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FAVOSAMACERIA COOPERI NEW GROUP AND FORM: A WIDELY DISPERSED, TIME-RESTRICTED THROMBOLITE

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ABSTRACT—The distinctive, branched thrombolite, *Favosamaceria cooperi* new group and form, is found widely in the Great Basin, USA, where it is restricted to the Late Cambrian *Saukia* trilobite Zone. This thrombolite is distinguished by a hedgerow, mazelike organization of ridges similar to garden walls (maceriae) in plan view, branching of ridges into daughter ridges and columns, the polymorphic nature of dark, 1–4 mm mesoclots, and the relative consistency of maceria width (approximately 1 cm). As a group, *Favosamaceria* is found elsewhere in Upper Cambrian strata of the Argentine Precordillera, Appalachians, and Upper Mississippi Valley, as well as in Lower Ordovician deposits of the Canadian Arctic and Newfoundland. The distribution of the group around Laurentia illustrates the use of microbialites in biogeographic studies.

INTRODUCTION

THROMBOLITES ARE a distinctive type of microbialite (''organosedimentary deposits that have accreted as a result of a benthic microbial community trapping and binding detrital sediment and/or forming the locus of mineral precipitation'': Burne and Moore, 1987, p. 241) characterized by a nonlaminated, clotted fabric (Aitken, 1967). Thrombolites are not as well known and abundant as stromatolites (=laminated). Thrombolites have been reported from strata as old as 1.9 Ga (Kah and Grotzinger, 1992) and are still forming today (Moore and Burne, 1994).

Microbialites have a rich and varied fossil record extending back almost 3.5 billion years (Hofmann et al., 1999). The diversity and abundance of microbialites decreased in the late Proterozoic and continued to diminish into the Cambrian (Awramik and Sprinkle, 1999). Though microbialites are found throughout the Phanerozoic, the details of abundance and diversity patterns are poorly known except for the Cambrian (Rowland and Shapiro, 2002). Microbialite abundance and diversity increased in the Middle Cambrian–Early Ordovician, in all major microbialite categories (stromatolites, thrombolites, and dendrolites). This revival is herein termed the ''Cambro–Ordovician Microbialite Resurgence.'' During this time, microbialites were widespread in shallow-marine carbonate environments that resembled Proterozoic stromatolitic facies, and invertebrates were rare (Wood, 1999; Pratt et al., 2001; Rowland and Shapiro, 2002). This Resurgence occurs between the demise of the Early Cambrian archaeocyath reefs and the stromatoporoid-coral-receptaculitid reef development of the Middle Ordovician.

Detailed descriptions of Cambro–Ordovician microbialites are limited despite the abundance. Few papers have used Cambrian and Ordovician microbialites for biostratigraphic correlation purposes (e.g., Dolnik, 2000, who named or identified stromatolite taxa; Shapiro and Awramik, 2000, who did not identify taxa, but used morphologically distinctive stromatolites and thrombolites). This contrasts sharply with Proterozoic microbialites, for which there are many examples of named stromatolites that provide reliable biostratigraphic and chronostratigraphic data (e.g., Grey and Blake, 1999; Semikhatov and Raaben, 2000). This paper presents the first taxonomic description of a thrombolite, *Favosamaceria cooperi* new group and form from the Upper Cambrian of the southern and eastern Great Basin, USA (Fig. 1) and discusses the biostratigraphic and chronostratigraphic significance of this thrombolite within a regional and global context.

MICROBIALITE NOMENCLATURE, TAXONOMY, AND BIOSTRATIGRAPHY

The naming of microbialites is a long and unresolved debate (e.g., Høeg, 1929; Grotzinger and Knoll, 1999). From a pragmatic point of view, the ability to name a fossil provides an identity and facilitates communication. This presumes and requires that there is a set of unique, definable attributes that can, or have the potential to, be recognized elsewhere. Microbialites present a particularly intriguing challenge. Unlike other fossils that are either 1) the remains or trace of a single species, 2) the trace produced by several different species but produced by an individual, or 3) the colony of many individuals or cell types, microbialites (based on Recent examples) are generally the product of a few different microbial species organized into complex ecosystems (Golubic, 1976; Riding et al., 1990; Reid et al., 2000).

Despite the rather unconventional nature of microbialites, characteristic shapes, combinations of morphological features, and microstructures for some (stromatolites) have been used to describe and name formally the structures (e.g., Maslov, 1938; Semikhatov, 1962; Grey, 1994). The first microbialite to be named, the stromatolite *Cryptozoon proliferum* Hall, 1883, was from the Upper Cambrian of New York State (Hall, 1883). Since that publication, at least 1,187 taxa (=forms) have been formally described (Awramik and Sprinkle, 1999). Practitioners of microbialite taxonomy recognize that the system used is empirical and artificial (Semikhatov, 1976). Group and form, rather than genus and species, are used (Maslov, 1953, p. 109). The names are latinized and italicized. At the suggestion of Maslov (1953), microbialite taxonomists have followed the International Code of Botanical Nomenclature (ICBN) to add rigor to their taxonomy.

The naming and taxonomy of microbialites is a convenience that enables comparison and the determination of any temporal significance. Arguments against nomenclature and taxonomy based on the parallels drawn between group and form in microbialites and genus and species in whole organisms (fossil or recent) are unproductive. By following the ICBN, formally described microbialites are subject to a rigorously applied nomenclature that has the potential to produce unambiguous descriptions. This should also result in stable names that facilitate discussion. A formal name has immense archival qualities and is the key to its literature. Adherence to a code requires that type specimens be established, properly curated, and available for study. This, along with type-locality information, facilitates comparisons. The Linnean-style nomenclature used is universally understood by biologists and paleontologists. Other naming systems have been proposed (e.g., Maslov, 1960; Logan et al., 1964; Cao and Bian, 1985); however, none of these have been adopted. Despite all the reservations expressed with regard to microbialite nomenclature and taxonomy, the fact remains that this approach has resulted in microbialites being successfully used in biostratigraphy and chronostratigraphy (Grey and Corkeron, 1998; Semikhatov and Raaben, 2000). Stromatolites described in one region

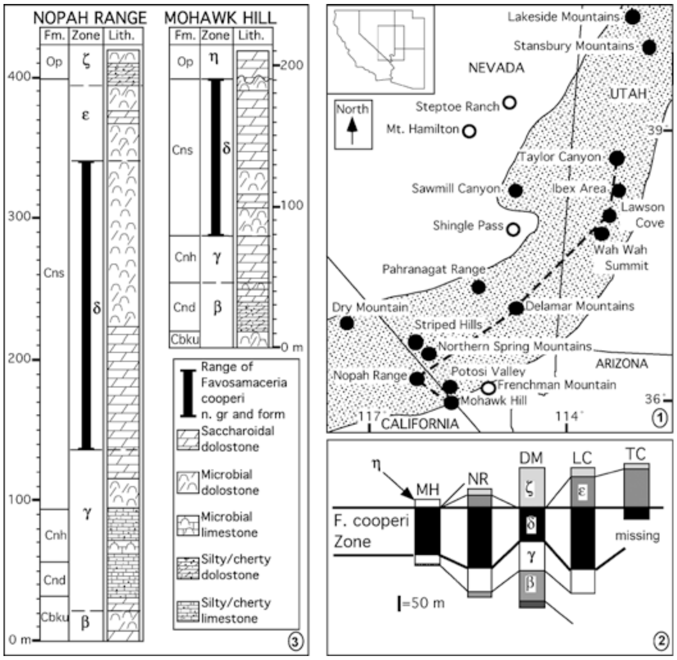


FIGURE *1*—Distribution of *Favosamaceria cooperi* n. gr. and form in the Great Basin. *1*, Map of the Great Basin (nonpalinspastic) showing the locations (stippled area) of Upper Cambrian deposits containing *F. cooperi*. Open circles denote localities where coeval strata do not contain the thrombolite form. *2*, Simplified stratigraphic columns along dashed line in *1* showing vertical distribution of the form. Microbialite morphozones accented by different grey tones. *3*, More detailed stratigraphic columns of the Nopah Range (middle ramp) and Mohawk Hill (craton margin) sections showing the distribution of *F. cooperi* and simplified lithologic units. Greek letters refer to microbialite morphozones of Shapiro and Awramik (2000). The boundary between the Steptoean and Sunwaptan is approximately at the boundary with the β and γ morphozones. Cbku = Upper Bonanza King Formation; Cnd = Dunderberg Shale Member, Nopah Formation; Cnh = Halfpint Member, Nopah Formation; Cns = Smoky Member, Nopah Formation; Op = Pogonip Group.

