

VASE-SHAPED MICROFOSSILS FROM THE NEOPROTEROZOIC CHUAR GROUP, GRAND CANYON: A CLASSIFICATION GUIDED BY MODERN TESTATE AMOEBAE

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ABSTRACT—Vase-shaped microfossil (VSM) assemblages from early diagenetic carbonate nodules in $>742 \pm 6$ Ma black shales of the Chuar Group, Grand Canyon, provide evidence for affinities with testate amoebae. Not only are VSMs exceptionally preserved in Chuar rocks, they exhibit a much higher degree of morphological diversity than was previously known. Using the taxonomy of modern testate amoebae as a guide, nine new species and eight new genera of VSMs are described, augmenting the eight species and two genera already recognized. Taxa described here are *Melanocyrrillium hexodiadema* Bloeser, 1985, *Trigonocyrrillium horodyskii* (Bloeser, 1985) n. comb., *T. fimbriatum* (Bloeser, 1985) n. comb., *Cyrciocyrrillium simplex* n. sp., *C. torquata* n. sp., *Bonniea dacruchara* n. sp., *B. pyatinaia* n. sp., *Trachycyrrillium pudens* n. sp., *Palaeoarcella athanata* n. sp., *Hemisphaeriella ornata* n. sp., *Bombycion micron* n. sp., and *Melicerion poikilon* n. sp. All of the test characters observed in VSM taxa (e.g., collars; indentations; hexagonal symmetry; lobed, triangular or invaginated apertures; curved necks) occur in modern testate amoeban taxa, though not always in the same combinations. Some VSM species have characters found today in diverse extant taxa, making it difficult to assess their relationships. A few species, however, have character combinations that closely approximate those found in specific genera of both lobose and filose testate amoebae, suggesting that at least stem group, and possibly crown group, representatives of these taxa were present ~ 742 Ma.

These fossils indicate that ecosystems were diverse and complex, that eukaryotic biomineralization had already evolved, and that the last common ancestor of animals+fungi had already appeared by ~ 750 Ma.

INTRODUCTION

VASE-SHAPED MICROFOSSILS (VSMs) are widespread and abundant in Neoproterozoic rocks. Although discovered almost 70 years ago (Ewetz, 1933), their affinities remained problematic until new assemblages preserved in carbonate nodules from $>742 \pm 6$ Ma black shales (Karlstrom et al., 2000) near the top of the Chuar Group, Grand Canyon (Fig. 1.1, 1.2), provided morphological details sufficient to indicate a close taxonomic relationship with the testate amoebae (“thecamoebians”; Porter and Knoll, 2000). As such, VSMs extend the stratigraphic record of testate amoebae by ~ 500 million years and provide the earliest body fossil evidence for heterotrophic protists, shedding new light on ecosystem complexity ~ 750 Ma (Porter and Knoll, 2000). Continuing study of these densely concentrated assemblages (up to 4,000 per mm³) reveals that the morphological diversity of VSMs is much greater than previously thought.

Here we use the taxonomy of modern testate amoebae as a guide to the identification of eight new genera and nine new species of VSMs, adding considerably to the two genera and eight species previously recognized [*Melanocyrrillium hexodiadema*, *M. horodyskii*, and *M. fimbriatum* from the Chuar Group (Bloeser, 1985); and *Caraburina granulosa*, *C. microgranulosa*, *C. ovalica*, *C. pyriforma*, and *C. spatiosa* described from Neoproterozoic successions in Kyrgyzstan (Kraskov, 1985, 1989)]. Drawing comparisons between VSMs and specific testate amoeban taxa, we evaluate the systematic relationships between VSMs and testate amoebae, and review the implications of high VSM diversity for early protistan evolution.

EVIDENCE FOR AFFINITIES BETWEEN VSMS AND TESTATE AMOEBAE

Porter and Knoll (2000) argued for an affinity between VSMs and testate amoebae on the basis of the resemblance between the distinctively perforate ‘honeycomb’ VSMs and members of the filose testate amoeban family Euglyphidae, as well as of the more general observation that the range of morphologies displayed by

VSMs is observed today only in lobose and filose testate amoebae. Since the publication of that paper, Martí Mus and Moczyłowska (2000) have reported phosphatized VSMs from the Visingsö Group, Sweden, that preserve evidence of a spheroidal structure inside the test. This is consistent with the interpretation of VSMs as vegetative structures, and with the presence of internal cysts observed in some testate amoebae (Deflandre, 1953). Also, one of us (SMP) has discovered VSM specimens from the Red Pine Shale, Uinta Mountain Group, that are clearly attached at their apertures (Fig. 2.1). Where asexual reproduction has been documented in testate amoebae, the daughter and mother cell’s tests remain attached at their apertures while the cell divides, presenting a morphology similar to the Red Pine Shale VSMs (Fig. 2.2). Comparable cell division is known from other protists as well, for example, tintinnids (Tappan, 1993). The most compelling new evidence for testate amoeban affinities, however, is a range of VSM test morphologies reported for the first time here. These morphologies, in particular that of *Palaeoarcella athanata* n. sp. (Fig. 11.1–11.6), are indistinguishable from those of specific testate amoeban taxa.

MODERN TESTATE AMOEBAE AS A GUIDE TO VSM CLASSIFICATION

The combination of characters observed in VSMs identifies these fossils as testate amoebae; therefore, we used character variation in modern testate amoebae to guide VSM classification. Most modern testate amoebae genera are distinguished on the basis of qualitative characters, such as test shape or apertural modifications. We adopt that practice here, distinguishing genera on the basis of qualitative test characters such as the presence or absence of indentations and test curvature, the shape of the aperture, and the shape of the test. This practice resulted in a revision of Bloeser’s (1985) VSM classifications, as the species placed in the genus *Melanocyrrillium* Bloeser, 1985 were distinct enough by these standards to be designated new genera.

Distinguishing among species within genera is more difficult. The predominant mode of reproduction among modern testate

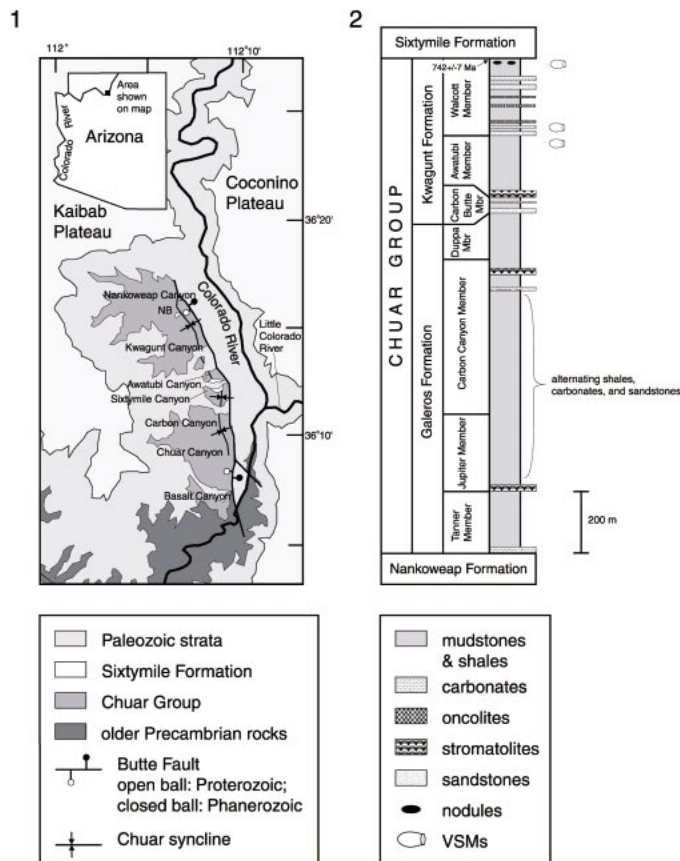


FIGURE 1—1, Geological map of the Chuar Group, northeastern Grand Canyon (modified from Link et al., 1993). NB = Nankoweap Butte; 2, Generalized stratigraphic column of the Chuar Group, indicating horizons where VSMs have been found (modified from Dehler et al., 2001). Radiometric date from Karlstrom et al. (2000).

amoebae is asexual division. As a result, the definition of species in modern testate amoebae is problematic (Charman, 1999). A morphospecies concept is commonly adopted, and many species are distinguished on the basis of test characters related to size, shape, and composition (Charman, 1999; Ogden and Meisterfeld, 1989). Studies of clonal cultures grown under different environmental conditions indicate, however, that intraspecific variability in test morphology can be high [e.g., Wanner and Meisterfeld 1994; see discussion in Charman (1999) and Wanner (1999)]. In this taxonomy, we have refrained from making arbitrary distinctions between species when the variation appears continuous. Instead, we have separated specimens into different species only if they exhibit consistent qualitative differences or cluster discretely with respect to quantitative characters (cf. Ogden and Meisterfeld, 1989). Note that ontogenetic variation is not relevant for these taxa. Testate amoeban tests do not grow during an individual's lifetime; rather, the test is formed in its entirety during reproduction and remains morphologically stable thereafter (Verworm, 1888).

MATERIALS AND METHODS

The new Chuar VSMs are preserved as siliceous casts (e.g., Figs. 4.1–4.9; 5.1–5.17; 6.1–6.8, 6.11–6.20; 9.1–9.13, 9.16–9.21; 10.1–10.4; 17.1–17.3; 18.1–18.4) and internal and external molds, in some cases coated with pyrite or iron oxides [e.g., Figs. 4.11, 4.13; 5.18, 5.19; 6.9, 6.21–6.23; 9.14, 9.15, 9.22, 9.23; 11.1–11.6; 12.1–12.3; 13.1–13.4; 15.1–15.8; see Porter and Knoll (2000) for

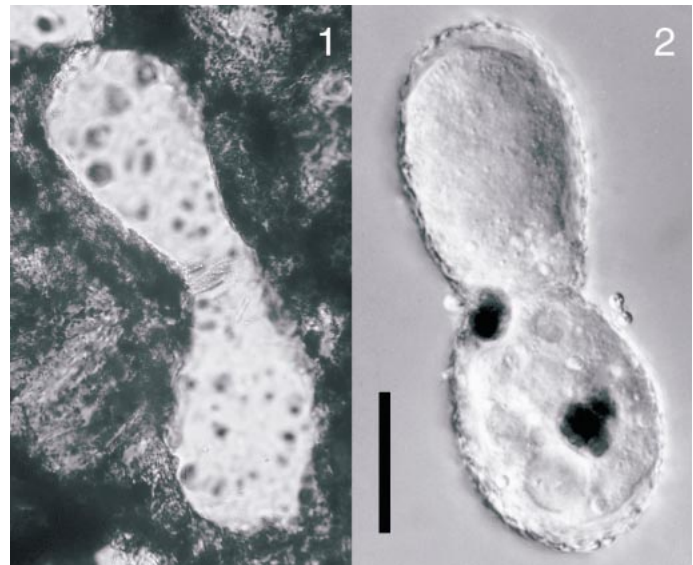


FIGURE 2—For this and all following captions, SEM stub name or thin section name and England Finder coordinates are given in parentheses; thin section oriented such that label is opposite fixed corner. Unless otherwise indicated, photos of modern testate amoebae from R. Meisterfeld. 1, VSMs attached at the aperture, from the Neoproterozoic Uinta Mountain Group, Utah; HUPC# 64459 (RP00B-40; A47); 2, The modern lobose testate amoeba, *Diffflugia lucida*, undergoing asexual reproduction. Scale bar is 60 μm for 1; and 25 μm for 2.

a more extensive discussion of their taphonomy]. VSMs occur in very high densities in early diagenetic carbonate nodules within black shales of the uppermost Chuar Group. The fossils lie two meters beneath an ash bed dated by U-Pb zircon chronology as 742 ± 6 Ma (Karlstrom et al., 2000). For a more extensive description of the locality, see Porter and Knoll (2000); for details of Chuar Group geology, see Dehler et al. (2001). Samples were either thin sectioned and viewed with a compound light microscope or macerated in 15 percent acetic acid. Macerated specimens were mounted on slides with Euparal[®] (WALDECK GmbH & Co. KG. Division Chroma[®]) and viewed with a compound light microscope, or mounted on stubs, coated with gold or palladium and viewed with a LEO 982 scanning electron microscope at 5 or 10 kV. Approximately 1,000 specimens were examined in thin section, and 215 specimens were viewed with scanning electron microscopy. Auto-Montage[®] software (Synoptics, Ltd.) was used to create composite images of some specimens (e.g., *Melicerion poikilon* n. sp.; Fig. 15.1–15.8), combining multiple images of the same specimen taken at different focal levels. In all descriptions, with the exception of species in the genus *Bonniea* n. gen. (see below), length is defined as the distance between the aboral and oral poles; width, or cross-sectional diameter, is perpendicular to length and is measured at the point of maximum distance.

SYSTEMATIC PALEONTOLOGY

Repository.—All specimens have been repositied in the Paleobotanical Collections of the Harvard University Herbaria, under accession numbers 62988, 62990, 62991, 64401–64457. Table 1 provides a list of the Chuar species with a summary of their distinguishing characteristics and global distribution, and Figure 3 indicates their relative abundance in the Chuar carbonate nodule assemblage.

Higher taxonomic ranks.—As discussed below (see the section, “How are the fossils related to modern testate amoebae?”), we believe that some VSM taxa are unquestionably related to specific

TABLE 1—Chuar Group VSM species, their distinguishing characters, and their geographic distributions beyond the Chuar Group. Number of specimens measured for length is the same as that measured for length-width ratio. BF = Backlundtoppen Formation, Spitsbergen; DCF = Draken Conglomerate Formation, Spitsbergen; EBG = Eleonore Bay Group, Greenland; EF = Elbobreen Formation, Spitsbergen; JR = Jabal Rockham dolostone, Saudi Arabia; PG = Pahrup Group, California; TG = Togari Group, Tasmania; UMG = Uinta Mountain Group, Utah; VB = Visingsö Beds, Sweden.

Species	Length-width ratio [# specimens]	Length (µm)	Aperture shape	Apertural modifications	Other characters	Geographic distribution
<i>Melanocyrrillium hexodiadema</i>	1.2–1.5 [N = 17]	30–140	circular	invaginated; apertural face hexagonal in shape	six indentations around aperture	?BF
<i>Trigonocyrrillium horodyskii</i>	1.2–1.8 [N = 20]	75–125	triangular	—	—	?VB; ?DCF
<i>Trigonocyrrillium fimbriatum</i> ¹	1.3–2.5 [N = 238]	38–170	triangular	—	three triangular fringes around aperture	?VB
<i>Cyclocyrrillium simplex</i>	1.1–1.9 [N = 10]	40–110	circular	—	—	EBG; ?JR, ?TG; ?VB; ?RF; ?BF; ?PG; ?UMG
<i>Cyclocyrrillium torquata</i>	1.4–1.9 [N = 12]	60–120	circular	collared	—	?EF; ?VB; ?RF; ?UMG
<i>Bonniea dacruchares</i>	1.5–2.1 [N = 21]	65–180	circular	—	strongly curved	?EF
<i>Bonniea pytinaia</i>	2.0–3.2 [N = 20]	80–160	circular	—	weakly curved	—
<i>Trachycyrrillium pudens</i>	1.4–1.8 [N = 2]	90–140	lobed	—	—	—
<i>Palaeoarcella athanata</i>	0.4–0.6 [N = 18]	20–40	circular	invaginated	hemispherical test	—
<i>Hemisphaeriella ornata</i>	0.6–0.8 [N = 2]	36–48	?	invaginated	hemispherical test, indentations	?BF; ?EF
<i>Bombycion micron</i>	1.5–2.0 [N = 8]	60–95	circular	steeply inclined	—	—
<i>Melicerion poikilon</i>	1.3–2.8 [N = 59]	50–160	?	—	circular mineralized scales, 1–13 µm in size, regularly arranged in organic test	?EF
Unnamed form	1.6–2.2 [N = 3]	110–130	circular	funnel-shaped	—	—

¹ Character data for *Trigonocyrrillium fimbriatum* taken from Bloeser (1985).

