

Research paper

Phylogenetic affinities and taphonomy of *Brooksella* from the Cambrian of Georgia and Alabama, USA

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Abstract

Siliceous “star cobbles”, referred to the enigmatic genus *Brooksella*, are abundant in the Conasauga Formation of the Coosa River Valley of Alabama and Georgia, USA. Explaining the phylogenetic affinities and taphonomic history of *Brooksella* has been difficult and contentious. *Brooksella* has, at times, been referred to: 1, the cnidarian order Scyphomedusae; 2, the cnidarian class Protomedusae (order Brooksellida); 3, as algae; 4, as a trace fossil; and 5, as a feature of inorganic origin.

Macroscopic, microscopic, and computer-assisted tomographic analysis of *Brooksella* from the Conasauga Formation suggests that the “star cobbles” represent exceptionally preserved body fossils of simple construction. Morphology of star cobbles is most consistent with a siliceous (hexactinellid) sponge interpretation. Specimens show wide morphologic variation, including gradational patterns, suggesting that a single species name (*Brooksella alternata*) should be used to embrace all forms described from the Coosa Valley. *B. alternata* includes specimens having a variable number of radially disposed lobes divided by radial grooves, and often a central opening inferred to be an osculum on one side. Lobes in many specimens terminate in small openings. Small craterlike structures, inferred to be ostia, are present on the external surface. Radial internal cavities occupy the lobes. Specimens from the Conasauga Formation have siliceous spicules preserved surficially and internally.

The three-dimensional nature of most “star cobbles” suggests rapid fossil diagenesis, perhaps mediated by the activities of microbial consortia that quickly formed biofilms around the dead hosts.

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Keywords: *Brooksella*; Cambrian; Porifera; Hexactinellida; Scyphozoa; Georgia

1. Introduction

The enigmatic Cambrian fossil *Brooksella* was first described by Walcott (1896) from “star cobbles” composed of chert that occur abundantly in the Conasauga Formation of the Coosa River Valley of Alabama

(Walcott, 1896, 1898) and adjacent areas of Georgia (Allen and Lester, 1954; Ciampaglio et al., 2005), USA (Fig. 1). *Brooksella* specimens exhibit a wide range of morphologic variation, including a variable number of radial lobes divided by relatively deep grooves, and often a central opening on one side (Fig. 2). Interpretation of the origin of *Brooksella* has been contentious. Historically, views concerning the identity of the fossils include: 1, body fossils of cnidarians of the order Scyphomedusae (Walcott, 1896, 1898); 2, body fossils of cnidarians

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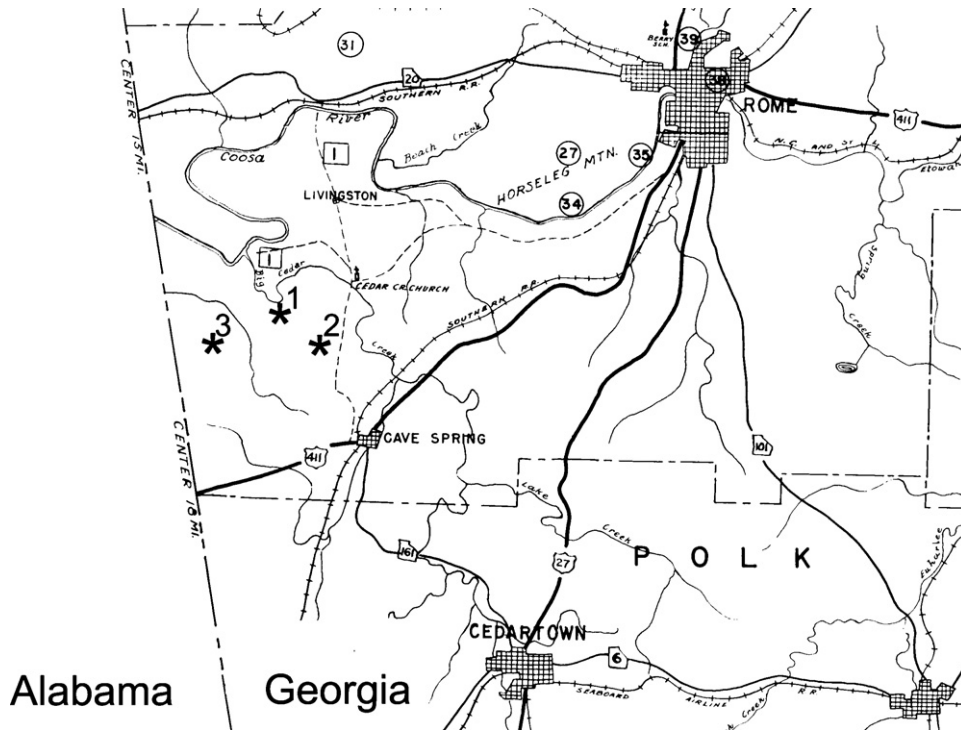


Fig. 1. The Coosa River Valley, northwest Georgia, and adjacent part of eastern Alabama, USA (modified from Allen and Lester, 1954). New specimens of *Brooksella* used in this study were collected from exposures 1–3 in Georgia.

of the monogenic class Protomedusae (Caster, 1945) and order Brooksellida (Harrington and Moore, 1956); 3, algae (Resser, 1938); 4, trace fossils (Seilacher, 1956; Häntzschel, 1975; Fürsich and Bromley, 1985; Seilacher and Goldring, 1996); and 5, inorganic structures (Cloud, 1960). Recently, Ciampaglio et al. (2005) reported preliminary information suggesting that *Brooksella* represents a siliceous sponge. The purpose of this paper is to expand on our earlier observations and interpretations about *Brooksella*, and to provide additional information bearing on the phylogenetic affinities and taphonomy of the fossil.