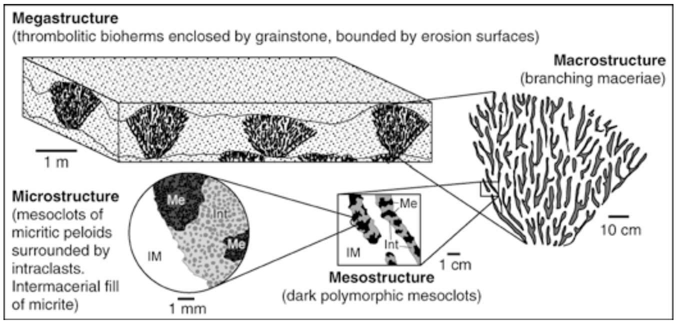


FIGURE *2*—Schematic diagram showing examples of the spatial relationships between the different scales of observation used in microbialite studies.

can be confidently recognized in another region (e.g., Bertrand-Sarfati and Awramik, 1992; Grey, 1994). *Linella avis* Krylov, 1967, for example, is restricted worldwide to the middle Neoproterozoic, about 800 Ma (Grey and Blake, 1999; Grey, personal commun., 2001).

Thrombolites are most abundant in Cambro–Ordovician strata (Rowland and Shapiro, 2002). Papers that describe thrombolites in detail are few (Howe, 1966; Pratt and James, 1982; Kennard, 1994; de Freitas and Mayr, 1995; Pratt, 1995; Armella et al., 1996; and Turner et al., 2000). Therefore it is not surprising that large-scale trends in both distribution and abundance patterns of Cambro–Ordovician microbialites have not been determined (Rowland and Shapiro, 2002).

Cambro–Ordovician microbialite-rich sections can be correlated with strata containing body fossils that offer independent, biostratigraphic control. Previous work established that assemblages of distinctive Cambro–Ordovician microbialites in the Great Basin can be used for biostratigraphy (Shapiro and Awramik, 2000). Sedimentological and paleoecological analyses demonstrated that the microbialite shapes are not necessarily tied to specific facies.

This paper describes a distinctive, branched thrombolite, *Favosamaceria cooperi* n. gr. and form, which is unusual in shape and differs from any microbialite that has been treated taxonomically. It consists of a honeycomb or mazelike network of ridges that resembles complex labyrinthine hedge mazes from sixteenth- and seventeenth-century English gardens (Matthews, 1922). 'Maceria' is a new term that describes the mazelike pattern of the microbialite (from the Latin *maceria*, meaning "wall of a garden"). The thrombolite is easily recognized and it can be used as a biostratigraphic marker in the Great Basin (Fig. 1). This is important because the enclosing, shallow-ramp dolostone of the Great Basin generally lacks invertebrate and conodont fossils. All occurrences are from within the *Saukia* trilobite Zone of the Sunwaptan Stage.

SYSTEMATIC PALEONTOLOGY

FAVOSAMACERIA new group

Type.—*Favosamaceria cooperi* new group and form.

Diagnosis.—Macrostructurally distinguished by the labyrinthine to honeycombed pattern of coalesced maceriae in cross section (plan view) (see Fig. 2 for scales of observation). Maceriae polylobate, crescentic, or meandroid in plan view (Fig. 3), one to several centimeters wide, of nearly constant width throughout the thrombolite, with margins of maceriae parallel, commonly ragged, darker than the surrounding intermacerial fill; branching upward, parallel to parent maceria.

Etymology.—Latin *favus*, honeycomb, and *maceria*, garden wall.

Discussion.—*Favosamaceria* is distinguished from other microbialites by the dominance of branched, labyrinthine maceriae (Figs. 3–5). Lack of three-dimensional serial sectioning, rarely done on Phanerozoic microbialites, has probably led to oversight of the characteristic geometry of the macrostructural elements of this thrombolite (see Howe, 1966). Most thrombolites do not possess the richness in macrostructural features that is found in stromatolites. However, there are enough significant features and differences in this group to enable characterization.

Favosamaceria has some similarities to the so-called "tube rock" of the Neoproterozoic Noonday Dolomite of the Death Valley region, California (Cloud et al., 1974; Wright et al., 1978; Marenco et al., 2002), and the Maiberg Formation of Namibia (Hegenberger, 1987). These have been interpreted as microbialites (Hoffman and Schrag, 2002). Kerans (1985) and Playford (2002) recognized similar microbialites in the Windjana and Nullara formations (Devonian) and in isolated blocks in the Kimberley Region, Western Australia.

Content.—*Favosamaceria cooperi*.

FAVOSAMACERIA COOPERI new form

Figures 6, 7

Synonymy.—Thrombolites now assigned to *Favosamaceria cooperi* were figured in Cooper, 1989 (untitled plate, p. 86). Shapiro and Awramik (2000) referred to this thrombolite as Form F (p. 176–177, figs. 4, 5).

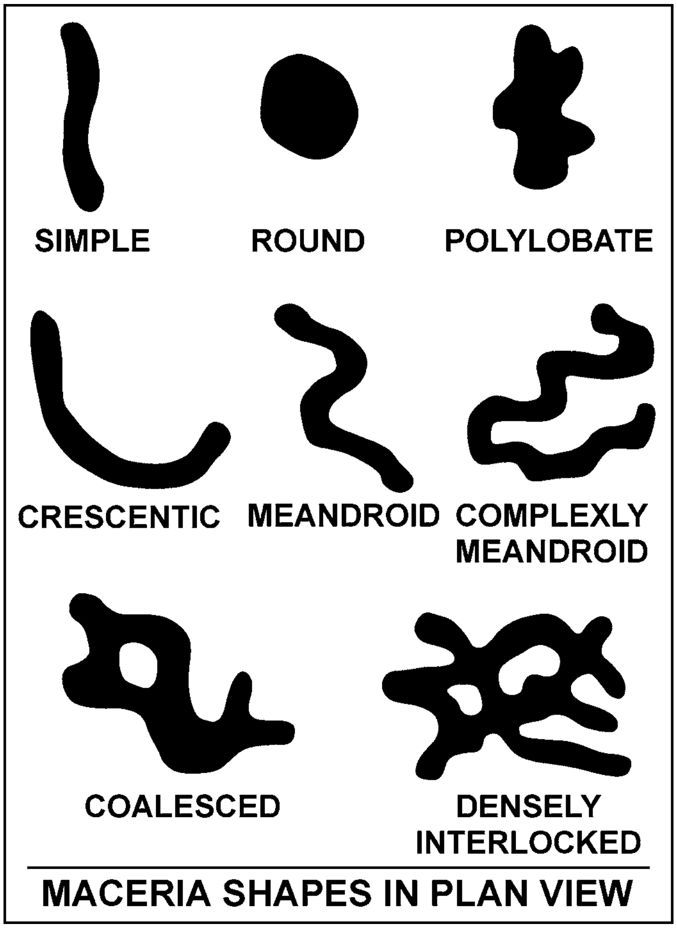


FIGURE *3*—Schematic diagram displaying the variety of maceria shapes of *Favosamaceria* n. gr. in plan view.

