

EXCEPTIONAL FOSSIL PRESERVATION IN THE CONASAUGA FORMATION, CAMBRIAN, NORTHWESTERN GEORGIA, USA

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ABSTRACT

Mudstones and siliceous concretions in the middle Cambrian Conasauga Formation, northwestern Georgia, contain body and trace fossils showing nonmineralized preservation and represent two temporally and spatially different marine environments. Identifiable, nonbiomineralized taxa include components of a Burgess Shale-type biota with red and green algae, primitive sponges, and the arachnomorph arthropod *Naraoia compacta*. Also exceptionally preserved are the filamentous appendages of a large ptychopariid trilobite and assemblages of oriented hyolithid tests we interpret as priapulid coprolites and cololites. Exceptional preservation in the Conasauga Formation has multiple causes. The Conasauga contains superabundant siliceous concretions, many with skeletal, trace, and some nonbiomineralized fossils. Shale specimens, especially sponges with preserved details, and whole-body trilobite preservations, often have iron (Fe) oxide halos that resulted from a biochemical cascade including bioimmuration, decomposition gas anoxia, Fe-sulfide crystallization, and Fe oxidation. Preservation of soft tissue is also partly attributable to the well-sorted clay matrix of inner shelf Conasauga shales, which allowed mechanical imprinting of body fossils. Several nonbiomineralized fossils show algal overgrowths, suggesting an additional form of bioimmuration. Exceptional preservation in the Conasauga Formation is relatively poor compared with such better-known Cambrian Lagerstätten as the Burgess and Wheeler Shales; nevertheless, it is significant for three reasons. The siliceous concretions are a rare vehicle for exceptional preservation and feature three-dimensional fossils rather than the more common compressed specimens. The older Conasauga biota occupied a shallow-shelf environment, a setting in which exceptional preservation is poorly understood. The Conasauga Formation extends the geographic range of a Burgess Shale-type biota to the extreme southeastern USA.

INTRODUCTION

The Cambrian Conasauga Formation of northwestern Georgia, United States (Fig. 1), contains two assemblages of soft-bodied and lightly mineralized organisms preserved as carbonaceous or ferrous impressions in shale, along with some specimens preserved in siliceous concretions, the latter being a largely overlooked mode of Cambrian soft-tissue preservation. Several types of organisms also occur, at least generically, in the Burgess Shale and penecontemporaneous deposits in the western United States. The report here, therefore, contains examples of an exceptional Cambrian biota in the southeastern United States, including some Burgess Shale taxa, not preserved in Burgess Shale-type preservation (Butterfield, 1995, 2003).

Exceptionally preserved biotas, termed Konservat Lagerstätten (Seilacher, 1970; Seilacher et al., 1985), are of extraordinary paleobiological interest. The current use of the term Lagerstätten commonly includes

fossil assemblages or preservational conditions where nonbiomineralized organisms, articulated skeletons, internal soft parts, or such rarely preserved associated body materials as gut contents or feces are present along with more typical shelly fossils. The Cambrian Burgess Shale biota is among the archetypal Konservat Lagerstätten and continues to receive intensive scrutiny for both the modes of preservation (e.g., Butterfield, 1990, 1996; Orr et al., 1998; Petrovich, 2001; Briggs, 2003; Butterfield, 2003) and taxic composition in it (Conway Morris, 1986, 1989a, 1989b, 1998; Gould, 1989; Briggs et al., 1992, 1994; Hagadorn, 2002b). Cambrian Lagerstätten with diverse biotas are being increasingly discovered and described, partly due to the intensity of the search and partly due to new exploration, notably in the Early Cambrian Chengjiang biota, Yunnan Province, China (Hou and Bergstrom, 1997; Shu et al., 1999; Babcock et al., 2001; Zhang et al., 2001; Hagadorn, 2002a; Hou et al., 2004).

Exceptional preservation occurs throughout the fossil record (Allison and Briggs, 1991; Martin, 1999; Bottjer et al., 2002; Briggs, 2003), but the most widespread and abundant exceptionally preserved marine biotas are of Cambrian age (Conway Morris, 1985; Allison and Briggs, 1991, 1993; Hagadorn, 2002c; Orr et al., 2003), particularly in the early and middle Cambrian (Yochelson, 2006; see the discussion of chronostratigraphic terminology). The apparent temporal bias toward Cambrian Lagerstätten preservation has been termed the Cambrian taphonomic window (Allison and Briggs, 1991), implying that Late and post-Cambrian marine conditions, especially in deeper waters, were generally less suitable for exceptional preservation than were conditions in the earlier Cambrian.

GEOLOGIC SETTING

Stratigraphy and Setting of the Conasauga Formation

All specimens we discuss come from mostly shaly facies of the Conasauga Formation in Floyd County, northwestern Georgia. The study area (Fig. 1) is in the Appalachian Ridge and Valley Province, in a zone characterized by relatively low topography with valleys floored by folded, incompetent strata mostly of the Conasauga shales. Tectonically, this area is situated on the Rome Thrust Sheet (Thomas, 1985), which extends from northwestern Georgia to northeastern Alabama as part of a series of northeast-striking, northwest-trending thrust sheets (Osborne et al., 2000). The Conasauga Formation, sometimes recognized as Group status, reaches local thicknesses to 885 m (Hasson and Hasse, 1988) and represents multiple depositional environments formed on inner-shelf and shelf-edge basins along the Laurentian margin of the Cambrian Iapetus Ocean. These paleoenvironments include shallow-water, peritidal clastic wedges, admixed outer-shelf carbonates and shales, and carbonate shoals along the shelf-to-slope boundary (Hasson and Haase, 1988; Astini et al., 2000).

In the collecting area for this study, the Coosa River Valley in northwestern Georgia (Fig. 1), the Conasauga Formation is represented largely by broad exposures of shale facies. These are complexly faulted, making the total thickness difficult to estimate, but certainly it is greater than 400 m thick (Osborne et al., 2000). Samples from the proximal area are from the upper portion of the Conasauga Formation, with outcrops commonly in small drainages adjacent to the Coosa River (e.g., site MB in Fig. 1)

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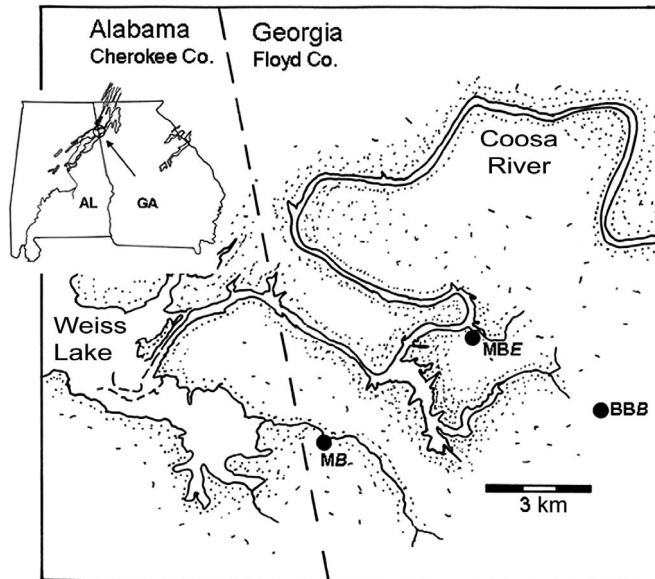


FIGURE 1—Localities with middle Cambrian Lagerstätten in the Conasauga Formation, Coosa River Valley, Georgia; inset map of regional Cambrian outcrop. Locality abbreviations: **BBB** = Black's Bluff Road, *Bolaspidella* Zone; **MB** = Melson, Georgia, *Bolaspidella* Zone; **MGE** = McGee Bend Road, *Ehmaniella* Zone.

and in road cuts and roadside ditches (e.g., site BBB in Fig. 1). Clear-cut, logged-and-dragged timberlands in the area expose broad surfaces yielding siliceous concretions that weather from soils developed on the soft shale. Many of these concretions preserve skeletal and trace fossils, and some preserve nonbiomineralized fossils. In addition, a small quarry cut into the lower Lagerstätte facies (site MBE in Fig. 1) has yielded some of the best specimens.