The *Brooksella* star cobbles show great variability in external shape. Three species assigned to *Brooksella* (Walcott, 1896, 1898; Harrington and Moore, 1956; Willoughby and Robison, 1979) have been reported from the Conasauga Formation: *Brooksella alternata* Walcott, 1896 (Fig. 2B, D–F and H–I), the type species of *Brooksella* Walcott, 1896; *B. confusia* Walcott, 1896 (Fig. 2E); and *Laotira cambria* Walcott, 1896 (Fig. 2A, C and G), the type species of *Laotira* Walcott, 1896. Large collections of new specimens from northwest Georgia show that the morphology of *Brooksella* (incorporating *Laotira* as a junior synonym) is highly gradational, and that the described species seem to represent morphologic end members. Herein, all *Brooksella* specimens from the

Coosa Valley are treated as a single species, *B. alternata* Walcott, 1896.

Methods used to analyze *Brooksella* specimens from northwest Georgia include standard light microscopy of external surfaces, examination of polished specimens, examination of polished cross sections, scanning electron microscope (SEM) analysis, and computer-assisted tomographic (CT) scanning.

2. Geologic setting

The original collections of *Brooksella* (Walcott, 1896, 1898; Fig. 2) consist of more than 9000 chert concretions obtained from two stratigraphic intervals within the Conasauga Formation in the watershed of the Coosa River, from Yancey's Bend to Centre, Cherokee County, Alabama (Resser, 1938; Rindsberg, 2000). Walcott's collections, originally part of the U.S. Geological Survey collections, are repositied in the U.S. National Museum of Natural History, Smithsonian Institution, Washington, D.C. Today, the area from which those specimens were collected is now under Weiss Lake, a reservoir formed behind Weiss Dam. Collecting of concretions in Alabama in recent years has been limited to times when the reservoir was at its lowest levels. Exposures of the Conasauga Formation occur around the Coosa Val-

