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► **To cite this version:**

Joan Bernhard, Emmanuelle Geslin. Introduction to the Special Issue entitled “Benthic Foraminiferal Ultrastructure Studies”. *Marine Micropaleontology*, 2018, 138, pp.1-11. <10.1016/j.marmicro.2017.11.002>. <hal-02872786>

HAL Id: hal-02872786

<https://univ-angers.hal.science/hal-02872786v1>

Submitted on 19 Jun 2025

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Introduction to the Special Issue entitled “Benthic Foraminiferal Ultrastructure Studies”

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Foraminifera are unicellular eukaryotes. These protists have membrane-bound nuclei, a microtubule-based cytoskeleton, intracellular membranous organelles, and anastomosing granuloreticulate pseudopodia. The name derives from the combination of two neo-Latin terms (“foramen”, meaning an opening, hole or passage; “fer”, meaning bearing), equating to “hole-bearing”, referring to the presence of a hole in each chamber wall of the mineralized shells observed by Alcide d’Orbigny, who coined the moniker in 1826 (Lipps et al., 2011). The shell, formally called a “test”, is typically considered as protection to the foraminiferal cell and commonly preserved in the geological record. Easily fossilized tests can be composed of either calcium carbonate secreted by the foraminifer, or mineral grains that are adhered with either organic or carbonate cement. Foraminifera with carbonate tests are informally referred to as “calcareous”; those forms that bind inorganic grains are “agglutinated”, most of which are multichambered. Some foraminifera such as the “thecate” allogromiids and “naked” forms, have organic tests that do not fossilize well because of the lack of mineralized test components. Most of these organic-walled forms are single chambered, or “monothalamous”. These “soft-walled” forms have largely been overlooked until recent decades. There are instances where monothalamid forms also have rigid agglutinated tests (Bowser et al. 1995). For a recent classification of foraminifera, the reader is directed to Pawlowski et al. (2013).

Foraminifera are nearly ubiquitous in the marine environment. To our knowledge, more limited representation exists in freshwater and terrestrial habitats. Thecate forms are generally marine while naked forms are generally freshwater or terrestrial. Three informal groups may be differentiated among common foraminiferal forms, based according to their habitats and life strategies: 1) planktonics, which live in the upper water column of the open ocean, 2) large benthic foraminifera (LBF) living on the seafloor in warm shallow waters and bearing photosynthetic symbionts, 3) “small” benthic foraminifera (SBF), which typically

lack photosynthetic symbionts and live in or on substrate such as unconsolidated “soft” sediment or megafauna and megafloa (seaweed). We focus this special issue on the ultrastructure of “small” marine benthic foraminifera (SBF); we do not extensively consider small benthic freshwater or terrestrial foraminifera.

During the mid-1800s foraminifera became widely appreciated, with studies by researchers such as Christian Gottfried Ehrenberg, William Benjamin Carpenter, and Henry Bowman Brady. Due to their long and diverse fossil record, much early research on foraminifera focused on biostratigraphy and paleoecology, eventually as a means to identify source rocks for hydrocarbon reserves. The global H. M. S. *Challenger* Expedition (1872-1876) collected hundreds of samples that received devoted study over decades by experts on every marine life form, including foraminifera (e.g., Brady (1884), see also updated report by Jones (1994)). Naturalists such as Ernst Haeckel popularized foraminifera at the turn of the century by including them in their artistic scientific illustrations. Because foraminifera can be abundant in shallow to deep waters from low to high latitude, their distribution and ecology also received concentrated research efforts by investigators such as Joseph A. Cushman, in the early to mid-1900s. Beginning in the middle of the last century, the chemical records of foraminiferal carbonate tests were used extensively to decipher past oceanographic and paleoclimate conditions (reviewed in Katz et al., 2010). For more thorough insights into the history of foraminiferal research, the reader is directed to recent compilations and historical perspectives (e.g., Bowden et al., 2014).

Due to the nineteenth century and twentieth century focus on fossil, relict and modern foraminiferal remains, relatively little research was done on the living organism. Research of the past few decades has revealed diverse foraminiferal adaptations, in the context of cell biology and physiology, especially to chemocline habitats and additional “stressful”

environmental conditions. Such adaptations implicate their importance to biogeochemical cycling.

A short history of transmission electron microscopy

A transmission electron microscope (TEM) uses an electron beam to pass (or transmit) through a specimen, to produce an image that is dependent on the interaction of the beam with the specimen; the image is subsequently magnified for viewing. Materials investigated by TEM are typically very thin, either being a thin slice ($<0.1 \mu\text{m}$) of a larger specimen or very fine particles accumulated on an appropriate surface (i.e., grid).