Age and Composition of the Lagerstätten

The age of the Conasauga Formation in the immediate study spans the portion of the Cambrian polymerid trilobite zones including the *Ehmaniella* and *Bolaspidella* Biozones. The Conasauga Lagerstätten are placed in the currently recognized Laurentian Marjuman Stage (Fig. 2; *vide* Ludvigsen and Westrop, 1985, as modified in Palmer, 1998, 1999). Traditionally, the Marjuman Stage would be placed in the uppermost Middle Cambrian to lowermost Upper Cambrian Series (Lochman-Balk and Wilson, 1958; Robison, 1964a, 1976; Yochelson, 2006); however, efforts at revision of Cambrian chronostratigraphy (Palmer, 1998, 1999; Geyer and Shergold, 2000; Peng et al., 2004; Gradstein et al., 2005; Babcock et al., 2005) indicate that the traditional three-part Cambrian series nomenclature is inapplicable to Laurentia. A developing, but not yet formally ratified, global chronostratigraphy would place the Conasauga Lagerstätten in unnamed Series 2 and Series 3 of the proposed four-part Cambrian Global Standard Stratotype Section (Peng et al., 2004; Babcock et al., 2004, 2005).

Lower (Inner-Shelf) Lagerstätte Unit.—The lower Lagerstätte unit corresponds to the upper portion of the Cordilleran *Ehmaniella* polymerid trilobite Biozone (Sundberg, 1994; Palmer, 1998, 1999; Geyer and Shergold, 2000; Babcock et al., 2005). This interval has also been termed the *Oryctocephalus* Zone (Robison and Hintze, 1975; Robison, 1976; Schwimmer, 1989) and the *Altiocculus* Subzone (Sundberg, 1994). This Conasauga Formation unit correlates with the Swasey Formation in the Great Basin (Robison and Hintze, 1975; Robison, 1976) and shares several trilobite genera (e.g. *Glyphaspis*, *Bolaspis*) with the Swasey. The strata in this unit are very well sorted, flaggy-bedded, slightly petroliferous, tan mudstones. It contains few discrete siliceous concretions, as compared with the upper unit, but the mudstones are hard and contain inter-

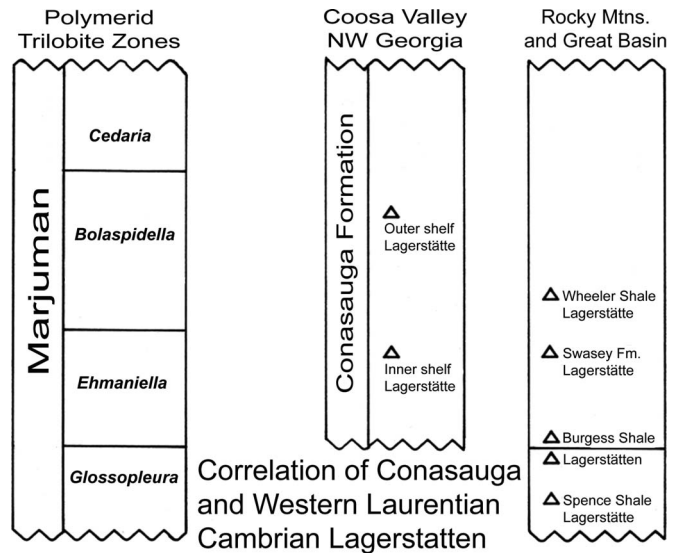


FIGURE 2—Biostratigraphic correlations of Conasauga Lagerstätten and representative middle Cambrian strata in the western continent. Note: Conasauga biotas are younger than both Burgess Shale biotas, but correlate well with the Swasey and Wheeler Lagerstätten.

stitial silica cement. The mudstone does not show significant endolithic trace fossils, suggesting that there was minimal deep infaunal activity.

We interpret the depositional environment as having been the inner marine clastic shelf, perhaps near to the shore, based on the nearly carbonate-free, light-colored mud matrix, the low-diversity, endemic polymerid trilobite assemblage, and the extreme rarity of pelagic and possibly planktonic agnostoid trilobites (Robison, 1972). Similar faunal characteristics are observed in such other presumably nearshore middle Cambrian environments as in the Pika Formation in Alberta (Melzak and Westrop, 1994) and the Wolsey Shale in Montana (Deiss, 1939; Schwimmer, 1973, 1975). Skeletal fossils in this lower Conasauga Lagerstätte unit (Table 1) are dominated by the large, asaphiscid trilobite, *Glyphaspis capella* (Walcott, 1916). Nonsclerotized organisms preserved in this unit (Table 1) include red and green algae, sponges, a nektaspid arthropod, and a remarkable specimen of *G. capella* that preserves several of its filamentous appendages.

Upper (Mid-to-Outer Shelf) Lagerstätte Unit.—The upper Conasauga Lagerstätte assemblage is in the *Bolaspidella* polymerid assemblage zone (Robison, 1976; Schwimmer, 1989). This stratum represents a somewhat deeper water, outer-shelf setting based on a fauna (Table 2) dominated by such polymerid trilobites as *Elrathia antiquata* and *Asaphiscus gregarius* (Resser, 1938; Schwimmer, 1989) and an abundance of agnostoids (primarily *Peronopsis* sp.). This unit correlates biostratigraphically and environmentally with the outer-shelf Wheeler Formation in the Great Basin (Robison, 1976; Babcock et al., 2004; Gaines et al., 2005).

The upper Lagerstätte unit is olive-gray to gray fissile shale containing numerous syndiagenetic siliceous concretions. In addition to a moderately diverse trilobite fauna (Schwimmer, 1989; Table 2), this unit also contains abundant hyolithids (*Haplophrentis*? sp.) and fairly common sponge and algal fossils. This unit includes skeletal fossils, trace fossils, and nonmineralized fossils in siliceous concretions, which preserve globular calcisponges, a high-relief priapulid cololite, and algal-encrusted sponges and hyolithids. Such siliceous preservation is noteworthy also for preserving three-dimensional, nonbiomineralized specimens that reveal unusual structures. As a noteworthy example, star-cobbles are extraordinarily abundant in this facies (see Fig. 3A). These lobate, radially symmetrical concretions were first identified as jellyfish of the genera *Brooksella* and *Laotira* by Walcott (1896, 1898) and recognized as such by authors for many subsequent years (e.g., Resser, 1938; Harrington and Moore, 1956; Willoughby and Robison, 1979). More recently, *Brooksella* (incorporating *Laotira* as a junior synonym) has been reinterpreted as a

TABLE 1—Representative biota of the *Ehmaniella* Zone in the Conasauga Formation (Walcott, 1916; Resser, 1938; Schwimmer, 1989; Schwimmer and Robinson, 1990; Montante and Schwimmer, 2005; field observations). Taxa discussed in text indicated with an asterisk.

Trilobita

- **Glyphaspis capella* Walcott, 1920
- **Naraoia compacta* Walcott, 1912
- Asaphiscus* sp.
- Bolaspis* cf. *B. labrosa* Deiss, 1939
- Tonkinella* sp.
- Olenoides* sp.
- Solenopleurella* sp.
- Peronopsis* sp.

Brachiopoda

- Wimanella aurialis* Bell, 1940
- Acrothyra* sp.
- Lingulella* sp.
- Micromitra* sp.

Hyolithida

- **Haplophrentis*? sp.
- Hyolithida, gen. & sp. indet.

Porifera

- **Leptomitius* cf. *L. zitteli* Walcott, 1886
- *cf. *Choia* sp.
- *Hexactinellida, gen. & sp. indet. (= *Brooksella alternata* spicules?)

Rhodophyta

- **Dalyia racemata* (Walcott, 1919)

Chlorophyta

- *Chlorophyta, gen. & sp. indet.

feeding trace (Fürsich and Bromley, 1985; Rindsberg, 2000), rather than as a body fossil, with the consequence that *Brooksella*, in this interpretation, would be subsumed into the senior synonym *Dactyloidites* Hall, 1886.

