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PRESERVATIONAL AND MORPHOLOGICAL VARIABILITY OF ASSEMBLAGES OF AGGLUTINATED EUKARYOTES IN CRYOGENIAN CAP CARBONATES OF NORTHERN NAMIBIA

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ABSTRACT

Laminated carbonates of the Rasthof Formation, deposited in the aftermath of the early Cryogenian low-latitude glaciation (Sturtian, 717–662 Ma), preserve abundant round tests of agglutinated microscopic eukaryotes. Previously, fossil tests were reported in two localities (Ongongo and Okaaru) from microbially laminated carbonates in the Rasthof Formation, which revealed a previous unexplored Cryogenian taphonomic window. In order to better understand the lateral variability in these microfossil assemblages, this work systematically examines fossil tests from two additional localities, South Ombepera and Ombepera, and compares their preservation in thinly and thickly laminated microbial laminites. Cap carbonates in South Ombepera and Ombepera contain abundant, hollow, spheroidal agglutinated tests (50 to 225 μm in diameter). Some of these tests exhibit slitlike or triangular apertures. In contrast, much larger, oval tests with a tapering end dominate the assemblages at Okaaru, whereas oval, laterally compressed and round structures with slits, visors, or central apertures are found at Ongongo. The thinly laminated microbial laminites from Ombepera, South Ombepera, and Okaaru also preserve rare agglutinated tubes attributed to fossils of early Foraminifera. At all four localities, the thinly laminated microbial laminites preserve more microfossils than thickly laminated microbial laminites although these two facies commonly interfinger and are interbedded. This difference shows that conditions present during formation of the thinly laminated microbial laminites favored the preservation of round agglutinators, perhaps during early burial, lithification, and fossilization of the test walls.

INTRODUCTION

Few times in Earth history match the captivating Neoproterozoic potpourri of climatic, biological, geochemical, and tectonic changes (Halverson et al., 2005; Knoll et al., 2006; Li et al., 2008; Pierrehumbert et al., 2011). Among other defining events that took place between 1000–541 Ma, geological evidence exists for the presence of ice at sea level at low latitudes, indicating at least two severe glaciations: the older, Sturtian, and the younger, Marinoan, glaciation (Hoffman et al., 1998; Hoffman and Schrag, 2002). Both the Sturtian and Marinoan glacial deposits are capped by carbonates, which have unique geochemical and sedimentological characteristics that have been interpreted to reflect an extreme alkalinity flux during a postglacial super greenhouse (Hoffman and Schrag, 2002; Bao et al., 2008). Although the severity and duration of the Sturtian glacial period has been questioned on geochemical and sedimentological grounds (Allen and Etienne, 2008; Kasemann et al., 2010), existing geochronology constrains the duration of the Sturtian glaciation(s) to between 5 and 55 myr (Macdonald et al., 2010). Here, we seek to improve the fossil record of eukaryotes in the immediate aftermath of the Sturtian glaciation by exploring the preservation and diversity of agglutinated tests across lateral environments preserved in cap carbonates of the Rasthof Formation, northern Namibia.

The Rasthof Formation preserves a cap carbonate of Sturtian age that is composed predominantly of thickly and thinly laminated microbial laminites (Pruss et al., 2010). Recently, microfossils were reported in the cap carbonates at two different sections of the Rasthof Formation: Ongongo and Okaaru (Bosak et al., 2011a, 2012). The microfossil assemblages from Ongongo and Okaaru contain various abundant agglutinated oval and round three-dimensional rigid and hollow tests whose organic walls are covered by platy, 2–10-μm-long grains of muscovite, microcline, and hematite (Bosak et al., 2011a). The morphologies and compositions of the oval and round tests are consistent with those of modern agglutinated testate amoebae, probably related to the arcellinid amoebozoans (Bosak et al., 2011a). Microbial laminites at Okaaru also preserve rare tubular agglutinated forms and large oval forms with one blunt end, resembling modern monothalamous tubular and globular foraminiferans (Bosak et al., 2011a, 2012). These initial findings from the Rasthof Formation at Ongongo and Okaaru, as well as a recent report of large phosphatized forms named *Otavia* from pre-Sturtian Namibian carbonates and the interglacial carbonates of the Ombaatjie Formation (Brain et al., 2012), inspire questions about the stratigraphic occurrence and variations of fossils within the Rasthof Formation. To this end, this study investigates microfossil morphology and preservation in similar facies at two additional localities of the lower Rasthof Formation: Ombepera and South Ombepera. The lateral variations of test morphologies across different exposures, but within similar facies, provide evidence for morphological and ecological diversity of testate eukaryotes following the Sturtian glaciation. Moreover, detailed comparisons of test abundances and preservation in the thinly and thickly laminated microbialites of the Rasthof Formation identify the potential of thinly laminated microbial laminites to preserve numerous tests in other, currently unexamined localities and formations.

GEOLOGICAL SETTING

The Neoproterozoic Otavi Group is a 2–4-km-thick carbonate-dominated succession exposed on the Congo Craton of northern Namibia (Fig. 1). Within the Otavi Group is the Rasthof Formation (Abenab Subgroup; Hedberg, 1979), a Cryogenian cap carbonate overlying glacial deposits of the Chuos Formation, which have been correlated globally with the early Cryogenian Sturtian glaciation (Hoffman and Schrag, 2002). Northeast of Sesfontein, the Rasthof Formation is 200–400 m thick (Hoffman et al., 1998; Hoffman and Halverson, 2008; Pruss et al., 2010) and is chronostratigraphically constrained below by the 746 ± 2 Ma Naauwpoort volcanics (Hoffman et al., 1996) and above by the 635.5 ± 1.5 Ma Ghaub Formation (Hoffmann et al., 2004).

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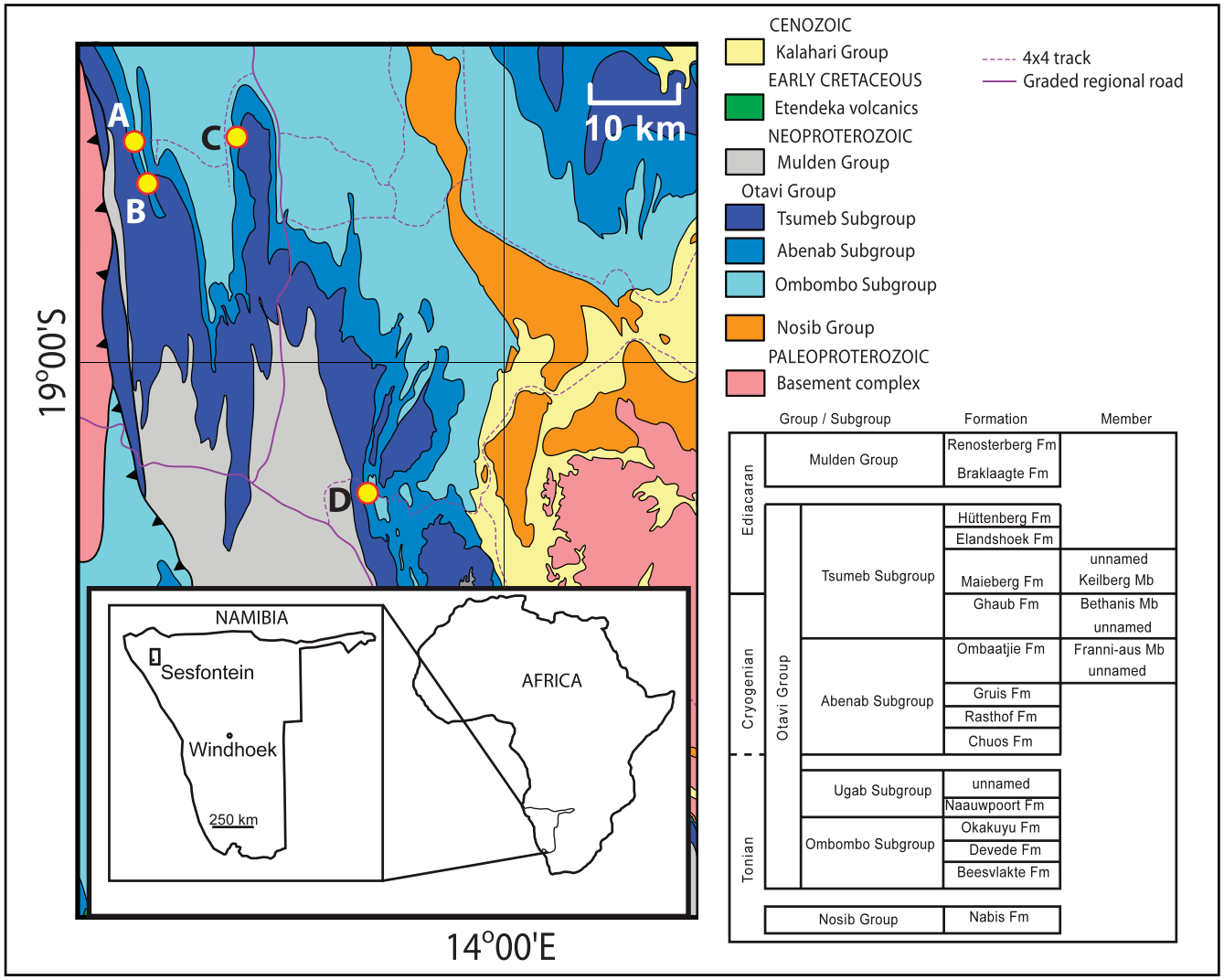

FIGURE 1—Geological map of the Rasthof Formation showing the fossiliferous localities. Inset map of Namibia in southern Africa shows mapped area in the north. Geological map shows the four localities: Ombepera = A, South Ombepera = B, Okaaru = C, and Ongongo = D. Stratigraphic names used in this paper are provided below the key. Modified from P. Hoffman and Pruss et al. (2010).