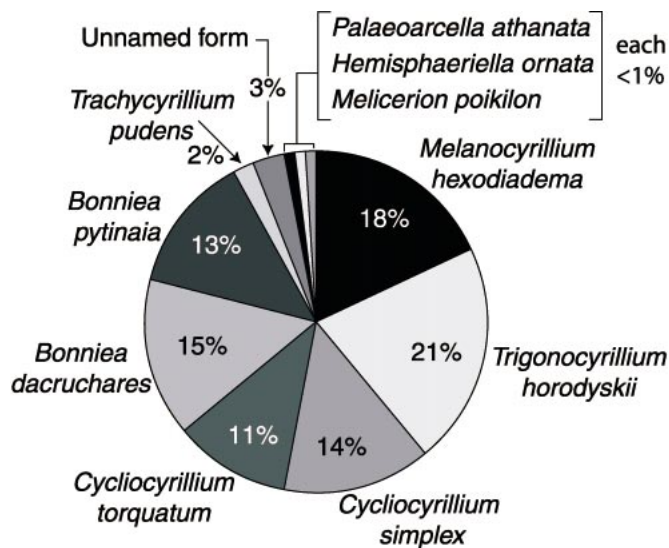


FIGURE 3—Pie chart indicating the relative abundances of VSM species in the Chuar carbonate nodule assemblage. *Trigonocyrrillium fimbriatum* (Bloeser, 1985) n. comb. has been found lower in the Chuar Group, but it has not been found in the carbonate nodule assemblage. Therefore, its relative abundance cannot be calculated.

modern testate amoeban groups, and that others are likely to be related as well. Nevertheless, we have refrained from providing a supra-generic taxonomy for VSMs, for two reasons. First, supra-generic classifications of modern testate amoebae may themselves be unstable: relationships among modern testate amoeban taxa and among testate amoebae and other eukaryotic groups remain unresolved (see, e.g., Meisterfeld, 2002a, 2002b; Schuster, 1990; Patterson, 1994, 1999). Second, recognizing that our interpretations may be revised in the future, we prefer the conservative route of maintaining a distinction between our descriptions of VSM species and our interpretations of them. This is not unusual in Precambrian and Cambrian micropaleontology: *Tasmanites*, for example, though widely regarded as a fossil prasinophyte (e.g., Mendelson, 1993), is nevertheless classified as an acritarch (e.g., Moczyłowska, 1991). Following this precedent, we maintain the informal designation, vase-shaped microfossils or VSMs, for this group of fossils united by similar preservation and morphology.

Domain EUCARYA Woese, Kandler, and Wheelis, 1990
Vase-Shaped Microfossils

Chitinozoans, BLOESER, SCHOPF, HORODYSKI, AND BREED, 1977, p. 676–679, fig. 2.
‘Chitinozoan-like’ microfossils, VIDAL, 1979, p. 24–25, pl. 6.
Chitinozoan-like microfossils, BINDA AND BOKHARI, 1980, p. 70–71, fig. 1.
Vase-shaped microfossils, KNOLL AND VIDAL, 1980, p. 207–211, fig. 1.
Vase-shaped organic walled microfossils, KNOLL, 1981, p. 46–47, fig. 2.32.
Vase-shaped microfossils, KNOLL AND CALDER, 1983, p. 476–480, 489, pl. 61.
Incertae sedis, KRASKOV, 1985, p. 150–152, pl. 53.
Vase-shaped microfossils, GREEN, KNOLL, AND SWETT, 1988, p. 837, fig. 4.3, 4.4.

- Chitinozoan-like microfossils, SAITO, TIBA, AND MATSUBARA, 1988, p. 60, pl. 1.
- Vase-shaped microfossils, VIDAL, 1994, p. 308, fig. 3A–B.
- Vase-shaped microfossils, KNOLL, SWETT, AND BURKHARDT, 1989, p. 135, figs. 7.9, 7.10, 8.2.
- Vase-shaped microfossils, KNOLL, SWETT, AND MARK, 1991, pp. 535, 537, fig. 7.1–7.3.
- Incertae sedis, KRASKOV, 1989, pp. 148–150, pl. 52.
- Vase-shaped microfossils, HORODYSKI, 1993, pp. 265–267, 270–271, fig. 10.C, 10.D, 10.H.
- Vase-shaped microfossils, MARTÍ MUS AND MOCZYDŁOWSKA, 2000, pp. 213–228, figs. 2, 3, 6, 7.
- Vase-shaped microfossils, PORTER AND KNOLL, 2000, pp. 360–385, figs. 2–8, 10.
- Vase-shaped microfossils, MARTÍ MUS, 2001, chapter 4, pp. 1–14, figs. 3, 4, 6–8.

Description.—Vase-like vesicles with a well-defined aperture at one end. Vesicles range in size from ~20 to ~300 μm in maximum dimension. They are presumed to have been originally organic-walled [see Martí Mus and Moczydłowska (2000) and Porter and Knoll (2000) for evidence], or, in the case of *Melicerion poikilon* n. sp., organic-walled with embedded mineralized scales (Porter and Knoll, 2000), but are preserved as mineralized casts and molds.

Genus MELANOCYRILLIUM Bloeser, 1985 emend.

Type species.—*Melanocyrrillium hexodiadema* BLOESER, 1985, by monotypy.

Emended diagnosis.—VSMs with a hexagonal apertural margin formed by six distinctive indentations distributed evenly around the aperture. Indentations extend toward the aboral pole approximately one-half to one-sixth the test length. Below the indentations, the test is rounded in cross section. Between the indentations are six parallel longitudinal ridges.

Discussion.—In its original sense (Bloeser, 1985), *Melanocyrrillium* encompassed all VSMs (note that no diagnosis was published for the genus *Melanocyrrillium* nor for any of its three species; instead we have referred to the published genus and species descriptions). We have restricted the definition of *Melanocyrrillium*, however, because comparisons with modern testate amoebae make us recognize multiple genus-level taxa in the Chuar assemblage. Furthermore, the three species originally assigned to *Melanocyrrillium* (*M. hexodiadema*, *M. fimbriatum*, and *M. horodyskii*) are too distinctive by the standards of modern testate amoeban taxonomy to be placed within the same genus (cf. Meisterfeld, 2002a); therefore, only the type species, *M. hexodiadema*, is included in this now monotypic genus. Our synonymy list reflects this emendation. The name *Melanocyrrillium* has commonly been used to refer to vase-shaped microfossils in general; therefore, we list only those publications that provide evidence for *Melanocyrrillium* as defined here.

MELANOCYRILLIUM HEXODIADEMA Bloeser, 1985 Figure 4.1–4.9, 4.11, 4.13

Melanocyrrillium hexodiadema [sic] BLOESER, 1979, p. 420, [nom. nud.].
Melanocyrrillium hexodiadema BLOESER, 1980, p. 64, pl. 2, fig. 1a–d, [nom. nud.]; BLOESER, 1985, p. 748–755, figs. 7.2, 7.6, 7.9–7.15, 8, 9.1, 9.2, 9.4–9.8.

Description.—Test shape bulbous, with aboral pole directly opposite aperture. Test size ranges from ~30 to 140 μm in length ($\mu = 75 \mu\text{m}$; $\sigma = 19 \mu\text{m}$; $N = 17$, where μ is the mean, σ is the standard deviation, and N is the number of specimens measured), ~25 to 100 μm in width ($\mu = 57 \mu\text{m}$; $\sigma = 14 \mu\text{m}$; $N = 19$). The aperture diameter of *M. hexodiadema* is ~20 to 60 μm (measured from outer margin; $\mu = 36 \mu\text{m}$; $\sigma = 8 \mu\text{m}$; $N = 17$) but most specimens fall within a narrower size range (~70

to 80 μm in length, ~50 to 60 μm in width, and ~30 to 40 μm in aperture diameter). Length-width ratios range from 1.2 to 1.5 ($\mu = 1.3$; $\sigma = 0.1$; $N = 17$), and are significantly different from those of other VSM taxa ($P < 0.05$; two-tailed t -test). The outer margin of the apertural face is hexagonal (Fig. 4.1, 4.13); the inner margin is broadly circular (Fig. 4.3, 4.4, 4.13). Specimens in thin section indicate that the test is invaginated at the apertural pole such that the aperture is located ~10 μm deep within the test (Fig. 4.11; arrow indicates invaginated aperture). The six indentations are separated by raised longitudinal ridges (e.g., Fig. 4.2, 4.3, 4.5, 4.6). The preservational state of specimens from acid macerations suggests that the test wall may have been thinnest where it formed the indentations and the inner apertural rim, as casts of these areas are commonly not preserved (e.g., Fig. 4.1, 4.2, 4.4, 4.7, 4.8).

Material examined.—Twenty-two specimens from acid maceration residues, ~50 specimens strewn-mounted on slides, and ~200 specimens in thin section, samples AK10-53-13A, AK10-53-13B-C, and AK10-53-13F, all from a single carbonate nodule in upper Walcott Member shale, Chuar Group, Grand Canyon (locality discussed in Porter and Knoll [2000]). *Melanocyrrillium hexodiadema* commonly can be distinguished in thin section by its unusual longitudinal sections that exhibit the invaginated aperture and broad indentations (Fig. 4.11), and by its hexagonal aperture (Fig. 4.13). This species is relatively abundant, constituting approximately ten percent of specimens in maceration residues (18 percent of identifiable specimens; Fig. 3).

Occurrence.—Specimens that can be identified unambiguously as *M. hexodiadema* (Bloeser, 1985) have thus far been found only in the Chuar Group. They occur in Walcott Member black shales and carbonate nodules in shales at localities on or near Nankow-eap Butte (described in detail in Bloeser [1985] and Porter and Knoll [2000]). A hexagonal cross section reported from VSM assemblages in the Neoproterozoic Backlundtoppen Formation, Spitsbergen (locality and stratigraphic position described in Knoll et al. [1989]), may represent *M. hexodiadema*, but an affinity with the species *Hemisphaeriella ornata* n. sp. (described below) cannot be ruled out.

Discussion.—No modern testate amoeba possesses the specific combination of characters exhibited by *M. hexodiadema*, but all of the characters are found in different species in the genus *Arcella* (Deflandre, 1928). *Arcella conica* has a test with regularly distributed indentations (Fig. 4.10) and an invaginated aperture; the test of *A. mitrata* var. *pyriformis* is identical in longitudinal section to *M. hexodiadema* (Fig. 4.12); and *A. mitrata* var. *spectabilis* has a test with six-fold symmetry (e.g., its apertural face illustrated in Fig. 4.14; six-fold symmetry also occurs in *Sexangularia*, in the lobose family Diffugiidae) (Meisterfeld, 2002a).

Genus TRIGONOCYRILLIUM new genus

Type species.—*Melanocyrrillium horodyskii* BLOESER, 1985.

Other species.—*Melanocyrrillium fimbriatum* BLOESER, 1985.

Diagnosis.—[Based on the description of *M. horodyskii* (BLOESER, 1985)]. Pyriform to bulbous VSMs with an equilateral triangular aperture.

Etymology.—From the Greek, *trigonos*, triangular, and *kyrillion*, jug with narrow neck; with reference to the triangular aperture.

Discussion.—Bloeser (1985) originally included both *T. horodyskii* n. comb and *T. fimbriatum* n. comb. within *Melanocyrrillium*, but because they lack the distinctive characters exhibited by *M. hexodiadema* and are distinct in aperture shape from all other VSMs, they have been placed in a new genus. The two species differ in the ornamentation of the apertural margin.

In modern testate amoebae, triangular apertures occur only in

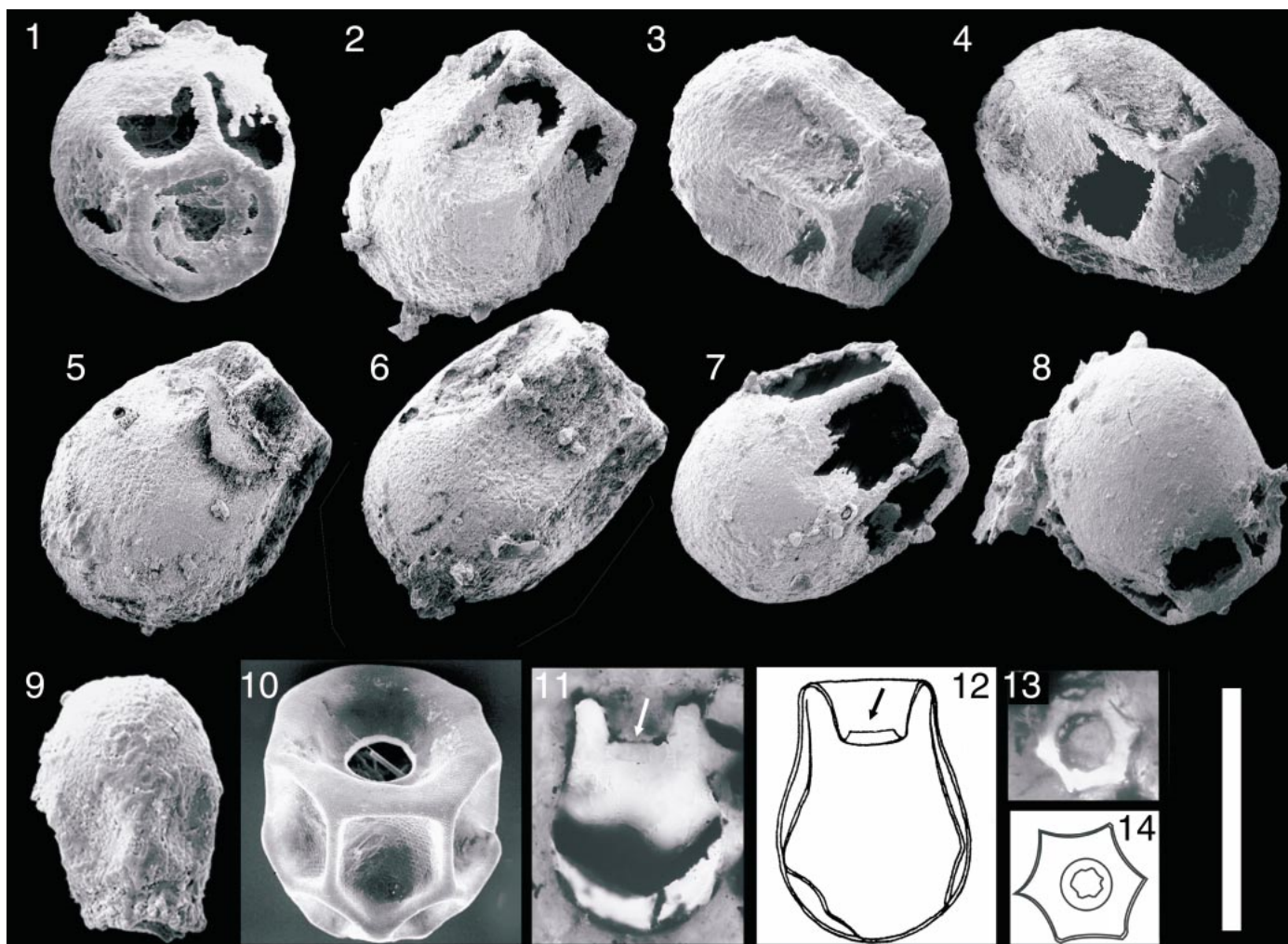


FIGURE 4—*Melanocyrrillium hexodiadema* Bloeser, 1985 and modern testate amoeban analogs. 1–9, 11, 13, *Melanocyrrillium hexodiadema*. 1, HUPC# 64429 (AK10-53-13A-5); 2, 3, HUPC# 64414 (AK10-53-13A-2); 4, HUPC# 64401 (AK10-53-13A-1); 5, HUPC# 64415 (AK10-53-13A-2); 6, HUPC# 64416 (AK10-53-13A-2); 7, HUPC# 64402 (AK10-53-13A-1); 8, HUPC# 64430 (AK10-53-13A-5); 9, HUPC# 64431 (AK10-53A-5). 10, The modern lobose testate amoeba, *Arcella conica*. 11, Longitudinal section of *M. hexodiadema*. Arrow points to invaginated aperture. HUPC# 62988 (AK10-53-13F-2B; Q68-1). 12, Drawing of a longitudinal section of the modern lobose testate amoeba, *Arcella mitrata* var. *pyriformis*, with arrow pointing to invaginated aperture (modified from fig. 386 in Deflandre [1928]; maximum length 97 μm). 13, Apertural face of *M. hexodiadema*; HUPC# 62991 (AK10-53-13F-2A; T65-1). 14, Drawing of the apertural face of the modern lobose testate amoeba, *Arcella mitrata* var. *spectabilis* (modified from fig. 391 in Deflandre [1928]; diameter of oral face 65–74 μm). Scale bar is 50 μm for 1; 60 μm for 2–5; 65 μm for 6, 7; 85 μm for 8, 10; 40 μm for 9; 70 μm for 11; and 140 μm for 13.

the lobose genus, *Trigonopyxis* (Fig. 5.20); however, unlike *Trigonocyrrillium*, *Trigonopyxis* tests are hemispherical in shape (Meisterfeld, 2002a).