Most recently, *Brooksella* has been identified as a hexactinellid sponge fossil (Ciampaglio et al., 2005, in press), which would resurrect *Brooksella* as a valid body-fossil genus. This current identification suggests that isolated hexactinellid spicules (discussed later) in the outer-shelf shale are derived from degraded *Brooksella* specimens. Notwithstanding their origin, the three-dimensional preservation of Conasauga *Brooksella* specimens shows that unusually good preservation of soft structures is present in siliceous concretions.

EXCEPTIONALLY PRESERVED BIOTA OF THE CONASAUGA FORMATION

The nonmineralized fossils in the Conasauga Formation represent moderately diverse organisms ranging from protocists to higher invertebrates. In addition to the taxonomic variety of soft-bodied fossils, there are multiple forms of preservation evident among various localities, with some clades exhibiting multiple types of exceptional preservations (cf. Zhu et al., 2005). For example, a red alga (*Dalyia*) occurs as both a carbonaceous and iron (Fe)-oxide film on a claystone surface (Fig. 3B) and as a three-dimensional mass in a siliceous concretion (Fig. 3C). To present the data in a comprehensible manner, we discuss nonbiomineralizing organisms and nonmineralized structures in animals that secrete biomineralized parts taxonomically and then discuss taphonomic observations that cut across biological affinities. All specimens described and figured here, unless otherwise indicated, are cataloged and housed in the Cambrian research collections at Columbus State University, Columbus, Georgia. Catalog numbers in the Columbus State collections are given in figure captions.

Red Algae (Rhodophyta): *Dalyia*? cf. *D. racemata* Walcott, 1919

Macroscopic (>1 cm) branching structures characteristic of the red algae are common in the lower (*Ehmaniella* Zone) Conasauga Lagerstätte horizon.

TABLE 2—Representative biota of the *Bolaspideella* Zone in the Conasauga Formation (data sources as in Table 1).

Trilobita

- Elrathia antiquata* Resser, 1938
- Asaphiscus gregarius* (Walcott, 1912)
- Alokistocare americanum* (Walcott, 1916)
- Peronopsis* sp.
- Solenopleurella*? sp.
- Bolaspideella* sp.
- Olenoides* sp.

Brachiopoda

- Acrothyra* sp.
- Lingulella* sp.
- Paterina* sp.

Porifera

- **Leptomitius* cf. *L. zitteli* Walcott, 1886
- **Eiffelia* cf. *E. globosa* Walcott, 1920
- *? *Brooksella alternata* Walcott, 1896

Rhodophyta

- **Dalyia racemata* Walcott, 1919

Hyolithida

- **Haplophrentis*? sp.

Priapulida

- *cf. *Ottoia prolifica* Walcott, 1911

Ichnotaxa

- **Dactyloidites* sp. (? = *Brooksella alternata*: Hexactinellida)

Several well-preserved specimens appear similar to *Dalyia racemata*, which was first described from slightly older *Ogygopsis* beds of the Burgess Shale (Walcott, 1919). Among the diagnostic characteristics of *Dalyia* are slender basal branches that bifurcate into second- and third-order branches of coequal thickness, terminating in thinner multiple branchlets (Walcott, 1919; Briggs et al., 1994). The best-preserved specimens comprise the basal portions of the thalli, since all the branches are bifurcate.

Conway Morris and Robison (1988) figured specimens identified as the green alga *Yuknessia simplex* Walcott, 1919, from the Marjum and Wheeler Formations, Utah. This taxon is characterized by having a central thallus with numerous unjointed stipes; however, a single Wheeler specimen figured by Conway Morris and Robison (1988, fig. 11–3) shows an obviously branched thallus, which closely resembles and may be the same taxon as the Conasauga *Dalyia*? specimens.

Green Algae: Chlorophyta, gen. & sp. indet

A small, <1 mm coccoidal algal form is abundant in the Conasauga Formation, usually observed as chains of linked spheres (Fig. 3D), with several chains typically entwined. The same coccoidal form is also found as an encrusting mass, such as the overgrowth on a hyolithid conch (Fig. 3E). Figures 3F–G show a specimen in which chains of coccoidal fossils are entwined around a small tubular sponge (*Leptomitius* sp., discussed later), to the extent that most of the sponge is obscured. Other specimens (e.g., Figs. 3D, H) show the same algal structures on sedimentary surfaces with no apparent shell or hard parts being encrusted. This algal form is very abundant in both Conasauga Lagerstätten horizons and, as with the red alga, is found in both shaly and concretionary siliceous preservations.

Identification of this algal taxon is tenuous since the preservation reveals only the external shape and colonial growth habit. We presume this is a green alga because the coccoidal colonial form and approximate colony size most closely resemble such chlorophytes as the modern Tetrasporales genus *Gloecoccus*, in which colonial masses developed from tetrads of cells surrounded by a gelatinous matrix (Bold and Wynne, 1985). Such spheres would be likely to leave fossils resembling the Conasauga specimens. In addition, the apparently multiple growth habits and barely



FIGURE 3—*Brooksella* and algae from the Conasauga Formation. A) Representative *Brooksella* from locality MB; note variations in symmetry, suggesting these are not bilateran body fossils; coin is 2.4 cm diameter. B–H) Representative algae from the Conasauga Formation, scale bars 5 mm unless indicated. B–C) *Dalyia* cf. *D. racemata*; B) CSUC 02-10-1, *Ehmaniella* Zone, on shale showing the bifurcating thallus; C) CSUC 01-10-21, concretionary specimen, *Bolaspidella* Zone, showing thallus composed of hollow tubes. D–H) Chlorophyta, gen. & sp. indet., all from *Bolaspidella* Zone; D) CSUC 01-10-2, colonies on shale surface; E) CSUC 01-10-5, hyolithid on shale encrusted with chlorophytes; F, G) CSUC 01-10-4, demosponge (*Leptomitrus* sp.) on shale encrusted with chlorophytes; H) CSUC 01-10-7, siliceous concretion with chlorophyte colonies.

