 32611, USA*
[3]*Geology Department, Lawrence University, Appleton, Wisconsin 54911, USA*
email: ross.anderson@yale.edu

ABSTRACT: **Continental siltstones of the Mesoproterozoic Copper Harbor Formation, Michigan contain macroscopic structures of a size and morphological complexity commonly associated with fossils of eukaryotic macroorganisms. A biogenic origin for these structures would significantly augment the Proterozoic continental fossil record, which is currently poor, and also add to a growing body of sedimentological and geochemical data that, albeit indirectly, indicates the presence of life in continental settings early in Earth's history. These three-dimensional structures occur abundantly within a single cm-scale siltstone bed. Along this bedding plane, these structures are generally circular-to-ovoid, range up to several centimeters in diameter, and most specimens possess a transecting lenticular element. Structures exhibit sharp, well-rounded external margins and, in contrast to the surrounding aluminosilicate-rich matrix, are calcitic in composition. Surrounding sedimentary laminae are deflected by and cross cut the structures. A fossiliferous origin is considered but rejected and an authigenic concretionary origin is favored based on these characters. However, a concretionary origin does not exclude the possibility of a biogenic precursor that served as a locus for early diagenetic calcite precipitation. This study highlights the need for careful analysis of morphological, mineralogical, distributional, and sedimentological characteristics when considering the origin of enigmatic structures; morphological complexity alone is an insufficient criterion for assignment of biogenicity. The unusual morphology of these concretions augments known concretion morphologies generally comparable to unusual fossil forms, and draws into question the biogenicity of similarly cryptic Proterozoic structures including, in particular, those of the 2.0 Ga Francevillian B Formation of Gabon.**

INTRODUCTION

Over the past five decades, substantial effort focused on reporting and describing fossilized remains of eukaryotic organisms from Proterozoic rocks (Knoll et al. 2006; Knoll 2014; Cohen and Macdonald 2015). The Proterozoic body fossil record is predominantly marine as well as microscopic (Cohen and Macdonald 2015; Planavsky et al. 2015). Indeed, Proterozoic continental landscapes have been envisioned as lifeless, windswept expanses, devoid of life. Recently, however, eukaryotic microfossils from a putative terrestrial lake system characterized by intermittent subaerial exposure—the 1.2–1.0 billion year old (Ga) Torridonian sequence—were reported, indicating that eukaryotic life may have existed on the continents during the Proterozoic (Strother et al. 2011; Wacey et al. 2014). Previous studies also reported macroscopic and microscopic structures of complex morphology potentially recording the presence of eukaryotes in Proterozoic continental settings, including *Horodyskia moniliformis* from freshwater siltstones within the 1.5 Ga Appekunny Formation, Montana (Horodyski 1982; Yochelson and Fedonkin 2000; Fedonkin and Yochelson 2002), enigmatic cm-scale pyritized objects interpreted as eukaryote colonies from deltaic deposits of the 2.0 Ga Francevillian B Formation, Gabon (Albani et al. 2010, 2014), and the urn-shaped structure *Diskagma* from a paleosol within the 2.2 Ga Hekpoort Formation, South Africa (Retallack et al. 2013b). However, the biogenicity and/or eukaryotic origin of many of these occurrences is ambiguous and, in many cases, these claims have proven controversial (e.g., Knoll et al. 2006; Knoll 2011).

A growing body of geochemical evidence indicates that continental ecosystems were biologically active as early as Proterozoic and potentially even late Archean time (Beraldi-Campesi 2013). Geochemical and sedimentological signatures for continental microbial activity are documented in Neoarchean and Paleoproterozoic paleosols, weathering profiles, and microbially mediated sedimentary structures (Ohmoto 1996; Gutzmer and Beukes 1998; Rye and Holland 2000; Watanabe et al. 2000; Driese and Medaris 2008; Sheldon 2012). However, the question of how common or spatially widespread eukaryotes were in Proterozoic continental environments remains poorly resolved.

Here we describe the morphological, mineralogical, distributional, and sedimentological characteristics of complex macroscopic structures preserved in continental facies of the 1.1 Ga Copper Harbor Formation, Michigan, and assess their potential biogenicity using criteria developed in previous studies (e.g., Anderson et al. 2013). A biogenic origin for these structures would add significantly to the Proterozoic continental fossil record.

GEOLOGICAL SETTING

The Midcontinent Rift, also called the Keweenaw Rift and one of the best-preserved ancient continental rifts, formed between 1.15 and 1.03 Ga

0883-1351/16/031-327/$03.00

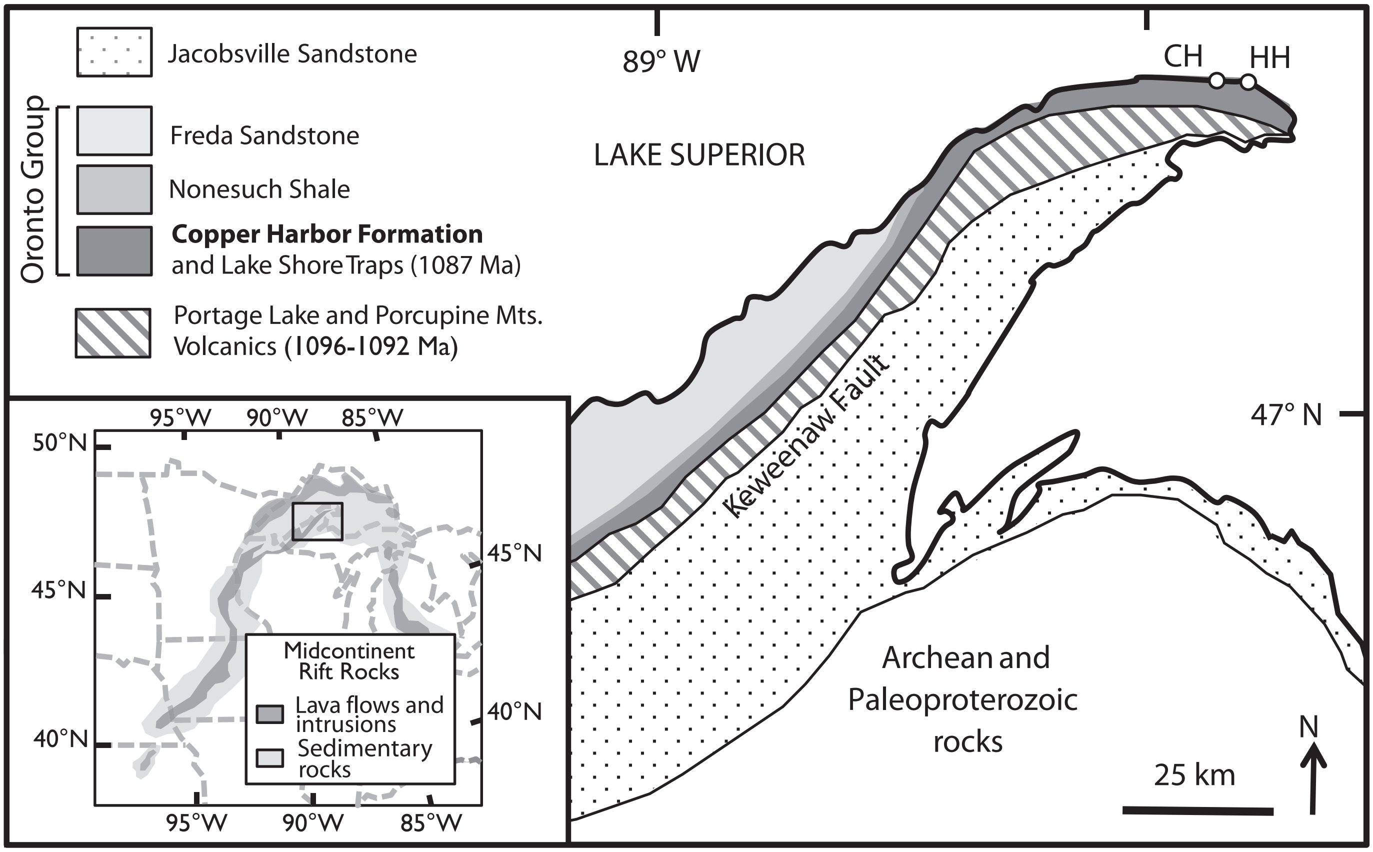


FIG. 1.—Generalized geological map of the Keweenaw Peninsula, northern Michigan, depicting the rocks of the Portage Lake and Porcupine Mts. Volcanics, Oronto Group, and Jacobsville Sandstone. Field localities are indicated with circles: CH = Copper Harbor, HH = Horseshoe Harbor. The Copper Harbor Formation, indicated in bold, is host of the enigmatic macrostructures discussed here. Inset: Geographic extent of the North American Midcontinent Rift system, based on the distribution of exposed rocks in the Lake Superior region, as well as subsurface information. Box shows the location of the Keweenaw Peninsula of Michigan.

(Cannon 1992). Lava flows, intrusive rocks, and sedimentary units related to the rifting event and exposed in the Lake Superior region can be traced as far southwest as Kansas due to their pronounced gravitational and magnetic signatures (Ojakangas and Dickas 2002). Seismic reflection profiling in Lake Superior has shown that, during this interval, the pre-existing Archean and Paleoproterozoic crust was thinned from approximately 35 km to less than 5 km, and lava flows and sedimentary strata totaling almost 30 km accumulated in the resulting rift valley (Hinze et al. 1990). The intercalation of paleosols, aeolian siltstones, and fluvial conglomerates within the volcanic sequence and the absence of pillow structures indicates that the Midcontinent Rift volcanics were extruded subaerially. The total volume of erupted material, estimated at 1.5 million km^3, extruded mainly over a six million-year interval (between 1.102 and 1.096 Ga) (Davies and Paces 1990; Cannon 1992; Miller and Vervoort 1996; Nicholson et al. 1997). The volcanic and sedimentary stratigraphy of the Midcontinent Rift is well known because the Rift is host to one of the world's largest stratiform native copper deposits, formed by pervasive hydrothermal fluid infiltration some 30 myr after rifting ceased (Cannon 1992).