Diagnosis.—Maceriate thrombolites composed of polymorphic, millimeter-scale, dark peloidal mesoclots and peloidal-intraclastic intermesoclot fill.

Description.—The description is divided into four scales of observation: megastructure, macrostructure, mesostructure, and microstructure (see Hofmann, 1977; Shapiro, 2000; Shapiro and Awramik, 2000) (Fig. 2, Table 1).

Megastructure.—Megastructure encompasses the thrombolite bed or buildup, at the meter to decimeter scale. *Favosamaceria cooperi* forms tabular biostromes. Where not obscured by recrystallization, lower biostrome boundaries developed on sharp, erosional surfaces with up to several decimeters of undulatory relief and may be coated by a lamina of silt. The biostromes either form the base or overly ooid-peloid grainstones in shallowing-upward subtidal cycles capped by erosional surfaces. Cycles range from 2.0 to 16.5 m in thickness (average 5.4 m) and form successions up to 150 m thick.

Assessing biostromes' true dimensions is hampered by exposure limitations. The longest measured biostrome was over 65 m long, truncated on one end by a normal fault. Thickness is also variable. Thin biostromes average 2.2 m thick (range = 0.7–4.1 m; n = 20) whereas thicker biostromes average 9 m thick (range = 0.9–13.1 m; n = 4). The vertical spacing between biostromes is variable, ranging from 0.2 m (one cycle) to over 40 m (over a few cycles). Near biostrome boundaries, turbinate to cylindrical columnar stromatolites or domical thrombolites are also present; the different microbialites are found in an arrangement in which one type serves as a substrate for the other.

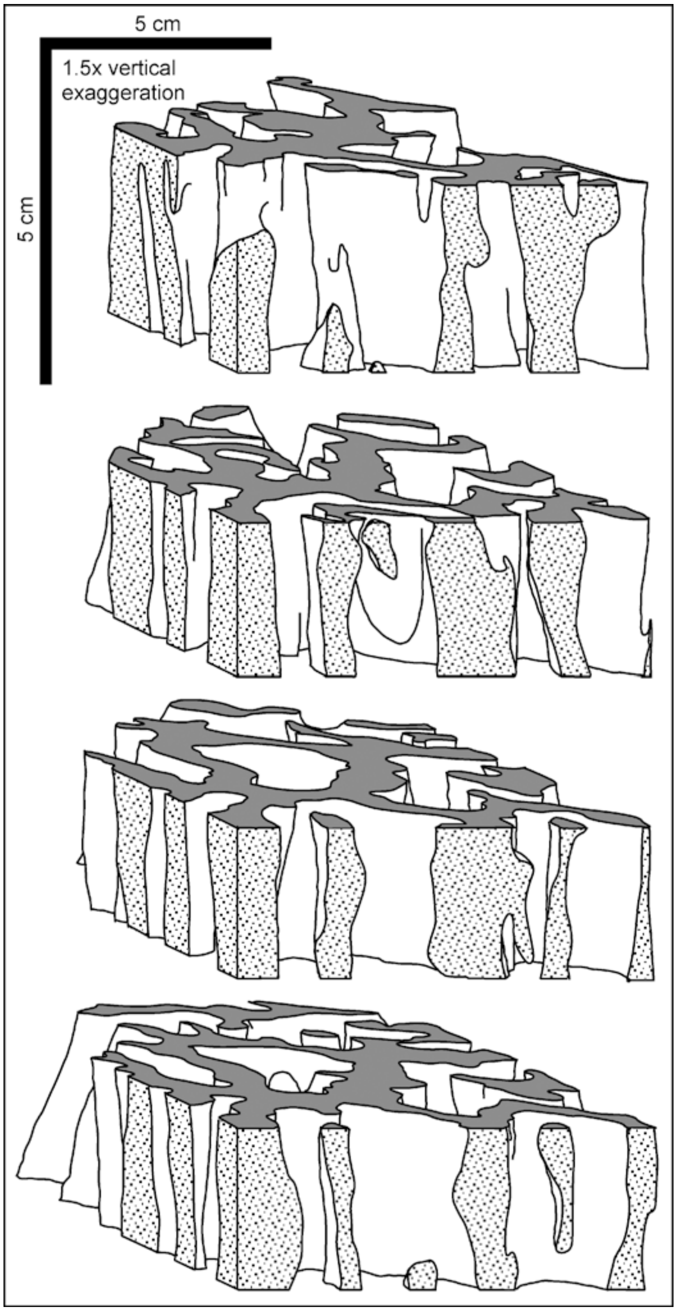


FIGURE *4*—Three-dimensional reconstruction of a representative example of *Favosamaceria cooperi* n. gr. and form. Stippled areas represent portions of maceriae trimmed by the rock saw. Specimen shown in section to illustrate the variability of maceriae in successive plan view. Differentiation between mesoclots and intermesoclot area not shown for clarity. Slabs used in reconstruction are part of the holotype UCMP 399741, 399742, 399743, 399744. True width = 9 cm. Vertical exaggeration = 1.5×.

The lateral boundaries of the biostromes interfinger with the ooid grainstone channel facies. Postlithification channels are also eroded into the biostromes. Where original sedimentary characteristics are preserved, the channel fill is typically cross-bedded ooid grainstone with lesser volumes of flat-pebble conglomerate and oncolite.