TRIGONOCYRILLIUM HORODYSKII (Bloeser, 1985)
new combination
Figure 5.1–5.19

Melanocyrrillium [sic] *horodyskii* BLOESER, 1979, p. 421, [nom. nud.].
Melanocyrrillium horodyskii BLOESER, 1980, p. 73, pl. 4, fig. 1a–c [nom. nud.]; BLOESER, 1985, fig. 11.1–11.2.

Diagnosis.—Specimens of the genus *Trigonocyrrillium* that have unadorned apertural margins.

Description.—The tests of *Trigonocyrrillium horodyskii* are bulbous to pyriform in shape, with the aboral pole directly opposite the aperture. Their length-width ratios range from 1.2 to 1.8 ($\mu = 1.5$; $\sigma = 0.1$; $N = 20$). The tests range from ~ 75 – 125 μm in length ($\mu = 96$; $\sigma = 19$; $N = 20$) and from ~ 45 – 90 μm in width

($\mu = 65$ μm ; $\sigma = 15$ μm ; $N = 22$). Both the outer and inner margins of the aperture are triangular in shape, with three equal sides and three subrounded points. In most specimens, the apertural rim is relatively thick (~ 3 μm) (Fig. 5.2, 5.5, 5.8, 5.15). One specimen, although possessing a triangular aperture, is different from the others in having a very thin apertural margin and, at the corners of the triangle, rounded outpocketings (Fig. 5.16, 5.17; see arrows).

Material examined.—Twenty-five specimens from acid maceration residues, and ~ 30 specimens in thin section, samples AK10-53-13A, AK10-53-13B-C, and AK10-53-13F, all from a single carbonate nodule in Walcott Member shales (see Porter and Knoll, 2000). It can be difficult to identify *T. horodyskii* in thin section because in side view (e.g., Fig. 5.4, 5.6, 5.10–5.12, 5.14) it is indistinguishable from specimens in the genus *Cycliocyrrillium* n. gen. (described below). In some specimens, however, the triangular aperture is recognizable (e.g., Fig. 5.18,

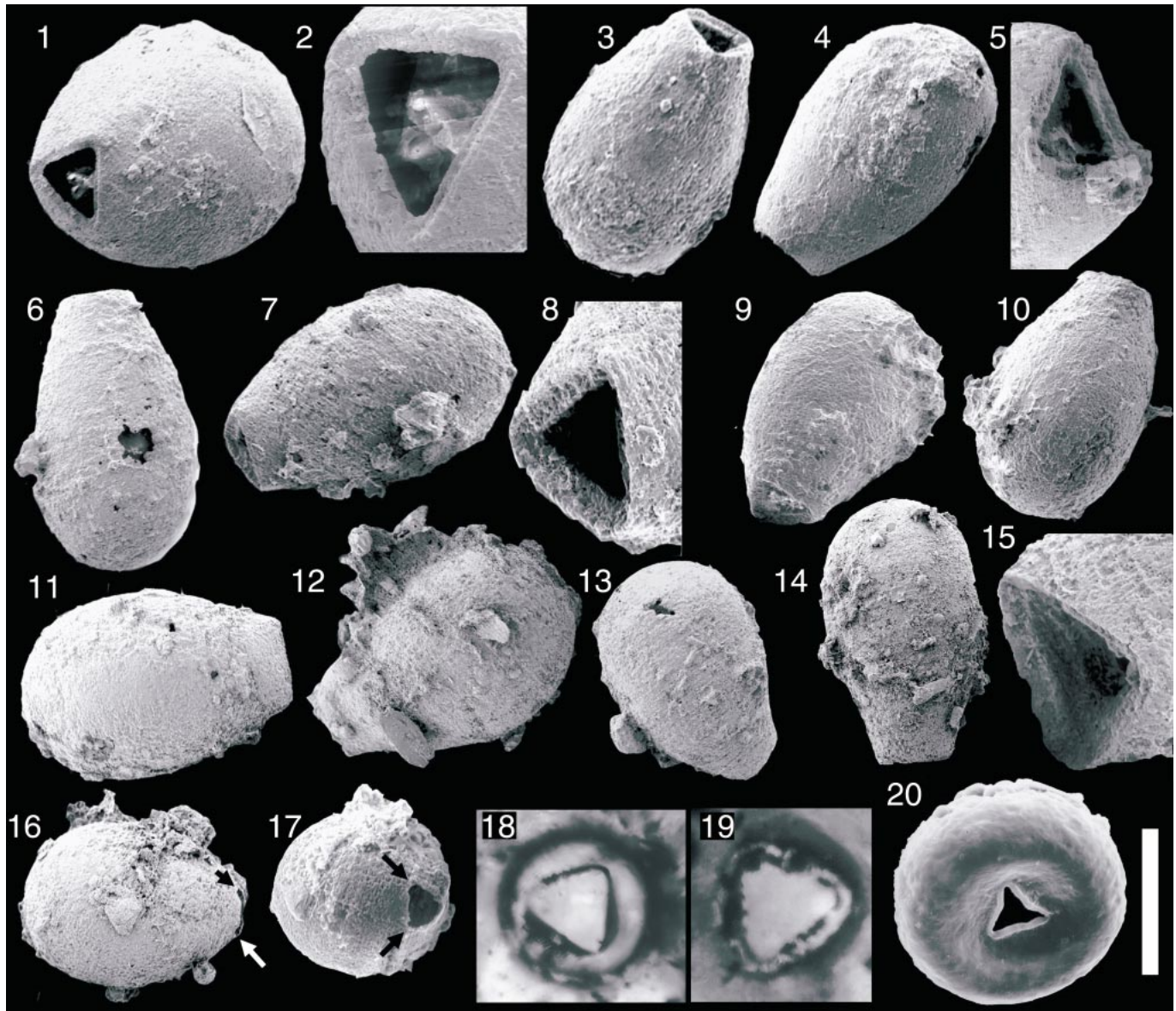


FIGURE 5.—*Trigonocyrrillium horodyskii* (Bloeser, 1985) n. comb. and a modern testate amoeban analog. 1–19, *Trigonocyrrillium horodyskii*; 1, 2, HUPC# 64432 (AK10-53-13A-5); 3, HUPC# 64433 (AK10-53-13A-5); 4, 5, HUPC# 64434 (AK10-53-13A-5); 6, HUPC# 64448 (AK10-53-13A-7); 7, 8, HUPC# 64449 (AK10-53-13A-7); 9, 10, HUPC# 64403 (AK10-53-13A-1); 11, HUPC# 64404 (AK10-53-13A-1); 12, HUPC# 64417 (AK10-53-13A-2); 13, HUPC# 64450 (AK10-53-13A-7); 14, 15, HUPC# 64454 (AK10-53-13A-9); 16, 17, HUPC# 64405 (AK10-53-13A-1); 18, looking through test (outer circle) at aperture (triangle) HUPC# 62988 (AK10-53-13F-2B; O64); 19, HUPC# 64457 (AK10-53-13F-2C; P54-2). 20, The modern lobose testate amoeba, *Trigonopyxis arcula*. Scale bar is 60 μm in 1, 4, 11, 20; 20 μm in 2, 8, 15; 45 μm in 3, 6, 7, 9, 10, 16; 30 μm in 5, 19; 65 μm in 12, 18; 75 μm in 13; and 50 μm in 14, 17.

5.19). *T. horodyskii* specimens constitute ~12 percent of specimens in maceration residues (~21 percent of identifiable specimens; Fig. 3).

Occurrence.—*Trigonocyrrillium horodyskii* occurs at the Nan-kowap Butte locality in black shales (Bloeser, 1985) and carbonate nodules in shales (Porter and Knoll, 2000) from the Walcott Member, Chuar Group, Grand Canyon. A specimen from the Elbobreen Formation, Spitsbergen, pictured in fig. 6I, Chapter 4, in Martí Mus (2001), exhibits a triangular aperture, and probably represents either *T. horodyskii* or *T. fimbriatum* (Table 1). A possible *T. horodyskii* specimen from the Draken Conglomerate Formation, Spitsbergen, is figured in Knoll et al. (1991; fig. 7.1). Many VSMs from elsewhere are comparable in

shape and dimensions to *T. horodyskii*, but the absence of preserved triangular apertures prevents definitive identification.

TRIGONOCYRILLIUM FIMBRIATUM (Bloeser, 1985)
new combination

Melanocyrrillium [sic] *fimbriatum* BLOESER, 1979, p. 420 [nom. nud.].
Melanocyrrillium fimbriatum BLOESER, 1980, p. 71, pl. 3, fig. 1a–d [nom. nud.]; BLOESER, 1985, p. 755–756, figs. 10, 11.3–11.12.

Diagnosis.—[Based on the description of *M. fimbriatum* (Bloeser, 1985)]. Specimens of *Trigonocyrrillium* with ornamentation around the apertural margin comprising roughly triangular fringes that project from the oral pole toward the aboral pole in three

distinct, equally spaced areas. The three sides of the triangular aperture coincide with the three areas of extension to produce a zig-zag pattern about the oral end.

Material examined.—Bloeser (1985) examined 238 specimens in thin section or acid-maceration residues. For this publication, figs. 10, 11.3–11.12 in Bloeser (1985) were examined.

Occurrence.—*Trigonocyrrillium fimbriatum* has been reported only by Bloeser (1985) in black shales of the Walcott Member, Chuar Group, Grand Canyon (see Bloeser [1985] for a detailed locality description).

Discussion.—No specimens of *T. fimbriatum* were found in the new Chuar Group populations and thus the description of this species is limited to that of Bloeser (1985). No modern testate amoebae have apertural margins like that of *T. fimbriatum*, although ornamented and/or thickened margins are common in the group (Meisterfeld, 2002a, 2002b).

Genus CYCLOCYRILLIUM new genus

Type species.—*Cycliocyrrillium simplex* n. sp.

Other species.—*Cycliocyrrillium torquata* n. sp.

Diagnosis.—Bulbous to pyriform VSMs with a circular aperture and uncurved “neck”; angle between the apertural plane and the aboral axis ~90 degrees.

Etymology.—From the Greek, *kyklios*, circular, and *kyrrillon*, jug with a narrow neck; with reference to the circular aperture of these VSMs.

Discussion.—The two species vary with respect to modification of the apertural margin.

CYCLOCYRILLIUM SIMPLEX new species

Figure 6.1–6.9

Diagnosis.—Specimens of *Cycliocyrrillium* whose apertural margin is not thickened or set off from the rest of the test by a short neck. Smooth apertural margin, flush with the rest of the test.

Description.—*Cycliocyrrillium simplex* tests are bulbous (Fig. 6.1, 6.4, 6.6) to pyriform (Fig. 6.2, 6.3, 6.5, 6.7–6.9) in shape. Length-width ratios range from 1.1–1.9 ($\mu = 1.5$; $\sigma = 0.2$; $N = 10$), and the tests range from ~40–110 μm in length ($\mu = 80$; $\sigma = 22$; $N = 10$) and ~35–75 μm in width ($\mu = 52$; $\sigma = 12$; $N = 10$). The aperture is circular, and ranges from ~10–25 μm in diameter. Test walls may curve inward toward aperture (Fig. 6.1, 6.2, 6.4, 6.6, 6.7) or may extend more or less straight toward it (Fig. 6.3, 6.5).

Etymology.—From the Latin, *simplex*, simple; referring to the undecorated apertural margin.

Type.—Holotype HUPC# 64455 (Fig. 6.7, 6.8) from sample AK10-53-13A (SEM stub AK10-53-13A-9), Nankowep Butte locality, Walcott Member, Chuar Group, Grand Canyon.

Other material examined.—Nine specimens from acid maceration residues, including HUPC# 64406, 64418, 64419, 64422, 64451, and 64452 (Fig. 6.1–6.6), all from same sample and locality as holotype; ~50 specimens in thin section (including Fig. 6.9), from samples AK10-53-13A, AK10-53-13B-C; AK10-53-13F; same locality as holotype. This species constitutes approximately seven percent of the specimens in maceration residues (~14 percent of identifiable specimens; Fig. 3).

Occurrence.—*Cycliocyrrillium simplex* occurs at the Nankowep Butte locality in carbonate nodules in black shales from the uppermost Walcott Member, Chuar Group, Grand Canyon, and in bed 18 at the Kap Petersens locality, Upper Limestone-Dolomite Series, Eleonore Bay Group, East Greenland (Vidal, 1979) (Table 1). Possible *C. simplex* specimens may occur in the Jabal Rockham dolostone (fig. 1C in Binda and Bokhari, 1980), the Togari Group, Tasmania (fig. 6 in Saito et al., 1988), the Backlundtoppen Formation, Spitsbergen (fig. 7.9 in Knoll et al., 1989), the Ryssö

Formation, Nordaustlandet, Svalbard (pl. 61, figs. 2, 7, 8 in Knoll and Calder, 1983), the Visingsö Group Sweden (fig. 1D–G in Knoll and Vidal, 1980), the Pahrump Group, California (e.g., fig. 47H in Link et al., 1993), and the Uinta Mountain Group, Utah (S. M. Porter, unpublished observations).

Discussion.—No modern testate amoebae are exactly comparable to *C. simplex*. Species in the genus *Diffugia* have similar test shape, but the tests are agglutinated (Fig. 6.10) (Meisterfeld, 2002a). Many species in the arcellinid genera *Nebela* and *Hyalosphenia* have tests that are superficially similar in shape to those of *C. simplex*, but they are compressed longitudinally (Meisterfeld, 2002a).

CYCLOCYRILLIUM TORQUATA new species

Figures 6.11–6.23, 18.1

Diagnosis.—Specimens of the genus *Cycliocyrrillium* with a distinctive, short ‘collar’: test walls narrow toward the aperture and then proceed in a parallel fashion for a short distance before terminating at the apertural edge. In some specimens neck appears thickened relative to the test wall.

Description.—*Cycliocyrrillium torquata* tests are pyriform in shape, with length-width ratios ranging between 1.4 and 1.9 ($\mu = 1.6$; $\sigma = 0.1$; $N = 12$). They range from ~60 to 120 μm in length ($\mu = 89$ μm ; $\sigma = 17$ μm ; $N = 12$) and from ~35 to 90 μm in width ($\mu = 57$ μm ; $\sigma = 12$ μm ; $N = 13$). The aperture ranges from ~15 to 45 μm in diameter ($\mu = 28$ μm ; $\sigma = 6$ μm ; $N = 12$), significantly larger than that of *C. simplex* ($P < 0.05$; two-tailed *t*-test).

The collar is set off from the test by a change in wall curvature: from the widest point of the test, the test walls curve toward each other orally and then bend sharply back such that they are roughly parallel to each other. This sharp bend marks the beginning of the collar. The collar is short, making up approximately ten percent or less of the test length. The collar may be thickened (e.g., Fig. 6.12, 6.20).

Etymology.—From the Latin, *torquata*, wearing a collar; with reference to the collar-like apertural margin.

Type.—Holotype HUPC# 64453 (Fig. 6.19, 6.20) from sample AK10-53-13A, Nankowep Butte locality, Walcott Member, Chuar Group, Grand Canyon.

Other material examined.—Twelve specimens, including HUPC# 64407, 64408, 64421, 64423, 64424, 64445, and 64447 (Figs. 6.11–6.18, 18.1) from acid maceration residues, all from same sample and locality as the holotype; ~30 specimens in thin section, including HUPC# 62990 (Fig. 6.21–6.23), from sample AK10-53-13F and sample AK10-60-19, same locality as the holotype. Approximately six percent of specimens in maceration residues were *C. torquata* (~11 percent of identifiable specimens; Fig. 3).