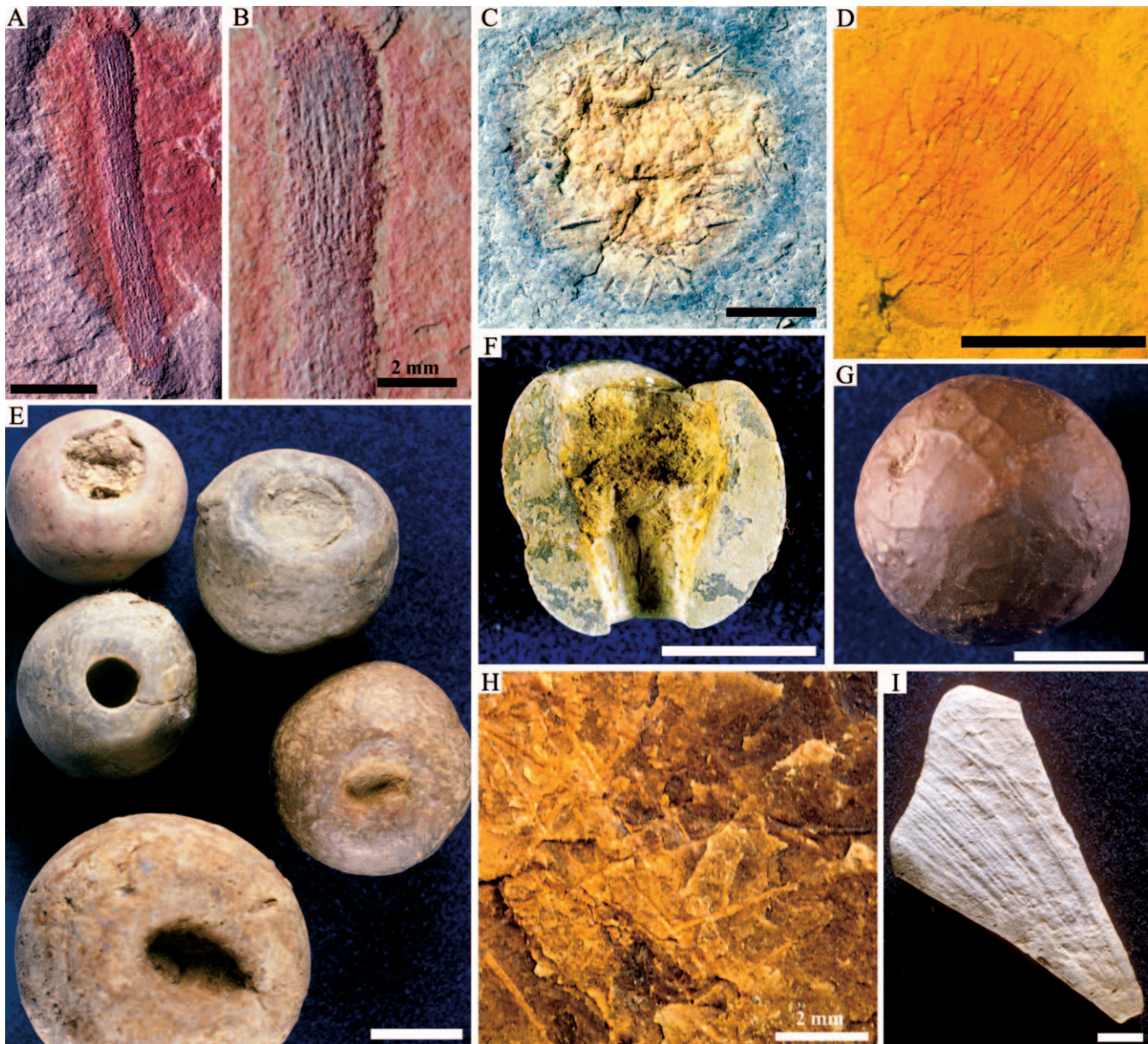


FIGURE 4—Conasauga Formation sponges showing nonmineralized preservation, scale bars 5 mm unless indicated. A–B) CSUC 02-10-4, *Leptomitius* sp., *Ehmaniella* Zone, shale specimen showing iron oxide (goethite) halo and well-preserved palisade of oxae; C–D) *Choia?* sp.; C) CSUC-01-10-10a, *Bolaspidella* Zone, showing body outline as goethite disk with broken monaxon spicules; D) CSUC-01-03-1a, small specimen with spicule fragments preserved across disk, *Ehmaniella* Zone. E–G) *Eiffelia globosa*; E) representative concretionary *Eiffelia* specimens, *Bolaspidella* Zone, showing globose morphology with distinct sulcus; F) cut specimen showing smooth lining of sulcus and possible decomposed spicular material; G) external surface showing possible expression of calcareous spicules. H–I) Hexactinellida indet., H) shale surface from *Bolaspidella* Zone with hexactinellid spicules; I) siliceous concretion from *Bolaspidella* Zone containing hexactinellid spicules.

megascopic size of this presumably single algal species suggests that it is a basal, photosynthetic protocystan. The same spherical fossils, however, could conceivably represent a cyanophyte structure.

This alga does not appear to be related to the long-stipe taxon *Yuknessia simplex* Walcott, 1919 (and see earlier) because of the distinctly coccoid morphology of the Conasauga form and its encrusting habit. While rare in the Burgess Shale (Briggs et al., 1994), *Yuknessia* appears to be more common in the Wheeler Shale (Conway Morris and Robison, 1988; Robison, 1991) and is also reported from the Chengjiang biota (Chen and Erdtmann, 1991; Hou et al., 1994). The specimens of *Yuknessia* from the Burgess Shale and those figured from the Wheeler show a relatively flat, striated stipe morphology, rather than the linked spheres of the Conasauga species. Further, no specimens of *Yuknessia* have been reported encrusting other organisms.

Porifera: Demosponges: *Leptomitius* cf. *L. zitteli* Walcott, 1886

Fossils attributed to this unbranched, tubular demosponge genus are typically 2–3 mm wide by 20–30 mm long. Many well-preserved specimens in the Conasauga (e.g., Figs. 4A–B) show parallel striations along the length, which we interpret as palisades of oxae (fibrous, siliceous monaxon spicules). Less well-preserved examples of *Leptomitius* show a concentration of spicules on the edges of the flattened tubes—a commonplace observation in other preservations of *Leptomitius* (e.g., in the Marjum Limestone; see Rigby, 1983). Specimens in the Conasauga Formation with the morphology of *Leptomitius* are found in both Lagerstätten horizons, but individuals with unambiguous structures (e.g., Fig. 4B) are only present in the older *Ehmaniella* beds. The genus *Leptomitius* is a basal monaxon demosponge (Rigby, 1986) widely distributed in middle

Cambrian deposits showing exceptional preservation, notably including the Marjum and Wheeler Formations (Rigby, 1978, 1983).

Many shale surfaces in the Conasauga Formation show dissociated parallel fibers, which may be poorly preserved siliceous monaxial spicules. This suggests that *Leptomitus* was abundant on the Conasauga shelf, but not commonly preserved in articulated condition. As shown previously (Figs. 4F–G), at least one *Leptomitus* specimen is preserved with nearly total encrustation by the unidentified coccooid green alga discussed above.

Choia? sp. (Figs. 4C–D)

Discoid specimens of 0.7–1.0 cm diameter are present in shales from both Lagerstätten horizons, with vague margins demarcated by halos of Fe oxide. A few specimens contain short, broken monaxon spicules, lying at various positions across the disk (Figs. 4C–D). These are tentatively identified as an undetermined species of *Choia*, a demosponge which in life had coronas of external siliceous monaxons (Walcott, 1920). In addition to these few better-preserved Conasauga specimens, there are numerous circular Fe stains of ~1.0 cm diameter on shale surfaces without evident spicules, which we interpret tentatively as poorly preserved individuals of *Choia?* sp.

Rigby (1986) proposed that *Choia* was a derived demosponge with *Leptomitus* near its basal ancestry. Several Cambrian species of *Choia* are known (Walcott, 1920; Rigby, 1983, 1986), with variations in the length of external spicules and overall disk sizes (6–70 mm) as the chief diagnostic specific character (Rigby, 1986). The relatively consistent size range of the Conasauga specimens suggests the species is closest to *C. carteri* Walcott, 1920, which is also known from the Wheeler and Marjum Formations (Rigby, 1978, 1983) and the Burgess Shale *Ogygopsis* beds (Rigby, 1986, Briggs et al., 1994).

Calcisponges: *Eiffelia globosa* (?) Walcott, 1920

Eroding shale exposures in the *Bolaspidella* Zone beds yield numerous globular, invaginated siliceous concretions of 12–18 mm diameter (Fig. 4E). Specimens cut sagittally (Fig. 4F) do not reveal differentiated internal structures, but there is a large sulcus present in each specimen that appears to contain remnants of degraded tissue or spicules. Several well-preserved individuals (Fig. 4G) have a surface pattern that we interpret as the remains of sexiradiate spicules. Based on the overall form, size, and apparent spicules, these appear to be calcareous sponges close to *Eiffelia globosa*, which is a monospecific genus known from the Burgess Shale (Walcott, 1920; Rigby, 1986).

No compressed shale specimens of *Eiffelia* have been found in the Conasauga Formation; the calcareous spicules may have dissolved in the siliceous and, thus, acidic bottom environment of the Conasauga shelf. These imperfect concretionary Conasauga specimens are the only known full-relief *Eiffelia* fossils.

Hexactinellid Sponges: Hexactinellida, gen. & sp. indet.

Disaggregated hexactinellid (glass) sponges are abundant in shales and siliceous concretions in both Lagerstätten horizons of the Conasauga. In the shales, the fossils assumed to be glass sponge spicules are bundles of fibers (Fig. 4H), often crossed at oblique angles by other fiber bundles or single fibers. These are interpreted to be degraded, thin-walled hexactinellids with largely parallel axes. Rigby (1983) described several groups of glass sponges from middle Cambrian deposits in the Great Basin with similar simple structural organization, including *Protospongia* and *Testispongia*; however, the ostensible hexactinellid material in the Conasauga shales is far too fragmentary to allow generic identification.