The first functional TEM was designed, built, and operated in the early 1930s by Ernst Ruska (Flegler et al., 1993). The development of the TEM was so influential that, in 1986, Ruska was co-recipient of the Nobel Prize in Physics (Bozzola and Russell, 1999). With the TEM, the use of an electron beam to image an item of interest allowed investigations at a much higher magnification than light microscopy. The resolution of the electron microscope was approximately three orders of magnitude higher than the light microscopes of the 1940s (Flegler et al., 1993). This ability to view materials at a much higher resolution resulted in unprecedented observations, opening entirely novel avenues of investigation. By the 1950s, the TEM was being used in many scientific disciplines, including biology, medicine, geology, and material sciences.

Over the years, the instrumentation has seen vast improvements and modifications that are beyond the scope of this short introduction. In sum, transmission electron microscopy has evolved to include a wide range of instrumentation, including High Voltage EM (HVEM), Low Voltage EM, Cryo-TEM, and Scanning TEM (STEM). These instruments can be paired with additional equipment such as an energy dispersive X-ray spectroscopy detector for elemental mapping and chemical characterization. Information on these methodologies is also beyond the scope of this contribution.

Use of the TEM relies not only on the instrumentation, but also on specimen preparation. Because most electron microscopes require a vacuum, and biological specimens are composed mostly of water, preparing specimens properly is crucial to successful TEM investigations. Different biological materials demand different preparation procedures. For example, even within the foraminifera, different protocols are required to adequately remove the test, if necessary. While this special issue includes information on foraminiferal preparations for TEM, the reader is directed to the primary literature for further details.

Brief history of foraminiferal TEM studies

To our knowledge, the first TEM investigations of foraminiferal cells were in the 1960s (e.g., Walfarth-Bottermann, 1961). In 1965, Lee et al. (1965) described for the first time in the literature the general ultrastructure of two planktonic (calcareous) foraminifera. In 1967, Robert Angell published two works on the calcareous benthic *Rosalina floridana*, being the first to document foraminiferal calcification and chamber addition using the TEM (Angell 1967a, b). Beginning in the late 1960s, several authors used the TEM to study the ultrastructure of soft-walled foraminifera (Table 1). The 1970s, 1980s and early 1990s saw numerous investigations into benthic foraminiferal reticulopods, extensively reviewed by Travis and Bowser (1991) and Bowser and Travis (2000).

Between 1974 and 1990, the number of publications about the ultrastructure of LBF and planktonics, and their photosynthetic symbionts, increased markedly (e.g., Lee et al., 1974, Anderson and Bé, 1976a, Lee and Bock, 1976, Müller-Merz and Lee, 1976, Lee et al., 1979, 1980a, b, Schmaljohann and Röttger, 1978, McEnery and Lee, 1981, Bé et al., 1982, Leutenegger, 1977a, b, 1983, 1984, Hemleben et al., 1985, Spero, 1987, Faber et al., 1988, 1989, Lee, 1990, Lee and Anderson, 1991).

Reviews of foraminiferal biology and cell structure exist mainly on planktonic foraminifera and LBFs. In 1977, important reviews were published by Leutenegger (1977a, b) on the ultrastructure of LBFs and planktonic foraminifera and their photosynthetic symbionts. Anderson and Bé (1978) and Anderson and Lee (1991) both describe the main organelles and features observed in foraminiferal cells (e.g., nuclei, ribosomes, endoplasmic reticulum, Golgi, lysosomes and digestive vacuoles, peroxisomes, mitochondria, fibrillar bodies, cytoskeletal structures) but the source of all their TEM images except for one was planktonic foraminifera or LBF. Hemleben et al. (1989) and Schiebel and Hemleben (2017) thoroughly described the cytology of planktonic foraminifera.

A published review presenting the ultrastructure of SBF does not exist, to our knowledge. Here we present a compilation of representative publications that present at least one micrograph of smaller benthic foraminiferal ultrastructure (Table 1). Using information from Table 1, we note that before 1990, most of the major published studies with the TEM micrographs of SBF ultrastructure were based on soft-walled species (Fig. 1) mainly studying attributes to the cell membrane and/or test wall, especially reticulopods (Fig. 2). Starting in the 1990s, increasingly more studies on calcareous SBF ultrastructure were published (Fig. 1) and, while these often focused on specific organelle type(s), some also focused on functions such as reproduction (Fig. 2). Also, in the 1990s, an interest to study cellular adaptations to specific environmental conditions increased. Much of this interest was and is presently focused on the response of foraminiferal ultrastructure to oxygen-depletion in either natural or laboratory-controlled experimental settings. In the 2010s, many correlative investigations are combining innovative methodologies with the TEM.