Occurrence.—*Cycliocyrrillium torquata* occurs at the Nankowep Butte locality in carbonate nodules in uppermost Walcott Member shales and in silicified dolomites lower in the same member, Chuar Group, Grand Canyon. It also occurs at the same locality in the upper Awatubi Member (fig. 10C in Horodyski, 1993). A VSM from the Elbobreen Formation, Spitsbergen (illustrated in Knoll, 1996), also has a collar, but unlike *C. torquata*, its test is curved. It may represent an abnormal specimen of *C. torquata* or a specimen of *Bonniea dacruchares* n. sp. Other specimens with elongate “necks” (e.g., pl. 1, fig. 13 in Knoll and Calder, 1983) are too distinct to be included in this species. Possible *C. torquata* specimens occur in the Visingsö Group (e.g., fig. 3A in Martí Mus and Moczyłowska, 2000), in the Ryssö Formation, Nordaustlandet (e.g., pl. 61, fig. 11 in Knoll and Calder, 1983), and the Uinta Mountain Group, Utah (e.g., Fig. 2.1) (Table 1).

Discussion.—The best analogs for *C. torquata* are species in

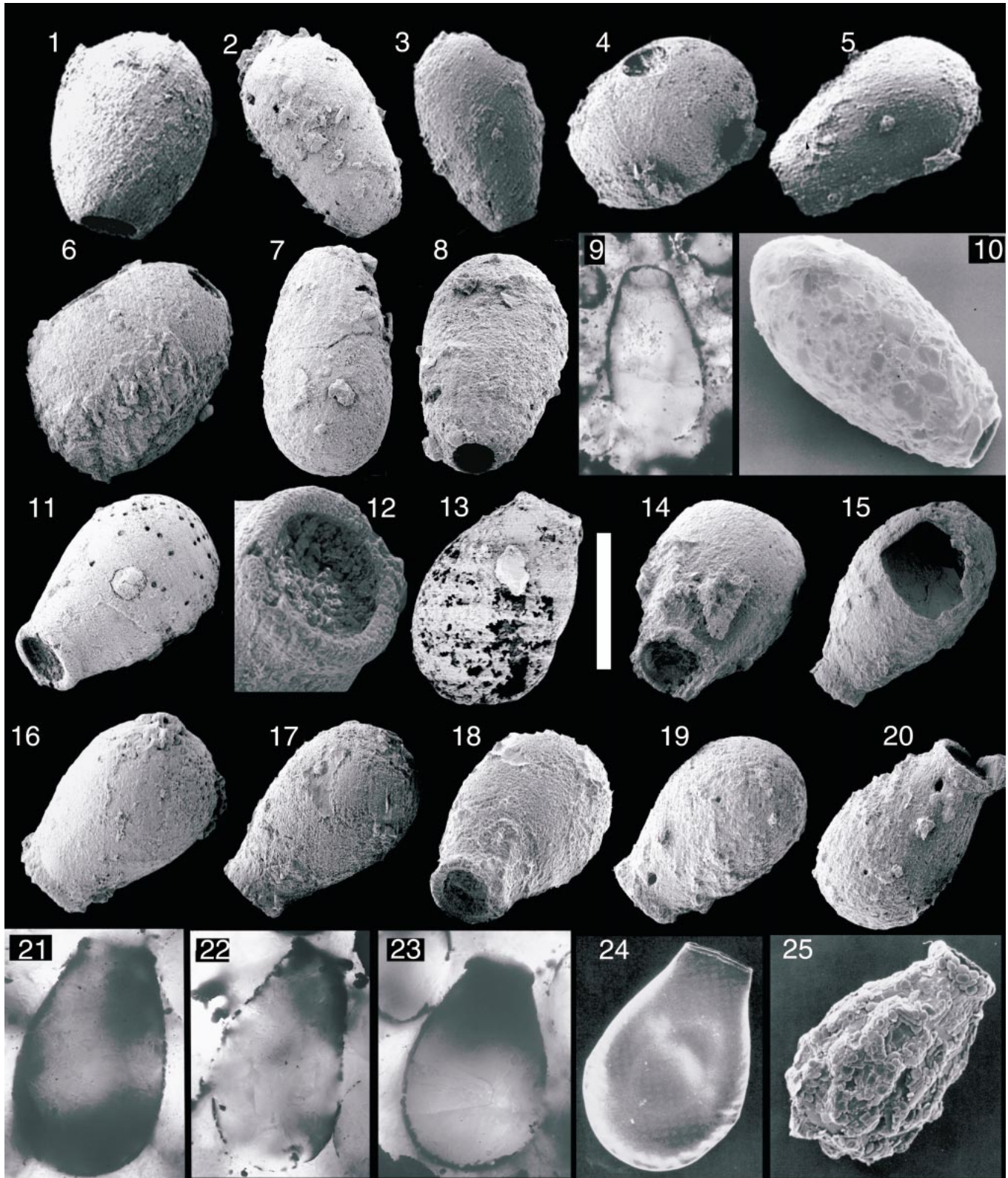


FIGURE 6—The genus *Cycliocyrrillium* n. gen. and modern testate amoeban analogs. 1–9, *Cycliocyrrillium simplex* n. sp.; 1, HUPC# 64422 (AK-53-13A-4); 2, HUPC# 64418 (AK10-53-13A-2); 3, HUPC# 64451 (AK10-53-13A-7); 4, HUPC# 64419 (AK10-53-13A-2); 5, HUPC# 64452 (AK10-53-13A-7); 6, HUPC# 64405 (AK10-53-13A-1); 7, 8, HUPC# 64455 (AK-53-13A-9); 9, HUPC# 62988 (AK10-53-13F-2B; S60-4). 10, The modern lobose testate amoeba *Diffflugia lanceolata*. 11–23, *Cycliocyrrillium torquata* n. sp.; 11, 12, HUPC# 64407 (AK10-53-13A-1); 13, HUPC# 64431 (AK10-53-13A-3); 14, HUPC# 64447 (AK10-53-13A-6); 15, HUPC# 64423 (AK10-53-13A-4); 16, HUPC# 64424 (AK-10-53-13A-4); 17, 18, HUPC# 64408 (AK10-53-13A-1); 19, 20, HUPC# 64453 (AK10-53-13A-7); 21, HUPC# 62990 (AK10-53-13F-1; P41-4); 22, HUPC# 62990

the arcellinid genera, *Hyalosphenia* and *Nebela* (Fig. 6.24, 6.25). Other species in both the filose testate amoebae and the Arcellinida have tests with “necks” (e.g., *Ampullataria rotunda* and *Difflugia gassowskii*) (Ogden, 1983; Meisterfeld, 2002a), but these are much longer than those of *C. torquata*, constituting as much as a third of the test length.

Genus *BONNIEA* new genus

Type species.—*Bonniea dacruchares* n. sp.

Other species.—*Bonniea pytinaia* n. sp.

Diagnosis.—VSMs with a curved “neck” and circular aperture.

Etymology.—In honor of Bonnie Bloeser, who first studied the Chuar VSMs.

Discussion.—The original rigidity of VSM tests (Martí Mus and Moczyłowska, 2000; Porter and Knoll, 2000) indicates that the curved neck of *Bonniea* is not diagenetic in origin, but rather that *Bonniea* tests were curved during the life of the organism.

In modern testate amoebae, test curvature may be a species-level character or it may vary intraspecifically. Curved tests in typically uncurved species are caused by unusual environmental factors, such as the presence of an obstacle encountered during the construction of the daughter test (R. Meisterfeld, unpublished observations). As a result, curved variants are rare (1 per 1,000 specimens). The regular form and relative abundance of test curvature in the VSM assemblage suggests that it is a species-level character, justifying its use as such here.

The two species of *Bonniea* are divided on the basis of length-to-width ratio and concavity of the lower wall. “Lower” refers to the side of the test to which the neck curves; Figure 7 provides an example of how length, width, concavity and curvature are measured. Clustering of specimens with respect to length-to-width ratio and concavity allowed distinction between *B. dacruchares* and *B. pytinaia* (Fig. 8). Supporting this division is a significant difference in aperture diameter ($P < 0.05$; two tailed *t*-test).

Many different modern testate amoeban species, both lobose and filose, have curved tests, including all species in the filose amoeban genus *Cyphoderia* (Fig. 9.24), many species in the filose family Psammonobiotidae, the lobose species *Nebela retorta* (Fig. 9.25), and the lobose genus *Lamtoquadrula* (Meisterfeld, 2002a, 2002b).

BONNIEA DACRUCHARES new species

Figure 9.1–9.23

Diagnosis.—Specimens of the genus *Bonniea* with a test that has length-to-width ratios less than two and concavity greater than 30 degrees. Aperture may be slightly thickened.

Description.—Body of test bulbous in shape. Length-width ratio ranges between 1.5 and 2.1 ($\mu = 1.8$; $\sigma = 0.1$; $N = 21$). Tests range from 65 to 180 μm in length ($\mu = 108 \mu\text{m}$; $\sigma = 25 \mu\text{m}$; $N = 21$), 35 to 90 μm in width ($\mu = 61 \mu\text{m}$; $\sigma = 13 \mu\text{m}$; $N = 21$), and ~15 to 50 μm in aperture diameter ($\mu = 28 \mu\text{m}$; $\sigma = 7 \mu\text{m}$; $N = 21$). Curvature, the angle between the aboral and oral axes (Fig. 7), varies between 30 degrees and 60 degrees ($\mu = 45$ degrees; $\sigma = 10$ degrees; $N = 12$). Concavity, a measure of the bend in the “lower” wall (Fig. 7), ranges between ~40 degrees and 70 degrees ($\mu = 47$ degrees; $\sigma = 8$ degrees; $N = 12$). Some specimens exhibit a slight thickening around the apertural margin (e.g., Fig. 9.7, 9.11, 9.12, 9.15).

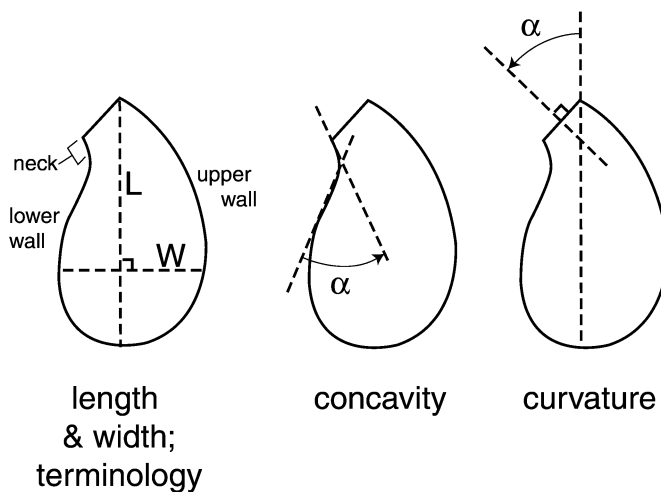


FIGURE 7—Diagram illustrating terminology used to describe *Bonniea* n. gen. and indicating how length, width, concavity, and curvature are measured in *Bonniea* specimens.

Etymology.—From the Greek, *dakrychares*, delighting in tears; with reference to the pleasure derived from studying the tear-shaped VSMs.

Type.—Holotype HUPC# 64409 (Fig. 9.9, 9.10) from sample AK10-53-13A, Nankoweap Butte locality, Walcott Member, Chuar Group, Grand Canyon.

Other material.—Twenty specimens from acid maceration residues, examined with SEM, including HUPC# 64420, 64425, 64426, and 64435–64440 (Fig. 9.1–9.8, 9.11, 9.12), from same sample and locality as holotype; ~100 specimens in thin section, including HUPC# 62988 (Fig. 9.14, 9.15) from samples AK10-53-13A, AK10-53-13B-C, and AK10-53-13F, same locality as holotype; and ~40 specimens in strew-mounted slides, including HUPC# 64458 (Fig. 9.13), from samples AK10-53-13A and AK10-53-13F, same locality as holotype. *B. dacruchares* is relatively common, constituting approximately ten percent of the specimens in maceration residue (15 percent of identifiable specimens; Fig. 3).

Occurrence.—Abundant in carbonate nodules in shales from the Walcott Member, Chuar Group, Nankoweap locality, Grand Canyon. A curved VSM from the Elbobreen Formation, Spitsbergen [illustrated in pl. 3, fig. 12 in Knoll (1996)], possesses a short neck that, in contrast to some specimens of *B. dacruchares* that possess a thickened apertural margin, is apparently thinner than the test wall. A VSM illustrated in Martí Mus (2001; fig. 3I; also from the Elbobreen Formation) is probably a specimen of *B. dacruchares*.

Discussion.—Many modern testate amoebae that exhibit curvature have relatively strongly curved necks and high concavity, and many are comparable in size to *B. dacruchares* as well. The best analog for *B. dacruchares* is *Cyphoderia ampulla* (Fig. 9.24), although, unlike *B. dacruchares* (see Porter and Knoll, 2000), it has a siliceous test made of small scales (Meisterfeld, 2002a, 2002b).

A number of modern testate amoebae with curved necks also have thickened apertural margins, including species in the filose

←

(AK10-53-13F-1; O45-3); 23, HUPC# 62990 (AK10-53-13F-1; N46-2). 24, The modern lobose testate amoeba, *Hyalosphenia papilio*, courtesy of Ogden and Hedley (1980). 25, The modern lobose testate amoeba, *Nebela griseola*, courtesy of Ogden and Hedley (1980). Scale bar equals 40 μm for 1, 2, 11, 13, 19, 20; 35 μm for 3, 6–8, 16; 30 μm for 4, 9; 45 μm for 5, 10, 15–18, 23; 15 μm for 12; 65 μm for 14; 50 μm for 21, 24; and 85 μm for 25.

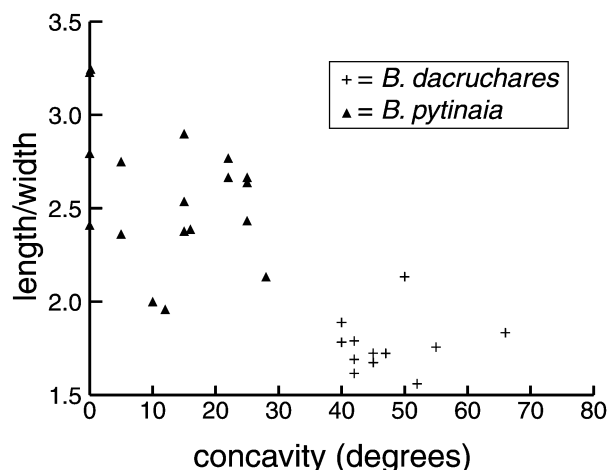


FIGURE 8—Plot of length/width ratios vs. concavity in 30 specimens of the genus *Bonnia* n. gen. Length, width, and concavity are measured as shown. Crosses represent specimens of *B. dacruchares* n. sp. ($N = 12$), and triangles represent specimens of *B. pytinaia* n. sp. ($N = 18$). Specimens from both thin sections and acid macerations were measured.

Psammonobiotidae and Cyphoderiidae families, and the lobose species *Nebela retorta* (Fig. 9.25) (Meisterfeld, 2002a, 2002b). Some species in the Psammonobiotidae have almost entirely organic-walled tests (e.g., *Psammonobiotus communis*), but they differ from *B. dacruchares* in having a strongly flared aperture (Meisterfeld, 2002b).

BONNIEA PYTINAIA new species
Figures 9.16–9.23, 18.2

Diagnosis.—Specimens of the genus *Bonnia* that have a test with a length-to-width ratio of two or greater and concavity less than 30 degrees.

Description.—Body of test elongate. Tests have length-to-width ratios that range from 2.0 to 3.2 ($\mu = 2.5$; $\sigma = 0.3$; $N = 20$). Tests range from ~ 80 to $160 \mu\text{m}$ in length ($\mu = 110 \mu\text{m}$; $\sigma = 21 \mu\text{m}$; $N = 20$), ~ 30 to $70 \mu\text{m}$ in width ($\mu = 45 \mu\text{m}$; $\sigma = 9 \mu\text{m}$; $N = 21$), and ~ 15 to $30 \mu\text{m}$ in aperture diameter ($\mu = 20 \mu\text{m}$; $\sigma = 5 \mu\text{m}$; $N = 19$). Curvature ranges between 15 degrees and 65 degrees ($\mu = 40$ degrees; $\sigma = 13$ degrees; $N = 18$). Concavity ranges between 0 degrees (e.g., Fig. 9.20) and 30 degrees ($\mu = 15$ degrees; $\sigma = 10$ degrees; $N = 17$). Curvature and concavity are not necessarily correlated in these species; some tests have high curvature but low concavity (e.g., Fig. 9.16, 9.20, 9.21, 9.22).

Etymology.—From the Greek, *pytinaios*, willowy; with reference to the long, thin shape of the tests.