The Rasthof Formation is composed of dark-gray carbonate composed of thickly laminated microbial laminites, thinly laminated microbial laminites, rhythmite, and grainstone facies (Hoffman and Halverson, 2008; Pruss et al., 2010). Facies of the lower Rasthof Formation are consistent with relatively deep-marine deposition. Rhythmites, the distal ends of turbidites, occur at the base of many Rasthof sections and overlying thinly and thickly laminated microbial laminite facies lack any evidence for wave or current activity, including bedforms, or shoaling (Pruss et al., 2010). These strata were likely deposited upon considerable topography due to both active tectonism and glacial erosion that preceded deposition (Pruss et al., 2010). Nonetheless, in exposures northeast of Sesfontein, shale and marl become more common to the west, both in the Rasthof and in overlying formations, suggesting deepening to the west on the western margin of the Congo Craton. This is in contrast to the Fransfontien region, which records southward deepening on the southern margin (Hoffman and Halverson, 2008).

Carbonate samples were collected from four exposures of the Rasthof Formation along a northwest transect, northeast of Sesfontein (Fig. 1). Two new localities, Ombepera and South Ombepera, are described herein. The lower Rasthof Formation is ~50 m thick at South Ombepera (Fig. 2), and alternating and interfingering thickly and thinly laminated microbial laminites comprise the basal 10 m of the section. The overlying 40 m of section is broadly similar to the underlying facies, but contains more brecciated microbial laminites. At Ombepera, located to the northwest of South Ombepera (Fig. 2), the lower Rasthof Formation is 21 m thick (Fig. 2). The base of the section consists of 2 m of thickly laminated rhythmite which is overlain by thickly laminated microbialite interbedded with thinly bedded microbial laminites with synsedimentary roll-up structures (Pruss et al., 2010). The Rasthof Formation at Ombepera and South Ombepera is lithologically similar to the exposures at Ongongo and Okaaru, with one important difference: the thinly laminated and thickly laminated microbial laminites occur at different stratigraphic intervals at Ongongo and Okaaru, whereas these facies are distinctly interfingered and interbedded at Ombepera and South Ombepera (Fig. 2).

Thickly laminated microbial laminites are characterized by 1–4-mm-thick alternating dark and light laminae. This facies typically contains dome-shaped features interpreted as the relics of soft sediment deformation (Pruss et al., 2010). Thinly laminated microbial laminite facies are characterized by <1-mm-thick alternating dark and light laminae and contain unique roll-up structures (Pruss et al., 2010). Differences in the thickness of the laminae may be related to varying accumulation and/or lithification rates (Pruss et al., 2010). Thinly laminated microbial laminites preserve extensive textural evidence of organic-rich microbial mats, while abundant early cements and fewer organic-rich layers are found in thickly laminated microbial laminites.

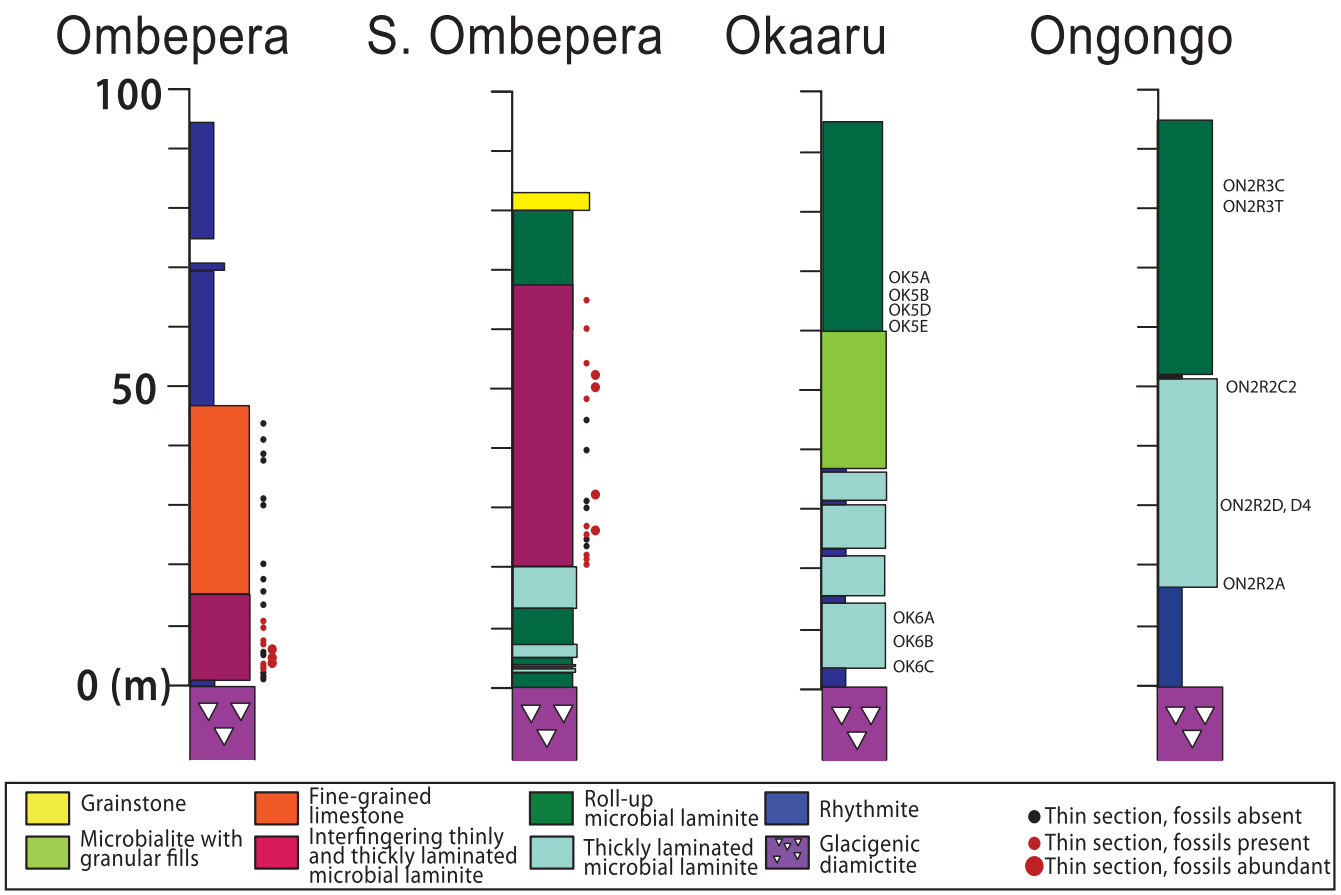

FIGURE 2—Stratigraphic columns of the Rasthof Formation at the four localities. Colored dots at Ombepera and South Ombepera mark the stratigraphic positions of fossiliferous and unfossiliferous samples, respectively. Fossiliferous samples from Ongongo and Okaaru described in Bosak et al. (2011a, 2012) are shown at the appropriate stratigraphic horizons.

METHODS

Carbonates of the Rasthof Formation at Ombepera and South Ombepera were sampled at a 1–4 m resolution in 2009. Forty-five of these samples were thin sectioned (Fig. 2). Each thin section was analyzed by transmitted light microscopy, using a petrographic microscope (Olympus BH-2, Olympus Optical Co., Tokyo, Japan). Microfossils in thin sections were identified by color, shape, size, presence of walls, and occurrence in clusters, and imaged using the petrographic microscope. Microfossils in thin section were characterized as abundant, present, or not present or rare (Tables 1, 2). Thin sections containing abundant microfossils typically contained microfossil clusters and/or >10 microfossil tests with clear, identifiable walls.

Samples corresponding to fossiliferous thin sections were dissolved in 10% acetic acid buffered with 10% ammonium acetate. From each of these samples, ~3–16 g of carbonate rock (limestone and dolostone) were dissolved. Residues were collected via suction filtration at >100 µm and 41–100 µm using Millipore nylon net filters and examined under a dissecting microscope (Nikon SMZ645, Nikon Corporation, Tokyo, Japan). Structures with recurring morphologies and colors were collected by brush and placed on clear glass slides prior to placement on SEM stubs.

Putative microfossils from each sample were analyzed by scanning electron microscopy (SEM) using an FEI Quanta 450 Scanning Electron Microscope at the Center for Biological Microscopy at Smith College, or Zeiss EVO 50 at the Electron Microprobe/SEM Facility, University of Massachusetts, Amherst. Samples were coated in gold and palladium with a Hummer V Sputter Coater and analyzed by SEM using 5kV acceleration voltage. Energy Dispersive X-Ray Spectrometer (EDS) with 20 kV acceleration voltage and Team EDS Analysis System software (EDAX Inc., Mahwah, New Jersey, United States) were used in conjunction with the SEM to analyze the chemical composition of samples. Lengths and widths of 114 microfossils from South Ombepera were measured using Olympus BH-2 microscope and DP Controller imaging software. Two-sample *t*-tests were employed to compare these dimensions to the dimensions of previously reported microfossil assemblages (Bosak et al., 2011a).

Raman spectra were collected nondestructively at room temperature with a WITec Confocal Raman Microscope/SNOM/AFM and WITec Control software. Point targets were excited using a 532-nm-wavelength laser of 50mW output power in an enclosed hood system for better noise performance and higher resolution. Laser shutter and aperture were adjusted to maximize a silica standard peak (>400 counts) during basic alignment of the system, which was performed prior to each measurement procedure. Parameters of 500 spectral counts, 20 spectral accumulations, and 0.1s integration time were set. Points of interest were located with a transmitted light microscope connected to the spectrometer by means of a fiber-coupling unit with optical output. Raman spectra were obtained in the interval of 0–2,500cm^{-1} for carbonaceous compounds and reviewed with WITec Project software (external data manager).

RESULTS

Petrographic Analysis

Of the 44 thin sections examined from Ombepera (N = 25) and South Ombepera (N = 20), 23 thin sections contained 100–300-µm-long, oval

TABLE 1—Description of facies, thin section and residue analysis from South Ombepera. N/A under residue description means sample was not dissolved.