Following the main stage of volcanic activity, which produced the North Shore Volcanic Group in Minnesota and the Portage Lake and Porcupine Mountain Volcanics sequences in Michigan, the central valley of the rift filled with > 5000 m of clastic sediments of the Oronto Group: the Copper Harbor Formation, the Nonesuch Shale, and the Freda Sandstone (Ojakangas et al. 2001) (Fig. 1). These are, in turn, overlain by the Jacobsville Sandstone (which may be as young as Neoproterozoic in age), the uppermost preserved unit in the Midcontinent Rift sequence (Stein et al. 2014a, 2014b; Stein 2015; Mitchell and Sheldon 2016). The sedimentary rocks of the central part of the rift valley provide a detailed record of a Mesoproterozoic landscape; this sequence is extensively exposed on the Keweenaw Peninsula of Michigan (Fig. 1) as well as in northernmost Wisconsin and Isle Royale, Michigan.

The macroscopic structures of interest occur in the lowest unit of the Oronto Group, the Copper Harbor Formation, which consists primarily of conglomerates and is > 2000 m thick at its type locality on the Keweenaw Peninsula of Michigan (Fig. 1). Conglomerates interbed with late-stage basaltic lava flows, known as the Lake Shore Traps, which yield a U-Pb zircon age of 1087.2 ± 1.6 Ma (Davies and Paces 1990). Clasts in the conglomerates appear to be derived almost entirely from volcanic rocks of the rift; very few have lithologies typical of the Paleoproterozoic or Archean rocks that today are exposed only tens of kilometers from Copper Harbor outcrops of the Keweenaw Peninsula (Hamblin and Horner 1961; Daniels 1982; Mitchell and Sheldon 2016) (Fig. 1). This indicates that the valley in which the conglomerates accumulated formed as a relative topographic low within a generally elevated region which was probably a thermally supported high similar to the modern East African Rift.

Detailed study of sedimentary structures on the Keweenaw Peninsula indicates that the Copper Harbor Formation was deposited in an

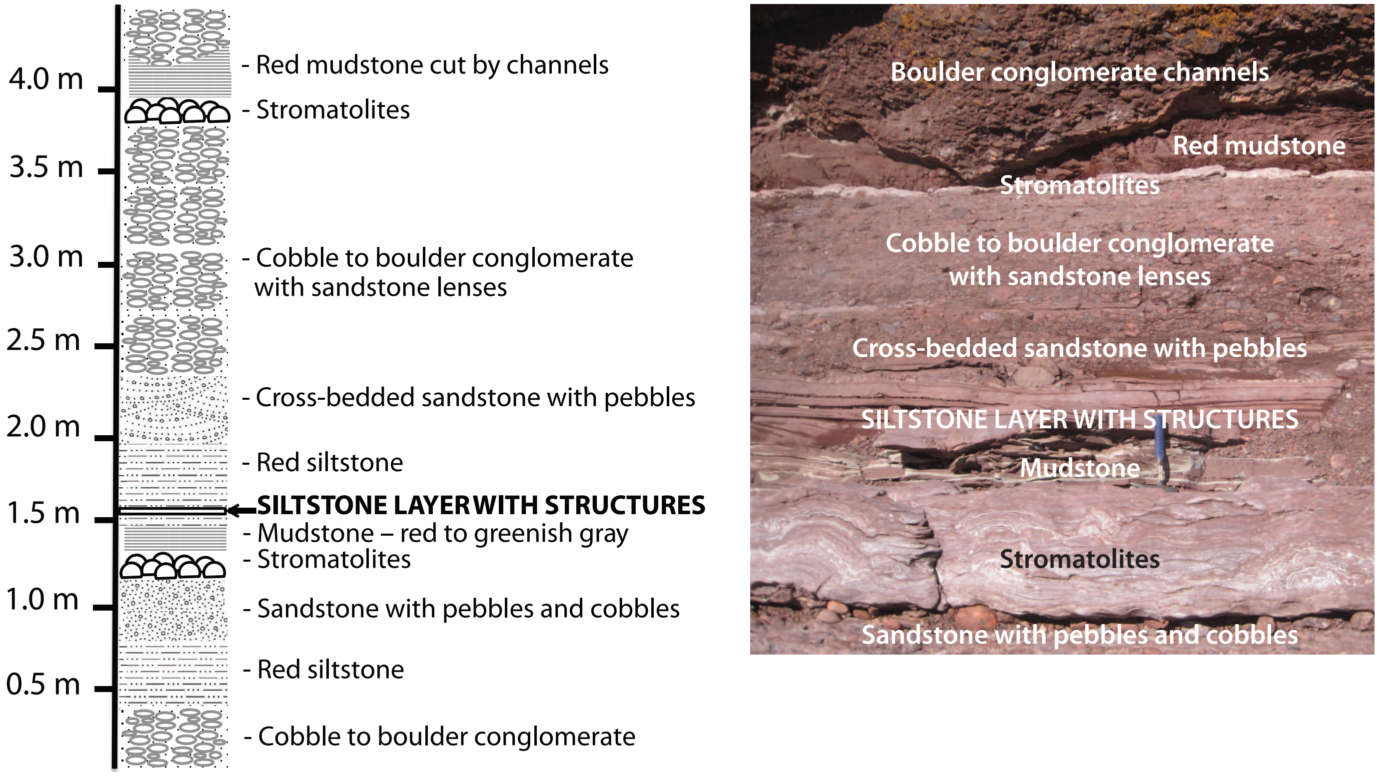


FIG. 2.—Sedimentology and stratigraphy of the Horseshoe Harbor locality. Left, detailed stratigraphy of the portion of the Copper Harbor Formation exposed at Horseshoe Harbor, with the macrostructure-yielding horizon indicated in bold. Right, photograph of outcrop showing the same stratigraphy, including the two stromatolitic horizons bracketing the macrostructure-yielding horizon.

environment characterized by alluvial fans, braided streams, and ephemeral lakes (Elmore 1984). Paleocurrent indicators in the Copper Harbor Formation, including cross beds, ripple marks, current lineations, and imbricated clasts, indicate consistent flow directionality from the flanks toward the center of the rift (currently located beneath western Lake Superior). The Copper Harbor Formation is characterized by an overall fining-upward trend, with conglomerates predominating in the lower part of the formation and sandstones dominating the lithology of the upper portion of the formation, but many second-order reversals of that pattern suggest episodic rejuvenation of topographic relief, probably by normal faulting synchronous with evolution of the rift (Elmore 1984).

At the type locality of Copper Harbor, Michigan (Fig. 1), most of the Copper Harbor Formation consists of clast-supported conglomerate characterized by cobble- to boulder-sized clasts and 0.1–0.5 m deep channel structures, reflecting a high-energy depositional environment, although beds and lenses of arkosic sandstone and siltstone record periods of lower flow velocity. Localized mudstones, commonly associated with desiccation cracks, likely record shallow playa lakes that persisted until they were buried by another series of coarser alluvial or fluvial deposits (Mitchell and Sheldon 2016). Some of the mudstones are gray to green in color. Many of the finer-grained rocks, as well as the matrix of the conglomerates, are red in color.

Calcareous, hemispheroidal stromatolites, up to 10–15 cm in diameter and characterized by rare pseudocolumnar branching, occur along several horizons in the upper part of the Copper Harbor Formation at the northern end of the Keweenaw Peninsula (Elmore 1984; Sheldon 2012; Fedorchuk et al. 2016). Some of these grew on substrates of mud, while others encrusted cobbles and boulders (Fig. 2). Stromatolitic laminae are replicated in crystalline calcite, reflecting late-stage recrystallization of the primary stromatolitic calcite.

METHODS

At Horseshoe Harbor (47.473323°N, 87.80501°W), approximately 7 km east of Copper Harbor (Fig. 2), several distinct stromatolite-bearing beds occur in outcrops, partly buried by beach cobbles, situated immediately south of prominent offshore outcrops of boulder conglomerate. The uppermost of these stromatolitic layers, exposed near the base of the offshore sequence, is continuous along strike for at least 800 m. Two slabs (total area approximately 900 cm^2), bearing a total of 58 individual macroscopic structures, were collected from a cm-scale red siltstone bed between the two uppermost stromatolitic horizons at Horseshoe Harbor.

All specimens were imaged using a Leica MZ16 binocular microscope combined with a Leica DFC420 camera. Images were taken at different focal planes and combined using Leica Applications Suite software to create a “z-stack” composite image. Specimen dimensions (maximum long axis, maximum short axis, surface area and perimeter) were measured from photomicrographs, where demarcation of the structures from the matrix was sufficiently clear, using the Leica Application Suite (49 of 58 specimens were measured). The orientation of the long axis of individual specimens was measured from photomicrographs in ImageJ software in all instances where the long axis could be confidently identified (43 of 58 specimens).