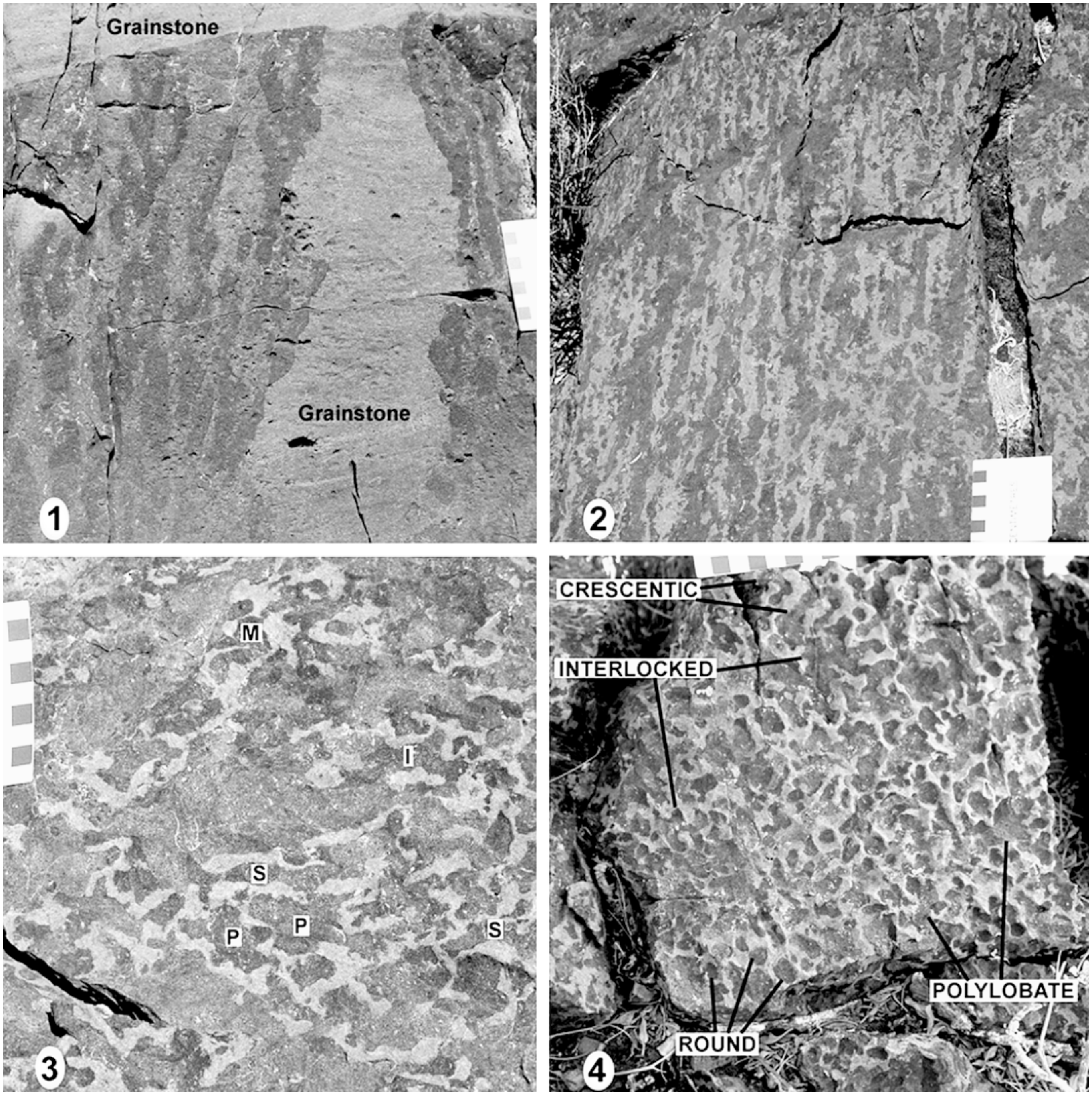


FIGURE 5—Field photographs showing the macrostructure of *Favosamaceria cooperi* n. gr. and form. *1*, *2* are vertical exposures and *3*, *4* are bedding-parallel exposures. *1*, Sharp erosional contact divides the thrombolites below from ooid grainstone above. Note the erosional channel between thrombolites filled with similar coarse ooid grainstone. *2*, Detail from the center of a thrombolite mound showing the ragged margins of the maceriae. Grey sediment between maceriae is micrite. *3*, Variable forms of maceriae in plan view. *4*, Maceriae preferentially weather in relief above the matrix. Scale bar in all photos is in centimeters.

Macrostructure.—Macrostructure describes the shape of the individual microbialite. Common macrostructures include columns, domes, and stratiform examples. *Favosamaceria cooperi* thrombolites are typically domical in external form, though some turbinate examples are present. Thrombolites measure between 0.35 and 2.8 m high (mean = 1.0 m; n = 95) and range from 0.1 to 2.0 m in maximum diameter. Rare small thrombolite columns (1 cm across by 3 cm high) are locally present separate from and adjoined to the larger domes.

Maceriae range from 1 to 10 cm wide (although most are about 3 cm wide) and 2 to 30 cm between branching points. The broad height range is due in part to irregularities in the location of branching points. Maceriae at the top of a buildup are not as densely packed as those in the center. In plan view, the maceriae

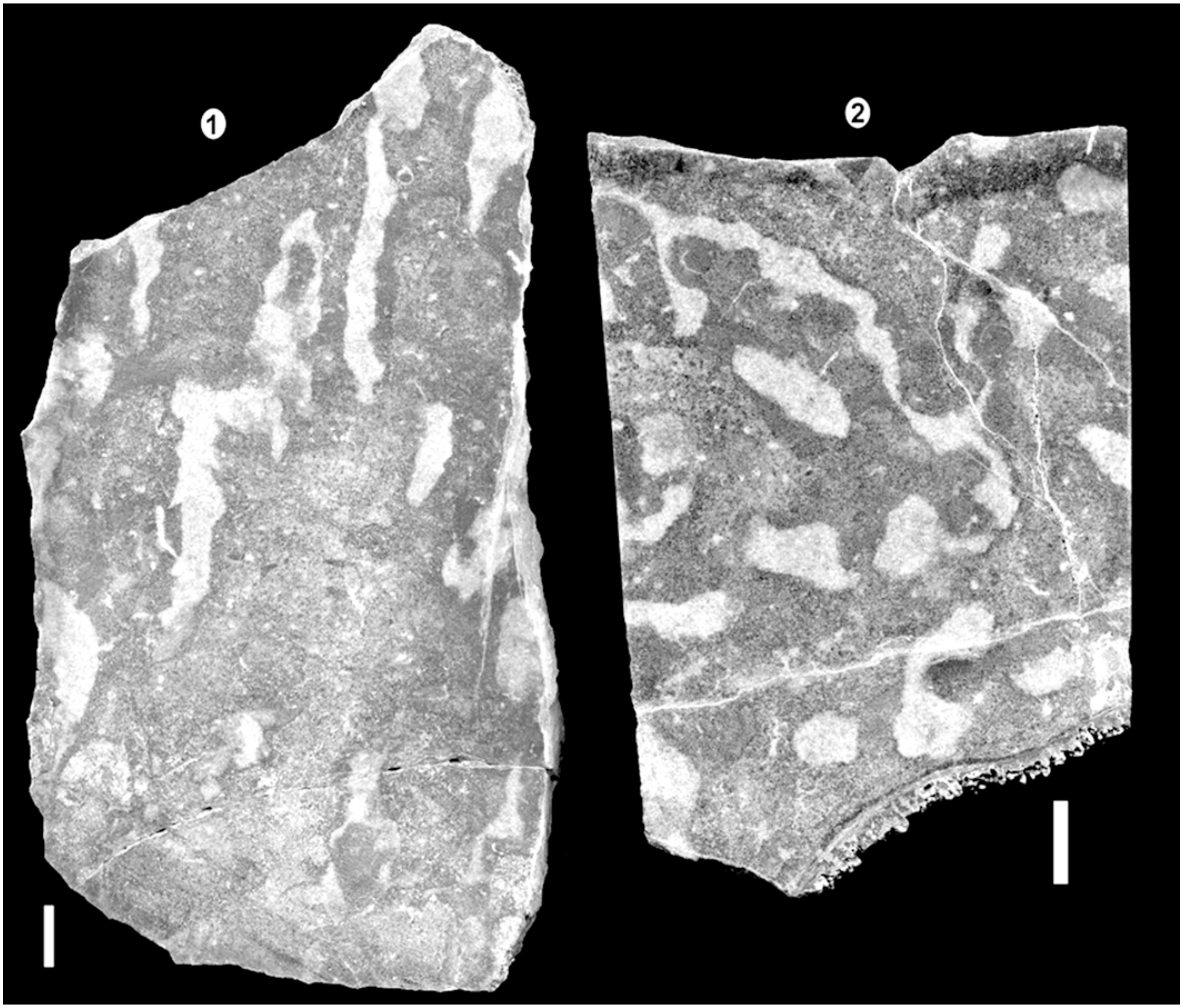


FIGURE 6—Polished sections showing the typical forms of maceriae. *1*, Vertical section, holotype UCMP 399745. *2*, Plan section, holotype UCMP 399746. Scale bar in both photos is 1 cm.

show a range of shapes that include relatively simple meandroid, polylobate, highly coalesced, and densely interlocked shapes. Smaller, crescentic to complexly meandroid maceriae located toward the center of a buildup are commonly surrounded by wider meandroid maceriae. In plan view, the length to width ratio of the smaller maceriae ranges from 1:1 to 20:1. In all of the maceriae, there is no net expansion or reduction of the width in the upward direction. Maceria branching is sparse, branching angle is moderately divergent to parallel, and the width of the parent maceria remains constant before branching (alpha branching). A new maceria (branch) diverges from the parent maceria over a short vertical distance, suggesting that branching develops over time and is not a 'single' event. Both the large and the small maceriae contain side maceriae projections of equal width that are normal to the main branch. These projections either terminate (with a rounded margin) or, more commonly, merge into adjacent maceriae and form the honeycombed, interlocked meshworks diagnostic of the group.