Sample #	Facies description	Thin section description	Residue descriptions
F903 20.4	Thickly laminated microbial laminite (ML)	Microfossils present	Microfossils absent
F903 20.8	Thinly laminated some interfingering with thickly laminated ML	Microfossils present, poor preservation	Microfossils absent
F903 21.0	Thinly laminated ML	Microfossils present, poor preservation	N/A
F903 23.8	Interfingered thickly and thinly laminated ML	Microfossils absent	N/A
F903 24.4	Interfingered thickly and thinly laminated ML	Microfossils absent	N/A
F903 24.8	Mostly thickly laminated interfingering with some thinly laminated ML	Microfossils present, poor preservation	Microfossils absent
F903 26.0	Thinly laminated ML	Microfossils abundant	Few tests, fragments
F903 27.5	Thickly laminated ML	Microfossils present	Tube present, no spherical microfossils
F903 30.5	Interfingered thickly and thinly laminated ML	Microfossils absent	N/A
F903 31.5	Thinly laminated ML	Microfossils absent	N/A
F903 32.5	Thinly laminated ML	Microfossils abundant in dark laminae	Microfossils not present, possible fragments
F903 40.0	Thinly laminated ML	Microfossils absent	N/A
F903 44.0	Thinly laminated, dark ML	Microfossils absent	Microfossil not present, possible fragments
F903 48.0	Thinly laminated, dark ML	Microfossils present	Microfossils abundant
F903 50.0	Thinly laminated ML	Microfossils abundant	Abundant fragments, few whole microfossils
F903 52.0	Thinly laminated ML	Microfossils abundant	Abundant microfossils with many fragments
F903 54.0	Thinly laminated ML	Microfossils present	Abundant fragments few whole microfossils
F903 60.0	Thinly laminated ML	Microfossils present	Few microfossils, possible fragments
F903 64.0	Thinly laminated ML	Microfossils present	Abundant fragments, few whole microfossils

or round, gray or brown structures (Figs. 3–4, Table 1). These structures are easily discernible from the surrounding matrix and have similar sizes and appearances to the previously described fossil tests at the Okaaru and Ongongo localities (Bosak et al., 2011a). At South Ombepera, most structures are round and ~200 to 250 μm in diameter (Figs. 3C–E), but rare forms include 250-μm-long ovals with apparent blunt ends (Figs. 3B, F) and 400-μm-long tubular forms (Figs. 3A, 4E). Structures from South Ombepera occasionally preserve well-defined walls in thin section (Figs. 3D–F). Similarly sized round structures in thin sections from Ombepera are sometimes darker than those at South Ombepera and, in some cases, preserve less distinct walls (Fig. 4A, C), which may be relicts of recrystallization. Ombepera thin sections preserve microfossils occurring in clusters within individual light laminae (Fig. 4D), and tubular forms (Fig. 4E). The ovals and tubes do not commonly appear hollow in thin section (Figs. 3B–F, 4A–D). This is not surprising because the thin sections cut many of their ~20-μm-thick mineral-rich walls at oblique angles.

Six thin sections from South Ombepera do not contain any visible fossils (Table 1). Microfossils are present but not abundant in 9 others (Table 1). The remaining four samples had abundant microfossils

TABLE 2—Description of facies, thin section and residue analysis from Ombepera. N/A under residue description means sample was not dissolved.

Sample #	Facies description	Thin-section description	Residue description
F905 1.4	Thickly laminiated, iron-rich microbial laminite (ML)	Microfossils absent	N/A
F905 2.0	Interfingered thickly and thinly laminated ML	Microfossils absent	N/A
F905 2.2	Interfingered thickly and thinly laminated ML	Microfossils absent	N/A
F905 2.8	Thinly laminated ML	Microfossils present, poor preservation	N/A
F905 3.0	Thickly laminated ML	Microfossils present, but rare	N/A
F905 3.6	Interfingered thickly and thinly laminated ML	Microfossils present, poor preservation	N/A
F905 3.8	Interfingered thickly and thinly laminated ML	Microfossils abundant	Rare spherical, microfossils, tube present
F905 4.4	Thinly laminated ML	Microfossils abundant	Poorly preserved microfossils
F905 4.8	Thinly laminated ML	Microfossils absent	N/A
F905 5.6	Interfingered thickly and thinly laminated ML	Microfossils absent	N/A
F905 6.0	Interfingered thickly and thinly laminated ML	Microfossils abundant	Microfossils absent
F905 7.0	Interfingered thickly and thinly laminated ML	Microfossils present	Tube present (partial), spherical microfossils absent
F905 8.0	Interfingered thickly and thinly laminated ML	Microfossils present	Tube present, poorly preserved microfossils
F905 10.0	Thinly laminated ML	Microfossils present	Tubes (N = 2) present, spherical microfossils absent
F905 11.0	Thickly laminated ML	Microfossils present	Poorly preserved microfossils
F905 13.0	Thinly laminated ML	Microfossils absent	N/A
F905 15.0	Thinly laminated ML	Microfossils absent	N/A
F905 17.0	Micrite	Microfossils absent	N/A
F905 20.0	Micrite	Microfossils absent	N/A
F905 30.0	Micrite	Microfossils absent	N/A
F905 31.0	Micrite	Microfossils absent	N/A
F905 38.0	Thickly laminated ML	Microfossils absent	N/A
F905 39.0	Micrite	Microfossils absent	N/A
F905 41.0	Micrite	Microfossils absent	N/A
F905 43.0	Micrite	Microfossils absent	N/A

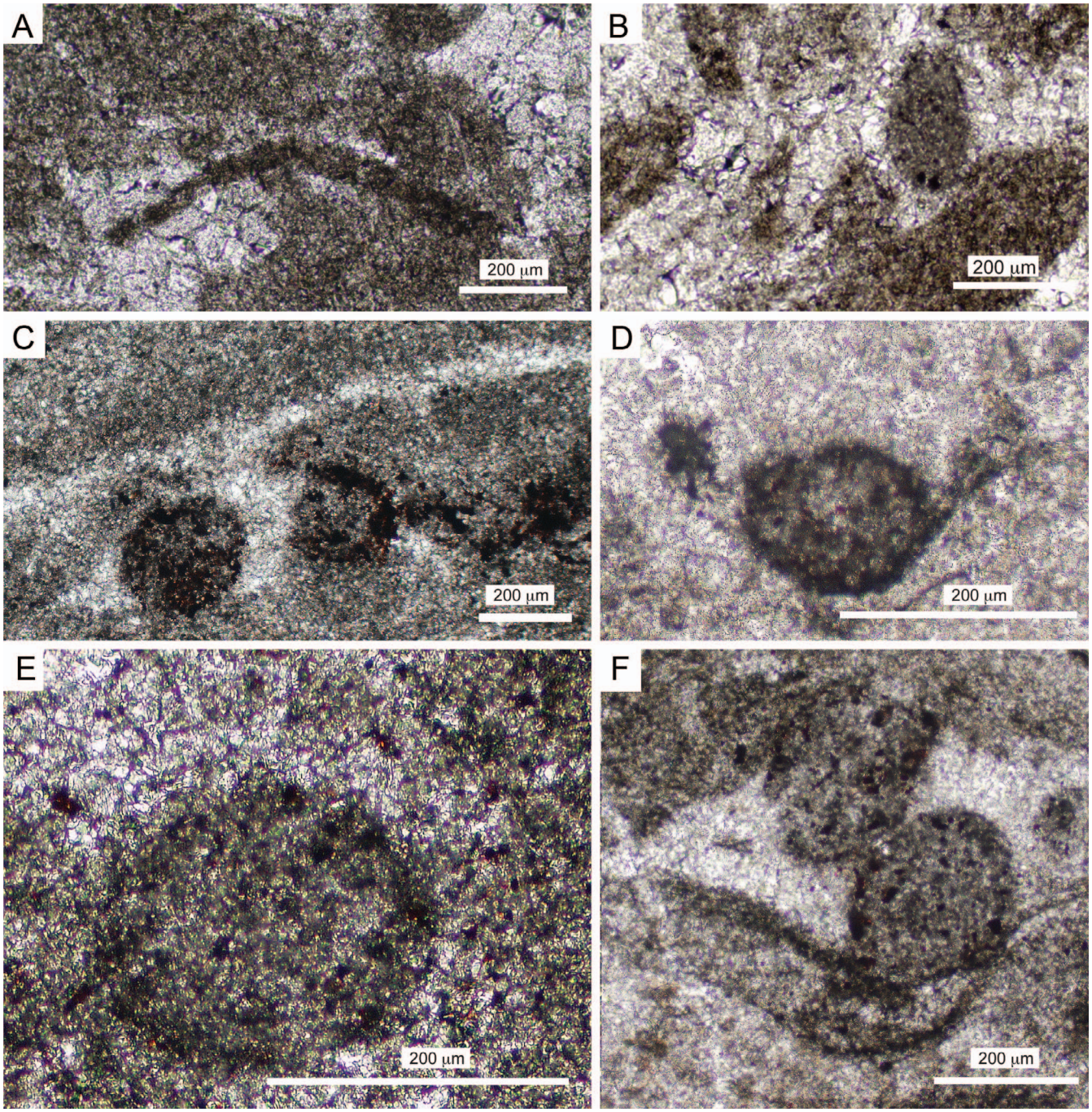

FIGURE 3—Photomicrographs of thinly laminated microbial laminite showing microfossils from South Ombepera. A) Tube with distinct, dark walls (52 m). B) Elongated test with a blunt end (52 m). C) Round tests with distinct walls (32.5 m). D) Round test (26 m). E) Round test (50 m). F) Two tests; bottom one shows elongated form with a blunt end (26 m).