Energy dispersive X-ray spectroscopy (SEM-EDS) was used on a Zeiss EVO MA15 scanning electron microscope in variable pressure mode to produce elemental maps of a specimen in an oblique 30 μm-thick thin-section. Four maps were produced in order to capture not only key regions

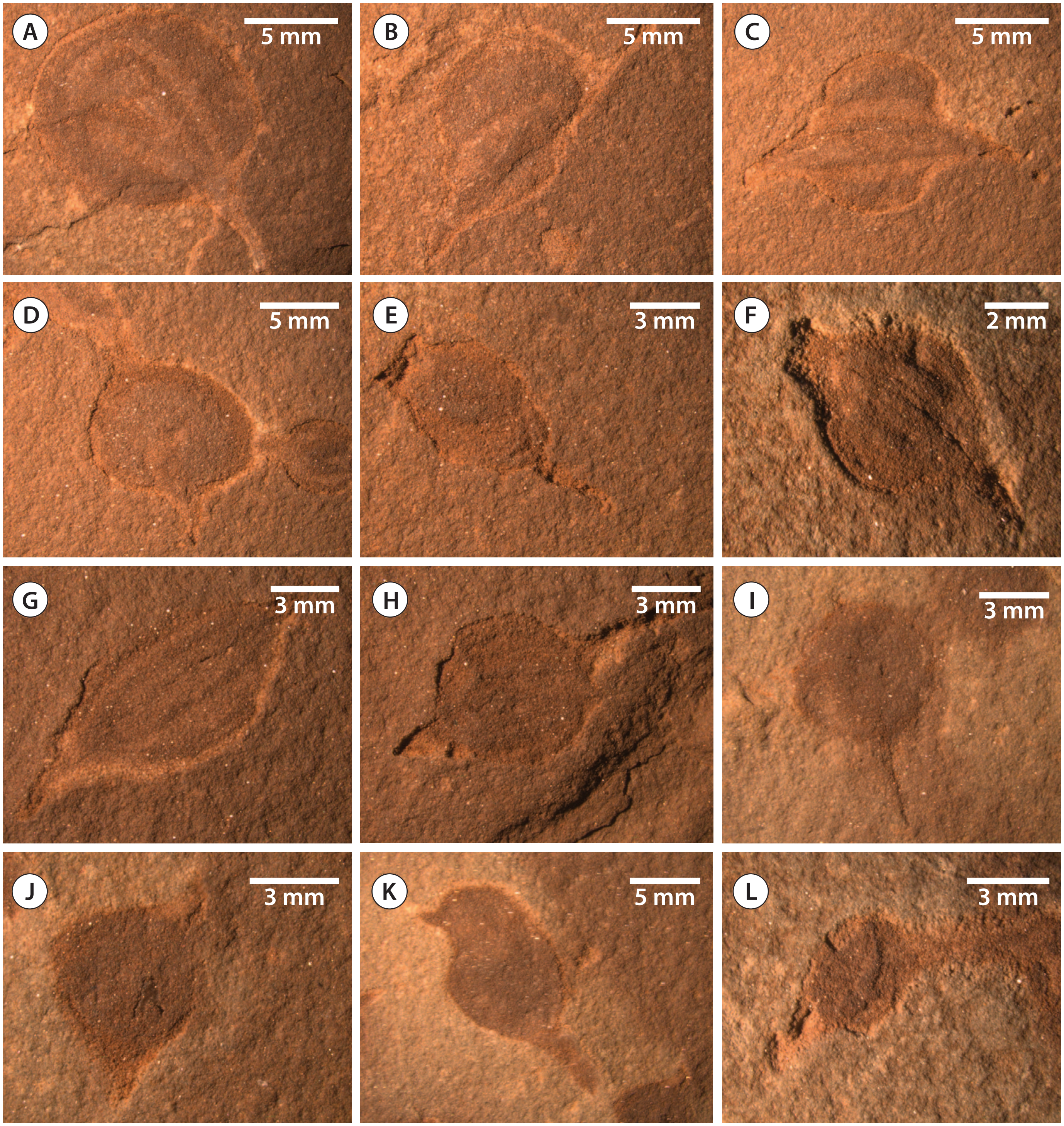


FIG. 3.—Photomicrographs of macroscopic structures depicting the range of morphologies characteristic of the Copper Harbor assemblage.

of the sectioned structure but also the surrounding sedimentary matrix. The entire suite of elemental data was collected for each analysis; herein we present concentration data for abundant (> 1 %) elements and discuss the potential paleobiological and geochemical significance of the observed elemental distributions.

Three-dimensional morphology was mapped using X-ray computed tomography (XRCT) on a North Star X5000 high-resolution microCT system with a twin head 225 kV X-ray source and a Dexela area detector. Two specimens were scanned for approximately 75 minutes with a focal spot size of six microns and frame capture rate of 1.1 fps.

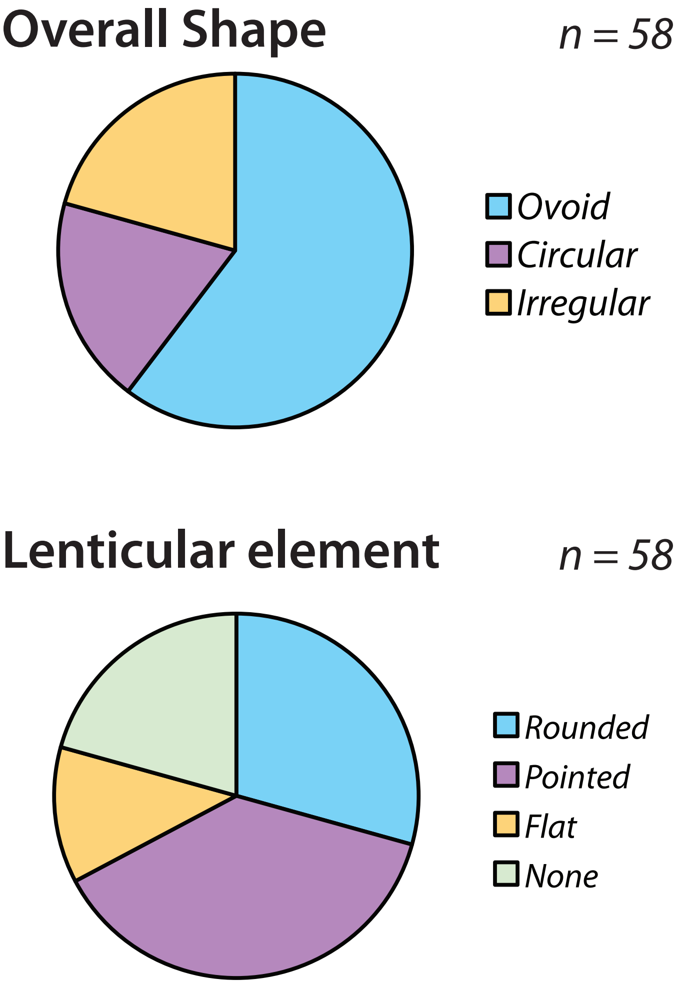


FIG. 4.—Pie charts representing distribution of morphologies among the Copper Harbor assemblage. Top, classification of structures according to shape: ovoid, circular, or irregular. Bottom, classification according to morphology of lenticular element: rounded, pointed, flat, or none (i.e., not present).

MACROSCOPIC STRUCTURES: DEFINING CHARCTERISTICS

Morphology

In plan view, the macroscopic structures exhibit a wide range of complex morphologies (Fig. 3). The majority of structures, however, are characterized by an ovoid to circular shape (60% ovoid, 19% circular, 21% irregular, n = 58) and distinguished from the surrounding matrix by a darker color and sharp, well-rounded external margins. All structures characterized by a well-defined ovoid or circular shape (79% of specimens) are transected by a lenticular element that, in 20% of specimens, extends beyond the margins of the rounded portion of the structure (Fig. 4). The terminations of these lenticular elements can be classified as rounded (29% of specimens, e.g., Fig. 3E, 3K), pointed (38% of specimens, e.g., Fig. 3B, 3D, 3F), or blunt (12% of specimens, e.g., Fig. 3C, 3F). Some specimens contain more than one type of lenticular element termination (e.g., Fig. 3F). The range of morphologies characterizing these structures may reflect variable orientation (upon burial or formation) with respect to the bedding plane. Fifty-seven percent (57%) of specimens are characterized by a rough symmetry with the lenticular element aligned along the central axis of the ovoid or circular structure (Fig. 3C), whereas in some specimens the lenticular element lies to one side of this axis (Fig. 3B). Some of the structures are three-dimensional (i.e., bed-penetrative) and are funnel-shaped in cross section. X-ray computed tomography suggests that some specimens are oblate spheroids with "wings" oriented perpendicular to the bedding plane (Fig. 5).

The macroscopic structures have a mean long axis (including lenticular elements) of 13.0 ± 4.6 mm and a mean short axis of 7.5 ± 2.7 mm (see Fig. 6 for histograms of the surface area, perimeter, long axis length [including lenticular elements], and short axis length [perpendicular to long axis] of each measurable structure). For each size metric (surface area, perimeter, long axis length, and short axis length), specimens are characterized by a single modal distribution with a lower abundance of smaller-sized specimens (right-skewed size distribution).

Mineralogy

SEM-EDS elemental analysis (Fig. 7) of a single specimen indicates that the macroscopic structures are, in contrast to the sedimentary matrix, strongly enriched in calcium and oxygen, and associated with carbon. Mapping at mineral-scale resolution indicates that both the structures and the surrounding matrix are associated with distinct mineralogical phases containing silicon and oxygen, moderate amounts of aluminum, and relatively rare magnesium, sodium, potassium and iron. The surrounding matrix is, relative to the specimen, preferentially enriched in silicon-, oxygen-, aluminum-, magnesium-, sodium- and—less strikingly—iron- and potassium-associated phases. Elemental abundances, phase associations, and petrographic examination indicate that the entirety of the specimen is enriched in calcite, whereas the matrix is comprised primarily of aluminosilicate material.

Distribution and Sedimentology

Macroscopic structures are randomly distributed across the bedding plane surface and appear to display no preferential orientation (with respect to their long axis) (Fig. 8). The cm-scale siltstone bed on which the structures occur is finely laminated and homogeneous, with no pronounced vertical gradients in grain size or composition to indicate that it represents a paleosol (Fig. 2). The mudstone layer immediately underlying this siltstone ranges from greenish gray to red in color. Overlying the siltstone is a coarse-grained and cross-stratified sandstone. No systematic association of the structures with cracks or veins is evident. Petrographic and XRCT analyses indicate sedimentological laminae transect the intra-bed portion of the three-dimensional structures (Fig. 9). In cross section, laminae are also observed to deflect upward and downward in the vicinity of the structure (Fig. 9).

DISCUSSION

Observations of the morphological, mineralogical, distributional, and sedimentological characteristics of these macroscopic structures permit critical evaluation of their origin and syngeneity and, in particular, allow us to distinguish between biogenic and abiogenic origins. In addition to a potential biological affinity, a range of abiogenic explanations for the structures must also be considered, including authigenic features formed during diagenesis (e.g., Seilacher 2001) and metamorphic features (e.g., Bucher and Grapes 2011). Both biogenic and abiogenic structures are associated with a suite of particular characters, which allows evaluation of these alternatives in light of our observations of the morphology, mineralogy, distribution, and sedimentology of the Copper Harbor structures (Fig. 10).