In general, multilocular (multichambered) agglutinated foraminifera are not well studied by TEM methods (Fig.1) generally due to the added complexities of removing their test. Even large agglutinated foraminifera, such as the Xenophyophores and komokiaceans,

have rarely been the subject of a TEM study (e.g., Lecroq et al. 2009), presumably due to the issues with recovery of deep-water materials.

Why this special issue?

Of course all foraminifera have similar overall cellular ultrastructure, including organelles typical to most eukaryotic cells. Additionally, the cellular ultrastructure of symbiont-bearing planktonic foraminifera and LBF are highly similar because both predominantly host photosynthetic symbionts. As noted, published reviews of foraminiferal ultrastructure are based on TEM micrographs of LBF (e.g., Leutenegger, 1977b) and planktonic foraminifera (Hemleben et al., 1989); a compilation of studies presenting TEM micrographs of SBF does not exist. This special issue is intended to fill the gap in existing reviews of SBF ultrastructure in a general context.

To improve our knowledge of the role of foraminifera in biogeochemical cycling and ecosystem functioning, it is imperative that we understand their physiology, metabolism and ecology. Such information is also critical to understanding foraminiferal biomineralization and geochemical signatures. One powerful means to better understand foraminiferal physiology, metabolism and ecology is to return to cell-scale studies, using transmission electron microscopy in combination with additional state-of-the-art imaging approaches.

This special issue includes the following contributions. An overview of typical smaller benthic foraminiferal ultrastructure and organelles is presented in LeKieffre et al., which also includes observations on some fine-scale structures of unknown function. An overview and synthesis of the observed associations between smaller benthic foraminifera and prokaryotes, as symbionts or parasites, is presented by Bernhard et al. A synthesis regarding a type of specialized “symbiosis” involving chloroplast sequestration is presented for shallow-water smaller benthic foraminiferal species (Jaufrais et al.). High-pressure freezing and freeze

substitution (HPF-FS) were used to document the ultrastructure of the chloroplast-sequestering *Haynesina germanica* (Goldstein and Richardson); this contribution also includes some comparisons between conventional chemical fixation and the HPF-FS approach. The ultrastructural response of *Ammonia* spp. to anoxia is presented by Koho et al. Similarly, the ultrastructural response of selected smaller benthic foraminifera to heavy metals is presented by Frontalini et al. Finally, an overview of methods that merge the TEM with additional powerful analytical tools is presented in Nomaki et al.

Acknowledgments

The idea for this Special Issue of *Marine Micropaleontology* resulted from the “Foraminiferal Ultrastructure Workshop” organized by the FRESCO (Foraminiferal Research Consortium) project in conjunction with The Micropalaeontological Society’s Foraminifera and Nannofossil Groups Joint Meeting 2016 held at the University of Angers. For this introductory review, we gratefully appreciate the insights from Sam Bowser and Sue Goldstein for their vast knowledge of the subject and extensive reprint collections as well as Charlotte LeKieffre for sharing her knowledge of planktonic foraminiferal ultrastructure. We also thank the *Marine Micropaleontology* Editors, Ric Jordan and Frans Jorissen for their support in our efforts to create this special issue. JMB acknowledges support from the WHOI Robert W. Morse Chair for Excellence in Oceanography and The Investment in Science Fund at WHOI.

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Figure and Table captions

Table 1. Publications including TEM images of the ultrastructure of small benthic foraminifera, categorized in very general terms of ABF = multichambered Agglutinated Benthic Foraminifera, CBF = Calcareous Benthic Foraminifera (generally multichambered), SWF = Soft-walled Benthic Foraminifera. The list is not exhaustive but representative of major research efforts. Note that the nomenclature given is from the original publication; taxa could have been reassigned or updated. In some cases, a publication could be considered in multiple categories but each is typically listed under the main focus of the contribution. Table updated from Stouff (1998).

Figure 1. Histogram plotting number of publications presenting TEM images of Smaller Benthic Foraminiferal ultrastructure binned by decade and according to test composition. All publications are listed in Table 1, which is not exhaustive.

Figure 2. Histogram showing number of publications with TEM images of Smaller Benthic Foraminiferal ultrastructure binned by decade and presented by major topic (“general characterization” = general description of diverse organelles in one to a few species; “link to membrane and wall” = includes publications aimed at cell membrane features such as reticulopods or the test wall; “link to cell body” = includes works dealing with the description of specific organelles or structures; “link to function” includes papers dealing with TEM approaches to understand cell function; “link to specific conditions” includes contributions dealing with *in situ* or experimental works using the TEM to understand the foraminiferal adaptation to specific conditions (e.g., low oxygen, heavy-metal contamination); “link to methods” include papers that combine the TEM with other methods, such as NanoSIMS). All publications are listed in Table 1, which is not exhaustive; Table 1 category “other topics” is not included in this figure.