Assuming *Brooksella* is a hexactinellid sponge fossil (Ciampaglio et al., 2005, in press), the *Protospongia*-type spicules in the Conasauga were secreted by *Brooksella*. Such fossils as the siliceous concretion from the *Bolaspidella* Zone (Fig. 4I), with tightly organized, long, parallel stria-

tions that penetrate through the entire concretion, however, do not conform to the radial morphology of *Brooksella* and must represent a different hexactinellid taxon.

Priapulida: *Ottoia* cf. *O. prolifica* Walcott, 1911

Priapulid worms are minor constituents of modern marine ecosystems, whereas during the Cambrian the clade was apparently more diverse and included important benthic marine predators (Huang et al., 2004). Cambrian priapulids are abundant in the Maotianshan Shale (Chengjiang) biota in Yunnan, China (Huang et al., 2004), and in the Burgess Shale (Conway Morris, 1977; Briggs et al., 1994) where the abundance of priapulid fossils is attested to by the specific name (*prolifera*) of the thick-bodied genus *Ottoia* (Walcott, 1911). Priapulids are also well represented in lesser Cambrian Lagerstätten, including such deposits as the Spence and Marjum Formations (Conway Morris and Robison, 1986). Despite their abundance in other rock units, however, body fossils of priapulids have not been clearly identified in the Conasauga Formation, although some suggestive structures in shales have the shape and size of typical *Ottoia*. Nevertheless, some of the most interesting Conasauga trace fossils are cololites—isolated fossilized guts—or coprolites attributable to priapulid worms.

Numerous *Ottoia prolifica* have been found in Lagerstätten with preserved gut contents (Fig. 5A), and these usually include hyolithid conchs, with minor amounts of brachiopod and small trilobite fragments (Conway Morris, 1977; Babcock and Robison, 1988). More than 30 such *O. prolifica* have been found in the Burgess Shale (Briggs et al., 1994), and similar remains have been found in the Spence Shale (Conway Morris and Robison, 1986). One of the notable characters of these gut contents is the preferred orientation of the ingested hyolithids, which are parallel to the body outline of the worms, and with the hyolithid conchs oriented with their apertures towards the anal end of the priapulids (Conway Morris, 1977; Babcock and Robison, 1988). Conway Morris (1977) observed that in 11 *Ottoia* studied containing hyolithids in the guts, only one hyolithid conch was oriented opposite the others.

The overall configurations of the intestines in several Cambrian priapulid taxa include relatively simple curvilinear morphologies (e.g., in *Selkirkia*) and slightly coiled or convoluted structures (in *Ottoia*: e.g., Conway Morris and Robison, 1986, fig. 3). Isolated fossil priapulid guts (i.e., cololites) are known previously from the Chengjiang biota (S. Hu, personal communication, 2004).

Coprolites attributed to Cambrian priapulids by Vannier and Chen (2005) from the Lower Cambrian Maotianshan Shale (Chengjiang) biota in Yunnan, China, are based on ribbonlike accumulations of small hyolithids (*Haplophrentis* sp.) with preferential orientation of the conchs. Vannier and Chen recognized several categories of fecal accumulations, including concentric and elongate aggregates; elongate aggregates were attributed to priapulids. Other than our study, priapulid coprolites have not been reported with certainty, but Conway Morris and Robison (1986) discussed a nondescript vermiform coprolite from the Marjum Formation of possible priapulid origin.

Conasauga priapulid traces consist of the gut contents from two specimens, each identifiable by masses of oriented hyolithids. It is not certain whether either or both are coprolites or the remains of the actual gut (i.e., cololites); but, in either case, the orientation and concentrations of small hyolithids clearly shows they are priapulid digestive products. The two masses occur in different modes of preservation: the first in a siliceous concretion (Fig. 5B) from the *Bolaspidella* Zone, containing 31 conchs tentatively referred to *Haplophrentis?* (cf. Babcock and Robison, 1988). The hyolithids extend along a 50 mm long by ~10 mm wide, slightly curvilinear trace, with ~0.8 mm of vertical relief on the concretion. Detailed examination also reveals a few trilobite fragments, which may have been part of the gut contents or a later accretion. For comparison, the elongate aggregates reported by Vannier and Chen (2005) were 45–70 mm long and contained 40–150 conchs each. The high relief of the Con-



FIGURE 5—Ecdysozoan fossils, scale bars 5 mm unless indicated. A–C) Priapulid body and ichnofossils; A) *Ottoia prolifica* from Burgess Shale (USNM 188616 counterpart) with three *Haplophrentis carinatus* conchs in gut; note apertural ends of hyolithids oriented toward anus of the worm, at upper left. B–C) Conasauga ichnofossils, both from *Bolaspidella* Zone, interpreted as *Ottoia* gut contents; B) CSUC 01-10-1, siliceous concretion containing 31 hyolithids (*Haplophrentis?* sp.) in elongate mass, 5.4 cm length, interpreted as an *Ottoia* cololite; C) CSUC 90-16-1, shale specimen with *Haplophrentis?* sp. conchs in tightly compacted bilateral mass, apertures uniformly oriented away from midline, interpreted as impacted hindgut cololite. D–E) Conasauga Formation *Glyphaspis capella*, CSUC 95-91-1a,b, *Ehmaniella* Zone, showing filamentous (gill) limb branches; D) ventral view of exoskeleton with filamentous branches visible under left thorax; E) counterpart internal cast with filamentous branches evident on posterior pleural segments. F–H) *Naraoia compacta*; F) Burgess Shale specimen, USNM 235852 for comparison; G–H) Conasauga Formation CSUC 01-10-12a,b, *Bolaspidella* Zone shale specimen; G) ventral view of chitinous exoskeleton, (H) dorsal surface of internal cast, showing five transverse lines along axis. Comparison specimens are from the Smithsonian Institution, National Museum of Natural History (USNM), Washington, D.C.

asauga specimen indicates that these hyolithid conchs comprised a massive quantity of ingested food. Like Burgess Shale analogs (e.g., Fig. 5A) and the Chinese specimens, hyolithids in the Conasauga specimen are preferentially oriented with the conch apices pointing anteriorly.

The second priapulid gut fossil (Fig. 5C) comes from an outer-shelf shale (*Bolaspidella* Zone) and consists of two sets of five or more laterally appressed *Haplophrentis?* sp. conchs. This specimen is poorly preserved, and the detailed configuration is not clear, but the appearance is that of a bilateral pair of clusters, with the hyolithid apertures in each half all pointing away from the midline, and with the two sets of hyolithids facing oppositely. Hyolithids are found commonly in current-sorted mass accumulations (e.g., Hou et al. 2004, fig. 13.3); however, in the Conasauga specimen, the strongest evidence for a priapulid origin is the bilaterally paired, opposed orientation of the conchs, which is likely not current induced. No other such accumulations of hyolithids have been found in the Conasauga Formation.

Both accumulations contain oriented hyolithids in numbers exceeding those in the guts of most priapulids in other Cambrian Lagerstätten. Based on these anomalous concentrations, we assume they are most likely the remains of distressed (i.e., impacted) priapulid guts. The siliceous concretionary mass (Fig. 5B) most likely represents the in situ configuration of the priapulid gut, therefore a cololite, with the hyolithid conchs approximating the configuration of the intestine. In support of this hypothesis, the length and width of the specimen corresponds to that of a typical *Ottoia*. Interpretation of the flattened shale specimen (Fig. 5C) is more tenuous: it is tentatively identified as an impacted digestive mass from the posteriormost intestine of a larger priapulid, probably also an *Ottoia*. The hindgut likely split apart from decay gases and was preserved in two halves after the host animal died.

Both identifications presume that hyolithids do not aggregate in such masses on their own. Hyolithids are generally considered vagrant, sediment deposit-feeding benthonic organisms (e.g., Babcock and Robison, 1988; Briggs et al., 1994; Marek et al., 1997) frequently found in great numbers, especially in the Cambrian and Ordovician, but they are presumed to have been solitary, albeit gregarious, organisms (Pojeta, 1987). Such compacted and oriented hyolithids described here can only be explained as the result of the organisms forced into such configurations by predator's digestive processes.