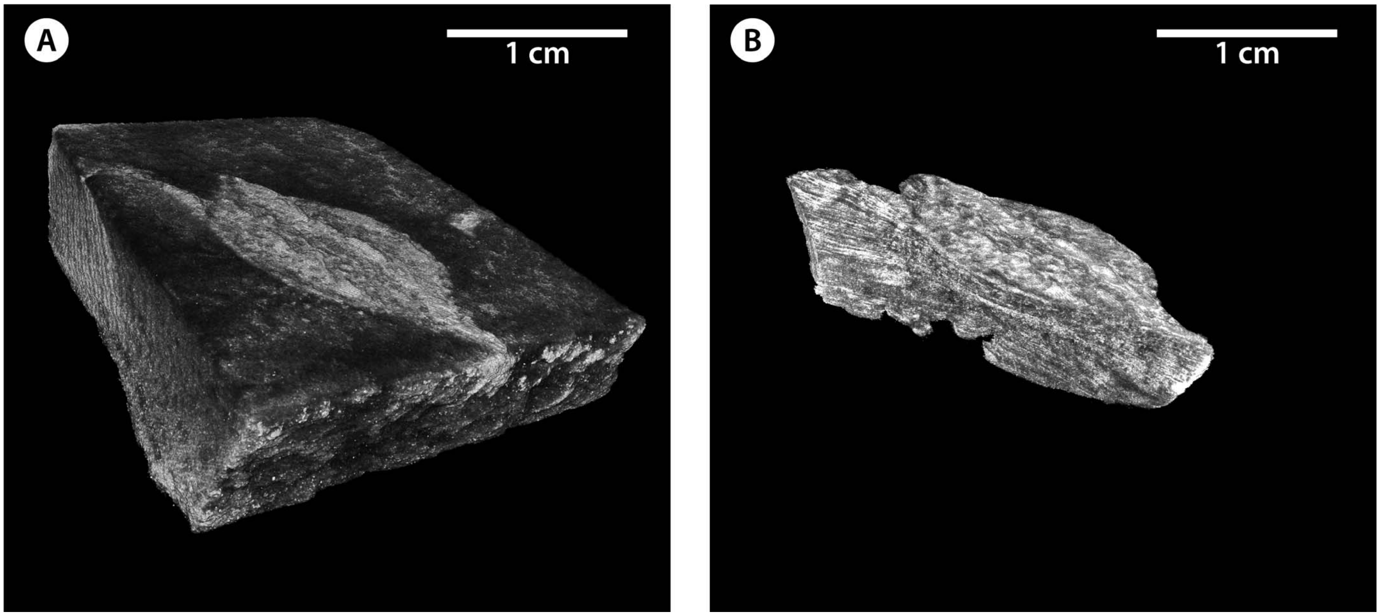


FIG. 5.—X-Ray Computed Tomography (XRCT) of a Copper Harbor structure. **A**) structure within rock matrix. **B**) Copper Harbor structure with matrix digitally removed, showing three-dimensional morphology and "funnel-shape" at depth. Lighter colors reflect higher average density and/or atomic number.

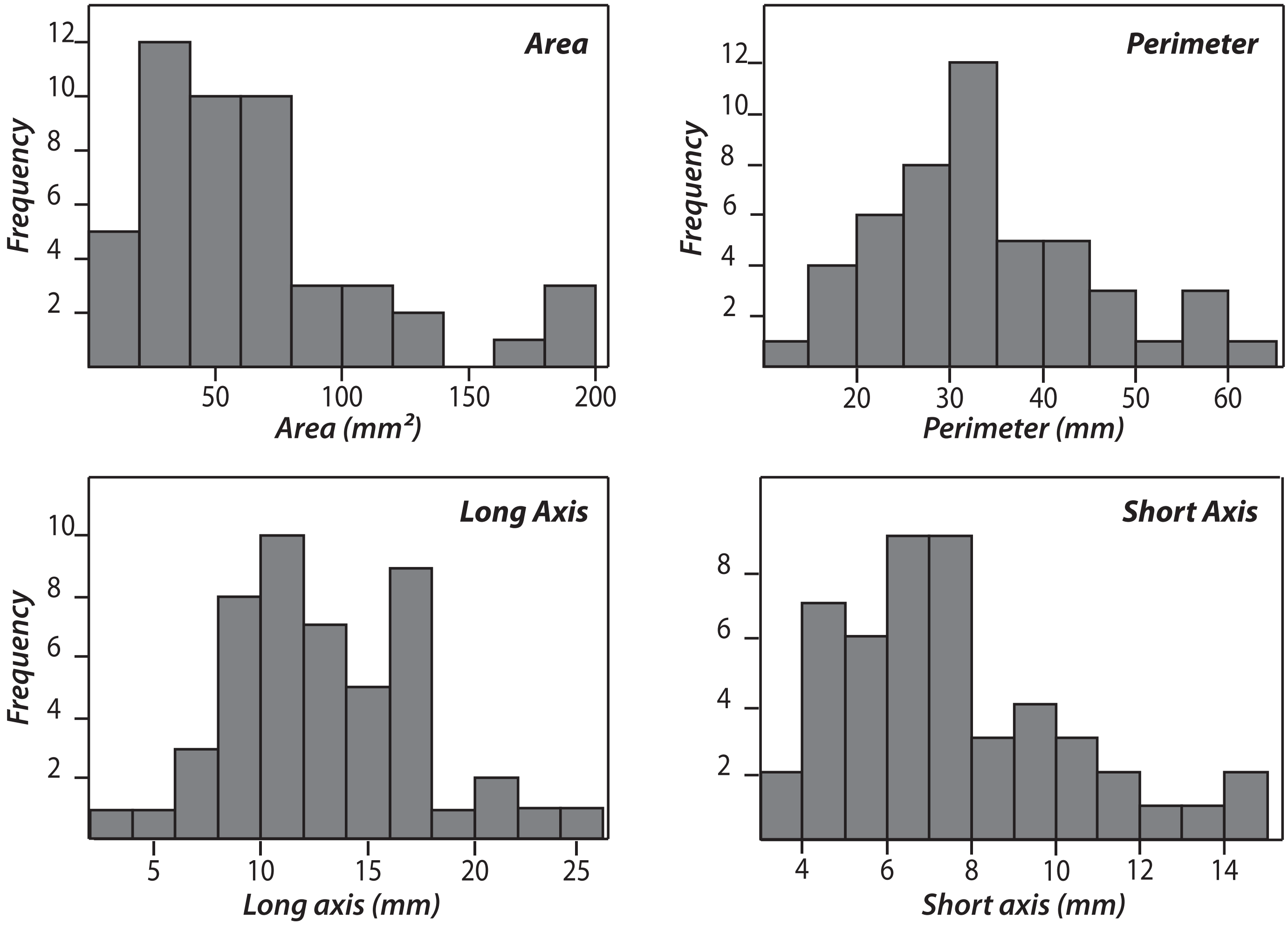


FIG. 6.—Size frequency distributions of macroscopic structures of the Copper Harbor Formation.

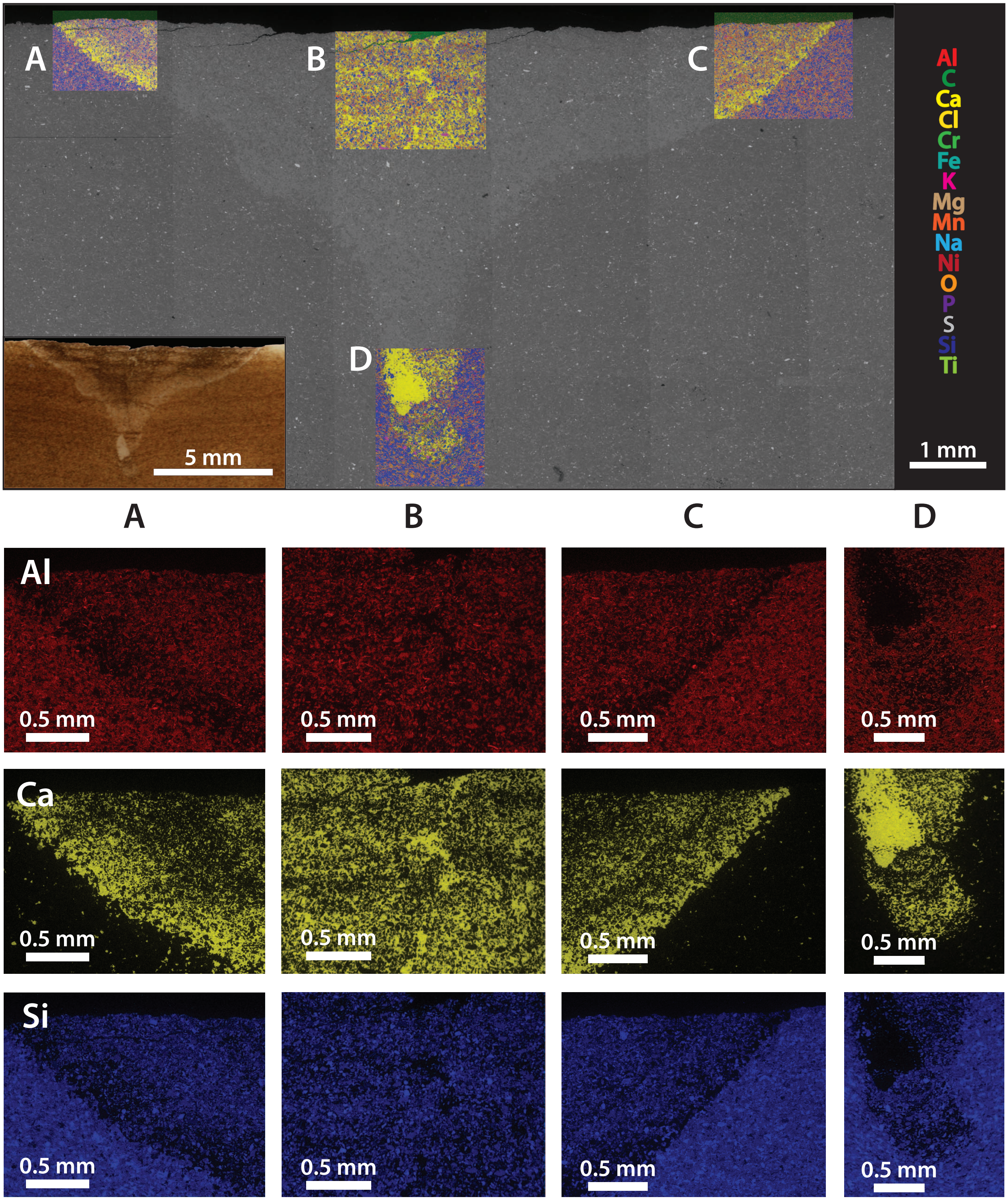


FIG. 7.—Textural and elemental analysis of macroscopic structures using backscatter electron microscopy and SEM-EDS. Top, composite backscatter electron micrograph of oblique cross section through a macroscopic structure. Light photomicrograph of same structure inset. Composite SEM-EDS elemental maps are overlain on the backscatter image at sites A, B, C, and D. Bottom, detailed SEM-EDS elemental maps showing distribution of major associated elements aluminum (Al), calcium (Ca), and silicon (Si) at sites A, B, C, and D.