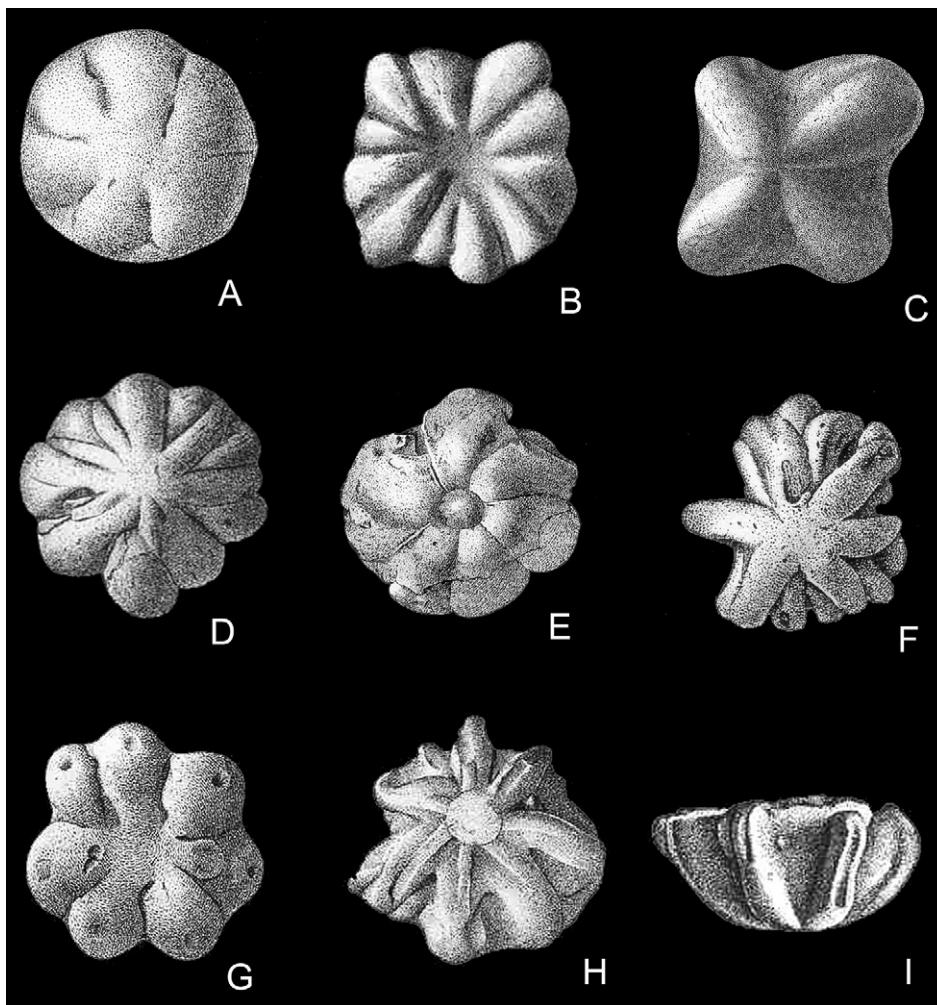


Fig. 2. *Brooksella alternata* Walcott, 1896 preserved as cherty star cobbles from the Conasauga Formation (Cambrian), Coosa Valley, Cherokee County, Alabama (all figures reprinted from Walcott, 1898). (A, C and G) Specimens previously referred (Walcott, 1898) to *B. cambria*. (E) Specimen previously referred (Walcott, 1898) to *B. confusa*. (B, D, F, H and I) Specimens previously referred (Walcott, 1898) to *B. alternata* (I, lateral view showing internal radial cavities in the lobes). As illustrated, specimens in B and G are regarded as showing the bottom side of the organism, and specimens in C–F, and H are regarded as showing the top side of the organism. The specimen illustrated in I is in lateral view, and the lower surface of the fossil is the convex side pointing downward as illustrated here.

ley, however, and include locations in Floyd County, Georgia, which borders Cherokee County, Alabama. Exposures in northwestern Georgia (Fig. 1) have produced numerous concretions (or nodules), including those examined in this study.

In northwestern Georgia and northeastern Alabama, the Conasauga Formation (Cambrian) consists mostly of gray to gray-green clayshales interbedded in some intervals with limestone layers. Chert nodules, usually 1–10 cm in diameter and gray with reddish-brown or yellowish color, weather free from gray shales apparently representing multiple stratigraphic intervals. Specimens reported here are from strata containing polymerid trilobites indicative of the *Bolaspidella* Zone

(Schwimmer, 1989), equivalent to the Drumian Stage (Babcock et al., 2005b) of the developing global chronostratigraphic framework (Babcock et al., 2005b,c). In some Conasauga Formation localities, most concretions are *Brooksella*, whereas in other localities, *Brooksella* star cobbles are much less common, and various other faunal elements (e.g., polymerid and agnostoid trilobites, hyoliths, chancelloriids, and isolated protospongiid-type sponge spicules) occur on the outer surfaces of irregularly shaped concretions (Butts, 1926; Resser, 1938; Allen and Lester, 1954; Schwimmer, 1989).

The Conasauga Formation (alternatively referred to as the Conasauga Group) has been mapped across parts of Alabama, Georgia, Tennessee, and Virginia (e.g.,

Palmer, 1971; Hasson and Haase, 1988). Thicknesses up to 885 m have been reported (Hasson and Haase, 1988). Paleoenvironments and lithologies represented include shallow peritidal siliciclastic environments through shelf carbonates and shales and carbonate shoals, to shelf-edge environments (Hasson and Haase, 1988; Astini et al., 2000). The lithologies and biota of the Conasauga Formation in northwestern Georgia and northeastern Alabama (e.g., Walcott, 1896, 1898; Resser, 1938; Allen and Lester, 1954; Schwimmer, 1989, 2000) suggest a marine shelf setting comparable in part to the Spence Shale and some Wheeler Formation localities in Utah (see Robison, 1991). However, the shelf may have been at least partly restricted, as suggested by a low diversity of agnostoid trilobites.

The Coosa Valley, which is part of the Appalachian Valley and Ridge Province, is structurally complex (Butts, 1926; Cressler, 1970; Thomas, 1985; Osborne et al., 2000). This area forms part of the Rome thrust sheet, which consists of a complex of northwest-trending thrust slices extending across northwestern Georgia and northeastern Alabama (Osborne et al., 2000). Individual thrust faults are northeast trending. Structural complexity, coupled with considerable vegetative cover, low topography, and limited exposures, inhibits precise stratigraphic correlation of individual localities.

3. Phylogenetic interpretations and taphonomy

3.1. *Brooksella* as a cnidarian

Walcott (1896, 1898) interpreted *Brooksella* as a dorsally convex, medusoid cnidarian. After examination of external surfaces, broken specimens, and polished cross-sections, Walcott (1898) reported the presence of radial canals, one per lobe that opened into a central rounded cavity in some specimens, and provided a model for how *Brooksella* appeared in life. He (Walcott, 1898) erected the family Brooksellidae Walcott, 1898 (embracing *Brooksella* and *Laotira*) and assigned the family to the order Scyphomedusae. Later, Caster (1945) erected the class Protomedusae to embrace *Brooksella* Walcott, 1896 and the family Brooksellidae. Harrington and Moore (1956) erected the cnidarian order Brooksellida to embrace the family Brooksellidae.