Type.—Holotype HUPC# 64410 (Fig. 9.16) from sample AK10-53-13A, Nankowep Butte locality, Walcott Member, Chuar Group, Grand Canyon.

Other material examined.—Fifteen specimens from acid maceration residues, including HUPC# 64411, 64412, 64427, 64428, and 64441 (Figs. 9.17–9.21, 18.2) all from same sample, locality as holotype; ~ 25 specimens in thin section from samples AK10-53-13A, AK10-53-13B-C, and AK10-53-13F; same locality as holotype; and ~ 20 of specimens strew-mounted on slides, all from same sample and locality as holotype. Tests are easily identifiable in thin section, and are relatively common in the Chuar Group carbonate nodules, accounting for approximately seven percent of the specimens from maceration residues (13 percent of identifiable specimens; Fig. 3).

Occurrence.—Abundant in carbonate nodules in shales from the upper Walcott Member, Chuar Group, Grand Canyon.

Discussion.—Degree of curvature varies widely in modern testate amoebae, but most are more strongly curved than *B. pytinaia*. [There are specimens of modern testate amoebae that are only slightly curved, but these are normally considered to be deformed specimens of straight species (R. Meisterfeld, unpublished observations). The abundance of *B. pytinaia* suggests this is not the case.] Many taxa have similar length-to-width ratios, however, including both *Cyphoderia ampulla* and *Nebela retorta* (Fig. 9.24, 9.25) (Meisterfeld, 2002a, 2002b). In some specimens of *B. pytinaia* (e.g., Fig. 9.20, 9.21), low to absent concavity suggests a similarity with the modern testate amoeban genus *Trinema* (shown in Fig. 13.5, 13.6; Ogden and Hedley, 1980; Meisterfeld, 2002a).

TRACHYCYRILLIUM new genus

Type species.—*Trachycyrellium pudens* n. sp., by monotypy.

Diagnosis.—VSMs with a lobed aperture. Lobed aperture results from evenly spaced, inwardly directed points.

Etymology.—From the Greek, *trachys*, jagged, and *kyrillion*, jug with narrow neck; with reference to the inwardly directed points around apertural opening.

Discussion.—The regular form of the *Trachycyrellium* aperture indicates that it is not diagenetic in origin: all points of the aperture are identical in size and shape and are evenly spaced, and a second specimen confirms these regularities. The distinctiveness of this character warrants the erection of a new genus.

TRACHYCYRILLIUM PUDENS new species
Figure 10.1–10.4

Diagnosis.—As for genus.

Description.—Test pyriform to bulbous in shape. Although only two specimens have been found, they are very different in test size and shape, indicating a large range of variability for this species, that may, with larger populations, justify the recognition of greater species diversity within this genus. Length-width ratios for the two specimens are 1.8 and 1.4, test lengths are ~ 90 and $\sim 140 \mu\text{m}$, test widths are ~ 50 and $\sim 100 \mu\text{m}$, and aperture diameters are ~ 15 and $\sim 40 \mu\text{m}$, respectively. Apertural margin consists of rounded “outpocketings” divided by inwardly directed points. Points extend into aperture a distance of $\sim 3 \mu\text{m}$. Lobed aspect of aperture barely visible in side view (see arrows in Fig. 9.1).

Etymology.—From the Latin, *pudens*, bashful, shy, modest; with reference to the difficulty of identifying these fossils and their relative rarity in the assemblage.

Type.—Holotype HUPC# 64413 (Fig. 10.1, 10.2) from sample AK10-53-13A, Nankowep Butte locality, Walcott Member, Chuar Group, Grand Canyon.

Other material examined.—One specimen from acid maceration residues (HUPC# 64442; Fig. 10.3, 10.4) from same sample, locality as holotype. *Trachycyrellium pudens* is rare, accounting for about one percent of the specimens from maceration residues (two percent of identifiable specimens). It is difficult to differentiate *Trachycyrellium pudens* and *Cycliocyrellium simplex* n. sp. in thin sections. Thus, it is possible that some *T. pudens* specimens may be misidentified as *C. simplex*, partly contributing to the relative rarity of *T. pudens* in thin section.

Occurrence.—Carbonate nodules in shales from the upper Walcott Member, Chuar Group, Nankowep Butte locality, Grand Canyon. VSMs from the Chatkaragai suite possess crenulated apertures (e.g., table LII, figs. 1–5, 7 in Kraskov, 1989; fig. 10A in Porter and Knoll, 2000), but the crenulations are formed by longitudinal grooves that extend aborally $\sim 35 \mu\text{m}$, and can be observed in side view.

Discussion.—Due to difficulties in viewing the specimens, only three points in the apertures of each of the two specimens can be definitively identified, but the angles between the points (~60–70 degrees) suggest either five- or six-fold symmetry (in Fig. 10.2 there appear to be five points; in Fig. 10.4 it is difficult to tell). The specimen of *Trigonocyrrillium horodyskii* (Bloeser, 1985) n. comb. illustrated in Figure 5.16, 5.17 looks superficially similar to *Trachycyrrillium pudens* specimens, but its aperture is characterized by rounded outpocketings at each corner of a triangular opening, rather than five or six inwardly directed points distributed around a roughly circular aperture.

Lobed apertures are found in a number of lobose testate amoeban taxa, including the genera *Difflugia* and *Cucurbitella*, the genus *Netzelia* (Fig. 10.5) (Ogden and Meisterfeld, 1989), and the species *Pseudonebela africana* (Meisterfeld, 2002a). The number of lobes varies within and between taxa, but many have five- or six-lobed apertures very similar in design to *T. pudens*. All of the taxa differ from *T. pudens* in having either agglutinated tests (*Difflugia*, *Cucurbitella*, and *Netzelia*) or tests with mineralized plates embedded in an organic wall (*Pseudonebela africana*) (Meisterfeld, 2002a).

PALAEORCELLA new genus

Type species.—*Palaeoarcella athanata* n. sp., by monotypy.

Diagnosis.—Hemispherical VSMs with a test length approximately half that of test width. Test rounded, without indentations. Aperture circular, invaginated.

Etymology.—Combination of the Greek, *paios*, old, and the modern testate amoeban genus name, *Arcella*; alluding to the similarity between the modern and fossil tests.

Discussion.—The original rigidity attributed to VSM tests (Martí Mus and Moczydłowska, 2000; Porter and Knoll, 2000) and their regular form indicates that the shape of *Palaeoarcella* specimens is not simply the result of post-mortem deformation. Their form is also unable to be accommodated within any other taxon as either extreme morphological variants or unusual cross sections; for comments regarding the distinction between *Palaeoarcella*, *Melanocyrrillium* Bloeser, 1985, and *Hemisphaeriella* n. gen., see the discussion section of *Hemisphaeriella ornata* n. sp.

PALAEORCELLA ATHANATA new species

Figure 11.1–11.6

Diagnosis.—As for genus.

Description.—Tests hemispherical in shape; length-width ratios range between 0.4 and 0.6 ($\mu = 0.5$; $\sigma = 0.1$; $N = 18$). Tests range from ~20 to 40 μm in length ($\mu = 27 \mu\text{m}$; $\sigma = 4 \mu\text{m}$; $N = 18$), ~40 to 70 μm in width ($\mu = 52 \mu\text{m}$; $\sigma = 9 \mu\text{m}$; $N = 18$), and ~8 to 15 μm in aperture diameter ($\mu = 12 \mu\text{m}$; $\sigma = 3 \mu\text{m}$; $N = 8$). Aperture centered in flattened part of hemisphere, invaginated relative to surrounding test wall. Test wall curves smoothly inward toward aperture; transition from flat part of hemisphere to rounded part is also smooth.

Etymology.—From the Greek, *athanatos*, undying; with reference to the similarity of form to modern *Arcella* tests.

Types.—Holotype HUPC# 62988 (Fig. 11.3) from sample AK10-53-13F, Nankowep Butte locality, Walcott Member, Chuar Group, Grand Canyon.

Other material examined.—Twenty-six specimens in thin section (including Fig. 11.1, 11.2, 11.4–11.6) from samples AK10-53-13F, AK10-53-13B-D, and AK10-53-13F, same locality as holotype. *Palaeoarcella athanata* is easy to identify in thin section because of its distinctive shape, but it is relatively rare, constituting less than one percent of fossils identified in thin section. No specimens of *P. athanata* fossils have been found in maceration residues.

Occurrence.—*Palaeoarcella athanata* occurs in carbonate nodules in shales from the upper Walcott Member, Chuar Group, Nankowep Butte locality, Grand Canyon.

Discussion.—The tests of *P. athanata* are nearly indistinguishable from those of the modern lobose testate amoeban species *Arcella hemisphaerica* (Fig. 11.7). They are similar in shape, size, aperture shape and invagination, and, as assumed for *P. athanata*, based on taphonomic similarity with other VSMs (Porter and Knoll, 2000), are organic-walled in composition (Meisterfeld, 2002a). Other species with similarly shaped tests include *Arcella crenulata* (Fig. 11.8), *Arcella vulgaris*, and *Antarcella atava* (Meisterfeld, 2002a). Species in the lobose genus *Cyclopyxis* have similarly shaped tests, but are agglutinated (Meisterfeld, 2002a).

HEMISPHAERIELLA new genus

Type species.—*Hemisphaeriella ornata* n. sp., by monotypy.

Diagnosis.—Roughly hemispherical VSMs covered with broad, rounded indentations (~20 to 40 μm in diameter) on side and aboral wall.

Etymology.—From the Greek, *hemisphairion*, hemisphere, with the diminutive, *-ella*; with reference to their roughly hemispherical shape.

Discussion.—That VSM tests were originally rigid (Martí Mus and Moczydłowska, 2000; Porter and Knoll, 2000) indicates that these specimens are not simply *Palaeoarcella* tests that were dented during diagenesis, but rather that the indentations were present during life. This is consistent with their regular shape, size, and arrangement, which indicate a biological, rather than taphonomic origin. It is impossible to reconcile them as unusual cross sections of other taxa, and their distinctiveness indicates that they are unlikely to be variants of other taxa. Thus, even though there are only two specimens of *Hemisphaeriella*, they are distinct enough to warrant a new genus. The two specimens are slightly different from each other in appearance but this difference likely reflects different planes of intersection: one is probably cut near the center of the test (Fig. 12.1), the other appears to be cut off center (Fig. 12.2).

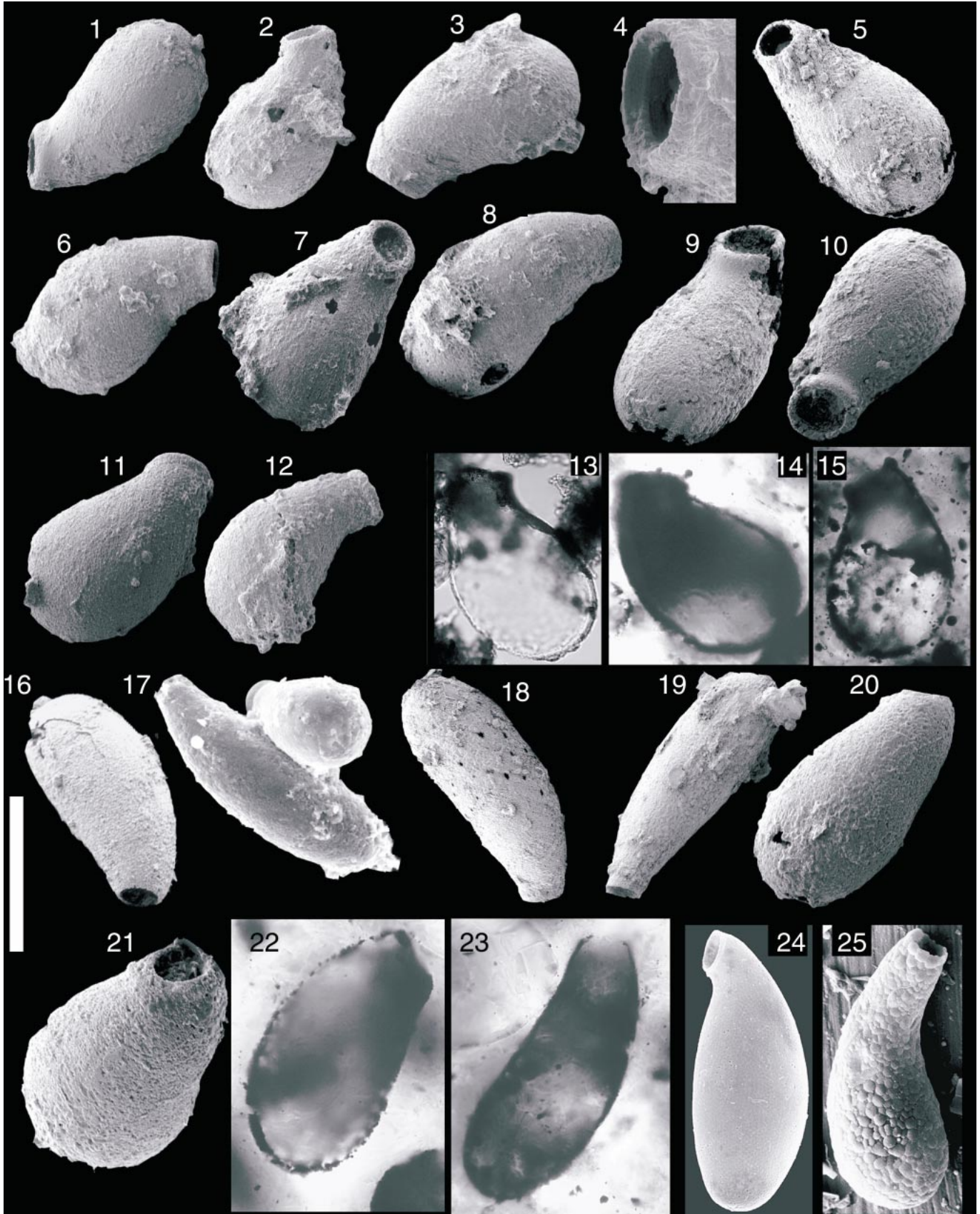
This genus is similar to *Melanocyrrillium* Bloeser, 1985 in having indentations on the test, and it is similar to *Palaeoarcella* n. gen. in its hemispherical shape, but uniting *Hemisphaeriella* with one or the other would imply that one character has greater phylogenetic significance, a distinction we are unable to make. In modern testate amoebae, taxa with any of these characters are united together in the genus *Arcella*, but the tests of this genus are unusually variable: species are linked by common cytological characters and a specific test composition rather than by any shared test morphology (Meisterfeld, 2002a). In the absence of cell characters linking *Melanocyrrillium*, *Palaeoarcella*, and *Hemisphaeriella*, and because of the discrete differences between their tests, we have kept these three taxa separate.

HEMISPHAERIELLA ORNATA new species

Figure 12.1, 12.2; possibly 12.3

Diagnosis.—As for genus.

Description.—Roughly hemispherical test with indentations distributed on presumed aboral side. The two specimens have tests that are 36 and 48 μm in length, 62 and 64 μm in width, and length-width ratios that are ~0.6 and 0.8, respectively. Indentations are ~20 to 40 μm in diameter; indentations that are symmetrically opposite the presumed aboral-oral axis have the same diameter. Ridges separate indentations. Walls bend sharply from rounded part of hemisphere to flattened part, and then slope inward toward apparently invaginated aperture. Shape in cross section unknown, but specimen in Figure 12.3 provides a possible example (see discussion).



Etymology.—From the Latin, *ornata*, ornate; with reference to the indentations which ornament their tests.

Type.—Holotype HUPC# 62990 (Fig. 12.1) from sample AK10-53-13-F, Nankowep locality, Walcott Member, Chuar Group, Grand Canyon.

Other material.—One specimen in longitudinal section (HUPC# 62990; Fig. 12.2), and a possible specimen in cross section (HUPC# 62990; Fig. 12.3); both in thin section from same sample, locality as holotype.

Occurrence.—*Hemisphaeriella ornata* occurs in carbonate nodules in shales from the upper Walcott Member, Chuar Group, Nankowep Butte locality, Grand Canyon. A possible specimen is preserved in the Neoproterozoic Backlundtoppen Formation, Spitsbergen (Knoll et al., 1989).