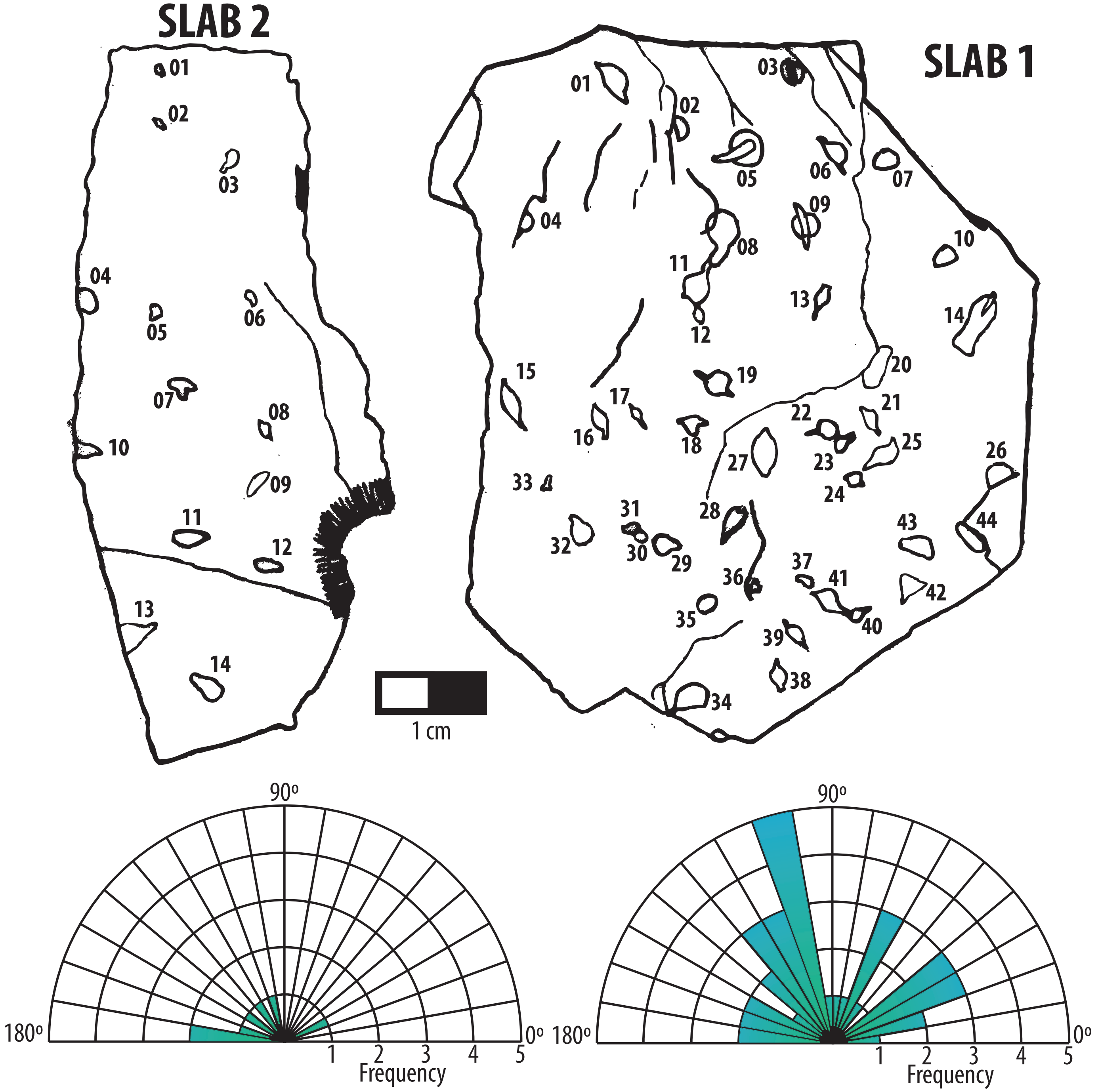


FIG. 8.—Bedding plane distribution of Copper Harbor macroscopic structures. Top, line drawing of two slabs containing all specimens recovered from Horseshoe Harbor. Bottom, frequency distribution (per slab) of long axis orientations of collected assemblage of Copper Harbor structures. Rose diagram orientations reflect depicted orientation of slabs.

Morphology

The smooth, abrupt boundary that differentiates the Copper Harbor structures from the surrounding matrix is inconsistent with a metamorphic or reduction spot origin. Such structures generally form via diffusion (Bucher and Grapes 2011) and, as such, are characterized by irregular and/or diffusive boundaries, reflecting properties of the surrounding rock matrix. However, distinct and regular margins are potentially consistent with either an authigenic or biogenic origin.

The morphology of the Copper Harbor macroscopic structures is distinctive and unusually complex. The combination of an ovoid to circular outline with a transecting lenticular element is dissimilar to any concretion morphology known to us (cf. Sellés-Martínez 1996; Seilacher 2001). However, concretions are also notoriously heterogeneous in both

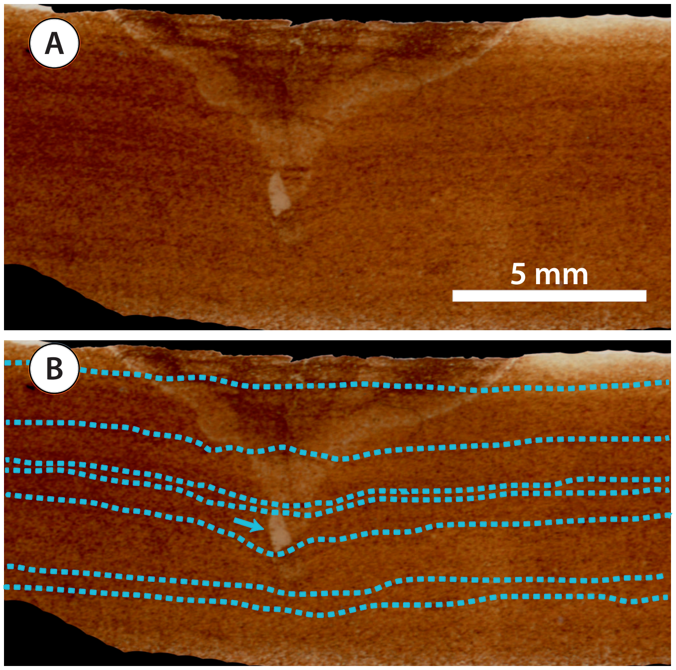


FIG. 9.—Light photomicrographs. **A**) Oblique cross section cut through a macroscopic structure. **B**) Transecting laminae of A highlighted in blue; arrow denotes particularly clear deflection of laminae around a grain within the macroscopic structure

morphology and size (Seilacher 2001) and therefore a lack of precedent does not preclude a concretionary origin.

However, this unusual morphology does not preclude a biogenic origin. The Copper Harbor structures are significantly larger than any known bacteria or archaea (Angert et al. 1993; Schulz and Jørgensen 2001) but do fall within the size range of bacterial/archaeal colonies or solitary eukaryotic organisms, e.g., myxobacterial resting colonies have been observed to overlap in size distribtutions with solitary eukaryotic organisms (Schlegel 1985). Bacterial/archaeal colonies are commonly circular/spherical (expanding equally in all available directions) or else highly irregular and variable in form where localized environmental conditions constrain growth in certain directions. Consequently, a colonial bacterial/archaeal interpretation for the Copper Harbor structures is unlikely, given the consistent presence of a transecting lenticular element observed to cross-cut the sharply bounded and generally ovoid Copper Harbor structures regardless of long-axis orientation.

Mineralogy

The calcitic composition of the Copper Harbor structures is consistent with an origin as a secondary mineral concretion. Calcitic concretions commonly form in siliciclastic rocks (Curtis et al. 1986; Dix and Mullins 1987; Morad and Eshete 1990; Wilkinson and Damier 1990; Coleman and Raiswell 1995; Seilacher 2001). The calcite associated with the Copper Harbor structures could potentially have formed during burial and the hydrothermal metamorphic episode that altered the rocks of the North American Midcontinent Rift region 30 myr after the deposition of the Copper Harbor Formation (Cannon 1992). However, the deflection of laminae associated with formation of these structures indicates that the calcite precipitated very early in the post-depositional history of this bed and therefore an early diagenetic origin for these structures may be more likely.