(Table 1). At Ombepera, samples were taken from the basal ~50 m of section (see Fig. 2, Table 2). Of the 25 thin sections examined, 15 samples do not contain obvious microfossils, 7 have microfossils that are present but not abundant, and 3 contain abundant microfossils (Table 2). Fossiliferous samples are concentrated at the base of the section (1.4 m to 13.0 m) within thinly laminated microbial laminites, but not in areas of the overlying fine-grained limestone (Fig. 2).

Analysis of Acid Macerates

Structures with recurring morphologies (Fig. 5) are present in macerates from all four localities, but the unfragmented structures are most abundant at Ongongo, Okaaru, and South Ombepera (Fig. 5). These structures are interpreted as fossil tests because they are hollow, contain uniformly thick organic-rich walls coated by Si-Al-K and Si-Al-Mg rich minerals, and have recurring sizes, shapes, and compositions (Bosak et al., 2011a). Fossil tests occur in thirteen residues from South Ombepera and Ombepera. Most round or elongated, light-brown or gray acid-resistant tests are found in the filtered fraction greater than 100.0 μm (see Methods). The smaller-size fraction (41–100 μm) contains mostly broken tests and fragments whose appearance, composition, and thickness indicate that they were derived from the fossil tests. MicroRaman spectroscopy, energy dispersive X-ray spectroscopy (EDS), and scanning electron microscopy (SEM) of tests from South

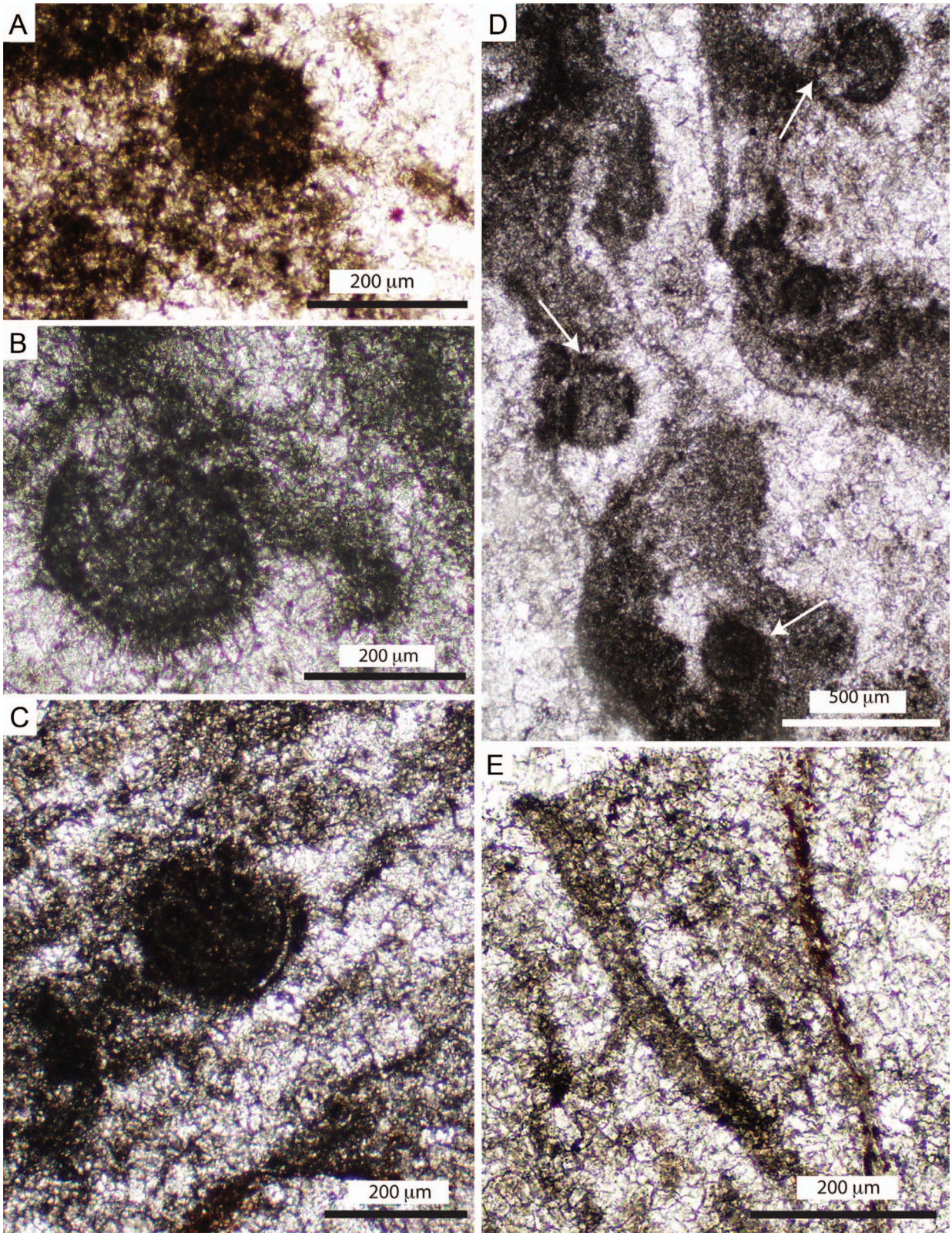

FIGURE 4—Photomicrographs of interfingered and thinly laminated microbial laminite showing microfossils from Ombepera. A) Round test with an interior that is darker relative to the tests from South Ombepera (3.8 m). B) Round test that may be broken (13 m). C) Dark, round test (13 m). D) Several round tests visible in the light laminae (13 m). E) Tubular form. Note the darker wall and a lighter interior (8 m).

Ombepera and Ombepera confirm the presence of carbonaceous material, 2–10 µm long platy siliceous minerals (Figs. 6–8), ~10-µm-long acicular siliceous minerals (Figs. 6–8), rarer 20–30 µm platy grains (Figs. 6–8), and hollow interiors of tests (Fig. 8). Several lines of evidence show that the tests are hollow: (1) preservation of apertures in some tests (Figs. 6–8); (2) presence of a lumen visible in thin section (Figs. 3–4); and (3) the presence of curved fragments whose thickness matches that of the test walls (see Figs. 5, 8). The Raman spectra and

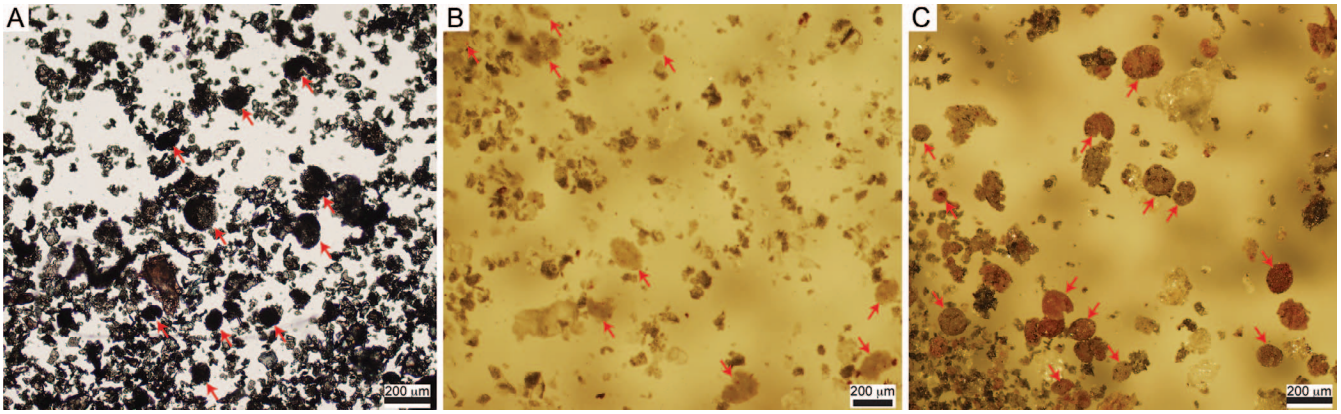

FIGURE 5—Acid macerates of the fossiliferous samples shown in transmitted light. A) South Ombepera residue, in water, with light source below sample. Note typical round forms (arrows) B) Okaaru residue sample, in water, with light source above. Note oval forms with blunt ends (arrows). C) Ongongo residue, dried, with light source above. Note abundant round but tapered forms (arrows). These residues were not filtered and were transferred directly from the acid macerates onto the slides by Pasteur pipettes.

EDS analysis (Fig. 9, and see Supplementary Data[1]) of tests from South Ombepera are identical to the already published spectra of tests from Ongongo and Okaaru (see Bosak et al., 2011a). Therefore, minerals with similar elemental compositions and similarly mature fossil organic material are present at all examined localities. At the previously described localities, these minerals were identified as muscovite, microcline, quartz, illite, and hematite by X-ray diffraction (Bosak et al., 2011a).

At South Ombepera, 8 samples of the thinly laminated facies yield round, unfragmented structures. Particularly abundant and well-preserved structures ($N > 100$, $N = 18$, $N = 50$, $N = 23$, and $N = 26$, respectively) occur in five samples (48.0 m, 50.0 m, 52.0 m, 54.0 m, and 64.0 m, respectively). One sample (60.0 m) contains many fragments whose colors and curvatures suggest that they were derived from larger, rounded structures. The same sample contained only three unbroken structures (Table 1). A tubular structure was recovered from a thickly laminated microbial laminites lower in the section (Table 1; 27.5 m; Fig. 10). Fewer than six tests with round or oval cross sections were collected in residues from interfingering thinly and thickly laminated facies at Ombepera; however, 4 of these samples (3.8 m, 7.0 m, 8.0 m, and 11.0 m) yielded 5 tubular structures. These structures are flexible in aqueous solutions, have variable lengths (300–700 µm), and are 30–60 mm wide, pinching and swelling along the length of the tube (Fig. 8). The tubes are coated mostly by very small mineral grains and have smoother surfaces than rounded tests extracted from the same samples (Fig. 10). The hollow nature of tubes could not be confirmed by SEM due to the small number of recovered individuals and the absence of broken specimens, but their composition and appearance are identical to the hollow forms reported from the Okaaru locality (Bosak et al., 2012).