Trilobites: *Glyphaspis capella* (Walcott, 1916)

Conasauga trilobites are diverse and well preserved, typical of the later middle Cambrian *Ehmaniella* and *Bolaspidella* Zones (see Tables 1 and 2), and described in a number of classic works by Walcott (1916), Butts (1926), Resser (1938), and, more recently, by Schwimmer (1989) and Schwimmer and Robinson (1990). Trilobites are commonly preserved in shales and siliceous concretions, with some beds containing abundant trilobite sclerites. Trilobites are mostly disarticulated, but there are many near-complete, dorsal exoskeletons lacking only the librigenae (free cheeks), and many complete specimens exist with the free cheeks attached (e.g., Figs. 5D, 6B).

The preservation of abundant trilobites in parts of the Conasauga constitutes a Konzentrat Lagerstätte (sensu Seilacher et al., 1985; dense fossil accumulation), similar to concentrations in parts of the Wheeler Shale. Although the trilobite components are comparable, shelly preservation in the Conasauga is generally different from that in some Wheeler quarries, where trilobite sclerites are in concretionary cone-in-cone carbonates (Robison, 1964b; Martin, 1999). In contrast, the Conasauga shaly facies have compressed trilobite sclerites, with the dorsal exoskeleton commonly preserved as thin, nearly transparent calcite. Such specimens sometimes have the flattened, intact dorsal exoskeleton peeled off along the ventral surface, exposing the hypostome and ventral cephalic doublure (Schwimmer, 1989, figs. 3.5, 3.16).

Conasauga trilobites preserved in siliceous concretions constituted a major part of the reference trilobite material of Walcott (1916) and Resser

(1938). The siliceous concretions preserve the original external dimensions of the exoskeletons without the compaction typical of shaly preservation, often with fine details of surface textures and skeletal morphology (Schwimmer, 1989). Collecting in the olive-gray shales of the *Bolaspidella* Zone has unearthed numerous concretions interbedded in many horizons of the shale beds, suggesting syndiagenetic formation of concretions.

One trilobite from the *Ehmaniella* Zone Lagerstätte, a complete dorsal exoskeleton (Fig. 5D) of the large ptychopariid trilobite *Glyphaspis capella* (Walcott, 1916), reveals nonbiomineralized appendages. Most specimens of *G. capella* in the Conasauga have been collected as disarticulated sclerites (Schwimmer, 1989) from molted or predated individuals (Pratt, 1998; Babcock, 2003). Preservation of a complete exoskeleton, in contrast, is most likely remains of a dead individual. Close examination of the thoracic region of the complete *Glyphaspis* (Fig. 5D) reveals two sets of anteroposterior striations under the left pleural region (Fig. 5E). These are imprints of the filamentous outer branch of the biramous limbs (Whittington, 1997). The outer limb rami of trilobites are termed gill branches because the filaments presumably served a respiratory function (Whittington and Almond, 1987; Whittington, 1992), as they do in other biramous arthropods (Barrington, 1979). Outer limb branches may have been relative stiff nonbiomineralized structures (Whittington, 1997) and have been preserved in many trilobites, including more than a dozen Burgess Shale trilobite species (especially *Olenoides*; see Briggs et al., 1994), and in such post-Cambrian trilobites as the pyritized Ordovician *Triarthrus* in Beecher's Trilobite Bed of New York (Etter, 2002).

Nektaspids: *Naraoia compacta* Walcott 1912

We interpret a specimen from the *Ehmaniella* Zone as *Naraoia compacta*, a nonbiomineralized arachnomorph arthropod (Wills et al., 1998). *Naraoiidae* are considered to be a sister group to trilobites (e.g., Briggs et al., 1992; Fortey, 1997; Edgecombe and Ramsköld, 1999); however, some researchers (e.g., Robison, 1984; Budd, 1999) treat the nektaspids, including naraoiids, as an aberrant order within the larger concept of trilobites. The low-diversity *Naraoia* species were widespread in the early and middle Cambrian, featuring several synapomorphies that separate them from typical trilobites. Besides lacking mineralized exoskeletons, the dorsal exoskeleton was nearly smooth with only two body divisions—assumed to be homologous with the cephalon and thoracopygon—and lacked large dorsal eyes. Some well-preserved specimens reveal the digestive structures (diverticula) in the cephalon and the limbs under the pygidium, perhaps because the dorsal surfaces of *Naraoia* species were chitinous rather than mineralized. Fortey (1997) observed that nektaspids resemble oversized, early meraspid trilobite larvae, based on their lack of thoracic segments. Paedomorphosis (i.e., neoteny) may in fact account for their evolution away from the basal trilobite lineage during the early Cambrian (see Caron et al., 2004, for a synopsis of the relationships).

Naraoia includes two species in the early Cambrian Chengjiang biota (Babcock and Chang, 1997), along with the middle Cambrian species *N. compacta*, in North America known from the Burgess Shale, the Marjum Formation in Utah, and the Gibson Jack Formation in Idaho (Robison, 1984). The Marjum Formation is penecontemporaneous with the Conasauga Formation, and the Conasauga *Naraoia* specimen is referable to the same species, *N. compacta*. Some morphological details of the Conasauga specimen (Figs. 5G–H) are poorly demarcated but compare favorably with *N. compacta* (Fig. 5F) in the similar proportions of anterior and posterior tagma and size. The Conasauga *Naraoia* lacks evidence of medial and pygidial marginal spines, suggesting it is not a *N. spinosa*. The fossil is flattened and slightly distorted, presumably by soft-sediment compaction. Remains of the internal surface of the chitinous exoskeleton are on one part (Fig. 5G), with at least seven transverse lines evident on the thoracopygon. The counterpart (Fig. 5H) appears to be an internal dorsal cast of the chitinous tissue and preserves traces of three transverse lines along the axial area.