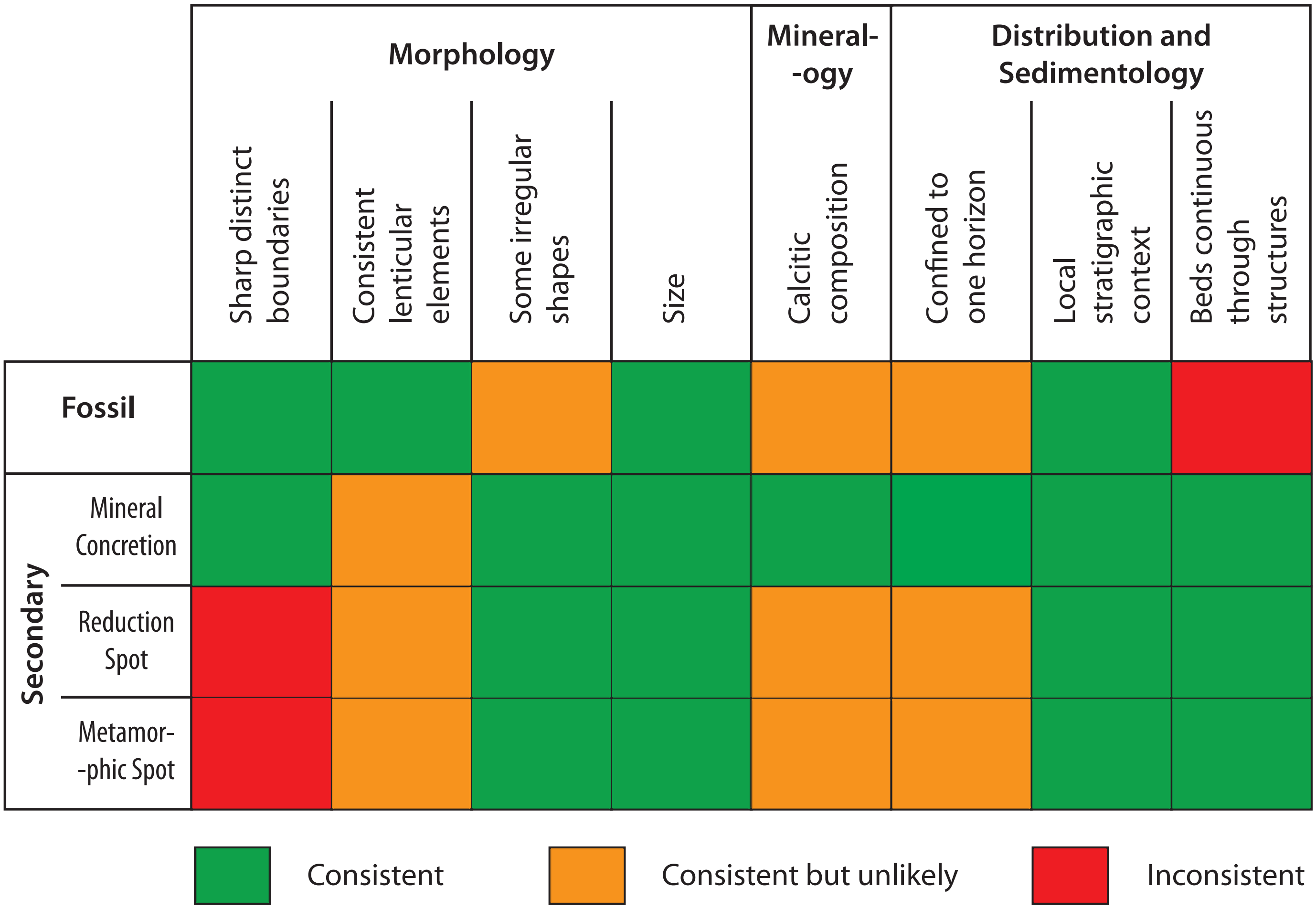
In contrast, given the age of these deposits, a biogenic (e.g., biomineral) origin for this calcite is unlikely. The oldest known examples of potential biomineralization appear some ~ 300 myr after deposition of the Copper Harbor Formation and consist of microscopic phosphatic scales (Cohen et al. 2011; Cohen and Knoll 2012). Calcite biomineralization of structures of comparable size to those of the Copper Harbor structures is unknown until late Ediacaran time (e.g., Knoll 2003), ~ 500 myr later than the interval recorded by the Copper Harbor sequence. Therefore, if the structures were fossils, they would have likely, in life, been composed entirely of organic compounds (i.e., soft-bodied), similar to other known Mesoproterozoic macroscopic fossils (Knoll et al. 2006). In this case, the original organic material comprising the carcasses must have been replaced by calcite, given the lack of organics and pervasive calcite characterizing these structures. However, the lack of evidence for localized replacement associated with the Copper Harbor structures or elsewhere in the formation suggests that a replacement scenario is unlikely.

Distribution and Sedimentology

A secondary origin for the structures as metamorphic features, reduction spots, or mineral concretions is consistent with the local stratigraphic setting of these structures. Secondary mineralization is common within the Copper Harbor Formation, often in the guise of copper deposits, which formed following pervasive hydrothermal fluid infiltration approximately 30 myr after deposition of the unit (Cannon 1992). It is not improbable that such fluids could have facilitated the growth of authigenic mineral concretions and/or influenced the redox state of this sequence, thus forming discrete structures on bedding plane surfaces. The metamorphic history of the Copper Harbor Formation, which did not exceed prehnite-pumpellyite facies (i.e., < 300°C) (Cannon 1992), does not preclude the presence of fossils. Fossils occur in other Proterozoic rocks that have experienced metamorphism (e.g., Anderson et al. 2013). However, metamorphism can also deleteriously impact the preservational fidelity of fossils and impede reconstruction of their biological affinity (Knoll et al. 1988).

The Copper Harbor structures appear to be confined to a single bedding plane. While unusual, this is not uncommon for fossils and may reflect localized productivity (e.g., a spatially confined environment optimal for recruitment and colonization), locally variable preservation potential (e.g., Seilacher et al. 1985), or primary rarity. The Copper Harbor Formation structures are ~ 300 myr older than the earliest known fossils of putatively biomineralizing organisms (Cohen et al. 2011; Cohen and Knoll 2012) and therefore, if biogenic in origin, the original organisms were most likely entirely soft-bodied. Exceptionally preserved soft-bodied fossil assemblages are usually rare and commonly characterized by extremely localized distributions (e.g., Seilacher et al. 1985). A limited spatial distribution is not inconsistent with a secondary (e.g., diagenetic) origin. Even minute differences in porosity and permeability can have a relatively major impact upon pore fluid flow and thus the extent and manifestation of diagenetic alteration.

Observation of intra-bed laminae cross-cutting the Copper Harbor structures is, however, inconsistent with an entirely biogenic origin for these structures. Burial of a carcass and, subsequently, differential compaction of the surrounding sediment could cause deflection of laminae around the carcass (e.g., Seilacher et al. 1976). However, observation of transecting (structure-penetrative) laminae directly conflicts with a carcass origin for the Copper Harbor structures. In contrast, such a relationship between individual laminae and secondary (but early stage) mineral growth is expected. Under this scenario, mineral precipitation would occur in the pore space. As authigenic



		Morphology				Mineral-ogy	Distribution and Sedimentology		
		Sharp distinct boundaries	Consistent lenticular elements	Some irregular shapes	Size	Calcitic composition	Confined to one horizon	Local stratigraphic context	Beds continuous through structures
Fossil		🟩	🟩	🟧	🟩	🟧	🟧	🟩	🟥
Secondary	Mineral Concretion	🟩	🟧	🟩	🟩	🟩	🟩	🟩	🟩
	Reduction Spot	🟥	🟧	🟩	🟩	🟧	🟧	🟩	🟩
	Metamor-phic Spot	🟥	🟧	🟩	🟩	🟧	🟧	🟩	🟩

🟩 Consistent 🟧 Consistent but unlikely 🟥 Inconsistent

FIG. 10.—Chart depicting the multiple lines of evidence used to evaluate the origin of the macroscopic structures as either fossils or secondary structures. Lines of evidence are binned into three distinct categories: morphological, mineralogical, and distributional and sedimentological.

mineralization proceeds, nucleating on the original inter-grain cements, the precipitate may displace laminae as precipitation continues (cf. Seilacher 2001, fig. 5) or subsequently promote differential compaction of sedimentary layers. The upward and downward deflection of laminae around a large grain within the Copper Harbor structure depicted in Figure 9 (see arrow) is, in this light, consistent with an authigenic origin for these features.

ORIGIN AS AUTHIGENIC MINERAL CONCRETIONS

Given the morphological, mineralogical, distributional, and sedimentological evidence reported herein, the Copper Harbor structures are most parsimoniously interpreted as authigenic calcite concretions. A biogenic hypothesis for their origin is rejected chiefly on the basis of disruption by penetrative laminae and the diffuse calcitic composition of these structures. Consequently, the Copper Harbor structures do not provide direct evidence in support of continental eukaryotic life at 1.1 Ga. However, a concretionary origin for these structures is not wholly inconsistent with a biological precursor. The morphology of the structures—in particular, the presence of a transverse lenticular element—is unusual for concretions. In spite of the high level of variability in the characteristics of these structures at the assemblage level, their shared general morphology is suggestive of a common growth history, possibly via nucleation on organic material. The random orientation of the long axis of the concretion could reflect disparity in the size, morphology, and orientation of this organic material. Concretions not uncommonly nucleate around organic materials (e.g., organic particles or carcasses) (McCoy et al. 2015) and may subsequently grow into unusually shaped structures (e.g., Seilacher 2001).

IMPLICATIONS FOR THE BIOGENICITY OF OTHER PROTEROZOIC MACROSCOPIC FOSSILS

The Copper Harbor structures add to a growing database of concretionary forms (e.g., Seilacher 2001) that display many of the complex morphological characteristics commonly associated with Mesoproterozoic and Neoproterozoic putatively eukaryotic fossils (e.g., Walter et al. 1976; Horodyski 1982; Albani et al. 2010; Maloof et al. 2010; Brain et al. 2012; Albani et al. 2014).

In particular, we can draw comparisons between the Copper Harbor structures and other Mesoproterozoic fossils. Although no other macroscopic body fossils of Mesoproterozoic age have been confidently assigned to particular eukaryotic groups, there are a number of potential candidates. The Mesoproterozoic Helena Formation of the Belt Supergroup of Montana, for instance, contains a variety of carbonaceous fossils, up to several centimeters in length, including *Grypania spiralis*, a coiled form (~ 2 mm wide), that have been interpreted as eukaryotic and are globally distributed (Walter et al. 1976; Walter et al. 1990; Han and Runnegar 1992; Kumar 1995). Another Mesoproterozoic macrofossil which has also been interpreted as eukaryotic (Horodyski 1982; Grey and Williams 1990; Yochelson and Fedonkin 2000; Fedonkin and Yochelson 2002; Retallack et al. 2014a), *Horodyskia moniliformis*, commonly consists of spheroidal (although other shapes have been reported) bodies, preserved as casts and molds, inter-connected via cylindrical strings to form "strings of beads." Each individual body comprising *Horodyskia* is 1–4 mm in diameter, but the total composite structure can reach up to 10 cm in length. The eukaryotic affinity of these organisms remains controversial (e.g., Knoll et al. 2006). However, while consistent with these fossil taxa in overall size, the Copper Harbor structures share few characteristics with them in terms of either shape or construction. Consequently, it is challenging to draw direct comparisons.