Morphologies and Size Distributions of Structures in Acid Macerates

Several recurring test morphologies are present in the residues from South Ombepera (Figs. 6–8). The same round and oval morphotypes are found in the residues from Ombepera, but these are much less common and less well preserved than their South Ombepera counterparts. The sizes and shapes of these extracted structures are comparable to the forms found in thin section. The most abundant structures in both residue and thin section from South Ombepera are round (Figs. 6–8). Oval shapes are rare (Figs. 6–8). The following descriptions catalog the primary morphological structures in order of abundance:

1. Spherical, hollow specimens. Some of these preserve more than 20-µm-long slitlike apertures (Figs. 6B, 7B–C, F). In better-preserved specimens, evenly sized platy grains coat these openings (Figs. 7B–C). Other spherical specimens contain 10-µm-wide triangular openings (Figs. 6D, 7D–E).
2. Round, dorsoventrally compressed specimens with a subterminal slit (Fig. 6E). The lower lip of the slit is invaginated and the surface surrounding the slit is smoother than the sides lacking the slit.
3. Oval specimens with apertures (Fig. 8A) and without apertures (Fig. 6F).
4. Rare forms (<1%) include tubular specimens with pointed or rounded terminal ends (Fig. 10), oval, dorsoventrally compressed structures with a blunt end (Fig. 4B), and teardrop-shaped structures (Fig. 8C). The latter structures are similar to the tests from Ongongo (Bosak et al., 2011a, fig. 8), but the ones from South Ombepera are less well preserved.

The average diameter of spheroidal structures from South Ombepera (48.0 m–64.0 m, $N = 114$) is 115.6 µm ± 27.83 µm (Fig. 11). The median diameter of these structures is 111.0 µm, but tests smaller than 80 µm are rare. Several data points indicating particularly large structures (>170 µm, and up to 218.0 µm) contribute to the observed skew (Fig. 11). Tests in acid macerates from South Ombepera are comparable in size to the tests from Ongongo and the few preserved tests from Ombepera, but are smaller than those at Okaaru (Fig. 11). Typical morphologies of agglutinated tests vary among these localities (Fig. 11). South Ombepera preserves small spherical or dorsoventrally compressed forms. In contrast, large elongated and asymmetrically indented ellipsoid forms are prominent at Okaaru (Bosak et al., 2011a), and round or dorsoventrally compressed, ellipsoidal, or heart-shaped forms with visors are more abundant at Ongongo (Bosak et al., 2011a).

We examined a subset of 52 well-preserved whole tests from 6 South Ombepera residues to determine the nature and distribution of apertures. Of the 52 tests examined, half were *Heleopera*-like in shape and should most likely exhibit a subterminal or terminal slitlike aperture (see Fig.7). Importantly, slitlike apertures were identified on at least 3 of these specimens (see Fig. 7B). We infer that on several of the other tests the aperture is present but not able to be seen under SEM, and in a few cases, the preservation of these, and the original size of the slit, may make the apertures difficult to identify. Of the remaining 26

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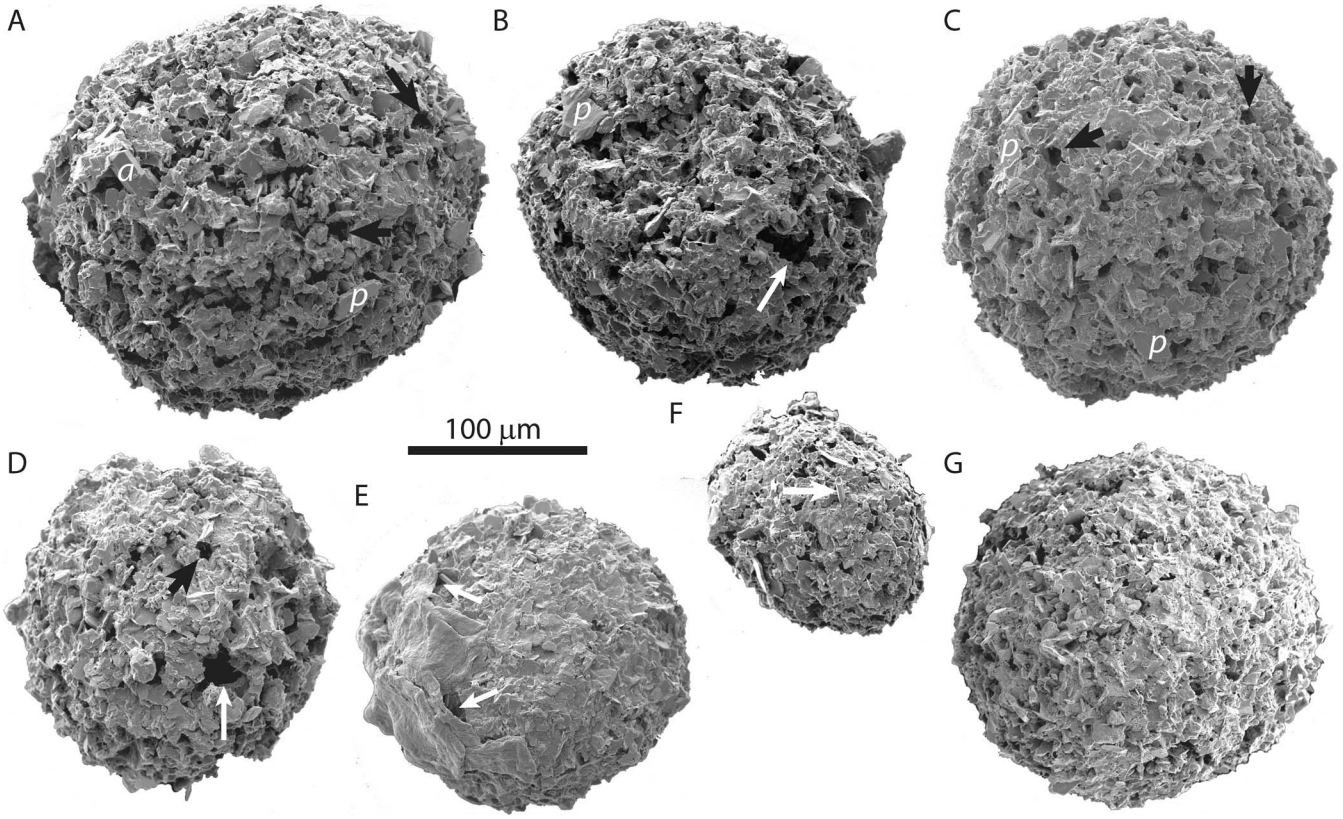

FIGURE 6—Typical morphologies of agglutinated tests in the residue from South Ombepera (SEMs). A) Round test covered by small platy mineral grains, rarer large platy mineral grains (*p*), and an acicular grain (*a*). B) Round test with a 50 µm long slit aperture (arrow) surrounded by imbricate platy minerals. C) Large round test covered by 2–5 µm long mineral grains (*p*). D) Round test with a possible remnant of a 20 µm wide aperture (arrow). This opening shows that the test is hollow. E) Dorsoventrally compressed test with a smoother ventral surface and a smoother area above the partially cemented subterminal slit. Arrows point to an invaginated lower lip, characteristic of the family Plagiopyxida (Meisterfeld, 2008). F) Smaller ovoid test with an acicular mineral (arrow). G) Round test. The walls of all tests contain small platy mineral grains. Some tests also contain 5–10 µm diameter surface pores (e.g., views A, C, D), indicated by short and thick black arrows. Scale bar is the same for all views.

tests, 5 (19%) contained well-preserved round or triangle-like apertures (See Figs. 7D–E) that could be viewed under SEM.

DISCUSSION

Interpretation and Paleoecology

Previous descriptions of fossils from the Cryogenian cap carbonates of the Rasthof Formation focused on two localities, Ongongo and Okaaru. These studies established similarities of fossil structures with agglutinated and organic-rich shells (tests) of modern agglutinated testate amoebae (Amoebozoa: Arcellinida; Bosak et al., 2011a), and modern agglutinated monothalamous Foraminifera (Bosak et al., 2011a, 2012). The residues from two additional localities, Ombepera and South Ombepera, also preserve round and agglutinated fossil tests similar to Arcellinida.

Although there are nonbiogenic hypotheses for the formation of these tests, we favor a biological interpretation (see also Bosak et al., 2011a, 2012). Importantly, the origin of these structures cannot be decoupled from the facies in which they are preserved, which limits the inorganic possibilities. For example, one possibility is that these structures represent some form of organo-coated sedimentary grains (similar to ooids). We reject this interpretation, based both on the morphology of the structures and the facies in which these are preserved. The teardrop shapes and oval, dorsoventrally compressed structures with a blunt end (which are present at all localities) and consistent wall thickness of all whole tests and test fragments, are inconsistent with rolled, coated grains, which should be rounded, would not exhibit blunt, tapering ends, would not have consistent wall thicknesses, and would lack apertures. Furthermore, as demonstrated in earlier work (Pruss et al., 2010), the facies that preserve these microfossils are microbial laminites that lack any evidence for wave or current activity that could have rolled these grains. Finally, the presence of agglutinated tubular microfossils (which are not round) at 3 of the 4 localities indicates that agglutinators from multiple groups were present at this time and do not reflect a consistent abiotic process.

Modern Arcellinida tests, which most closely resemble the tests at South Ombepera and Ombepera, exhibit considerable variations in size, from 30–600 µm, and have diverse morphologies, which may include vase-shaped, round, elongate or tapering tests with or without visors or bent necks (Lahr and Lopes, 2009). Arcellinida also have round, triangular, slitlike, and circular lobed or otherwise ornamented apertures whose characteristic dimension is commonly larger than 10 µm (Ogden and Hedley, 1980). The characteristics of modern agglutinating testate amoebae allow distinctions between the tests of Arcellinida (Amoebozoa) and other agglutinating organisms such as Foraminifera and filose testate amoebae (Rhizaria). In particular, the Rasthof microfossils are agglutinators (Ogden and Hedley, 1980) and have apertures, often smaller than 30 µm in diameter, which are distinct from vents, which are small holes in the test (see Figs. 8D, G).