3.2. Other interpretations of *Brooksella*

Differing hypotheses concerning the origin of *Brooksella* have been published. In addition to the medusoid cnidarian hypothesis, fossils assigned to *Brooksella* from

the Coosa Valley and elsewhere were interpreted as algae (Resser, 1938), as trace fossils (Seilacher, 1956; Häntzschel, 1975; Fürsich and Bromley, 1985; Seilacher and Goldring, 1996; Schwimmer, 2000), as sponges (Ciampaglio et al., 2005; see also Walcott, 1898), and as features of inorganic origin (Cloud, 1960).

Resser (1938) questioned Walcott's (1896, 1898) interpretation of a medusoid cnidarian origin of *Brooksella* on the grounds that the gastric cavities of jellyfish are unlikely to fossilize because they would need to become sufficiently hard to retain their shape while soft tissue decayed and a limestone nodule (a presumed precursor to a chert nodule) became entombed in mud. Problems related to interpreting the fossilization history, he stated, would disappear if it were assumed that *Brooksella* had an algal origin.

Fürsich and Bromley (1985) compared *Brooksella* to rosetted-spreite trace fossils and synonymized the genus with *Dactyloidites* Hall, 1886. Fürsich and Bromley (1985) reconstructed the trace fossil with a central radial shaft that leads to a rosette consisting of a series of vertical spreiten. Building on the *Dactyloidites* hypothesis, Seilacher and Goldring (1996) inferred the presence of radial tunnels and teichichnoid backfill structures in *Brooksella* based on examination of weathered specimens.

Fossils referred to *Brooksella* have been reported from localities other than the Coosa Valley of Georgia and Alabama, and some of these fossils have played roles in the interpretation of the genus. Notably, Willoughby and Robison (1979) reported rare *Brooksella* sp. preserved three dimensionally in shale from the Spence Shale (Cambrian) of Utah, USA. These specimens were originally referred to as impressions of medusoid cnidarians (Willoughby and Robison, 1979). Later, Robison (1991) noted that *Brooksella* specimens had also been considered to be fecal masses, organic burrows, and inorganic compaction structures. Cloud's (1960) suggestion that *Brooksella* was inorganic in origin (gas blisters formed by the escape of gas from sediment) was based on the Proterozoic form *Brooksella canyonensis* from the Grand Canyon, Arizona, USA. Following reinterpretation of *B. canyonensis* as a trace fossil (Kauffman and Fürsich, 1983; see also Seilacher, 1956; Häntzschel, 1975), Robison (1991) reinterpreted *Brooksella* specimens from the Spence Shale as complex burrowing and probing structures produced by an unknown metazoan. Here, we consider specimens from the Spence Shale of Utah (Willoughby and Robison, 1979; Robison, 1991) to be *Brooksella* (and possibly *B. alternata*), but we question the generic assignment of *B. canyonensis*. The species *B. canyonensis* may belong in *Asterosoma*, as