Maceria margins are parallel and often ragged. Synoptic relief was low (one-fifth to one-eighth of the maceria width), based on the intercalation of the enclosing ooid grainstone to the ragged edges of the maceria margins. Maceriae interspaces are about 1 cm wide and consistently thinner (67%–90%) than the maceriae themselves. Smaller projections extend from the maceriae at about 40° from the margin upward into the interspace area.

Mesostructure.—Mesostructure refers to the internal organization of the microbialite. For thrombolites, mesoclots are the distinctive mesostructural feature (Shapiro, 2000), and for *F. cooperi*, they define the new form. The mesoclots of *F. cooperi* are polymorphic, composed of dark dolomite, 2–4 mm across, and are surrounded by dark gray dolomite (Fig. 6). Mesoclots are found throughout the maceriae, but tend to be more concentrated along maceriae margins. In a hand-sample, mesoclots appear as closely to loosely packed granular masses. Grains are about 0.3–0.5 mm in diameter and very dark. The dark coloration is due to kerogen content, verified by thin section analysis. Vugs and

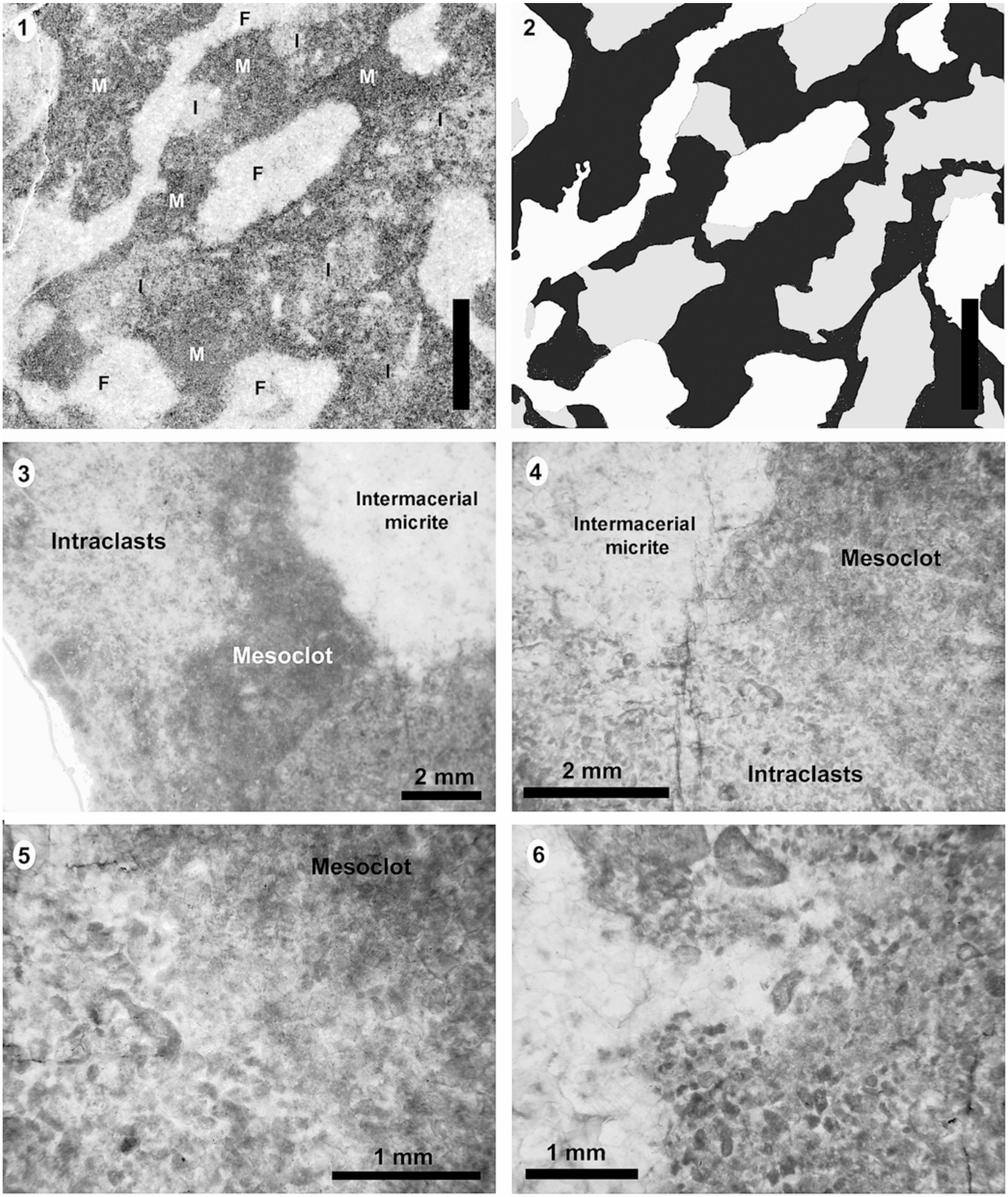


FIGURE 7—Meso- and microstructural attributes of *Favosamaceria cooperi* n. gr. and form. *1* and *2* show a polished plan surface in which the individual mesoclots (M) can be distinguished from the intermesoclot area (I) and the intermaceriae micrite fill (F). Slab is holotype UCMP 399747. *2*, Tracing emphasizing the details in *1*. Scale bar is 1 cm. *3–6*, Photomicrographs showing details of the different fabrics from holotype UCMP 399748. The mesoclots are composed of peloids with a high organic component in both the peloids and matrix. The intermesoclot area is dominated by micritic intraclasts and the intermacerial fill is micrite. All fabrics have been altered by late-stage dolomitization, creating the textural variation in the micrite. Photomicrographs were taken under transmitted light using a white card placed under the thin section.

TABLE *1*—Summary of the characteristics of *Favosamaceria cooperi* n. gr. and form.

MEGASTRUCTURE	Tabular biostromes. Thinner set averages 2.2 m thick (r = 0.7–4.1; n = 20) and thicker set averages 9.0 m thick (r = 0.9–13.1; n = 4). Vertical spacing variable, ranges from 0.2–40.0 m. Longest length at least 65 m.
MACROSTRUCTURE	Thrombolites average 1 m tall (r = 0.35–2.8; n = 95) and range from 0.1 to 2.0 m diameter. Maceriae average 3 cm wide (r = 1–10 cm) and 2–30 cm tall. Maceriae simple meandroid, crescentic, polylobate, highly coalesced, or densely interlocked. Length-to-width ratio 1:1–20:1. Synoptic relief one fifth to one eighth of width. Width of maceriae interspaces 67%–90% of maceria width.
MESOSTRUCTURE	Polymorphic mesoclots 2–4 mm wide, closely to loosely packed dark peloids, 0.3–0.5 mm in diameter.
MICROSTRUCTURE	Mesoclot peloids of dark masses, 130–250 μm diameter. Intermesoclot area of maceria is intrasparite. Intermacerial fill is micrite.

burrows filled with millimeter-sized white dolomite crystals occur within the dark dolomite.

Microstructure.—Microstructure describes the microscopic attributes of the microbialite. Mesoclots are composed of micritic peloids consisting of smaller masses, 130–250 μm in diameter, with a grumous fabric (Turner et al., 2000) (Fig. 7). The concentration of the small masses is higher near the mesoclot margins. Between the mesoclots, the maceriae are composed of intrapelsparite. The intermacerial sediment is predominantly micrite. The contact between the maceria and the micrite is depositional, rather than erosional. Locally, there appears to be a faintly preserved isopachous rim cement coating mesoclots, but preservation is too poor to be conclusive. No identifiable microfossils, including calcimicrobes, have been found.