South Ombepera and Ombepera tests do not always contain well-preserved apertures in their SEM images, but they do preserve a consistent, characteristic round test shape and wall thickness. When preserved, the triangular apertures and the slits are similar to those of modern *Trygonopyxis* and Plagiopyxidae, respectively (Penard, 1912; Deflandre, 1929). The dorsoventrally compressed, round fossil tests with invaginated slits are also smoother around the slit, but rough on the sides (Fig. 6E). This asymmetric roughness further underscores

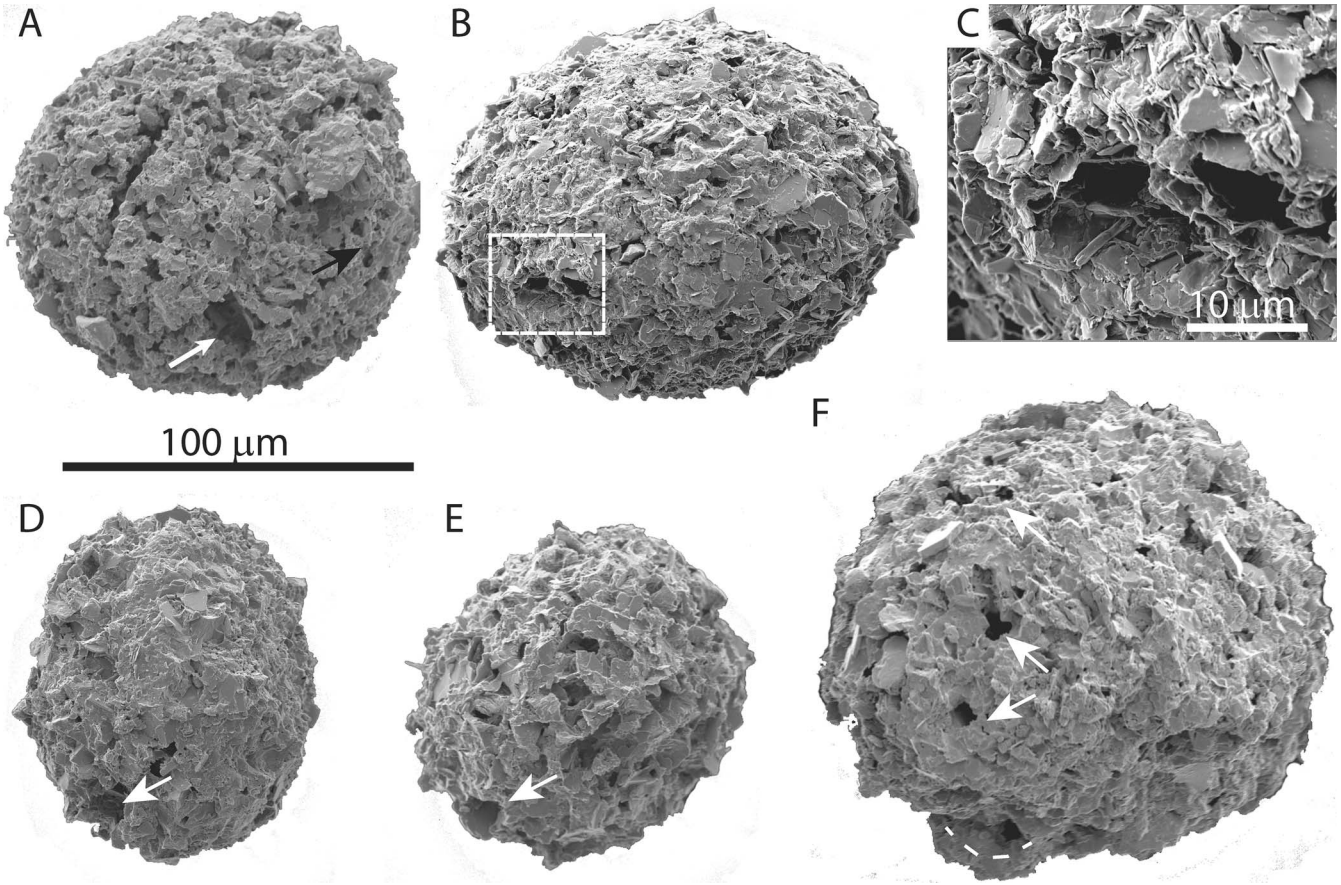

FIGURE 7—Apertures on round agglutinated tests from South Ombepera (SEMs). A) Remnant of an aperture. This aperture is interpreted as a slit covered by a broken visor whose former outline is indicated by a white arrow. B) Test with a slitlike aperture, ~ 25 µm long and covered by imbricate platy minerals. C) Magnified image of the area within the rectangle in view B. D–E) Triangular apertures (arrows). F) Slitlike aperture with an overhanging lip or visor (dashed line). Small pores (<10 µm wide) are numerous on the surfaces of views A and F (arrows). The 100 µm scale bar applies to views A, B, D–F. The smaller scale bar in view C applies to view C.

their similarity to some modern Centropyxidae and Plagiopyxidae (e.g., Meisterfeld, 2008). Tests with identical morphologies are found at Ongongo, (Bosak et al., 2011a, figs. 7A–C, E), but residues from the latter locality also contain heart-shaped forms with visors and hemispherical forms with central apertures (Bosak et al., 2011a) which are absent from South Ombepera.

Some of the other morphotypes at South Ombepera are compressed, oval tests (Figs. 6F, 7E). These forms are also similar to some Arcellinida, particularly the genus *Heleopera*, oval agglutinators with dorsoventrally compressed tests and a terminal thin slitlike aperture (Ogden and Hedley, 1980). The analysis of apertures on a subset of well-preserved tests from South Ombepera demonstrates that of the specimens that should preserve round or triangle-shaped apertures (N = 26), about 19% preserve them. Of the remaining 26 *Heleopera*-like tests, the slitlike apertures should be thin and located on the terminal or subterminal region of the test; slitlike apertures were well preserved on 3 of these specimens. The lack of preserved apertures on some tests of all morphotypes may have several explanations: (1) single apertures are very thin; (2) imaging these tests under SEM limits our view to ~50% of the fossil, which reduces the chance of seeing and imaging an aperture on a specimen, particularly in specimens that should preserve a terminal or subterminal slit; (3) some of the preserved tests were encysted individuals; for example, the modern *Trygonopyxis* sp. closes its aperture with agglutinated particles before encysting (Penard, 1912); or (4) microfossils are not Arcellinida testate amoebae. Because of the considerable similarity of the South Ombepera tests to tests recovered at previous localities, and to some modern testate amoebae, we consider 1, 2, and 3 to be the most likely interpretations.

The assemblages of agglutinated tests extracted from cap carbonates at different localities of the Rasthof Formation include different dominant forms, but preserve some common similar morphotypes. Besides the abundant spheroidal tests, South Ombepera also preserves a test morphology that is more abundant at Ongongo: the dorsoventrally compressed tests with subterminal curving slits and smoother ventral sides similar to modern Plagiopixidae (Bosak et al., 2011a). The large agglutinated tests from Okaaru (Fig. 11), similar to Heleoperidae or foraminiferans (Bosak et al., 2011a), are absent from Ombepera, S. Ombepera, and Ongongo. At the same time, the rare teardrop-shaped tests with blunt ends (Bosak et al., 2011a, fig. 9) and agglutinated tubes (Bosak et al., 2012) are found at South Ombepera, Ombepera, and Okaaru (Figs. 3A, 4E, 10). These differences (Figs. 6–7, 11), which represent common morphological variants in modern populations, are not easily explained by variable preservation and postmortem diagenesis of the same precursors. Instead, they likely reflect the original morphological and ecological variations of test-forming organisms between exposures of the Rasthof Formation. In modern assemblages of testate amoebae and foraminiferans, the species composition varies over horizontal distances that are often smaller than 1 km as a function of salinity, the height of the water table, detrital input, and the abundance of organic matter (e.g., Haynes, 1984; Mitchell et al., 2000; Gehrels et al., 2001). Similar factors, as well as the saturation with respect to calcium carbonate and the abundance of detrital sediment influence the abundances of calcareous and agglutinated foraminiferal forms in modern assemblages of marine foraminifera (reviewed by Haynes, 1984).Environmental factors that influenced the ecology of testate organisms in the Rasthof Formation are not