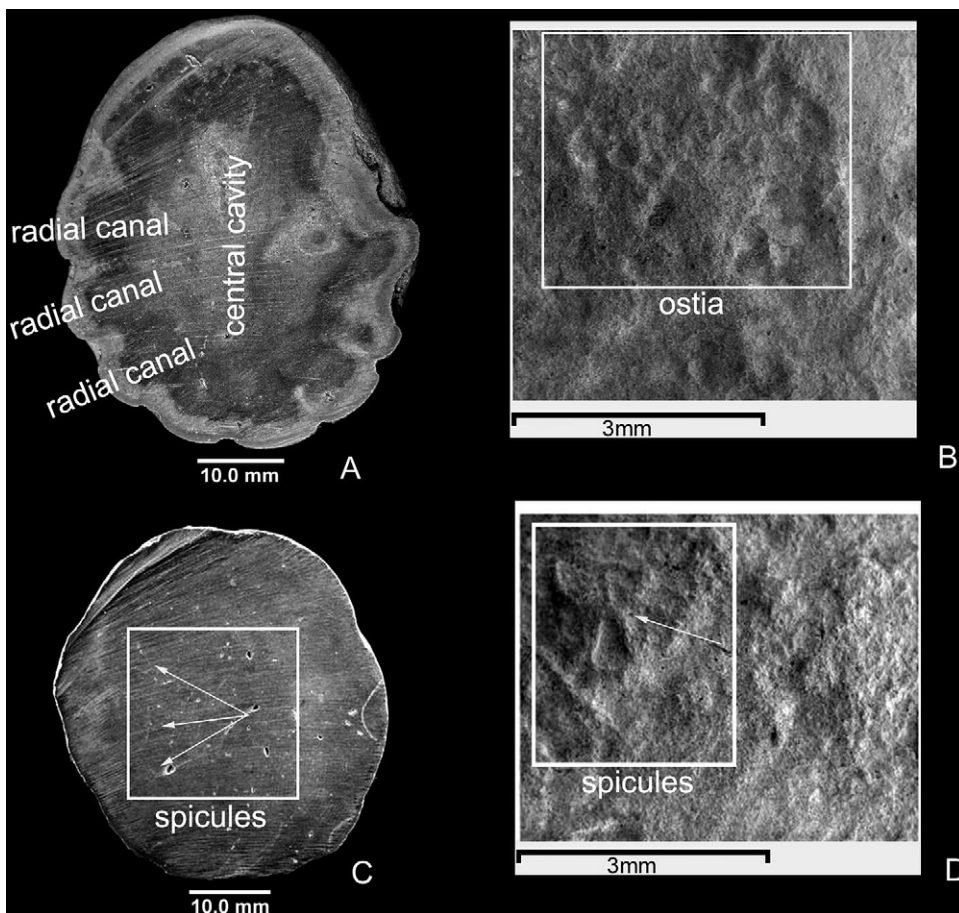


Fig. 3. *Brooksella alternata* Walcott, 1896 preserved as cherty star cobbles from the Conasauga Formation (Cambrian), Coosa Valley, Floyd, County, Georgia, USA. (A) Cross-sectioned specimen showing inferred radial canals and central cavity; PRI 33202. (B) SEM micrograph of surface of a specimen showing a cluster of rosette-shaped structures, each with a central depression, interpreted as possible ostia; PRI 33203. (C) Cross-sectioned specimen, arrows indicate siliceous spicules internally; PRI 33204. (D) SEM micrograph of surface of a specimen, arrow indicates *Protospongia*-type spicules; PRI 33205.

suggested by Glaessner (1969), but further evaluation is needed.

Walcott (1898) considered the possibility that *Brooksella* fossils from the Coosa Valley represent sponges. He noted the external morphologic similarity of *Brooksella* to that of *Hallirhoa costata* (Lamouroux, 1821) and *Brachiospongia digitata* (Owen, 1857), and the similarity of the interior canals to that of *B. digitata*. He also identified *Protospongia*? spicules on the surfaces of some star cobbles. Ultimately, however, Walcott (1898) did not find evidence for a poriferan affinity to be compelling and rejected the possibility.

3.3. Morphologic and phylogenetic reevaluation

Study of approximately 200 specimens of *Brooksella* from the Conasauga Formation of northwestern Georgia

suggests that the “star cobbles” represent body fossils of relatively simple radial construction. Their general regularity, surface features, and internal features are, as illustrated here (Figs. 3 and 4), consistent with an organic origin, and rule out the possibility that *Brooksella* is inorganic. The lack of structures that we can interpret as internal teichichnoid-type backfill structures tends to rule out the possibility that the fossil is a complex burrow. Overall morphology and details of the surface features tend to rule out the possibility that the fossil is a coprolite. We have found no direct evidence of an algal origin for *Brooksella*.

Brooksella specimens usually range from 1 to 10 cm in diameter, and show wide morphologic variation. The organism basically consists of a cup-shaped structure (in lateral view) with a variable number of radially disposed lobes (Fig. 4A) extending from a small central