Comparisons.—The new form, *Favosamaceria cooperi*, is distinguished from other forms and other thrombolites by its macrostructure (branched maceriae) and mesostructure (polymorphic mesoclots). Other older and younger thrombolites have more uniformly shaped mesoclots that have been described as pendant, arborescent, saccate, diffuse, prostrate, lobate, elongate, and crescentic (Kennard, 1994). Nearly all thrombolites described from the Neoproterozoic to the present share the same microstructure, namely a grumous fabric dominated by dark spherical masses one to several hundred μm in diameter (e.g., Turner et al., 2000). This uniformity in thrombolite microstructure precludes its use in differentiating forms.

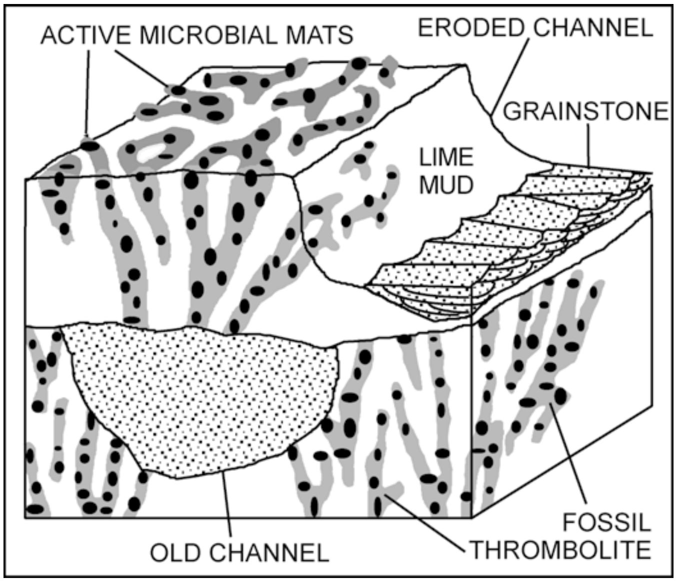


FIGURE *8*—Paleoecologic reconstruction of *Favosamaceria cooperi* n. gr. and form. The active microbial mats are composed of areas of microbial clusters (black) and intrapelsparite (grey). The microbial clusters fossilize to become the ‘mesoclots’ of the thrombolite. Between the mats, lime mud (white) accumulates. Following lithification, channels are eroded which later become filled with cross-bedded ooid grainstone.

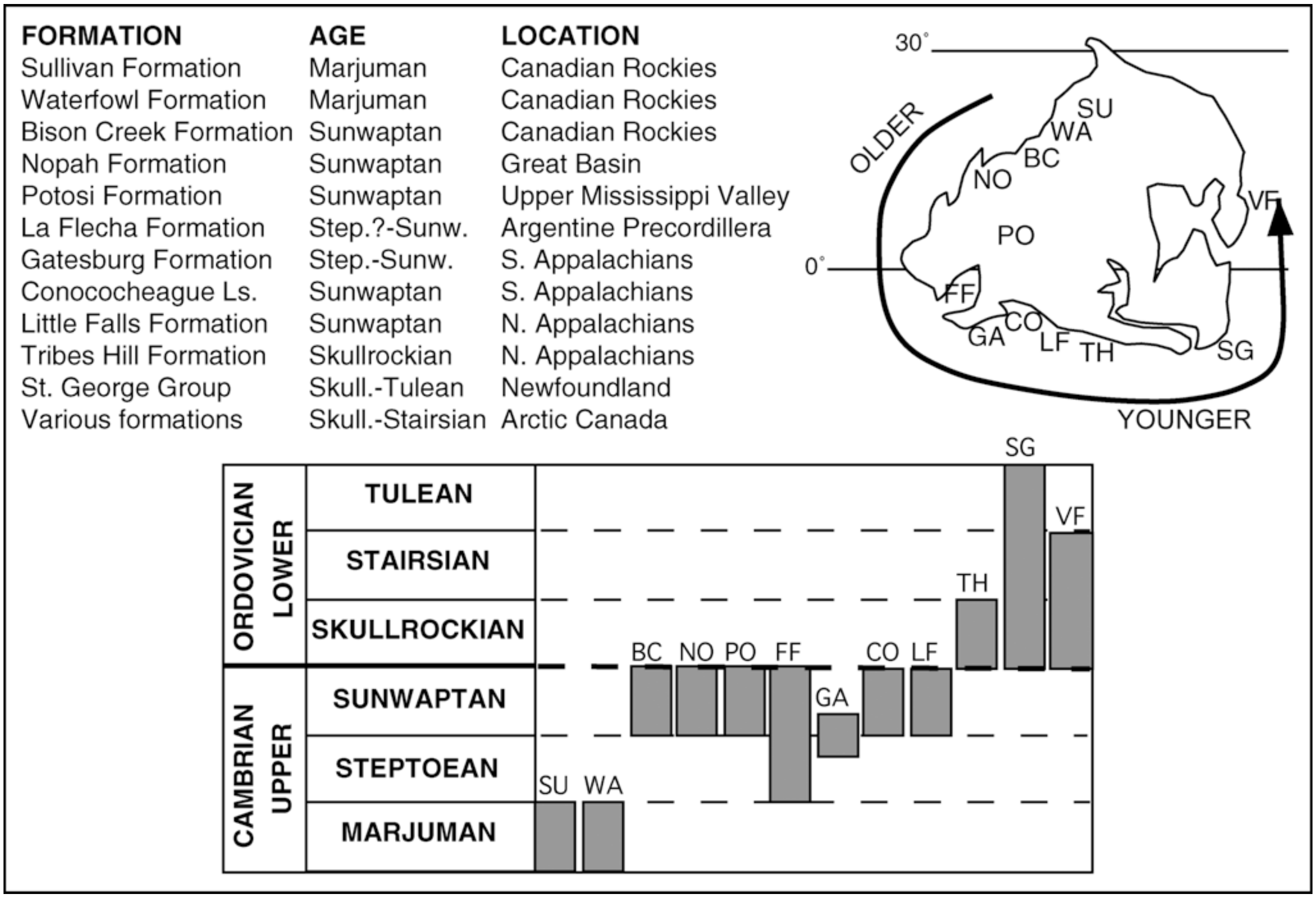
Etymology.—The form name honors Professor John Cooper of the California State University, Fullerton, who has devoted much effort to the study of the Cambrian and Ordovician of the Great Basin.

Types.—The holotype (deposited in the Museum of Paleontology, University of California, Berkeley) comprises four serial slabs, UCMP 399741, 399742, 399743, 399744, three polished slabs, UCMP 399745, 399746, 399747, and one petrographic thin section, UCMP 399748, from the Late Cambrian (Sunwaptan) Smoky Member of the Nopah Formation, Mohawk Hill, Clark Mountain, San Bernardino County, California. UTM: 11, 630792 mE 3928104 mN. A paratype comprising three polished slabs, SBO 473, 474, 475, one polished vertical specimen, SBO 476, and thin section SBO 475 made from one of the slabs is deposited in the Preston Cloud Research Laboratory, Department of Geological Sciences, University of California, Santa Barbara.

Material.—All figured specimens were collected between 1992 and 2002 from the Great Basin. More than 100 unfigured specimens from the other localities listed in Figure 1 are deposited at UCMP.

Occurrence.—Ubiquitous in the Sunwaptan (Upper Cambrian) carbonate ramp dolostone of the Great Basin, from the Nopah Formation, Desert Valley Formation, Whipple Cave Formation, Notch Peak Formation, and the Ajax Dolomite. The dolostone forms a several 100 m thick cliff that is easily recognized by its striped appearance. The stripes are caused by differential dolomitization of the *F. cooperi* buildups. The form has also been recognized in outer ramp deposits (Windfall Formation, northern Egan Range, Nevada) and is seen near the craton margin (Smoky Member of the Nopah Formation, Clark Mountain, California). The thrombolite has thus far not been recognized east of the cratonal-hinge zone in western North America.