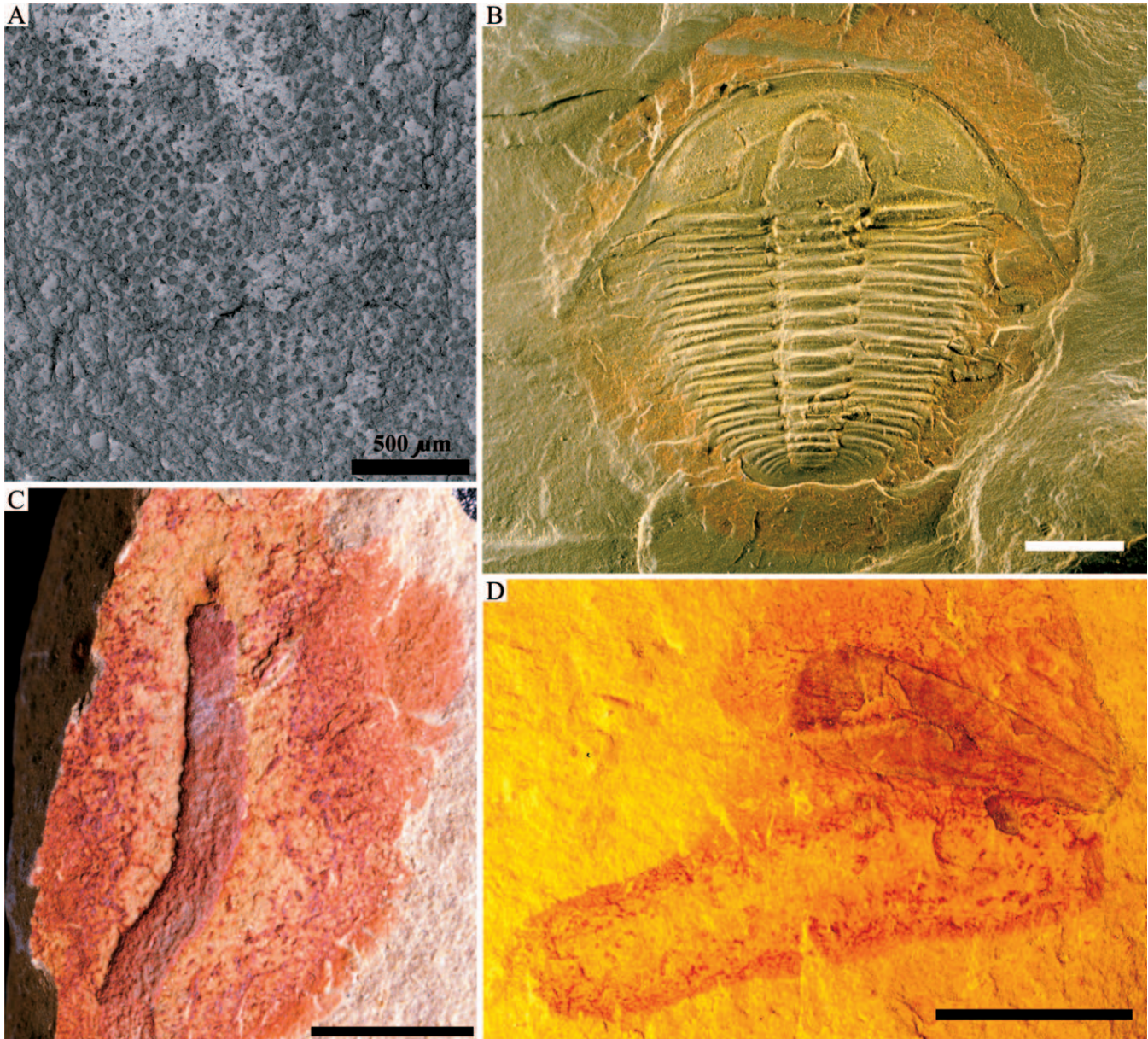


FIGURE 6—Conasauga Formation fossils illustrating taphonomy, scale bars 5 mm unless indicated. A) Scanning electron microphotograph of trilobite doublure fragment, probably *Bolaspis labrosa*, *Ehmaniella* Zone shale, showing extremely fine-grained preservation of detail. B–D) Conasauga specimens with Fe-oxide halos, indicating localized decay deoxygenation; B) CSUC 05-01-1a, *Elrathia antiquata* with intact free cheeks and goethite halo; C) CSUC 02-10-3, *Leptomitus* sp. with extensive goethite halo; D) CSUC 01-03-3, *Haplophrentis*? sp. with goethite outline and displaced conch, indicating the specimen was moved after initial Fe-mineral precipitation.

TAPHONOMY OF EXCEPTIONAL PRESERVATION IN THE CONASAUGA FORMATION

The Conasauga exceptional fossil assemblages are interesting for several reasons. The Conasauga Lagerstätten lithofacies are inferred to range from inner- to mid-shelf marine environments, whereas other Laurentian exceptional Cambrian biotas (e.g., Burgess, Wheeler, and Spence Shales) represent various shelf-to-slope environments. The Conasauga biota shows that the Cambrian preservational bias favoring nonmineralized fossils is not restricted to deeper marine environments. Also, the Conasauga Formation reveals neither biotic nor sedimentary evidence of such catastrophic phenomena as sediment flows or specific anoxic events associated with exceptional preservation. There is no evidence also of unusual sedimentary conditions present in proximal deposits forming on the Conasauga shelf, except for the great abundance of amorphous silica. The Conasauga shelly biota is similarly unexceptional, with abundant min-

eralized trilobite, hyolithid, and brachiopod fossils (Resser, 1938; Schwimmer, 1989) along with the sparse nonmineralized remains.

Given these observations, and the fact that other known Laurentian inner-shelf Cambrian faunas (e.g., the Wolsey Shale, Montana [Schwimmer 1975], and the Pika Formation, British Columbia [Melzak and Westrop, 1994]) usually feature only shelly fossils, one asks why any non-mineralized fossils are preserved in the Conasauga?

First, a multiplicity of preservational formats of Conasauga biota indicates that there was no single phenomenon causing the preservational (see also Skinner, 2005; Zhu et al., 2005). The causes of exceptional preservational events were implicitly low-key or unexceptional, and non-biomineralizing organisms had several taphonomic opportunities to be preserved. Similar conclusions about multiple but unexceptional causes of preservation of soft tissue were made for the lower Cambrian Kinzers Shale fauna in Pennsylvania (Skinner, 2005), but with the addition of

predation as a cause of macerated accumulations, not observed in the Conasauga biota.

Second, the admixture of abundant skeletal fossils with rare nonskeletal fossils in the Conasauga is unlike the Burgess Shale and Chengjiang biotas, where nonmineralized fossils are more diverse and abundant than are trilobites and other shelly fossils (e.g., Conway Morris, 1986; Briggs et al., 1994; Hou et al., 2004). The causes of Conasauga exceptional preservations appear to be unlike those of the Chengjiang and Burgess Shale biotas, therefore. A related and significant taphonomic observation is that the majority of trilobite fossils in the Conasauga are molted or predated dorsal exoskeletons, rather than remains of dead individuals. Most typical shelly middle Cambrian deposits with abundant remains of common ptychopariid and corynexochid trilobites (e.g. Schwimmer, 1973, 1989; Sundberg, 1994) contain mostly disarticulated trilobites with missing free cheeks, as in the Conasauga Formation. This indicates a relatively normal marine biocoenosis, rather than a death assemblage. Possible causes of the nonmineralized preservation are discussed next.

Limited Bioturbation

Important also to soft-tissue preservation in the Conasauga was the limited amount of bioturbation present at the time. The Cambrian and post-Cambrian diversification of infaunal bioturbators is an active topic of discussion, with some authors claiming there was a generally low level of deep burrowing infauna in the Cambrian (e.g., Bottjer and Ausich, 1986; Droser and Bottjer, 1989; Allison and Briggs, 1993; Bottjer et al., 2000), especially in the earlier series of the period; counterarguments generally support the presence of significant Cambrian bioturbating infauna (e.g., Crimes and Droser, 1992; Pickerell, 1994). These may not be globally opposed views, however, because most controversy focuses on the spread of significant bioturbating infauna to the deeper shelf and slope habitats. It is widely accepted that some Cambrian neritic environments were inhabited by a substantial shallow-tiering infauna, based on the frequent discovery of the *Skolithos* ichnofacies in the early Cambrian (Crimes and Droser, 1992).

Dzik (2005) has most recently described a shallow-tiering, diverse ichnofauna, just above the Neoproterozoic-Cambrian boundary in Ukrainian northern Siberia, and identified the tracemakers as priapulids or related bilaterans. Indeed, the existence of some infauna on the Conasauga shelf is indisputable, given the presence of priapulid fossils; however, there is no compelling ichnofossil evidence of a pervasive bioturbating fauna in the strata. There is no ready explanation for the paucity of infauna in the inner-shelf Conasauga lithofacies, especially since the light tan color of the mudstone suggests that the bottom waters were well oxygenated. The lack of endolithic trace fossils and extensive reworking evident in the sedimentary fabric suggests that pore waters just below the sediment-water interface must have been dysoxic. It may be argued by inverse reasoning that if there were major reworking of sediment on the Conasauga shelf, all soft-tissue remains would have been destroyed.

Amorphous Silica Fixation

The ubiquitous siliceous concretions interbedded within the Conasauga shales indicate that there was abundant free silica present on the marine shelf. Siliceous concretions are present in both shallow and midwater settings that contain the two Lagerstätten horizons, but they are locally superabundant in the deeper water (*Bolaspidella* Zone) unit. Siliceous concretions are present, but fewer, in the tan shale unit (*Ehmaniella* Zone) in the shallow shelf. In this unit are numerous zones of hard shales nearly constituting porcelanites with great amounts of interstitial silica, suggesting that the excess free silica in these facies was more effectively intercalated with clay minerals during deposition.

Bedding in Conasauga shales typically drapes around the siliceous concretions, indicating that they formed penecontemporaneously with mud compaction. Even without bedding evidence, the presence of such sizeable siliceous fossils as *Brooksella*, *Eiffelia*, priapulid cololites, and tri-

lobite exoskeletons in many siliceous concretions indicates that masses of free, amorphous silicic acid (H_4SiO_4) were abundant during primary deposition of the Conasauga Formation. These gelatinous silica masses likely covered and fixed organic matter by simple obrution and hardening into cherty concretions.