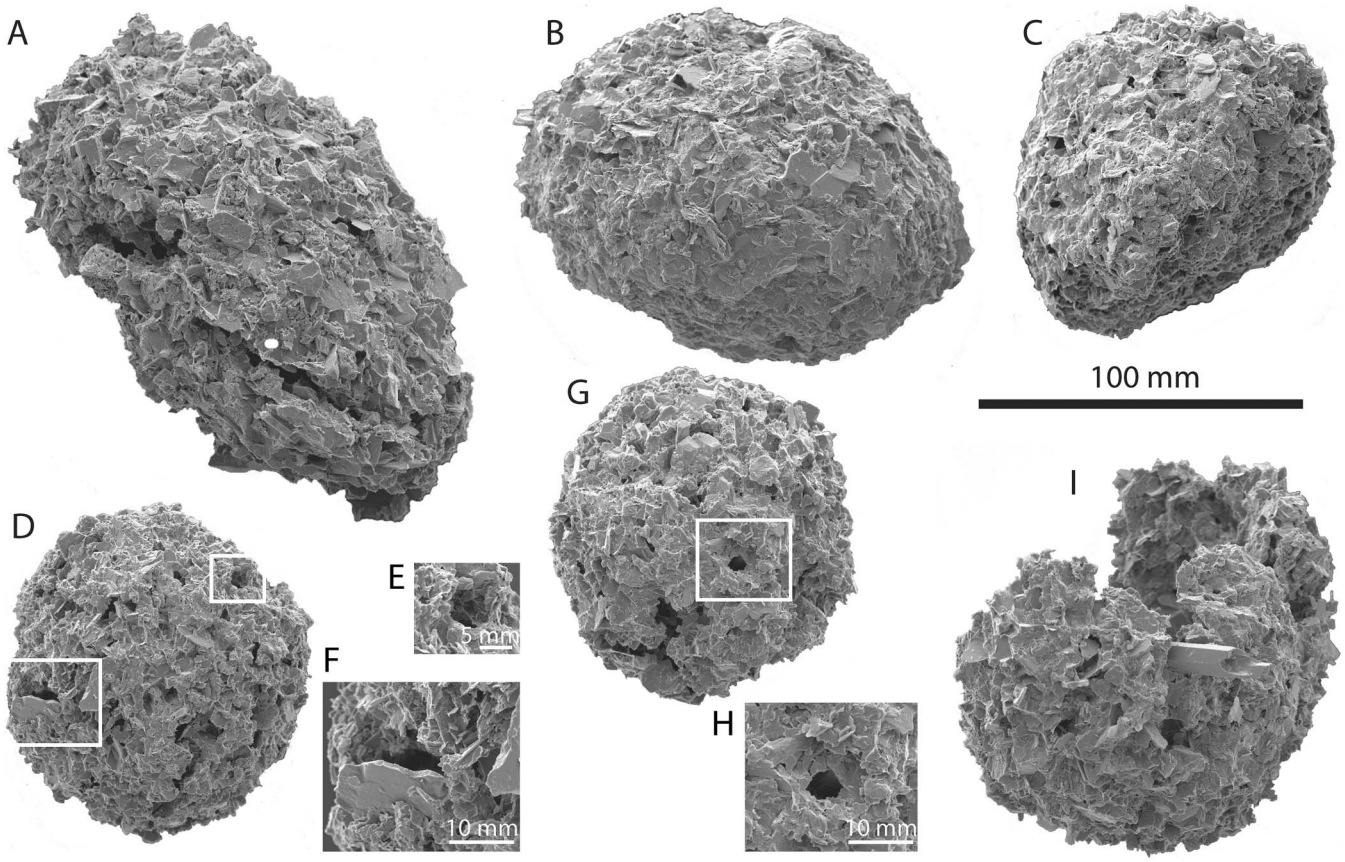

FIGURE 8—SEMs of less common test morphologies, broken tests, pores, and apertures from South Ombepera and Ombepera. A) Ovoid form with subterminal slitlike aperture. B) Ovoid form. C) Teardrop-shaped form. D) Test with a pore (upper right box) and a slit aperture (lower left box). E) Close-up of the pore from D reveals the ~7–10-µm-thick wall. F) Close-up of the ~20-µm-long slit aperture from D. The slit contains elongated platy minerals. G) Test with a small pore (white box). H) Close–up of the pore from G reveals the hollow inside surrounded by ~10- to 20-µm-thick wall. I) Broken test showing ~10- to 20-µm-thick walls. All structures, except for the close-ups, are shown on the same scale indicated by the 100 µm scale bar.

obvious, given the petrographic and sedimentological similarities of microbial laminite facies across all four examined localities of the Rasthof Formation. To the west, we might expect features consistent with somewhat deeper settings (e.g., more upwelling and nutrient supply), and to the east we might expect more detrital material near the craton; however, this generalization is complicated by postglacial topography underlying the Rasthof Formation (Pruss et al., 2010).

Preservation and Taphonomy

Systematic examination of lower Rasthof facies from Ombepera and South Ombepera reveals that the thinly laminated microbial laminite facies preserves more microfossils than thickly laminated microbial laminites. Several factors may explain this variation. Firstly, it is possible that much of the original organic matter in thickly laminated microbial laminites was remineralized, perhaps contributing to the abundant clear, often bladed, early cements seen in their thick light laminae (Pruss et al., 2010). In contrast, the thin light laminae of the thinly laminated microbial laminites preserve abundant inclusions, consistent with microbial microporosity (Bosak et al., 2004). An earlier burial of tests and a less extensive remineralization in the thinly laminated microbial laminites (e.g., Pruss et al., 2010) would have fostered the preservation of agglutinated tests in this facies. The dark laminae, which preserve textural evidence of organic-rich microbial mats, may have also provided a suitable habitat for the agglutinators with rounded tests, perhaps to the exclusion of other organisms. Thus, taphonomic and ecological factors may explain the prevalence of round agglutinated tests in the thinly laminated facies, and the preferential occurrence of the overall rare tubular forms in the thickly laminated facies. These differences are important to note, as they may inform the search for microfossils at other stratigraphic horizons.

We also note some interesting and confounding discrepancies between the abundances of microfossils in thin section and in residue. For example, several thin sections were designated as containing abundant microfossils, but few complete tests were recovered from their corresponding residues (see Tables 1, 2). Residues from Ombepera yield fewer whole tests than those of South Ombepera, yet many Ombepera thin sections contain distinct, round tests covered by siliceous minerals (see Fig. 4). This discrepancy suggests that during early, fabric retentive recrystallization, the distinct composition of microfossil walls was only partially preserved. Alternatively, the living organisms incorporated more carbonate particles into their tests. In either case, these carbonate minerals would have been dissolved during extraction. Both partial decay and the original presence of some carbonate grains in tests also may account for the presence of small pores on tests (e.g., Figs. 6A, C, D, 7A, F, 8D, G). In the future, the abundance of carbonate in fossil walls could be established by more EDS mapping (see Supplementary Data[1]); this technique demonstrated the prevalence of siliceous minerals in microfossil walls from Okaaru and Ongongo (see Bosak et al., 2011a) and South Ombepera (Supplementary Data[1]), but more abundant carbonate minerals may be expected in the walls of tests from Ombepera.

Microfossils in Other 715–635 Ma Carbonates

Organic-rich allodapic limestones in the Tayshir member of the Tsagaan Oloom Formation in Mongolia overlie glacial deposits and

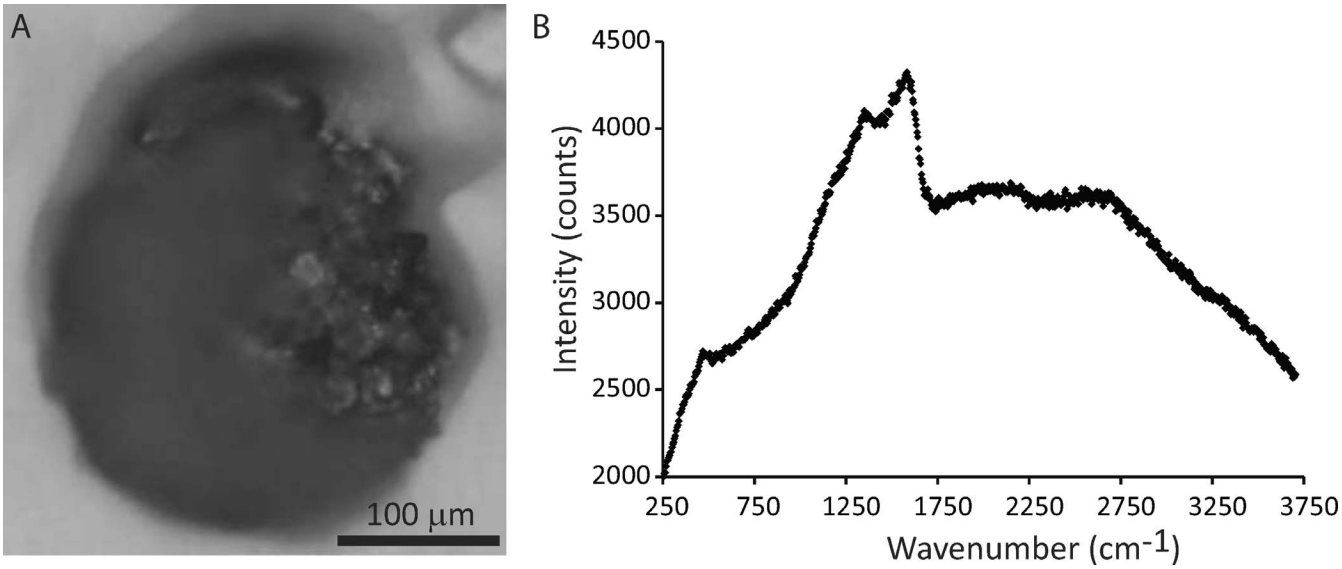

FIGURE 9—Representative Raman spectroscopic analysis of tests from South Ombepera. A) Analyzed test (transmitted light micrograph). B) Raman spectrum of the test from A. Peaks centered at 1352 relative cm^{-1} and 1608 relative cm^{-1} indicate the presence of carbonaceous material, peaks centered around 460 relative cm^{-1} and 692 relative cm^{-1} are consistent with the presence of siliceous minerals such as quartz and muscovite (see Bosak et al., 2011a). This spectrum is representative of three points on each of the four analyzed tests.

preserve isotopic signatures characteristic of other Sturtian-age cap carbonates (Macdonald et al., 2009). The thick 715–635 Ma carbonate strata of this formation preserve primarily smaller, elongated agglutinated tests (Bosak et al., 2011a) and various organic microfossils, including the organic tests of the oldest putative ciliates (Bosak et al., 2011b). The occurrence of these fossils in allodapic carbonates shows that, even in the absence of microbial mats, the depositional conditions of these carbonates favored preservation of organic-rich fossils via early burial. The early burial and lack of reworking, either by physical or biological processes, is likely a critical aspect of fossilization in Cryogenian carbonates that may have been diminished by the presence of bioturbation in younger late Ediacaran and early Paleozoic carbonates.