Discussion.—*Favosamaceria cooperi* formed in shallow, subtidal environments across a carbonate ramp along the continental shelf margin (Fig. 8). This was a dynamic environment, as demonstrated by cross-bedded ooid grainstone and flat-pebble conglomerate. Late Cambrian invertebrates such as trilobites, brachiopods, molluscs, and echinoderms are very rare in this environment. Oncoids that accumulated between the thrombolites contain calcified filaments (*Girvanella* Nicholson and Etheridge, 1878) and presumably were not transported far. The thrombolites developed on submerged, eroded surfaces, forming the bases of meter-scale, shallowing-upward cycles (Fig. 8). Cycles are entirely subtidal and bounded by erosional surfaces. Successive thrombolites nucleated on localized postlithification erosional highs. Individual biostromes were separated from one another much like patch reefs in modern shallow tropical seas. During growth, the synoptic relief of the maceriae above the sediment surface was probably less than 5 mm (Fig. 8), evidenced by the maceria-intermacerial sediment relationships.



FORMATION	AGE	LOCATION
Sullivan Formation	Marjuman	Canadian Rockies
Waterfowl Formation	Marjuman	Canadian Rockies
Bison Creek Formation	Sunwaptan	Canadian Rockies
Nopah Formation	Sunwaptan	Great Basin
Potosi Formation	Sunwaptan	Upper Mississippi Valley
La Flecha Formation	Step.?-Sunw.	Argentine Precordillera
Gatesburg Formation	Step.-Sunw.	S. Appalachians
Conococheague Ls.	Sunwaptan	S. Appalachians
Little Falls Formation	Sunwaptan	N. Appalachians
Tribes Hill Formation	Skullrockian	N. Appalachians
St. George Group	Skull.-Tulean	Newfoundland
Various formations	Skull.-Stairsian	Arctic Canada

FIGURE 9—Distribution of *Favosamaceria* n. gr. thrombolites around Laurentia. SU = Sullivan Formation; WA = Waterfowl Formation; BC = Bison Creek Formation; NO = Nopah Formation; PO = Potosi Formation; FF = La Flecha Formation; GA = Gatesburg Formation; CO = Conococheague Limestone; LF = Little Falls Formation; TH = Tribes Hill Formation; SG = St. George Group; VF = various formations.

DISTRIBUTION OF *FAVOSAMACERIA* N. GR. THROMBOLITES IN TIME AND SPACE

Thrombolites dominate many microbialite-bearing Cambro–Ordovician, shallow-water, carbonate successions. Although comparisons of the thrombolites in these successions have not been carried out, a survey of the published illustrations and descriptions shows that there are a variety of shapes, and that thrombolites have the potential for interbasinal correlation. Common shapes include domes, cylindrical columns, branched columns, and stratiform biostromes (for example, Ahr, 1971; Griffin, 1989; Kennard, 1994; Shapiro, 2000). Domes appear to be the most prevalent early Paleozoic thrombolite morphology; non-domal *Favosamaceria* are limited to the middle Late Cambrian (late Marjuman) to middle Early Ordovician (Tulean) of the Laurentian margins (Fig. 9; Table 2). Thrombolites that compare favorably with *Favosamaceria* differ in depositional environment. The examples that follow are limited to those published occurrences in which sufficient, significant detail of thrombolite morphology is provided and where the morphology is consistent with the diagnosis of *Favosamaceria* though not necessarily of the *F. cooperi*. Terminology has been modified from the original descriptions for uniformity following the usage of Grey (1989) and Shapiro (2000). The series/stage nomenclature follows Ross et al. (1997) and Palmer (1998).

Canadian Rockies.—Aitken (1967) described branched thrombolites from the Bison Creek Formation (Sunwaptan), Sullivan Formation (Marjuman), and Waterfowl Formation (Marjuman). The thrombolites are organized into large bioherms, up to 6 m thick and over 15 m across. Based on the published descriptions, the mesostructure is dominated by centimeter-sized polymorphic mesoclots of microcrystalline calcite with rare terrigenous grains. Fossil fragments, particularly trilobites, are common, as are spar- and sediment-filled burrows. Specific environment(s) of formation are not provided. Aitken (1967) compared the Canadian forms to those described by Howe (1966) from Missouri (see below), but he did not provide individual maceria width or height.

Appalachians.—Branched columnar thrombolites from the Hoyt Limestone Member of the Little Falls Formation (Sunwaptan) and Wolf Hollow Member of the Tribes Hill Formation (Skullrockian) of New York State form large bioherms, 2 m high and over 10 m long (Mazzullo and Friedman, 1977; Landing et al., 2003). Although Mazzullo and Friedman (1977) did not provide data on column height and diameter, their illustrations clearly show the thrombolites to be similar to *Favosamaceria* from the Great Basin (field confirmed by Shapiro in 1998). The thrombolites contain abundant invertebrate material, chiefly gastropods and cephalopods. Mazzullo and Friedman (1977) cited the presence of solution collapse breccias, relict anhydrite molds, length-slow chalcedony, and desiccation cracks as evidence for an intertidal origin, and identified the environment of formation as prograding intertidal flats.

Farther south in the Appalachians, thrombolites similar to New York examples have been reported from the Gatesburg Formation (Steptoean–Sunwaptan boundary) and Conococheague Limestone

TABLE 2—Distribution of *Favosamaceria* n. gr. thrombolites.

Location	Age	Associated fauna	Macrostructural dimensions	Maceriae dimensions	Environmental setting
Canadian Rockies[1]	Marjuman–Sunwaptan	trilobites	up to 6 m tall, over 15 m wide	no data	no data
Great Basin[2]	Sunwaptan	rare trilobites, brachiopods, molluscs	0.35–2.8 m tall, 1–2 m wide	1–10 cm wide (avg. 3 cm)	restricted subtidal ramp
Upper Mississippi Valley[3]	Sunwaptan	no data	no data	0.6–1.9 cm wide	pertidal intracratonic embayment
Argentine Precordillera[4]	Steptoean?–Sunwaptan	no data	no data	0.5–1.0 cm wide	peritidal carbonate ramp
Southern Appalachians[5]	Sunwaptan	gastropods, brachiopods,trilobites	0.5–2.0 m tall	cm-scale	open-marine subtidal bank
Northern Appalachians[6]	Skullrockian	gastropods, cephalopods	2 m tall, over 10 m long	no data	intertidal flats
Newfoundland[7]	Skullrockian–Tulean	calcareous algae, corals, sponges	0.5–1.8 m tall, up to 3 m wide	1–3 cm wide	open-marine, subtidal shelf
Arctic Canada[8]	Skullrockian–Stairsian	Renalcis, trilobites, cephalopods, gastropods, brachiopods, lithistid sponges	5 m tall, 5 m wide, tens of m long	up to 5 cm wide	shallow to deep subtidal inner shelf

References: [1]Aitken (1967); [2]this paper; [3]Howe (1966); [4]Baldis et al. (1981), Armella (1994); [5]Demicco (1985), Demicco et al. (1987), Taylor et al. (1999); [6]Mazzullo and Friedman (1977); [7]Pratt and James (1982); [8]de Freitas and Mayr (1995).

(Sunwaptan). The Gatesburg Formation thrombolites form 1–2 m thick buildups, analogous to patch reefs separated by extensive grainstone, hosting rich trilobite faunas (Taylor et al., 1999). Although data on column size are not reported, Taylor et al. (1999) compared the occurrences to those described by Pratt and James (1982) from western Newfoundland (see below). *Favosamaceria* appears in the Conococheague Limestone along with other thrombolites. The Conococheague Limestone thrombolites are centimeter-scale maceriae(?) composed of microspar (Demicco, 1985; Demicco et al., 1987). The thrombolites comprise 0.5–1.0 m high bioherms. Cross-bedded, oolitic-peloidal grainstone, flat-pebble conglomerates, and abundant remains of gastropods, brachiopods, and trilobites are associated with the thrombolites. The thrombolites formed subtidally on an open marine bank.