The most likely source of silica in the Conasauga is degraded siliceous sponge spicules. Demosponges are apparently the more basal Poriferan clade and were diverse in the Cambrian (Rigby, 1986). We assume that they were the primary source of much biogenic chert in the Cambrian (Carozzi, 1993). Degraded hexactinellids and their spicules, however, are also abundant in the Conasauga (e.g., Fig. 4H, I) and may have been a significant or coequal source of free silica, especially if the abundant *Brooksella* were hexactinellids (Ciampaglio et al., 2005, in press). Since other such silica-secreting organisms as radiolaria, silicoflagellates, and diatoms were apparently not present or yet common in the Cambrian, it is almost certain that sponges were the silica source. Further, since the peri-Iapetus continents Laurentia and Baltica were totally to largely submerged during the later half of the Cambrian (Frazier and Schwimmer, 1987), subaerial continental weathering was not a significant source of silica.

Well-Sorted Clay Matrix

The inner shelf *Ehmaniella* Zone Conasauga beds contain a few non-mineralized remains, and at least one noteworthy specimen appears to be the result of a mechanical imprint in the claystone. The trilobite filamentous appendages shown in Figures 5D–E were preserved in several segments of the unusually complete specimen of *Glyphaspis capella*. This specimen, which is characteristic of many other fossils in the same tan shale, shows no significant variations in the texture of the matrix immediately around the fossil and lacks signs of recrystallized sclera. There is also no evidence of algal or bacterial overgrowth in the preservation of this specimen or signs of anoxia or chemical processes enhancing preservation.

Whittington (1997) observed that the filamentous branches of trilobite appendages were relatively stiff chitin and contained backward-directed, overlapping sheets. The absence of signs of anoxia or chemical alteration in this specimen and the slightly resilient nature of the filamentous appendages suggests that trilobite tissue may have been preserved simply as the result of physical impression into a clay matrix, perhaps following partial dissolution of the prismatic calcite layer of the cuticle (Whittington and Wilmot, 1997).

The ability of the Conasauga clay lithofacies to preserve extremely fine detail is also demonstrated by the specimen shown in Figure 6A, which is small ventral area of a trilobite scleral fragment. Even at 60× magnification, the sclerite surface shows well-defined surface ornamentation (prosoxon) with granulations ranging down to the size of fine silt. Preservation by mechanical impression is not observed in the deeper water clayshales of the Conasauga Formation, suggesting that the same sorting and fineness of matrix was not present farther out on the marine shelf.

Anoxia, Bioimmuration, and Iron Mineral Precipitation

Many mineralized and nonmineralized fossils in the Conasauga Formation have well-formed, red halos in the sediment surrounding the specimens (e.g., Figs. 6B–D). These halos are composed of Fe-oxide crystals, which X-ray diffraction reveals are largely goethite with minor amounts of hematite. In addition, broad Fe-oxide zones that surround mineralized and nonmineralized fossils grade into generalized red stains in the clay matrix.

The general nature of sulfide and Fe-oxide compounds in association with many types of fossil preservation is moderately well understood (e.g., Borkow and Babcock, 2003; Lazar, 2004; Popa et al., 2004). Oxides are the end products of a cascade of chemical responses that begin with local reducing conditions induced by organic decay. Such conditions were

especially common in such anoxic, deeper-water Cambrian environments as the Burgess and deep Wheeler Shales (Gaines and Droser, 2005); however, the more shallow-water facies of the Conasauga show localized evidence of the same processes in the immediate vicinity of decaying organisms. Pyrite crystals would precipitate in such local anoxic sedimentary environments that contained sufficient sulfur and Fe. The primary pyrite crystals formed were subsequently oxidized to goethite or hematite by oxygenated groundwater or subaerial exposure. As evidence of this sequence, small hyolithids are found with coatings of unoxidized pyrite that are strikingly reflective when collected wet from the field.

Although the general chemistry of the Fe-sulfide-oxide decomposition sequence is fairly clear, the exact cause of the textural development of pyrite crystal aggregates is arguable (Ohfuji et al., 2003; Sawlowicz, 2000); however, the role of microorganisms has frequently been assumed as a necessary intermediate in the process (Popa et al., 2004; Wignall et al., 2005). Bacteria contributed to the deoxygenation of nonmineralized tissue and may have provided a physical means of maintaining the integrity of organisms through formation of biofilms (Meyer and Milsom, 2001; Borkow and Babcock, 2003; Briggs, 2003; Gabbott et al., 2004). The encrusting coccolidal green alga discussed here (Fig. 3D–H) also may have contributed to maintaining physical integrity and modifying the local chemistry of some nonmineralized organisms that were encrusted. For example, the spicules of the small *Leptomitus* demosponge (Figs. 3F–G) appear to be tightly appressed by the encirclement of the chains of algae.

The role of anoxia has been widely accepted as a critical factor in preservation of nonmineralized fossils. For example, Gaines et al. (2005) discussed the importance of anoxia in restricting microbial decomposition in the Wheeler Formation. Anoxia is also important in the precipitation of pyrite and other authigenic mineral proxies of organisms and may be the most critical factor in preserving the image of soft tissues in Burgess Shale-type preservation (Zhu et al., 2005). As discussed in the previous section, the evidence for widespread anoxia above the sediment surface on the Conasauga shelf, however, is absent in most sites and is localized and ephemeral where there is evidence (e.g., encrustations and decaying organisms). Anoxia below the sediment-water interface may have been widespread, as reflected by the absence of trace fossils. The light-colored, inner-shelf sediments seem to contraindicate the generalized extreme low-oxygen conditions; however, localized anoxic microenvironments were created owing to decay of individual organisms.

One very interesting preservational aspect of the Conasauga biota concerns the topic of dead trilobites versus molts. As discussed, both Conasauga Lagerstätten intervals contain abundant trilobite fossils, with most of the common opisthopteran trilobites lacking their free cheeks. Since the purpose of shedding free cheeks was an adaptation for molting, such trilobite fossils represent empty exoskeletons. Some Conasauga specimens, however, do preserve the entire cephalon with intact free cheeks (e.g., Fig. 6B). Also, Fe-oxide halos are found generally only on trilobites with intact free cheeks, rather than around the obvious molts. Thus, intact trilobites likely represent dead, decomposed animals, whereas the molts lacked sufficient organic tissue to attract the microbial growth that favors pyrite formation. Fe-oxide halos are ubiquitous around sponge fossils (e.g., Figs. 4A–B, 6C) and hyolithids (Fig. 6D), which are not ecdysozoans (molting animals), and, thus, always represent dead organisms. Figure 6D is a specimen in which a *Haplophrentis?* sp. is slightly displaced from an Fe halo, which conforms to its overall shape. The hyolithid partly decomposed, initiating precipitation of pyrite, and then was subsequently displaced from the ring of precipitated pyrite that remained in place and subsequently oxidized to the goethite halo.

CONCLUSIONS

The Conasauga Formation in northwestern Georgia yields a rare inner-shelf Laurentian biota with exceptional preservation. It is the combination of attributes—mixed types of fossil preservation modes and proximity to the Cambrian shore—by which the Conasauga contrasts with some well-

represented Cambrian outer-shelf-to-slope Cambrian Lagerstätten. The biota preserved in the Conasauga Formation is taxonomically comparable at the generic level with the biotas of the Burgess and Wheeler Formations, and this reinforces the view that Burgess Shale-type Cambrian biotas were geographically widespread around the Laurentian continent (Conway Morris, 1985; Conway Morris and Robison, 1988).

The occurrence of Konservat Lagerstätten in the Conasauga Formation is the first extension of exceptional Cambrian biota to the (present) southeastern margin of Laurentia, which further demonstrates the extensive geographic range of Burgess Shale-type biotas. The upper beds in the Conasauga Formation are among the younger examples of Cambrian strata containing a Burgess Shale-type benthos featuring priapulids, nektaspids, basal sponges, and common polymerid trilobites, indicating that this general biota was both geographically widespread and long-ranging temporally, at least into the later Cambrian.

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