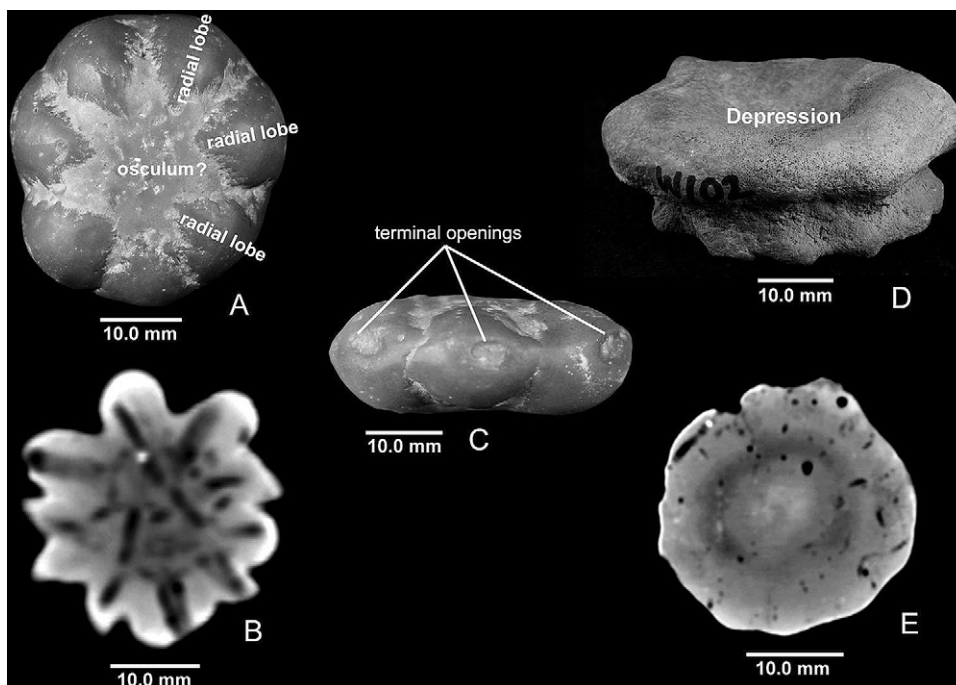


Fig. 4. *Brooksella alternata* Walcott, 1896 preserved as cherty star cobbles from the Conasauga Formation (Cambrian), Coosa Valley, Floyd County, Georgia, USA. (A) Polished specimen from inferred upper surface showing radial lobes and possible osculum; PRI 33206. (B) CT scan image of a specimen with an overall morphology similar to the specimen shown in (A). Black areas represent internal canals now filled with silica; white areas represent more dense concentrations of silica inferred to represent the original positions of spicule lattices. Note that the canals tend to radiate along the lobes from the central area of the fossil; PRI 33207. (C) Lateral view of specimen in (A), showing terminal openings interpreted as possible oscula at the distal end of each lobe. Lobes may represent individual, but fused spongocoels. Specimen is oriented with inferred upper surface toward top of figure. (D) Unusually shaped specimen showing conspicuous central depression on inferred upper surface; PRI 33208. (E) CT scan image of specimen in (D). Note the presence of a low density ring-shaped area in the center of the specimen and small, black, silica-filled canals extending radially and vertically through fossil.

area (in top or bottom view). Radial lobes commonly number four to seven (Fig. 2A, C, E and G–H), but other specimens have more (Fig. 2B, D and F). The radial lobes are divided by radial grooves and are variably distinct, leading to morphotypes that are nearly round through quadrate and star-like, to lobate. Lobes are usually present on both surfaces, but are wider on one side (Fig. 2A, C, F and I). Radial cavities are present in the lobes (Fig. 2I). Lobes sometimes terminate in small openings (Figs. 2G and 4C). If preserved three-dimensionally (Fig. 2I), the fossil is highly convex on one surface (here interpreted as the lower surface; see Discussion under *Brooksella alternata*), and much less convex to slightly concave on the other surface (interpreted as the upper surface). Some specimens consist of a single cup-shaped structure (Figs. 2A–C, I and 4C–D), whereas others resemble imbricate or otherwise more complex structures (Fig. 2D, F and H). Some siliceous concretions (e.g., Walcott, 1898, pl. 12, Figs. 1, 3–6; pl. 13, Figs. 1–3, 5, 6, pl. 14, Figs. 1–3, pl. 19, Figs. 1, 2)

show either compound individuals or multiple individuals of *Brooksella* preserved in close proximity to each other. The central area of an individual *Brooksella* may have a round protrusion (Fig. 2E and H), typically on the more convex side, and may have a shallow depression (Fig. 4A and D) on the other side. Surfaces of some specimens show four-rayed spicules of siliceous composition (Fig. 3D), and small, scattered, craterlike structures interpreted as ostia (Fig. 3B).

Polished cross sections (Fig. 3A) and CT scans (Fig. 4B and E) show radial internal canals occupying the lobes and central portions of specimens. Cross-sectioned specimens have a “spongy” latticework appearance internally (Fig. 3A and C). White siliceous spicules are scattered internally through most sectioned specimens (Fig. 3A and C).

The general internal and external morphology of the star cobbles seems to be most consistent with a poriferan interpretation. The star cobbles do not usually have radial lobes numbering in multiples of four (Fig. 2A–B, D–H;

exception: 1C), nor do they show tentacles or gonads, as expected if they had a scyphomedusan or other cnidarian affinity. The presence of four-rayed, stauract, siliceous spicules inside and on the surfaces of the concretions is even stronger evidence of a poriferan (hexactinellid) affinity.

3.4. Taphonomy

The star cobbles represent an unusual example of exceptional preservation: three-dimensional preservation in silica concretions. Although exceptional preservation in concretions is moderately common in the fossil record, instances of organisms that normally disarticulate quickly having been preserved through silicification are rare. A comparable example is articulated, often three-dimensional, conulariids in siliceous concretions in the Devonian *Conularienschichten* (“conulariid shales”) of Bolivia (Babcock et al., 1987; Babcock, 1994). Exceptional preservation within siliceous nodules is not the only type of exceptional preservation exemplified in the Conasauga Formation. Schwimmer (2000) reported preliminary information about the preservation of chitinous arthropod limbs and a possible annelid in Conasauga shales.

Protospongiid-type spicules, or other siliceous sponge spicules, are among the most common fossils in Cambrian rocks, and they range through Cambrian strata (e.g., Rigby, 1976, 1978, 1986; Robison, 1991; Rigby and Hou, 1995; Debrenne and Reitner, 2001; Dornbos et al., 2005; Ivantsov et al., 2005; Steiner et al., 2005; Xiao et al., 2005). Articulated siliceous sponges, and especially articulated, three-dimensionally preserved sponges, however, are unusual as fossils in most Cambrian strata. Cambrian sponges that secreted protospongiid-type spicules normally did not have fused spicule tips, so in most cases their skeletons disarticulated and scattered soon after death (Rigby, 1976).