Discussion.—No specimens of *H. ornata* have been found in acid maceration residues and thus reconstruction of its three-dimensional shape is conjectural. Apertures have not been definitively identified but are presumed to be where indicated by the arrows in Figure 12.1 and 12.2. The specimen shown in Figure 12.3 is a plausible cross section of *H. ornata*: its width (~65–80 μm , depending on whether width is measured from the points or the sides of the hexagon) is consistent with the width of *H. ornata*, its hexagonal shape is consistent with the presence of indentations on *H. ornata* tests, and the length of the hexagon's sides (40 μm) is consistent with the diameter of the indentations. Its hexagonal shape is also similar to cross sections of the apertural end of *Melanocyrrillium hexodiadema* Bloeser, 1985, but the width of the specimen in Figure 12.3 falls well outside the range of aperture diameters exhibited by *M. hexodiadema*, and in fact falls outside the range of *M. hexodiadema* test widths as a whole. (The single exception is an unusually large specimen of *M. hexodiadema* with an aperture diameter of 59 μm and a test width of 104 μm .)

Using the same line of reasoning, the specimen shown in figure 8.2 in Knoll et al. (1989; ~60 μm in diameter) may be a cross section of *H. ornata*, rather than a cross section of a *M. hexodiadema* aperture as originally suggested. Similarly, probable VSMS from the Neoproterozoic Elbobreen Formation, Spitsbergen, which exhibit polygonal (6–7+ sides) cross sections (Martí Mus, 2001), may also represent *H. ornata* or a related species in the same genus.

Among modern testate amoebae, species with indented, hemispherical tests are found only in the genus *Arcella*. Species most similar to *H. ornata* are *Arcella conica* (Fig. 4.10) and *A. costata*. They have tests comparable in size, shape, and composition, with indentations similar in size and distribution (Meisterfeld, 2002a).

BOMBYCION new genus

Type species.—*Bombycion micron* n. sp., by monotypy.

Diagnosis.—VSMS with apertural plane strongly tilted with respect to aboral axis; aperture flush with the lower test wall, such that tests lack a “neck.” Aperture is circular.

Etymology.—From the Greek, *bombykion*, cocoon; with reference to their cocoon-like appearance.

Discussion.—In both *Bombycion* and *Bonniea* n. gen., the apertural plane is tilted relative to the aboral-oral axis, rather than oriented perpendicularly as it is in all other taxa. The two genera are distinct, however, in the presence vs. absence of a “neck.” In *Bonniea*, the plane of the aperture is more or less at right angles to the part of the test walls that form the rim of the aperture. Thus, aperture and the test walls are distinct, and the test appears to have a “neck,” curved in *Bonniea*. In *Bombycion*, the angle between the “upper” wall and the plane of the aperture is 90 degrees or greater, but the angle between the plane of the aperture and the “lower” wall is zero. Thus, the aperture appears to be flush with the lower test wall, and the test appears to lack a “neck.” That this is used as a generic-level distinction is supported by modern testate amoeban taxonomy, which similarly distinguishes taxa with a curved “neck” [e.g., *Cyphoderia ampulla* (Fig. 9.24) and *Nebela retorta* (Fig. 9.25)] from those with apertures flush with the lower test wall [e.g., *Trinema enchelys* (Fig. 13.5, 13.6)] (Meisterfeld, 2002b).

BOMBYCION MICRON new species

Figure 13.1–13.4

Diagnosis.—As for genus.

Description.—Pyriform to bulbous tests, lacking “necks.” Instead, aperture is tilted to one side of the test, flush with the test wall (Fig. 13.1–13.4). Opposite aboral pole test appears pointed in thin section (Fig. 13.3, 13.4), representing upper margin of aperture. Aperture circular (arrow in Fig. 13.1 indicates faint outline of circular aperture; see also Fig. 13.2). Length-width ratios range between 1.5 and 2.0 ($\mu = 1.7$; $\sigma = 0.2$; $N = 8$). Tests range from ~60 to 95 μm in length ($\mu = 76 \mu\text{m}$; $\sigma = 14 \mu\text{m}$; $N = 8$), ~35 to 65 μm in width ($\mu = 44 \mu\text{m}$; $\sigma = 10 \mu\text{m}$; $N = 8$), and ~20 and 35 μm in aperture diameter ($\mu = 25 \mu\text{m}$; $\sigma = 7 \mu\text{m}$; $N = 8$).

Etymology.—From the Greek, *micron*, small.

Type.—Holotype HUPC# 62988 (Fig. 13.2) from sample AK10-53-13F, Nankowep Butte locality, Walcott Member, Chuar Group, Grand Canyon.

Other material examined.—Seven specimens in thin section, including HUPC# 62988 and 62990 (Fig. 13.1, 13.3, 13.4), from same sample, locality as holotype. Specimens of *Bombycion micron* are rare in thin section (less than one percent); none have been found in acid maceration residues.

Occurrence.—*Bombycion micron* occurs in carbonate nodules in shales in the upper Walcott Member, Chuar Group, Nankowep Butte locality, Grand Canyon.

Discussion.—Species with tests similar to those of *B. micron* are found in the lobose genus *Centropyxis* (e.g., *C. constricta*, *C. elongata*, or *C. platystoma*) and the filose genus, *Trinema* [e.g., *T. enchelys* (Fig. 13.5, 13.6), and *T. lineare*] (Meisterfeld, 2002a, 2002b). These differ from *B. micron*, however, in having either agglutinated tests (*Centropyxis*) or tests with mineralized scales (*Trinema*) (Meisterfeld, 2002a, 2002b).

FIGURE 9—The genus *Bonniea* n. gen. and modern testate amoeban analogs. 1–15, *B. dacruharens* n. sp.; 1, HUPC# 64425 (AK10-53-13A-4); 2, HUPC# 64435 (AK10-53-13A-5); 3, 4, HUPC# 64426 (AK10-53-13A-4); 5, HUPC# 64420 (AK10-53-13A-2); 6, HUPC# 64436 (AK10-53-13A-5); 7, HUPC# 64437 (AK10-53-13A-5); 8, HUPC# 64438 (AK10-53-13A-5); 9, 10, HUPC# 64409 (AK10-53-13A-1); 11, HUPC# 64439 (AK10-53-13A-5); 12, HUPC# 64440 (AK10-53-13A-5); 13, HUPC# 64458 (Euparal[®]-mounted slide AK10-53-13F-2; O50); 14, HUPC# 62988 (AK10-53-13F-2B; S45-2); 15, HUPC# 62988 (AK10-53-13F-2B; Q66-3). 16–23, *B. pytiniaia* n. sp.; 16, HUPC# 64410 (AK10-53-13A-1); 17, *B. pytiniaia* specimen is the one whose side is in view; the other specimen, viewed aborally, is in the species *Cycliocyrrillium torquata* n. sp. HUPC# 64411 (AK10-53-13A-1). 18, HUPC# 64412 (AK10-53-13A-1); 19, HUPC# 64427 (AK10-53-13A-4); 20, 21, HUPC# 64441 (AK10-53-13A-5); 22, HUPC# 62990 (AK10-53-13F-1; Q43-4); 23, HUPC# 62990 (AK10-53-13F-1; Q49). 24, The modern testate amoeba, *Cyphoderia ampulla*. 25, The modern testate amoeba, *Nebela retorta*. Scale bar is 60 μm for 1, 5, 17, 24; 80 μm for 2, 3, 7, 11; 30 μm for 4; 85 μm for 6, 14, 25; 100 μm for 8, 13; 55 μm for 9, 10, 12, 23; 45 μm for 20, 21; 70 μm for 16, 18, 19, 22; and 90 μm for 15.

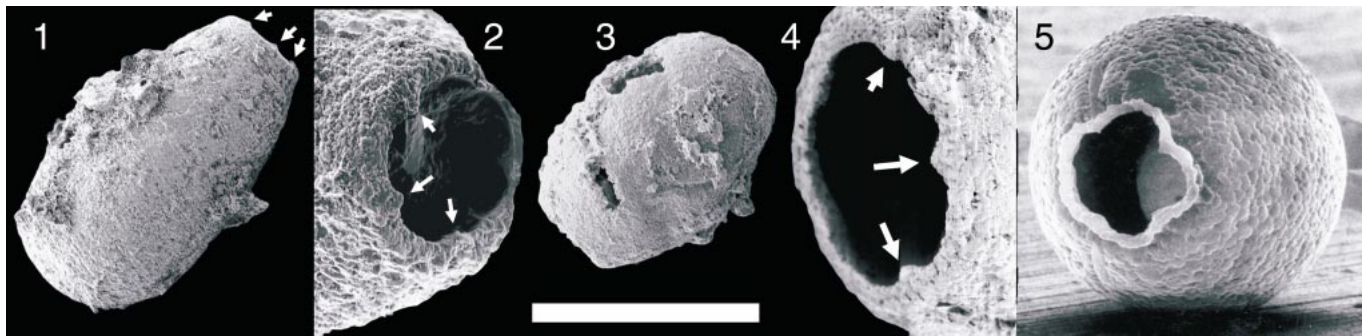


FIGURE 10—*Trachycyrrillium pudens* n. sp. and a modern testate amoeban analog. Arrows indicate inwardly directed triangular thickenings. 1–4, *Trachycyrrillium pudens*. 1, 2, HUPC# 64413 (AK10-53-13A-1); 3, 4, HUPC# 64442 (AK10-53-13A-5). 5, The modern testate amoeba, *Netzelia waillesi*. Scale bar is 60 μm for 1, 5; 20 μm for 2; 120 μm for 3; and 35 μm for 4.

MELICERION new genus

Type species.—*Melicerion poikilon* n. sp., by monotypy.

Diagnosis.—VSMs with organic wall embedded with regularly arranged circular to elliptical bodies commonly preserved as perforations; test with a length-to-width ratio less than three.

Etymology.—From the Greek, *melikerion*, honeycomb; with reference to the honeycomb-like wall pattern.

Occurrence.—*Melicerion* species occur at the Nankowear Butte locality within carbonate nodules in black shales from the uppermost Walcott Member. Possible *Melicerion* species have been reported from limestone in the upper reef of the Neoproterozoic Chatkaragai Suite, Talaskii Mountain range, near the Karabura and Urmalar Rivers, Tien Shan, Kyrgyzstan (Kraskov, 1989; see discussion below) and from a chert breccia in the Lower Carbonate Member of the Neoproterozoic Elbobreen Formation, ENE Dracoisen section, Spitsbergen (Martí Mus, 2001).

Discussion.—We believe that *Melicerion poikilon* may be closely related to *Caraburina granosa* Kraskov, 1989, a species

from Tien Shan, Kyrgyzstan, that has tests similar in size and shape and covered with regularly arranged, raised circles (see Porter and Knoll, 2000). Putting these two species together in the same genus, however, would require a revision of the genus *Caraburina* Kraskov, 1985 and its five morphologically diverse species (Fig. 14; Kraskov, 1985, 1989), an effort that is beyond the scope of this paper.

With the exception of heliozoans like *Clathrulina* and chrysophytes like *Mallomonas*, which differ from *Melicerion* in other respects (see Porter and Knoll, 2000), mineralized circular scales are found only in the tests of the filose testate amoeban order Euglyphida (Meisterfeld, 2002a, 2002b). Species in the lobose families Paraquadrulidae and Lesquereusiidae also secrete mineralized scales but these are rod-like, nail-like, or rectangular in shape (Meisterfeld, 2002a). Some species in the lobose genus *Nebela* have mineralized scales that are circular in shape, but these are not endogenous, i.e., they are not formed in the nebelid cell but rather are obtained by engulfing euglyphids and appropriating their scales (Gnekow, 1981).

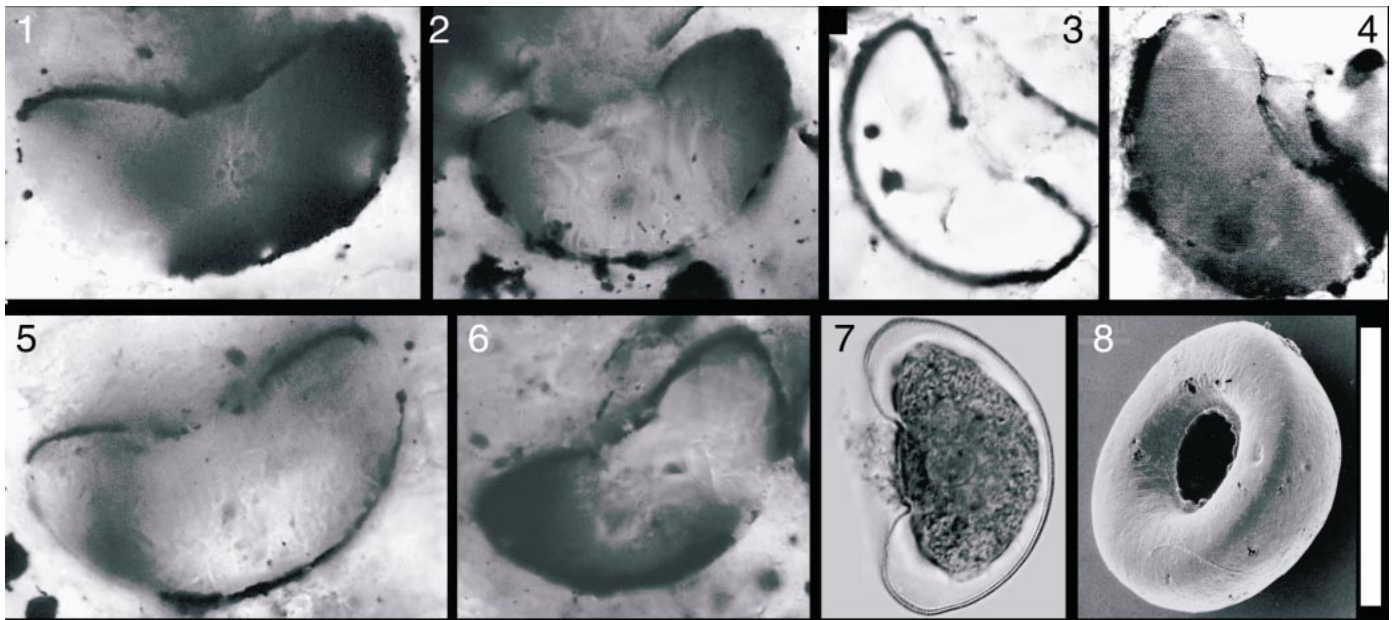


FIGURE 11—*Palaeoarcella athanata* n. sp. and modern testate amoeban analogs. 1–6, *Palaeoarcella athanata*; 1, HUPC# 64457 (AK10-53-13F-2C; S56); 2, HUPC# 64457 (AK10-53-13F-2C; P58-1); 3, HUPC# 62988 (AK10-53-13F-2B; S70-3); 4, HUPC# 62990 (AK10-53-13F-1; G57-2); 5, HUPC# 62990 (AK10-53-13F-1; O44-1); 6, HUPC# 62988 (AK10-53-13F-2B; O49-4). 7, The modern testate amoeba, *Arcella hemisphaerica*. 8, The modern testate amoeba, *Arcella crenulata*, courtesy of Ogden and Hedley (1980). Scale bar equals 35 μm for 1, 4; 40 μm for 2, 5, 6; 55 μm for 3; 70 μm for 7; and 120 μm for 8.

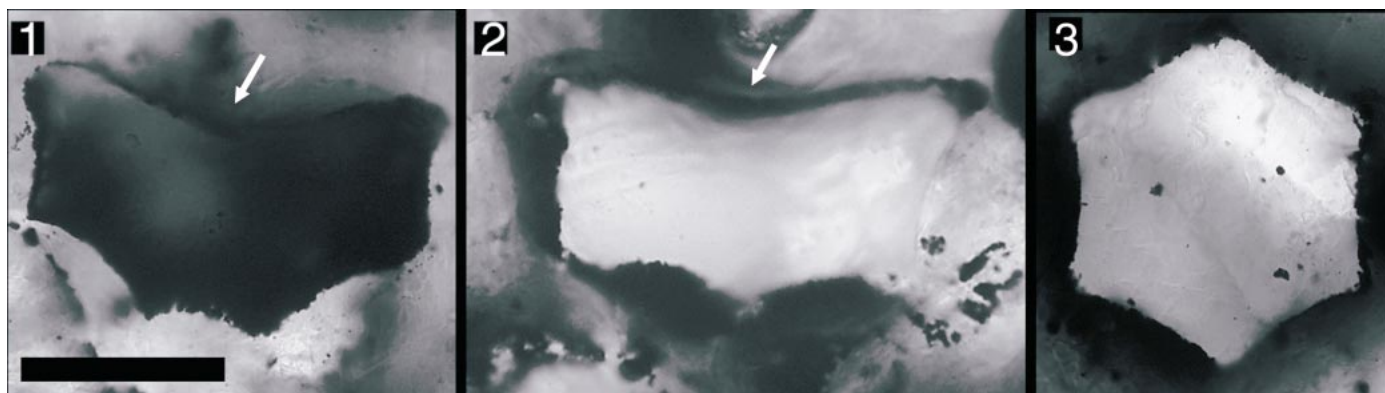


FIGURE 12—*Hemisphaeriella ornata* n. sp. Arrows indicate where apertures appear to be. 1, HUPC# 62990 (AK10-53-13F-1; P47-3); 2, HUPC# 62990 (AK10-53-13F-1; Q43-3); 3, HUPC# 62990 (AK10-53-13F-1; N-51). Scale bar equals 40 μm for 1; 30 μm for 2; and 50 μm for 3.