In contrast, the Copper Harbor structures do bear a gross morphological resemblance to unusual macroscopic, partially pyritized structures that occur in the ca. 2.0 Ga Francevillian B Formation of Gabon. These structures have been interpreted as fossils on the basis of complex repeated morphologies, large size, and compositional disparity (Albani et al. 2010, 2014) but their biogenicity is controversial (e.g., Knoll 2011). The Gabon structures, which also occur as aggregates up to ~ 12 cm in length, are characterized by a variety of shapes, ranging from elongate to isodiametric, but commonly possess a permeating radial fabric (Albani et al. 2010, 2014). The Copper Harbor structures resemble some of these structures—in particular those Gabon forms that possess a lenticular element (cf. Albani et al. 2010, fig. 5). The size range of the Copper Harbor structures overlaps with that of the Gabon structures. However, the aggregated (interpreted by the authors as colonial) nature of the Gabon structures, with individual structures often closely spatially associated along the bedding plane, is distinctive. Such an association between individuals is much rarer in the Copper Harbor structures. In addition, the Copper Harbor structures neither possess the distinctive permeating radial fabric of the Gabon structures nor are they pyritized.

Despite these disparities in composition and internal fabric, the gross morphological similarities between the Copper Harbor structures and the putative fossils of the 2.0 Ga Francevillian B Formation of Gabon (Albani et al. 2010, 2014), coupled with strong evidence for an authigenic concretionary origin for the former, calls into question the hypothesis that the Gabon structures represent biological remains, and highlights the need for careful consideration of not only morphology but also mineralogical, distributional, and sedimentological characteristics when assessing the biogenicity of similarly enigmatic structures in Proterozoic rocks. Moreover, interpretation of an abiogenic origin for the Copper Harbor structures is largely contingent upon observation of disruption of the structures by penetrative laminae. However, if the hosting lithology had been monolithic (i.e., laminae were not visible) this sedimentological relationship would not have been observed, and the absence of this evidence may possibly have led to interpretation of these structures as biogenic. Consequently, enigmatic and potentially biogenic structures occurring in homogeneous strata should be interpreted with particular caution.

ACKNOWLEDGMENTS

We thank two anonymous reviewers for helpful comments that greatly improved this manuscript. We thank Robert Dott, Jr. and Andrew Knoll for helpful correspondence. Derek Briggs provided valuable comments on drafts of this manuscript. We thank Anikó Bezur for assistance with SEM-EDS analysis at the Institute for the Preservation of Cultural Heritage, Yale University. X-ray scans were carried out by Brian Bagley at the University of Minnesota Department of Earth Sciences X-Ray Computed Tomography Laboratory. We thank Elizabeth Clark, Adam Pritchard, and Bhart-Anjan Bhullar for assistance in processing XRCT data. This material is based upon work supported by the National Aeronautics and Space Administration through the NASA Astrobiology Institute under Cooperative Agreement Nos. NNA15BB03A and NNA13AA90A issued through the Science Missions Directorate, and an NSF-ELT Program grant to NJP. RPA was supported by NASA Headquarters under the Earth and Space Science Fellowship Program (grant NNX14AP10H). LGT was supported by Yale University and NSF Earth Sciences Postdoctoral Fellowships.

REFERENCES

Albani, A., Bengtson, S., Canfield, D.E., Bekker, A., Macchiarelli, R., Mazurier, A., Hammarlund, E., Boulvais, P., Dubuy, J., Fontaine, C., Fürsich, F., Gauthier-Lafaye, F., Janvier, P., Javaux, E.J., Ossa, F., Pierson-Wickmann, A., Ribooleau, A., Sardini, P., Vachard, D., Whitehouse, M., and Meunier, A., 2010, Large colonial organisms with coordinated growth in oxygenated environments 2.1 Gyr ago: Nature, v. 466, p. 100–104, doi: 10.1038/nature09166.

Albani, A., Bengtson, S., Canfield, D.E., Riboulleau, A., Bard, C. R., Macchiarelli, R., Pemba, L.N., Hammarlund, E., Meunier, A., Mouele, I.M., Benzerara, K., Bernard, S., Boulvai, P., Chaussidon, M., Cesari, C., Fontaine, C., Chi-Fru, E., Ruiz, J.M.G., Gauthier-Lafaye, F., Mazurier, A., Pierson-Wickmann, A.C., Rouxel, O., Trentesaux, A., Vecoli, M., Versteegh, G.J.M, White, L., Whitehouse, M., and Bekker, A., 2014, The 2.1 Ga old Francevillian biota: biogenicity, taphonomy and biodiversity: PLOS One, v. 9, p. 1–18, doi: 10.1371/journal.pone.0099438.

Anderson, R.P., Fairchild, I.J., Tosca, N.J., and Knoll, A.H., 2013, Microstructures in metasedimentary rocks from the Neoproterozoic Bonahaven Formation, Scotland: microconcretions, impact spherules, or microfossils?: Precambrian Research, v. 233, p. 59–72, doi: 10.1016/j.precamres.2013.04.016.

Angert, E.R., Clements, K.D., and Pace, N.R., 1993, The largest bacterium: Nature, v. 362, p. 239–241, doi: 10.1038/362239a0.

Beraldi-Campesi, H., 2013, Early life on land and the first terrestrial ecosystems: Ecological Processes, v. 2, p. 1–17, doi: 10.1186/2192-1709-2-1.

Brain, C.K., Prave, A.R., Hoffman, K-H., Fallick, A.E., Botha, A., Herd, D.A., Sturrock, C., Young, I., Condon, D.J., and Allison, S.G., 2012, The first animals: ca. 760-million-year-old sponge-like fossils from Namibia: South African Journal of Science, v. 108, p. 1–8, doi: 10.4102/sajs.v108i1/2.658.

Bucher, K. and Grapes, R., 2011, Petrogenesis of Metamorphic Rocks: Springer, Berlin, 428 p.

Cannon, W.F., 1992, The Midcontinent Rift in the Lake Superior region with emphasis on its geodynamic evolution: Tectonophysics, v. 213, p. 41–48, doi: 10.1016/0040-1951(92)90250-A.

Cohen, P.A. and Knoll, A.H., 2012, Scale microfossils from the Mid-Neoproterozoic Fifteenmile Group, Yukon Territory: Journal of Paleontology, v. 86, p. 775–800, doi: 10.1666/11-138.1.

Cohen, P.A. and Macdonald, F.A., 2015, The Proterozoic record of eukaryotes: Paleobiology, p. 1–23, doi: 10.1017/pab.2015.25.

Cohen, P.A., Schopf, J.W., Butterfield, N.J., Kudryavtsev, A.B., and Macdonald, F.A., 2011, Phosphate biomineralization in mid-Neoproterozoic protists: Geology, v. 39, p. 539–542, doi: 10.1130/g31833.1.

Coleman, M.L. and Raiswell, R., 1995, Source of carbonate and origin of zonation in pyritiferous carbonate concretions: evaluation of a dynamic model: American Journal of Science, v. 295, p. 282–308, doi: 10.2475/ajs.295.3.282.

Curtis, C.D., Coleman, M.L., and Love, L.G., 1986, Pore water evolution during sediment burial from isotropic and mineral chemistry of calcite, dolomite, and siderite: Geochimica et Cosmochimica Acta, v. 50, p. 2321–2334, doi: doi: 10.1016/0016-7037(86)90085-2.

Daniels, P., 1982, Upper Precambrian sedimentary rocks: Oronto Group, Michigan-Wisconsin, *in* Wold, R. and Hinze, W. (eds.), Geology and Tectonics of the Lake Superior Basin, Geological Society of America Memoir 156, Boulder, p. 107–134.

Davies, D. and Paces, J., 1990, Time resolution of geologic events on the Keweenaw Peninsula and implications for development of the Midcontinent Rift system: Earth and Planetary Science Letters, v. 97, p. 54–64, doi:10.1016/0012-821X(90)90098-I.

Dix, G.R. and Mullins, H.T., 1987, Shallow, subsurface growth and burial alteration of Middle Devonian calcite concretions: Journal of Sedimentary Research, v. 57, p. 140–152, doi: 10.1306/212f8acb-2b24-11d7-8648000102c1865d.

Driese, S. and Medaris, L.G., 2008, Evidence for biological and hydrological controls on the development of a Paleoproterozoic paleoweathering profile in the Baraboo Range, Wisconsin, USA: Journal of Sedimentary Research, v. 78, p. 443–457, doi: 10.2110/jsr.2008.051.

Elmore, R.D., 1984, The Copper Harbor Conglomerate: a late Precambrian fining-upward alluvial fan sequence in northern Michigan: Geological Society of America Bulletin, v. 95, p. 610–617, doi: 10.1130/0016-7606(1984)95<610:TCHCAL>2.0CO;2.

Fedonkin, M. and Yochelson, E.L., 2002, Middle Proterozoic 1.5 Ga *Horodyskia moniliformis*: oldest known tissue-grade Eukaryote: Smithsonian Contributions to Paleobiology, v. 94, p. 29.

Fedorchuk, N.D., Dornbos, S.Q., Corsetti, F.A., Isbell, J.L., Petryshyn, V.A., Bowles, J.A., Wilmeth, D.T., 2016, Early non-marine life: evaluating the biogenicity of Mesoproterozoic fluvial-lacustrine stromatolites: Precambrian Research, v. 275, p. 105–118, doi:10.1016/j.precamres.2016.01.015.

Grey, K. and Williams, I.R., 1990, Problematic bedding-plane markings from the middle Proterozoic Manganese Subgroup, Bangemall Basin, Western Australia: Precambrian Research, v. 46, p. 307–327, doi: 10.1016/0301-9268(90)90018-L.