The three-dimensional nature of most *Brooksella* star cobbles suggests rapid fossil diagenesis of siliceous sponges. Retention of the general morphology of the sponge may be due to rapid development of a fungus-dominated microbial consortium (a fungal-bacterial biofilm) that enveloped the decaying sponge. Borkow and Babcock (2003) described the development of pyrite concretions as an outcome of such microbial consortia. Their work showed that organisms decaying in water became enveloped by a relatively resistant “halo” of microbes within a day or so of the host organism’s death. Microbes evidently played roles in decomposition of the host and in lithification. The microbial-consortium scenario may serve as a model for the devel-

opment of concretions generally, including the development of siliceous *Brooksella* concretions described here, or ones bearing Devonian conulariids and other fossils (Babcock et al., 1987; Babcock, 1994). In the Conasauga Formation concretions, metabolic activities of the microbial consortium may have contributed to dissolution of siliceous spicules and reprecipitation of colloidal silica. Microbial bodies were identified inside the pyrite concretions reported by Borkow and Babcock (2003), but the difficulty of breaking siliceous concretions from the Conasauga Formation precluded our attempts to find fossilized microbes within star cobbles. Silica precipitation leading to lithification of *Brooksella* star cobbles may have been initiated within days to weeks of the death of the sponges, as suggested by the empirical work of Borkow and Babcock (2003), and by three-dimensionally preserved fossils shown to have been enveloped by and preserved in fungal-bacterial biofilms (e.g., Borkow and Babcock, 2003; Babcock et al., 2005a). In these examples, and in the *Brooksella* star cobbles, fossil diagenesis had apparently occurred prior to the time of sediment compaction.

4. Systematic paleontology

Phylum PORIFERA Grant, 1861.

Class HEXACTINELLIDA Schmidt, 1870.

Order RETICULOSA Reid, 1958.

Family PROTOSPONGIIDAE Hinde, 1887.

Genus *Brooksella* Walcott, 1896.

1896 *Brooksella* Walcott, 1896 - *Brooksella* Walcott, p. 611.

1896 *Laotira* Walcott, 1896 - Walcott, p. 613.

1898 *Brooksella* Walcott, 1896 - Walcott, p. 22.

1898 *Laotira* Walcott, 1896 - Walcott, p. 31.

1956 *Brooksella* Walcott, 1896 - Harrington and Moore, p. F23.

2005 *Brooksella* Walcott, 1896 - Ciampaglio et al., p. 21.

Type species: Brooksella alternata Walcott, 1896, by original designation (Walcott, 1896).

Emended diagnosis: Body fossil consisting of asymmetrical cup-shaped structure (in lateral view) with variable number of radially disposed lobes extending from a small central area (in top or bottom view); central area may have round protrusion or depression; siliceous spicules variably present.

Discussion: *Brooksella*, based principally on specimens from the Conasauga Formation of Georgia and Alabama, is here considered to be a body fossil of a hexactinellid sponge. Spicules occurring in intimate

association with the Conasauga Formation material are mostly siliceous tetraxons (four-rayed stauract spicules of various sizes), and of the type commonly referred to in literature as *Protospongia* Salter, 1864 (see for example Walcott, 1898). Stauract protospongiid-type spicules are common in Cambrian rocks (e.g., Rigby, 1976, 1978; Xiao et al., 2005), often occurring in isolated condition (Rigby, 1976). As reported by Rigby (1976), the practice of assigning such spicules to *Protospongia* is unwise because similarly shaped spicules occur in several genera (Rigby, 1976, 1978, 1986; Xiao et al., 2005). Furthermore, the degree of spicule union in most of these related sponges was minimal, so individual spicules could easily become detached and individual sponge bodies could disarticulate after death. In reassigning *Brooksella* as a hexactinellid sponge, we now recognize that it was one of the genera that secreted four-rayed stauract spicules of siliceous composition.

Reassignment of *Brooksella* to the poriferan family Protospongiidae necessitates synonymization or abandonment of some taxonomic names above the species level. The rule of priority in nomenclature only applies up to the family level. The type species of *Laotira* Walcott, 1896, *L. cambria* Walcott, 1896, is considered a junior subjective synonym of *Brooksella alternata* Walcott, 1896, which is the type species of *Brooksella* Walcott, 1896. *Laotira* is thus a junior synonym of *Brooksella*. The family Brooksellidae Walcott, 1898 (type genus, *Brooksella*) is considered a junior subjective synonym of the family Protospongiidae Hinde, 1887. The monogeneric order Brooksellida Harrington and Moore, 1956, and the monogeneric class Protomedusae Caster, 1945, are abandoned.

As emended, *Brooksella* ranges at least from the *Glossopleura* Zone through the Furongian Series of the Cambrian, and possibly into the Ordovician. The genus includes *B. alternata* (incorporating as junior synonyms *B. confusa* and *Laotira cambria*) from the Conasauga Formation of Georgia and Alabama. Specimens referred to as *Brooksella?* sp. (Willoughby and Robison, 1979, text-fig. 1A–D; later assigned to *Brooksella* sp. by Robison, 1991) from the Spence Shale (*Glossopleura* Zone) of Utah are here referred to as *B. alternata?* A specimen referred to *Laotira cambria* from the upper Cambrian (Furongian Series) of Wyoming (Caster, 1942, pl. 1, Figs. 1 and 2; reassigned to *Brooksella cambria* by Harrington and Moore, 1956) appears to be *Brooksella*, and possibly *B. alternata*. An Ordovician form from Sweden assigned by Harrington and Moore (1956, Fig. 12,3) to *Brooksella silurica* (von Heune, 1904) may belong in *Brooksella*. The enigmatic *Brooksella canyonensis* Bassler, 1941 from the Grand

Canyon Series (Neoproterozoic) of Arizona is not here included in *Brooksella*. We provisionally agree with Glaessner's (1969) reassignment of the fossil as *Asterosoma? canyonensis* (Bassler), and tentatively interpret it as a trace fossil (Glaessner, 1969; Hüntzschel, 1975; Kauffman and Fürsich, 1983).