MELICERION POIKILON new species
Figure 15.1–15.8

Diagnosis.—As for genus.

Description.—Test shape pyriform, ~ 50 to 160 μm in length ($\mu = 104 \mu\text{m}$; $\sigma = 22 \mu\text{m}$; $N = 59$), ~ 30 –70 μm in width ($\mu = 53 \mu\text{m}$; $\sigma = 9 \mu\text{m}$; $N = 59$). Length-width ratios are highly variable, ranging from 1.3 to 2.8 ($\mu = 1.9$; $\sigma = 0.4$; $N = 59$). Test wall containing many circular bodies; in the Chuar nodules these appear as holes in a pyrite or iron oxide matrix. Holes appear to be more or less regularly distributed in rows that are slanted relative to the long axis of the test. Holes may be circular

to slightly elliptical in shape. Hole size is relatively uniform within a test, but varies widely between tests (Fig. 16), from $\sim 1 \mu\text{m}$ (e.g., Fig. 15.6–15.8) to 12 μm in average diameter ($\mu = 5 \mu\text{m}$; $\sigma = 2.5 \mu\text{m}$; $N = 107$).

Etymology.—From the Greek, *poikilos*, elaborate, decorated.

Type.—Holotype HUPC# 62990 (Fig. 15.3) from sample AK10-53-13-1, Nankoweap Butte locality, Walcott Member, Chuar Group, Grand Canyon.

Other material examined.—One hundred and seven specimens in thin section including HUPC# 64457, 62990, and 62991 (Fig. 15.1, 15.2, 15.4–15.8), from samples AK10-53-13A and AK10-53-13F, same locality as holotype. *Melicerion poikilon* specimens have only been observed in thin section thus far, where they constitute approximately one percent of the population.

Occurrence.—In carbonate nodules in shales from the Walcott Member, Chuar Group, Nankoweap locality, Grand Canyon.

Discussion.—The *M. poikilon* population is highly variable and may represent more than one species. Indeed, the range of hole sizes exhibited by *M. poikilon* is at least three times greater than the range of scale sizes observed within single euglyphid species (Ogden and Hedley, 1980). Two peaks in the distribution of hole sizes at 2 and 5 μm (Fig. 16) may represent mean hole sizes for two different species, but because no other characters, such as test length or shape, support a distinction between these two groups, and because the distribution of hole sizes is continuous within the population, we have grouped all of these specimens in a single species.

The sizes of the “holes” in *M. poikilon* fall within the range of scale sizes exhibited by the Euglyphida, although not by any single euglyphid species [$\sim 1 \mu\text{m}$ in length in the genus *Cyphoderia ampulla* to more than 14 μm in length in *Euglypha tuberculata* (Fig. 15.9)]. Circular to elliptical scales are common in the order (e.g., *C. ampulla* and the body scales of *E. tuberculata* or *Tracheleuglypha dentata*) (Meisterfeld, 2002a).

Unnamed form
Figure 17.1–17.3

Description.—Pyriform tests, ~ 110 –130 μm in length ($\mu = 120 \mu\text{m}$; $N = 3$), ~ 50 –80 μm in width ($\mu = 60 \mu\text{m}$; $N = 3$). Length-width ratios range from 1.6–2.2 ($\mu = 1.9$; $\sigma = 0.3$; $N = 3$). Test narrows toward aperture, then flares outward to form a funnel-like shape. The height of the “funnel,” measured from the point of constriction to the outer edge of the “funnel,” varies from ~ 5 to 15 μm . In one specimen (Fig. 17.1, 17.2), the outer edge of the “funnel” appears to be slightly thickened.

Discussion.—These VSMS have a distinct form; their shape cannot be accommodated within the range of variation observed

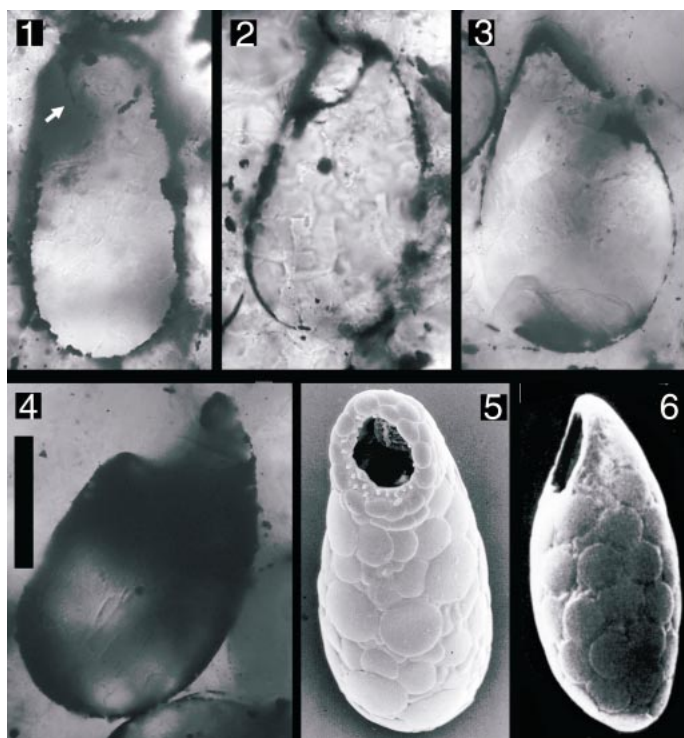


FIGURE 13—*Bombycion micron* n. sp. and a modern testate amoeba analog. 1–4, *Bombycion micron*. 1, HUPC# 62988 (AK10-53-13F-2B; P50); 2, HUPC# 62988 (AK10-53-13F-2B; O63); 3, HUPC# 62990 (AK10-53-13F-1; L43-2); 4, HUPC# 62990 (AK10-53-13F-1; K50-4). 5, 6, The modern testate amoeba, *Trinema enchelys*. 6, From Ogden and Hedley (1980). Scale bar equals 30 μm for 1; 40 μm for 2–4, 6; and 25 μm for 5.

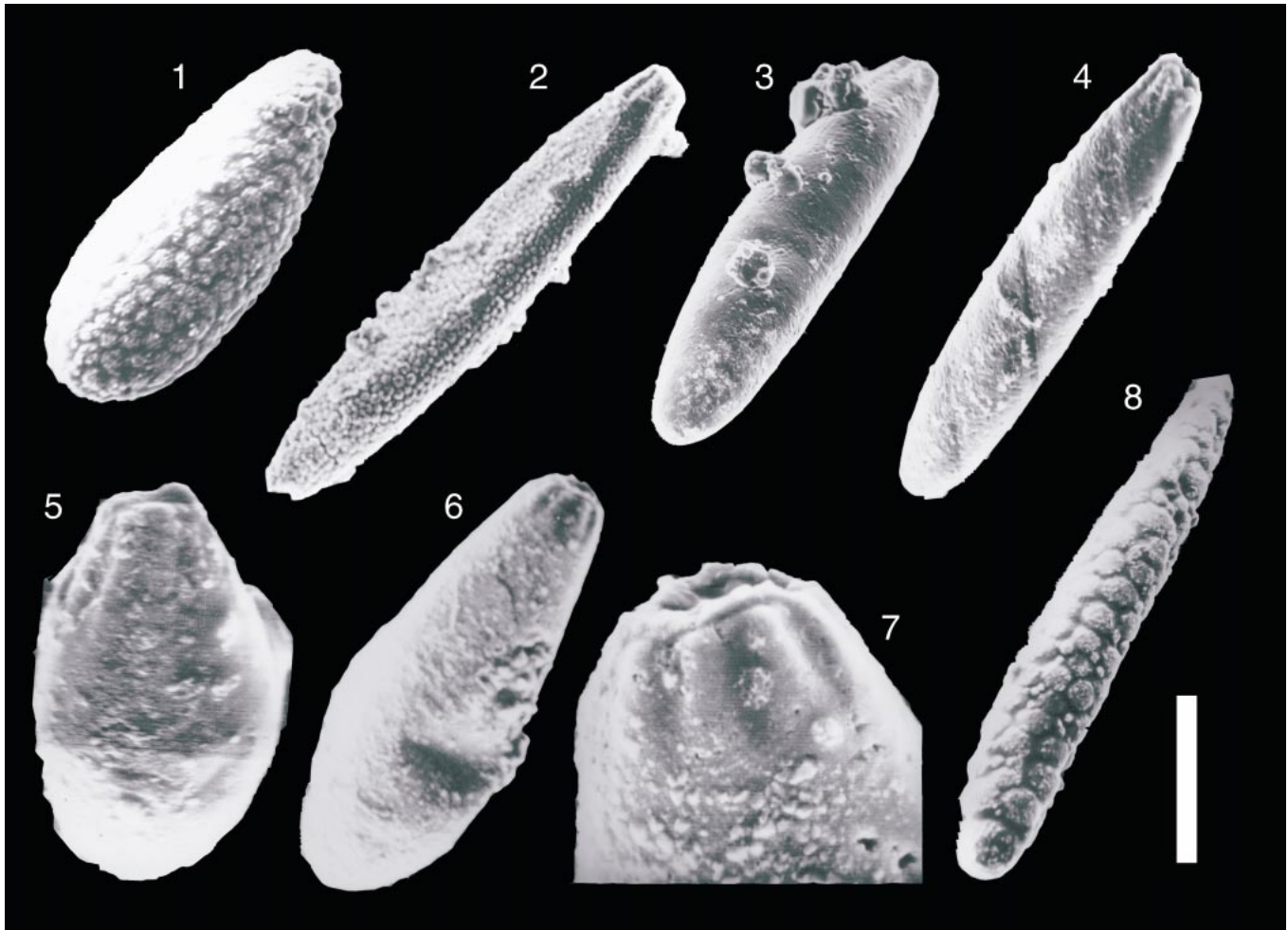


FIGURE 14—VSMs from Tien Shan, Kyrgyzstan. All images courtesy of L. Kraskov. 1, *Caraburina granosa* Kraskov, 1989; 2, *C. microgranosa* Kraskov, 1989; 3, 4, *C. spatiosa* Kraskov, 1985; 5, *C. pyriforma* Kraskov, 1989; 6, 7, *C. ovalica* Kraskov, 1985; 8, An undescribed specimen, distinct from the *Caraburina* Kraskov, 1985 species, hints at even greater diversity in the Tien Shan assemblage. Scale bar is 70 μm for 1 and 8; 130 μm for 2, 4; 90 μm for 3; 35 μm for 5; 75 μm for 6; and 25 μm for 7.

in any other VSM taxon. They may therefore represent a distinct taxon, characterized by a funnel-like aperture. [Funnel-like apertures are common in both lobose and filose testate amoebae, e.g., the filose amoeba, *Microamphora pontica* (Fig. 17.4) (Meisterfeld, 2001).] Another interpretation is possible, however. Some testate amoebae build daughter tests from the mother's aperture outward; these specimens may simply represent an aborted stage in the reproduction of *Cycliocyrrillium simplex* n. sp. or a similar species (R. Meisterfeld, unpublished observations). While the slight thickening of the "funnel" edge in one specimen (Fig. 17.2) appears to support the former possibility, without a larger number of specimens, the latter cannot be ruled out.

HOW ARE THE FOSSILS RELATED TO MODERN TESTATE AMOEBAE?

To assess the relationships between VSMs and specific modern testate amoeban taxa, we need to estimate the likelihood that similarities in fossil and modern test morphologies reflect homology rather than convergence. This requires a phylogeny for the testate amoebae, which, unfortunately, is not well resolved. Nevertheless, we can estimate homology by looking at the number of characters shared between specific fossil and modern taxa and the distribution of those characters in the modern testate amoebae. The more

characters shared and the more restricted those characters are to well-defined modern groups, the more likely they are to be homologous.

VSM species exhibit characters at both ends of the homology-convergence spectrum. The test characters observed in *Melicerion* n. gen. occur today only in the filose order Euglyphida, which recent rRNA phylogenies suggest is monophyletic (Wylezich et al., 2002). Similarly, the combination of characters observed in the tests of *Palaeoarcella* n. gen., *Melanocyrrillium* Bloeser, 1985, and *Hemisphaeriella* n. gen. are found today only in the lobose family Arcellidae. Because *all* of the observed test characters in these VSM taxa occur *only* in these specific modern groups, the fossil and modern test characters are likely to be homologous, implying that *Melicerion*, *Palaeoarcella*, *Melanocyrrillium*, and *Hemisphaeriella* are stem or crown groups of modern testate amoeban taxa. Thus, both lobose and filose testate amoebae are represented in this assemblage.

The remaining VSM taxa possess characters found in different combinations in a diversity of modern testate amoebae. Depending on testate amoeban phylogeny, they may be stem, or even crown, group relatives of one or more of these taxa, or their similar test characters may reflect convergent evolution. In principle,

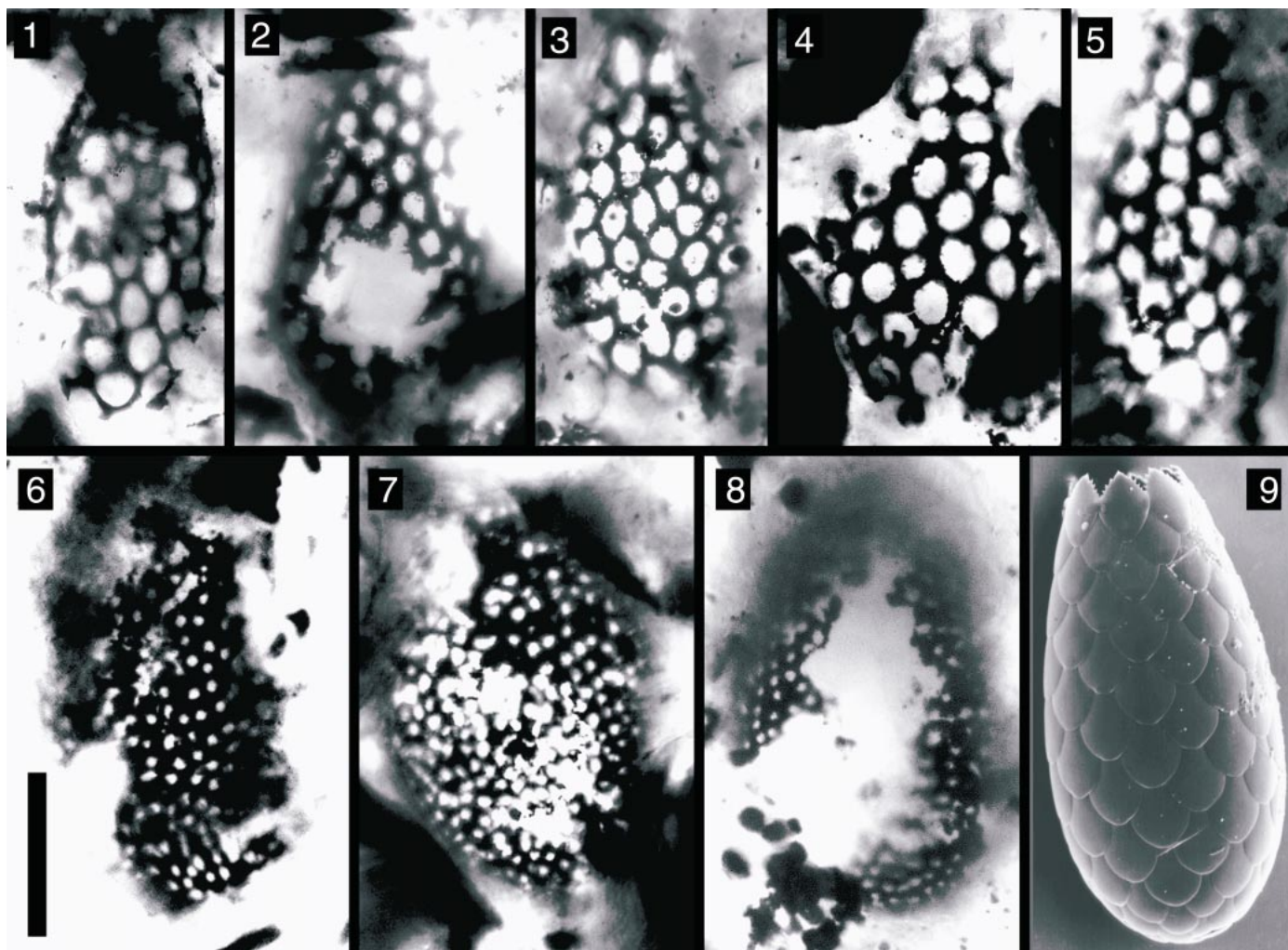


FIGURE 15—*Melicerion poikilon* n. sp. and a modern testate amoeban analog. 1–8, *Melicerion poikilon*; 1, HUPC# 64457 (AK10-53-13F-2C; W57-4); 2, HUPC# 62990 (AK10-53-13F-1; P44); 3, HUPC# 62990 (AK10-53-13F-1; P54-2); 4, HUPC# 62990 (AK10-53-13F-1; M61-1/2); 5, HUPC# 62991 (AK10-53-13F-2A1-3); 6, HUPC# 64457 (AK10-53-13F-2C; T52-3); 7, HUPC# 62990 (AK10-53-13F-1; R49); 8, HUPC# 62991 (AK10-53-13F-2A; V61-1). 9, The modern testate amoeba, *Euglypha tuberculata*. Scale bar is 45 μm for 1, 8; 40 μm for 2, 4, 5; 50 μm for 3; 30 μm for 6, 9; and 25 μm for 7.