Newfoundland.—Perhaps the best described branched thrombolites are found in the St. George Group of Newfoundland (Skullrockian–Tulean) (Pratt and James, 1982). The thrombolites comprise mounds, 0.5–1.8 m tall and up to 3 m wide. In plan view, the cerebroid pattern of the maceriae is pronounced. Maceriae range from 1 to 3 cm wide and exhibit a wide variety of shapes, expanding outward and upward. The margins are ragged and suggest only millimeters of synoptic relief. Polymorphic mesoclots are composed of small mudstone fenestrae and micrite peloids. Fossiliferous and burrowed mudstone or wackestone accumulated between the thrombolites. Calcareous algae, coral and/or sponges, and burrowing organisms are associated with the thrombolites. The thrombolites formed in shoals on an open, subtidal shelf.

Argentine Precordillera.—The most diverse assemblage of macrostructural shapes (i.e., columns and maceriae) of *Favosamaceria* appears to occur in the La Flecha Formation (Steptoean?–Sunwaptan) of the Argentine Precordillera (Baldis et al., 1981; Armella, 1994). The diverse shapes form encephalic, horizontal, concentric, vertical, radial, and lanceolate structures in plan view (Armella, 1994). Maceriae, where apparent, are 0.5–1.0 cm wide and intermacerial areas are 1–2 cm wide. Maceriae are composed of polymorphic mesoclots consisting of massive micritic or peloids. The peloids are composed of microclots 100–150 μm in diameter. The thrombolites of the La Flecha Formation formed on a stable carbonate ramp in a series of regressive peritidal cycles (Keller et al., 1989; Buggisch et al., 2000).

Upper Mississippi Valley.—The microbialites from the Potosi Formation (Sunwaptan) described by Howe (1966) as ''digitate stromatolites'' are more likely branched thrombolites, based on comparisons by Aitken (1967). The thrombolites are irregularly branched and constitute larger bioherms and biostromes. Howe (1966, p. 65) made a point of stressing that the individual columns were not circular in plan view, but 'meandrine' (=maceriae; see also Howe's text-fig. 5). Maceriae range from 0.6 to 1.9 cm wide and the maceria:interspace ratio is nearly always 1:1. The maceriae are slender, vertically to obliquely oriented, and range up to >1 m tall with little overall taper. The interspace area consists of calcarenite that includes eroded microbialite. Howe called these structures ''stromatolites.'' However, he noted that true lamination was found at only two localities, and that the lamination is ill-defined. He noted that these unique shapes might represent ''an important form-category that can be usefully distinguished from other types'' (Howe, 1966, p. 74). The thrombolites formed in peritidal environments across a broad, intracratonic embayment.

Arctic Canada.—A thick succession of strata containing branched thrombolites occurs in various formations of the Early Ordovician (Skullrockian–Stairsian) of Arctic Canada (de Freitas and Mayr, 1995). In one region, maceriate thrombolites are present in closely spaced mounds, tens of meters in length, 5 m in width, and more than 5 m tall. The mounds show elongation that is probably current-controlled. In plan view, individual maceriae are up to 5 cm wide and present complex meandroid patterns. The maceriae are composed of polymorphic mesoclots of pelmicrite, clotted micrite, and fenestral pelmicrite. The mesoclots also contain spar-replaced sponge spicules, dense, *Renalcis*-like micrite clots, and calcispheres (40–240 μm in diameter). The enclosing strata are rich in skeletal debris of trilobites, orthoconic cephalopods, planispiral and high-spired gastropods, brachiopods, and lithistid sponges. The various thrombolite-bearing deposits range from the shallow to deep subtidal along an inner carbonate shelf margin.

Discussion.—Branched thrombolites assigned to *Favosamaceria* are ubiquitous around the margins of Laurentia in uppermost Cambrian and lowermost Ordovician strata, with an apparent acme during the Sunwaptan. Although *Favosamaceria* thrombolites from the various sites are similar on all or most structural levels, they formed in different environments (Table 2). The central Appalachian thrombolites represent an excellent example of development on intertidal flats. Thrombolites from older, Late Cambrian Appalachian deposits, as well as the Early Ordovician examples from Newfoundland and Arctic Canada, grew on open-marine, subtidal shelves. The thrombolites of the Great Basin and Argentine Precordillera most likely formed under more restricted, shallow subtidal conditions on a carbonate ramp. Skeletal fossils associated with the thrombolites differ among the various locales. The fact that these similar thrombolites are found across a spectrum of intertidal to deep subtidal, open- to restricted-marine carbonate facies suggests a significant biological control on the group characteristics and a weaker environmental control. Environmental factors may play a role in the distribution of other microbialite types (oncoids, stromatolites, domical thrombolites) at the margins of or in successions with the *Favosamaceria* thrombolites.

An interesting pattern emerges when the ages of the occurrences of *Favosamaceria* thrombolites are plotted on a paleogeographic reconstruction of Laurentia (Fig. 9, Table 2). *Favosamaceria* shows a biogeographic distribution around Laurentia and has not been documented from elsewhere. Such provinciality is not unusual for microbialites; for example, Proterozoic stromatolites show provincialism (Semikhatov and Raaben, 2000). The distribution of *Favosamaceria* thrombolites around Laurentia (Fig. 9) begins in the Canadian Rockies and becomes younger in a counterclockwise direction. The youngest occurrences are in the Canadian Arctic. The cause of this diachronous pattern is unknown and it is not documented in other Laurentian biota. Similarly branched, maceriate thrombolites are absent from coeval thrombolitic deposits on continental margins that were not contiguous with Laurentia. For instance, thrombolites from the North China and Korean margins at this age are predominantly hemispheroids (Ming et al., 1996; Meng et al., 1997). Also, older and younger Laurentian margins contain abundant thrombolites (e.g., Ahr, 1971; Pereyra, 1987; Friedman, 1996; Glumac and Walker, 1997; Shapiro and Awramik, 2000) but not of the branched maceriate type described here. Interestingly, coeval deposits of the Franklin Mountains in Texas contain columnar-branched stromatolites (cylindrical columns) but not thrombolites (LeMone, 1976).

CONCLUSIONS

Favosamaceria cooperi n. gr. and form represents a new microbialite architecture that has not been systematically described. The distinctive maceriate structure and well-constrained chronostratigraphic occurrence (*Saukia* trilobite Zone of the Sunwaptan Stage) lends the thrombolite to taxonomic description and biostratigraphic utility throughout the Great Basin region.

Additionally, the distribution and abundance patterns of the *Favosamaceria* n. gr. show that individual microbialite types may be used for large-scale correlation in the Phanerozoic. Though the biological composition of the microbial ecosystems responsible for branched maceriate thrombolites has not been identified, the consistency of macro- to microstructural features of the thrombolites alludes to microbiological similarities among the various locales around Laurentia. Whether these thrombolites are the same form as the Great Basin examples remains to be seen. The thrombolites are found in a variety of facies and from different tectonic settings (ramps, shelves, intracratonic embayments), yet they are restricted to the same time interval. This pattern suggests the utility of microbialites in Phanerozoic biostratigraphy and justifies taxonomic treatment. Future research should look into other unique microbialite types and how they can be used for correlation. In addition to the Cambro–Ordovician interval that is the focus of this study, other target times include the (relatively) microbialite-rich Proterozoic, Late Devonian, Late Carboniferous, Triassic–Jurassic, and Neogene.

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