Gutzmer, J. and Beukes, N., 1998, Earliest laterites and possible evidence for terrestrial vegetation in the early Proterozoic: Geology, v. 26, p. 263–266, doi: 10.1130/0091-7613(1998) 026<0263:ELAPEF>2.3.CO;2.

Hamblin, W. and Horner, W., 1961, Sources of Keweenawan conglomerates of northern Michigan: Journal of Geology, v. 69, p. 204–211.

Han, T.M. and Runnegar, B., 1992, Megascopic eukaryotic algae from the 2.1-billion-year-old Negaunee Iron formation: Science, v. 257, p. 232–235, doi: 10.1125/science.1631544.

Hinze, W., Braile, L., and Chandler, V., 1990, A geophysical profile of the southern margin of the Midcontinent rift system in western Lake Superior: Tectonics, v. 9, p. 303–310, doi: 10.1029/TC009i002p00303.

Horodyski, R., 1982, Problematic bedding-plane markings from the middle Proterozoic Appekunny Argillite, Belt Supergroup, northwestern Montana: Journal of Paleontology, v. 56, p. 882–889.

Knoll, A.H., 2003, Biomineralization and evolutionary history: Reviews in Mineralogy and Geochemistry, v. 54, p. 329–356, doi: 10.2113/0540329.

Knoll, A.H., 2011, The multiple origins of complex multicellularity: Annual Reviews of Earth and Planetary Sciences, v. 39, p. 217–219, doi: 10.1146/annurev.earth.031208.100209.

Knoll, A.H., 2014, Paleobiological perspectives on early eukaryotic evolution: Cold Spring Harbor Perspectives in Biology, v. 6, p. 1–14, doi: 10.1101/cshperspect.a016121.

Knoll, A.H., Javaux, E.J., Hewitt, D., and Cohen, P., 2006, Eukaryotic organisms in Proterozoic oceans: Philosophical Transactions of the Royal Society B-Biological Sciences, v. 361, p. 1023–1038, doi: 10.1098/rstb.2006.1843.

Knoll, A.H., Strother, P.K., and Rossi, S., 1988, Distribution and diagenesis of microfossils from the lower Proterozoic Duck Creek Dolomite, Western Australia: Precambrian Research, v. 38, p. 257–279, doi: 10.1016/0301-9268(88)90005-8.

Kumar, S., 1995, Megafossils from the Mesoproterozoic Rohtas Formation (the Vindhyan Supergroup), Katni area, central India: Precambrian Research, v. 72, p. 171–184, doi: 10.1016/0301-9268(94)00085-6.

Maloof, A.C., Rose, C.V., Beach, R., Samuels, B.M., Calmet, C.C., Erwin, D.H., Poirer, G.R., Yao, N., and Simons, F.J., 2010, Possible animal-body fossils in pre-Marinoan limestones from South Australia: Nature Geoscience, v. 3, p. 653–659, doi:10.1038/ngeo934.

McCoy, V.E., Young, R.T., and Briggs, D.E.G., 2015, Factors controlling exceptional preservation in concretions: PALAIOS, v. 30, p. 272–280, doi: 10.2110/palo.2014.081.

Miller, J.D. and Vervoort, J., 1996, The latent magmatic stage of the Midcontinent rift: a period of magmatic underplating and melting of the lower crust: Proceedings of the Institute on Lake Superior Geology, v. 42, p. 33–35.

Mitchell, R.L. and Sheldon, N.D., 2016, Sedimentary provenance and weathering processes in the 1.1 Ga Midcontinent Rift of the Keweenaw Peninsula, Michigan, USA: Precambrian Research, v. 275, p. 225–240, doi: 10.1016/j.precamres.2016.01.017.

Morad, S. and Eshete, M., 1990, Petrology, chemistry, and diagenesis of calcite concretions in Silurian shales from central Sweden: Sedimentary Geology, v. 66, p. 113–134, doi: 10.1016/0037-0738(90)90010-q.

Nicholson, S., Shirey, S., Schulz, K., and Green, J., 1997, Rift-wide correlation of 1.1. Ga Midcontinent Rift system basalts: Canadian Journal of Earth Sciences, v. 34, p. 504–520, doi: 10.1139/e17-041.

Ohmoto, H., 1996, Evidence in 2.2 Ga paleosols for the early evolution of atmospheric oxygen and terrestrial biota: Geology, v. 24, p. 1135–1138, doi: 10.1130/0091-7613(1996)024<1135:EIPGPF>2.3.CO;2.

Ojakangas, R. and Dickas, A.B., 2002, The 1.1 Ga Midcontinent Rift System, central North America: sedimentology of two deep boreholes, Lake Superior region: Sedimentary Geology, v. 147, p. 13–36, doi:10.1016/S0037-0738(01)00185-3.

Ojakangas, R., Morey, G.B., and Green, J.C., 2001, The Mesoproterozoic Midcontinent Rift system, Lake Superior region, USA: Sedimentary Geology, v. 141, p. 421–442, doi: 10.1016/S0037-0738(01)00085-9.

Planavsky, N.J., Tarhan, L.G., Bellefroid, E.J., Evans, D.A.D., Reinhard, C. T., Love, G. D., and Lyons, T. W., 2015, Late Proterozoic transitions in climate, oxygen, and tectonics, and the rise of complex life: The Paleontological Society Papers, v. 21, p. 47–82.

Retallack, G.J., Dunn, K.L., and Saxby, J., 2013a, Problematic Mesoproterozoic fossil *Horodyskia* from Glacier National Park, Montana, USA: Precambrian Research, v. 226, p. 125–142, doi:10.1015/j.precamres.2012.12.005.

Retallack, G.J., Krull, E.S., Thackray, G.D., and Parkinson, D., 2013b, Problematic urn-shaped fossils from a Paleoproterozoic (2.2 Ga) paleosol in South Africa: Precambrian Research, v. 235, p. 71–87, doi: 10.1016/j.precamres.2013.05.015.

Rye, R. and Holland, H.D., 2000, Life associated with a 2.76 Ga ephemeral pond?: evidence from Mount Row #2 paleosol: Geology, v. 28, p. 483–486, doi: 10.1130/0091-7613(2000)28<483:LAWAGE>2.0.CO;2.

Schlegel, H.G., 1985, Allgemeine Mikrobiologie: Thieme Verlag, Stuttgart, 571 p.

Schulz, H.N. and Jørgensen, B.B., 2001, Big bacteria: Annual Review of Microbiology, v. 55, p. 105–137, doi: 10.1146/annurev.micro.55.1.105.

Seilacher, A., 2001, Concretion morphologies reflecting diagenetic and epigenetic pathways: Sedimentary Geology, v. 143, p. 47–57, doi:10.1016/S0037-0738(01)00092-6.

Seilacher, A., Andalib, F., Dietl, G., and Gocht, H., 1976, Preservational history of compressed Jurassic ammonites from southern Germany: Neues Jahrbuch für Geologie und Paläntologie, Abhandlungen, v. 152, p. 307–356.

Seilacher, A., Reif, W.-E., and Westphal, F., 1985, Sedimentological, ecological and temporal patterns of fossil Lagerstätten: Philosophical Transactions of the Royal Society B-Biological Sciences, v. 311, p. 5–23, doi: 10.1098/rstb.1985.0134.

Sellés-Martínez, J., 1996, Concretion morphology, classification and genesis: Earth-Science Reviews, v. 41, p. 177–210, doi: 10.1016/S0012-8252(96)00022-0.

Sheldon, N.D., 2012, Microbially induced sedimentary structures in the ca. 1100 Ma terrestrial Midcontinent Rift of North America, *in* Noffke, N. and Cahetz, H. (eds.), Microbial Mats in Siliciclastic Depositional Systems Through Time: SEPM Special Publication No. 11, p. 153–162.

Stein, C.A., 2015, Age of the Jacobsville sandstone and implications for the evolution of the Midcontinent Rift: Geological Society of America Abstracts with Programs, v. 47, p. 809.

Stein, C.A., Stein, S., Kley, J., Hindle, D., Keller, G.R., 2014a, Mid-continent Rift: rift, LIP, or both and implications for Rodinia reconstructions: Geological Society of America Abstracts with Programs, v. 46, p. 372.

Stein, C.A., Stein, S., Merino, M., Keller, G.R., Flesch, L.M., and Jurdy, D.M., 2014b, Was the Midcontinent Rift part of a successful seafloor-spreading episode?: Geophysical Research Letters, v. 41, p. 1465–1470, doi: 10.1002/2013GL059176.

Strother, P.K., Battison, L., Brasier, M.D., and Wellman, C.H., 2011, Earth's earliest non-marine eukaryotes: Nature, v. 473, p. 505–509, doi: 10.1038/nature09943.

Wacey, D., Saunders, M., Roberts, M., Menon, S., Green, L., Kong, C., Culwick, T., Strother, P., and Brasier, M.D., 2014, Enhanced cellular preservation by clay minerals in 1 billion-year-old lakes: Scientific Reports, v. 7, p. 5841 (1–11), doi: 10.1038/srep05841.

Walter, M.R., Du, R., and Horodyski, R.J., 1990, Coiled carbonaceous megafossils from the middle Proterozoic of Jixian (Tianjin) and Montana: American Journal of Science, v. 290A, p. 133–148.

Walter, M.R., Oehler, J.H., and Oehler, D.Z., 1976, Megascopic algae 1300 million years old from the Belt Supergroup, Montana: a reinterpretation of Walcott's *Helminthoidichnites*: Journal of Paleontology, v. 50, p. 872–881.

Watanabe, Y., Martini, J., and Ohmoto, H., 2000, Geochemical evidence for terrestrial ecosystems 2.6 billion years ago: Nature, v. 408, p. 574–578, doi: 10.1038/35046052.

Wilkinson, M. and Damier, M.D., 1990, The rate of growth of sandstone-hosted calcite concretions: Geochimica et Cosmochimica Acta, v. 54, p. 3391–3399, doi: 10.1016/0016-7037(90)90293-t.

Yochelson, E.L and Fedonkin, M.A., 2000, A new tissue-grade organism 1.5 billion years old from Montana: Proceedings of the Biological Society of Washington, v. 113, p. 843–847.

Received 29 January 2016; accepted 10 May 2016.