they could even represent an independent evolution of testate protists, although no positive evidence supports this interpretation. Apart from the simple test morphology of *Cycliocyrrillium simplex* n. sp. (which also occurs in, for example, the allogromiids), no VSM species display character combinations that are seen today outside of the testate amoebae. Insofar as *Melicerion*, *Palaeoarcella*, *Melanocyrrillium*, and *Hemisphaeriella* strongly suggest that filose and lobose lineages were present 750 million years ago, it is more parsimonious to regard other VSM taxa as relatives of one or the other (or both) of these groups, rather than to speculate on an independent acquisition of tests.

IMPLICATIONS FOR PALEOECOLOGY AND EVOLUTION

Ecological history of testate amoebae.—The diversity of testate amoebae in the Chuar Group is dwarfed by the diversity of modern testate amoebae in non-marine settings, but it is an appreciable proportion of testate amoeban diversity known today in the oceans (~100 species; Meisterfeld, 2001). Like their modern counterparts, these early testate amoebae probably lived in organic-rich environments such as microbial mats, which were widespread in Neoproterozoic oceans. Later, they may have expanded onto land,

following the diversification of land plants (Porter and Knoll, 2000). The presence of both filose and lobose testate amoebae in Neoproterozoic oceans indicates that this transition was made by at least two and perhaps more testate amoeban lineages. The reason for their relative scarcity in marine environments today is not known; their decline may be linked to the Paleozoic radiation of benthic foraminifera, organisms that appear to occupy the same niches that VSMS did in the Neoproterozoic (Porter and Knoll, 2000). VSMS apparently disappear before the terminal Proterozoic period (Neoproterozoic III), however, so it is not known whether they were displaced by other protists or decimated by Neoproterozoic climate change.

Neoproterozoic food webs.—A few Chuar VSMS have a semi-circular perforation in the side of their tests (Fig. 18). These holes are uniform in size (~20 μm) between different tests, and are typically oriented such that the flat side is parallel to the longitudinal axis of the test. Their origin is unknown. Their regular size and perfect geometrical shape, suggests that they are not the result of taphonomic destruction, but are biogenic in origin. They are probably not test characters, however: they are found in a variety of VSM species, but are rare within any single species,

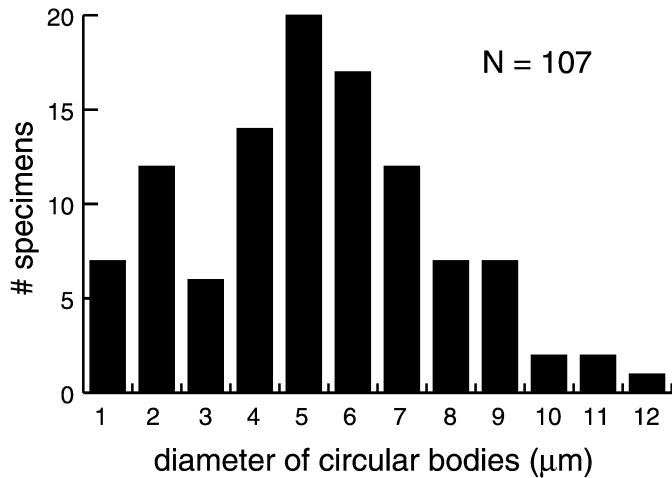


FIGURE 16—Histogram of “hole” size in *Melicerion poikilon* n. sp. For each specimen, a single, average hole size was used. Hole sizes do not vary much within individual specimens, but do vary widely between individuals. Bins are 1 µm in size and measurements were rounded off to the nearest 0.25 µm; a bin labeled ‘n’ includes specimens with holes greater than $n - 1$ µm and less than or equal to n µm.

and are unlike test characters in any modern testate amoebae. Instead, they may have been formed by the activity of other organisms.

The holes may reflect predatory activity, although cutting holes in the test to get at the cell inside seems unnecessary given the presence of the aperture. Alternatively, the holes may reflect scavenging on the organic test itself. Circular holes (Figs. 6.4, 9.8, 18.1) may reflect scavenging of the test as well, consistent with the presence of multiple holes cut in a single test (Fig. 18.1). Similar holes reflecting predatory or scavenging activity are not known in modern testate amoeban tests (Meisterfeld, unpublished observations). Most modern predators of testate amoebae swallow them whole [e.g., the naked amoeba *Thecamoeba sphaeronucleolus* (Ogden and Coûteaux, 1988)].

The only definitive evidence for eukaryotic predators or scavengers at this time is biomarker evidence for ciliates (Summons et al., 1988) and, of course, body fossil evidence for testate amoebae. Species of ciliates (e.g., *Grossglockneria*) and amoebae [both

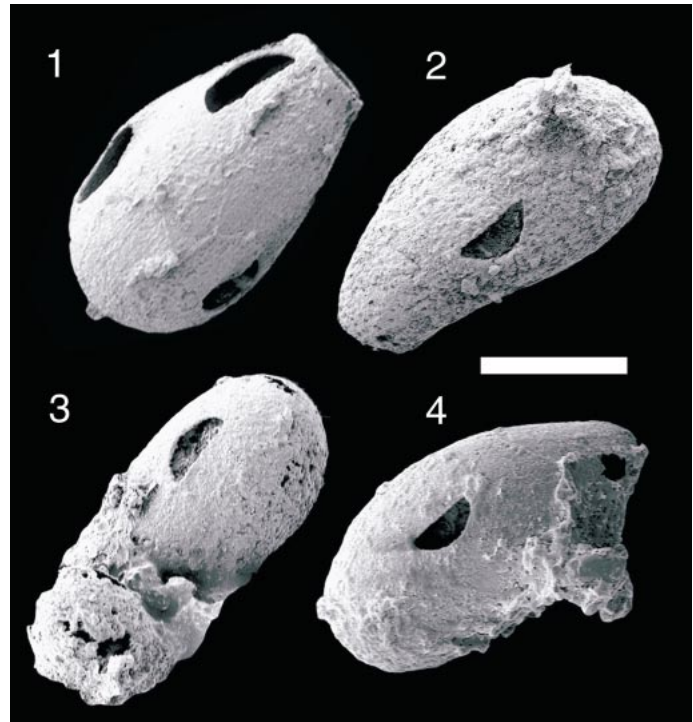


FIGURE 18—VSMs with semicircular holes in their tests, possibly due to predation or scavenging. 1, HUPC# 64445 (AK10-53-13A-5); 2, HUPC# 64428 (AK10-53-13A-4); 3, HUPC# 64456 (AK10-53-13A-9); 4, HUPC# 64446 (AK10-53-13A-5). Scale bar is 50 µm for 1; 35 µm for 2; and 30 µm for 3, 4.

testate, e.g., *Diffugia rubescens* (Hoogenraad and De Groot, 1941) and naked, e.g., the vampyrellid family (Old, 1978)] can form holes in fungal and algal prey, but these holes are much smaller in size and are circular. Other predators and scavengers were almost certainly present in the middle Neoproterozoic as well, including, possibly, the ancestor to the animals + fungi (see below); they may be responsible for the holes.

Regardless of the identity of the organisms that produced them, the holes indicate that by middle Neoproterozoic time, intricate food webs were beginning to appear. Bacteria were eating dead

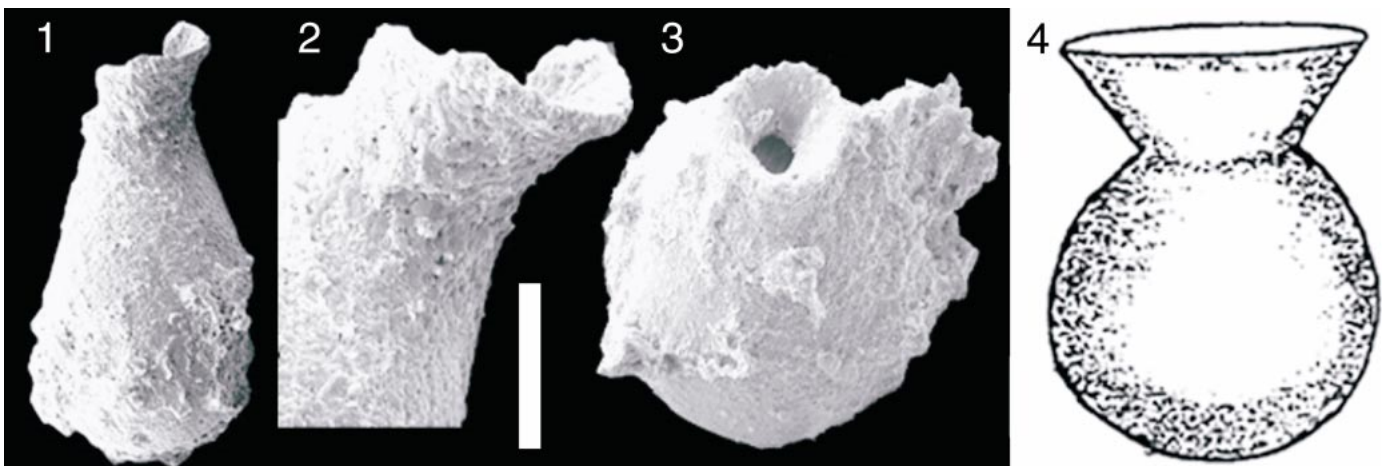


FIGURE 17—An unnamed form and a modern testate amoeban analog. 1–3, Unnamed Form; 1, 2, HUPC# 64443 (AK10-53-13A-5); 3, view looking downward into “funnel”; HUPC# 64444 (AK10-53-13A-5). 4, The modern testate amoeba, *Micramphora pontica*. Adapted from Meisterfeld (2001). Scale bar is 45 µm for 1, 3; 20 µm for 2; and 5 µm for 4.

primary producers (cyanobacteria and algae) and their secretory products; protozoa, including VSMS and ciliates, were eating both primary producers and bacteria; and additional organisms were eating these protozoa. Eukaryotes, with their ability to engulf particles, had begun building trophically complex ecosystems.

The evolution of eukaryotes.—Recent molecular phylogenies provide an increasingly clearer, though still not fully resolved, view of eukaryotic relationships and the position of testate amoeban groups in the eukaryotic tree. Phylogenies that include representatives of the euglyphid amoebae consistently place this taxon in the Cercozoa (e.g., Bhattacharya et al., 1995; Cavalier-Smith and Chao, 1996/7; Sims et al., 1999; Bolivar et al., 2001; Wylezich et al., 2002), a group that includes the chlorarachniophytes and the cercozoans (Cavalier-Smith, 1998). A recent analysis suggests that the Cercozoa is a paraphyletic group, from which the Foraminifera were derived (Keeling, 2001). Unfortunately, this analysis did not include any euglyphids, and therefore it is not known whether VSMS, and in particular, *Melicerion poikilon* n. sp., constrain the timing of origin of the Foraminifera. Likewise, the relationships between the Cercozoa and other eukaryotic groups are not well resolved, although most place the Cercozoa well within the crown of the eukaryotic tree (e.g., Philippe and Adoutte, 1995; Cavalier-Smith and Chao, 1996/7; Medlin et al., 1997; Bolivar et al., 2001). Thus, until better resolution is attained, *Melicerion poikilon* indicates only that the eukaryotic crown group had begun to diversify by ~750 Ma, consistent with evidence from a growing number of Late Mesoproterozoic/Early Neoproterozoic eukaryotic crown group fossils (e.g., Summons et al., 1988; German, 1990; Pratt et al., 1991; Butterfield et al., 1994; Woods et al., 1998; Butterfield, 2000).

VSMS related to the lobose testate amoebae, in particular, *Palaeoarcella athanata* n. sp., *Hemisphaeriella ornata* n. sp., and *Melanocyrrillium hexodiadema* Bloeser, 1985, may provide, at present, a more informative constraint on the timing of major eukaryotic divergences. Despite preliminary evidence suggesting that amoebae were widely polyphyletic (e.g., Clark and Cross, 1988), there is a growing consensus from molecular systematic studies that many amoeboid organisms, including the lobose testate amoebae, group together with the slime molds into an Amoebozoa clade (Cavalier-Smith, 1998; Baldauf et al., 2000; Bolivar et al., 2001; Baptiste et al., 2002; cf. Patterson, 1999). A number of recent phylogenies, including two based on combined protein or gene sequence data, indicate that the Amoebozoa is sister to the opisthokonts (animals + fungi) [e.g., Baldauf et al., 2000; Baptiste et al., 2002; Sogin and Silberman, 1998; although see Keeling (2001), which suggests a sister group relationship with the animals, to the exclusion of the fungi; and Bolivar et al. (2001), which suggests a sister group relationship with the opisthokonts + plants]. If this is correct, then, unless arcellid-like tests are a plesiomorphy of both the animals + fungi and the Amoebozoa—for which there is no evidence—VSMS indicate that branching between the animals + fungi clade and the Amoebozoa had occurred by ~750 Ma.

Biom mineralization.—Template-directed, enzymatic precipitation of minerals is commonly associated with animal skeletons, but it is also widely distributed among other eukaryotes, occurring in plants as well as a diversity of protists. Major events in protistan biom mineralization occurred in the Mesozoic (diatoms, coccolithophorids) and Paleozoic (foraminifera, radiolarians), but apparently siliceous scales from rocks now known to be older than 600 Myr (Allison and Hilgert, 1986; Kaufman et al., 1993) suggest that template-directed biom mineralization has deep Proterozoic roots. The honeycomb texture of *Melicerion poikilon* n. sp. walls suggests that testate amoebae evolved the ability to manufacture mineralized scales at least 750 Ma. Together with possible skeletal algae reported from the Pahrump Group, California (Horodyski

and Mankiewicz, 1990), this provides the oldest evidence of eukaryotic biom mineralization.

CONCLUSIONS

Vase-shaped microfossils preserved in carbonate nodules from the upper Chuar Group show that VSMS are not only widespread and locally abundant in Neoproterozoic oceans, but were taxonomically diverse as well. Features of test morphology suggest a systematic relationship between VSMS and extant testate amoebae. A few VSM species are morphologically indistinguishable from specific modern taxa; these indicate that both lobose and filose testate amoebae (crown or stem group taxa) were present in the assemblage. Other VSMS do not have exact modern analogs, but are probably related to modern testate amoeban groups as well. Collectively, the Chuar fossils provide an unusually clear glimpse of heterotrophic protists in the Neoproterozoic ocean.

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