Brooksella alternata Walcott, 1896.

See Figs. 2–4.

1896 *Brooksella alternata* Walcott, 1896 - *Brooksella alternata* Walcott, p. 612, pl. 31, Figs. 1–5.

1896 *Brooksella confusa* Walcott, 1896 - Walcott, p. 612, pl. 31, Figs. 7, 7a, 7b.

1896 *Laotira cambria* Walcott, 1896 - Walcott, p. 613, pl. 32, Figs. 1–8.

1898 *Brooksella alternata* Walcott, 1896 - Walcott, p. 23, pls. 1–4.

1898 *Brooksella confusa* Walcott, 1896 - Walcott, p. 30, pl. 3, Figs. 11–13.

1898 *Laotira cambria* Walcott, 1896 - Walcott, p. 32, pls. 5–19, 21–23.

1936 *Laotira cambria* Walcott, 1896 - Resser, p. 36.

1938 *Brooksella alternata* Walcott, 1896 - Resser, p. 36.

? 1942 *Brooksella cambria* (Walcott, 1896) - Caster, p. 104, pl. 1.

1954 *Brooksella?* cf. *Brooksella alternata* Walcott, 1896 - Allen and Lester, pl. 1, Fig. 1.

1956 *Brooksella alternata* Walcott, 1896 - Harrington and Moore, p. F23, Fig. 11,2.

1956 *Brooksella cambria* (Walcott, 1896) - Harrington and Moore, p. F23, Figs. 11,1a–c, 11,2a–f.

? 1956 *Brooksella cambria* (Walcott, 1896) - Harrington and Moore, p. F23, Fig. 12,1.

non 1956 ?*Brooksella cambria* (Walcott, 1896). Harrington and Moore, p. F23, Fig. 12,2.

? 1979 *Brooksella?* sp. Willoughby and Robison, p. 496–498, text-fig. 1A–D.

? 1991 *Brooksella* sp. Robison, Fig. 11.4.

1996 *Brooksella cambria* (Walcott, 1896) - Seilacher and Goldring, p. 210, Fig. 4.

2005 *Brooksella alternata* Walcott, 1896 - Ciampaglio et al., p. 21–23, Fig. 1.

New material: Approximately 200 specimens. Illustrated specimens are in the Paleontological Research Institution, Ithaca, New York, USA (PRI 33202–33208).

Emended diagnosis: *Brooksella* showing variable number of radial lobes (typically 4–7; rarely 15 or more); radial lobes variably distinct, resulting in range of morphologic shapes (from top or bottom view) including rounded, astraeiform, tetradial, regularly or irregularly

lobate, or compound-lobate; terminal openings may be present at distal end of each radial lobe; lateral profile variable from single cup-shaped structure to multiple, imbricate structures; siliceous, four-rayed, stauract spicules variably present; surface may show small, scattered, round, craterlike structures.

Discussion: Considerable morphologic variability exists in *Brooksella* star cobbles from the Coosa Valley. Walcott (1896) described three species, *B. alternata* (type species of *Brooksella*), *B. confusa*, and *Laotira cambria* (type species of *Laotira*; later reassigned to *Brooksella*; Harrington and Moore, 1956; Willoughby and Robison, 1979; Seilacher and Goldring, 1996), based on star cobbles from northeastern Alabama. Our observations reveal considerable morphologic gradation among star cobbles, and we interpret Walcott's (1896, 1898) species as morphologic endmembers of a single species, *B. alternata* (Fig. 2).

Uncertainty exists concerning top and bottom directions in *Brooksella alternata*. Although some of the specimens examined in this study were collected in place from surface exposures, it was not possible to determine whether they were preserved convex-up or convex-down because intense structural deformation in the region inhibited determination of stratigraphic younging direction in the shales. A star cobble is basically asymmetrically cup-shaped when viewed laterally (Figs. 2I and 4C–D) or in vertical cross section. One side is more convex than the other. The less convex side is commonly gently concave centrally (see especially Figs. 2B, G and 4D), and the more convex side often has a small round protrusion centrally (see especially Fig. 2E and H). If a poriferan interpretation is correct, we would regard the more convex side of the fossil as pointing downward in life, and the gently concave side of the fossil as pointing upward in life. This is opposite the configuration envisioned by Walcott (1896) in modeling the fossil as a medusoid cnidarian. In a specimen illustrated from the Spence Shale of Utah (Robison, 1991, Fig. 11.4) and questionably referred to *B. alternata*, we regard the side of the fossil protruding in the direction of the viewer as the lower surface of the organism.

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