Dark limestone from the Otavi Group and the Nama Group in Namibia also contain biological structures, which were extracted primarily from samples of shallow-water sections in Etosha National Park (Brain et al., 2012). These structures are irregularly shaped and 0.3–5 mm long across the longest axis, with numerous 5–20-μm-wide openings across the entire surface, and contain phosphatic walls of irregular thickness and an internal cavity, possibly surrounded by a network of pores (Brain et al., 2012). An interpretation of these structures as sponges (Animalia) was based on the large sizes, porosity, and lack of agglutinated minerals (Brain et al., 2012); however, organic and agglutinated tests of many modern representatives of agglutinated and organic-walled early diverging foraminiferans and other Rhizaria are large, irregularly shaped, and contain internal sediment grains (Gooday, 1994; Gooday and Bowser, 2005; Rothe et al., 2009).

Regardless of their biological affinity, the agglutinated and phosphatized structures from Namibia expand the record of organic, phosphatized, and agglutinated forms preserved in Neoproterozoic

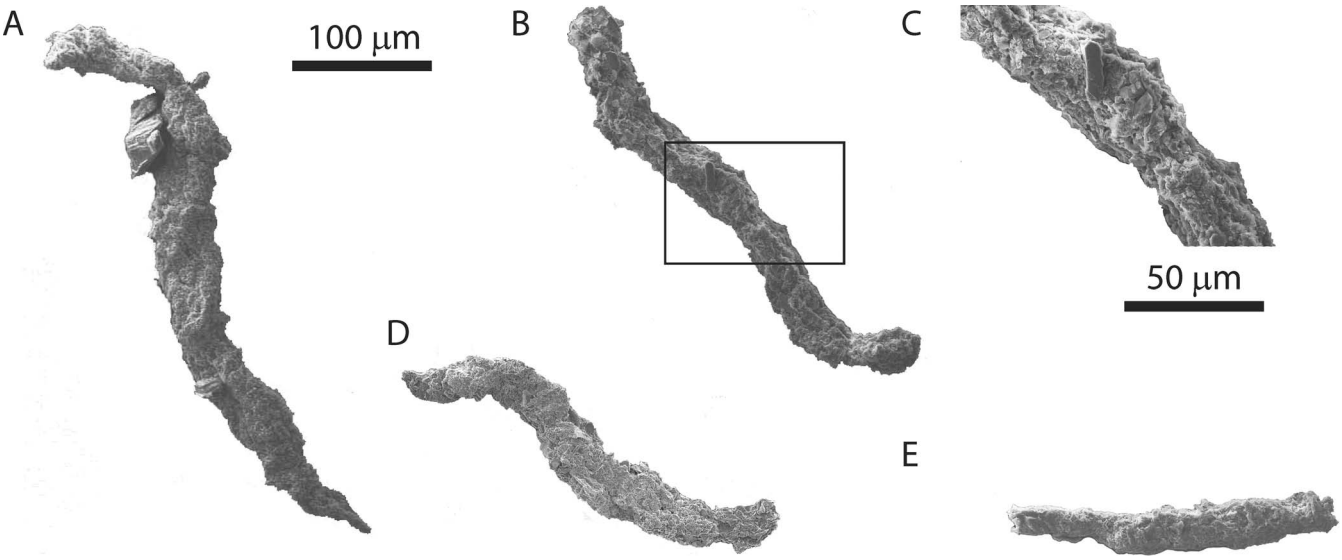

FIGURE 10—A–E) Agglutinated tubes from South Ombepera and Ombepera (SEMs). C) Magnified surface of the tube from B. The magnified area is outlined by a black rectangle in B. Structures in A, B, D and E are shown on the same scale, indicated by the 100 μm scale bar on the left. The magnified detail in C is shown on the scale bar indicated under the panel in C.

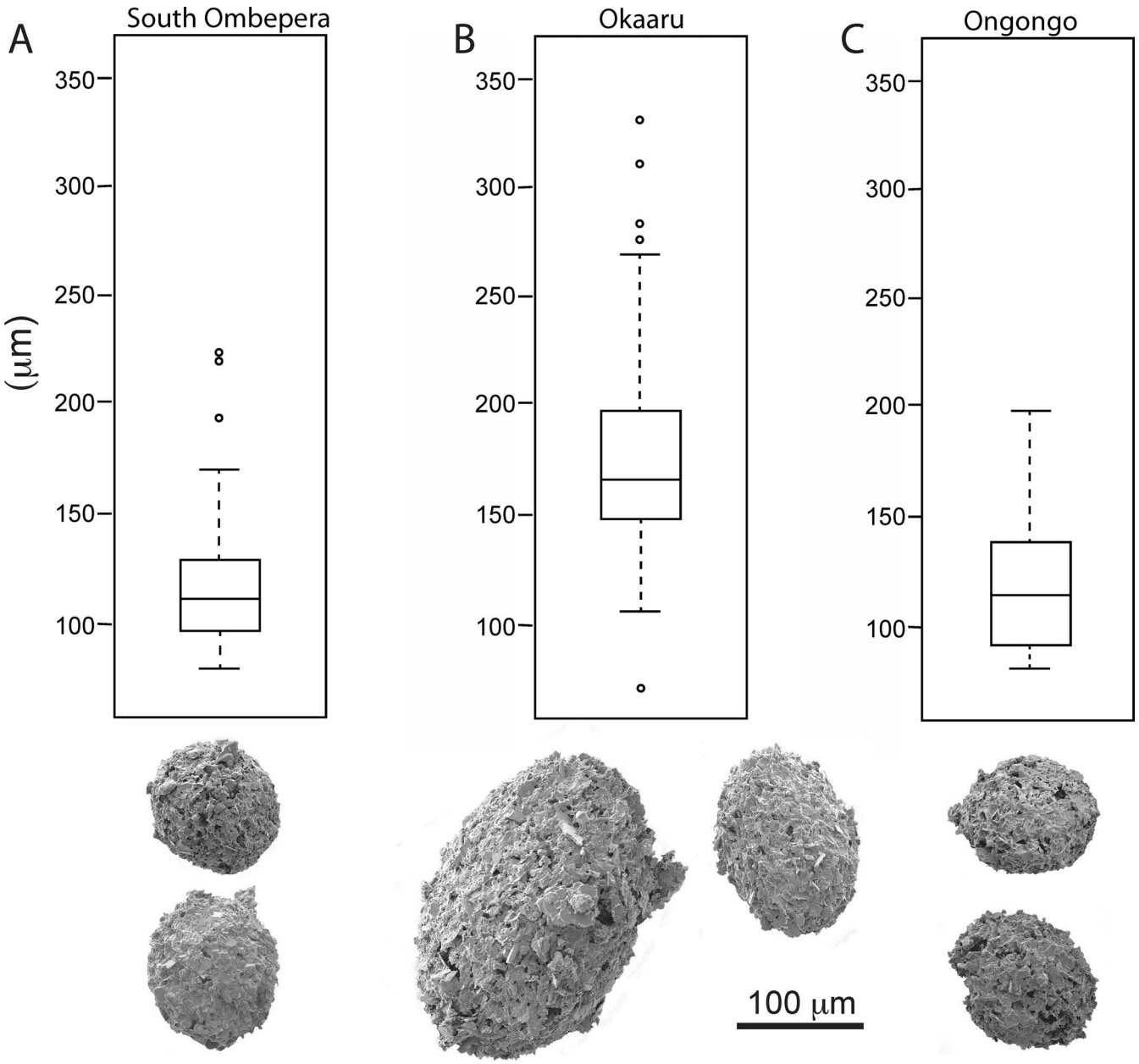

FIGURE 11—Box plots of length distributions of the maximum dimension of individual microfossils and SEMs of typical agglutinated forms from South Ombepera (N = 114), Okaaru (N = 149) and Ongongo (N = 85). All box plots are shown on the same scale. The length of the boxes spans the interquartile range, the horizontal bar within the boxes indicates the median, and the bars show the range of the data excluding outliers. Individual data points plotted outside of the boxes are outliers. A) Round tests from South Ombepera. B) Large, blunt oval tests from Okaaru. C) Subterminally indented tests from Ongongo (indentations on the left) similar to modern Plagiopixidae. The same scale bar applies to all shown tests.

successions ranging from pre-Sturtian (Hofmann and Aiken, 1979; Allison, 1981; Hofmann, 1985; Allison and Hilgert, 1986; Allison and Awramik, 1989; Hofmann and Rainbird, 1994; Porter and Knoll, 2000; Corsetti et al., 2003; Cohen et al., 2011; Brain et al., 2012), 715–635 Ma (Maloof et al., 2010; Bosak et al., 2011a, 2011b, 2012; Brain et al., 2012) to Ediacaran strata (Brain et al., 2012). The similarity of organic and agglutinated body fossils extracted from carbonate strata to various modern eukaryotes also hints at a more detailed and continuous record of eukaryotic evolution between the Sturtian and the Marinoan glaciation.

CONCLUSIONS

This study systematically examined microbial laminite samples of the Rasthof Formation from the South Ombepera and Ombepera localities and revealed preservational and ecological differences between facies and localities. Microfossil assemblages varied among the four examined localities: some similar forms were found at Ongongo, South Ombepera, and Okaaru, but the most abundant microfossils differed from one locality to another. These microfossils are ubiquitous in thinly laminated microbial laminite facies, but are less abundant in the thickly laminated microbial laminites. Agglutinated tubular forms, consistent with early Foraminifera, are preserved in thickly laminated microbial laminites of South Ombepera and Ombepera, like at Okaaru. The abundance of round agglutinators in thinly laminated microbial laminites suggests that the burial and early lithification in these facies fostered the preservation of globular agglutinated organisms. The identification of these fossiliferous facies in the Rasthof Formation informs the search for microfossils at other sections of the Rasthof as well as in other Neoproterozoic carbonate successions.

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