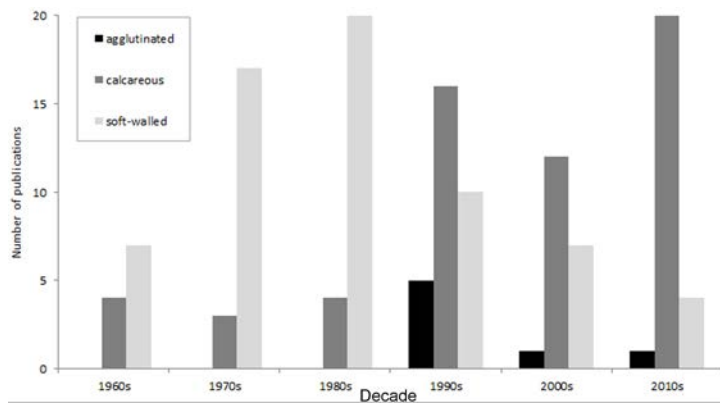


Figure 1.

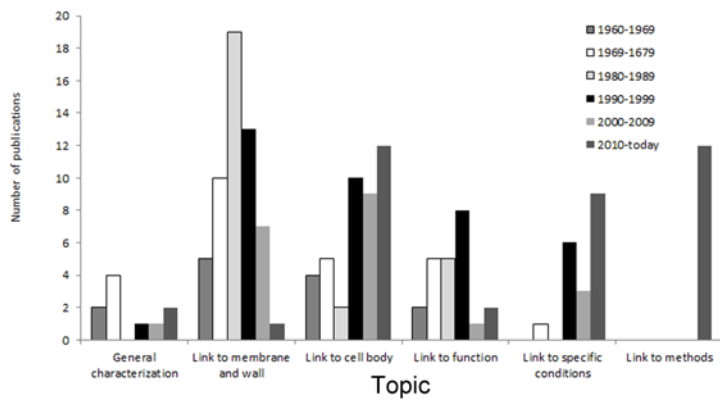


Figure 2.

Study Aim	Author(s)	Year	Foram Type	SBF species imaged with TEM
General description of cell	Boltovskoy and Wright	1976	SWF	<i>Allogromia laticollaris</i> , <i>Ovamina opaca</i> , <i>Hippocrepinella alba</i>
	LeKieffre et al.	in press	CBF	<i>Ammonia</i> sp., <i>Bulimina marginata</i> , <i>Bulimina tenuata</i> , <i>Elphidium oceanense</i> , <i>Globobulimina</i> sp., <i>Haynesina germanica</i> , <i>Nonionella</i> sp., <i>Nonionellina labradorica</i> , <i>Stainforthia fusiformis</i>
General knowledge of ultrastructure in specific species	Hedley et al.	1967	SWF	<i>Sfapheardella tceniformis</i>
	Lengsfeld	1969a	SWF	<i>Allogromia laticollaris</i>
	Schwab	1971	SWF	<i>Allogromia laticollaris</i> , <i>Myxotheca arenilega</i>
	Lena and Freire	1974	SWF	<i>Allogromia laticollaris</i>
	Schwab	1977	SWF	<i>Boderia albicollaris</i>
	Stouff	1998	CBF	<i>Ammonia tepida</i> , <i>Ammonia beccarii</i>
	Goldstein and Richardson	2002	SWF	<i>Myxotheca</i> sp., <i>Cribrorhammina alba</i> , <i>Hyperammina</i> sp.
	Altin-Ballerio et al.	2013	SWF	<i>Psammophaga sapela</i>
Organic layer / wall structure	Hedley et al.	1973	SWF	<i>Allogromia</i> spp., <i>Iridia diaphana</i> , <i>Boderia turneri</i>
	Pierce and Nathanson	1974	SWF	<i>Allogromia laticollaris</i> , <i>Allogromia</i> sp.
	Schwab and Schwab-Stey	1981	SWF	<i>Allogromia laticollaris</i>
	Goldstein and Barker	1988	SWF	<i>Cribrorhammina alba</i>
	Heeger	1990	CBF	<i>Cibicidoides wuellerstorfi</i>
	Anderson and Lee	1991	ABF	<i>Abyssotherma pacifica</i>
	Lee et al.	1991	ABF	<i>Abyssotherma pacifica</i>
	Bowser et al.	1995	SWF	<i>Astrammina rara</i> , <i>Notodendrodes antarctikos</i>
	Rützler and	1996	ABF	<i>Spiculidendron corallicum</i>

	Richardson			
	Goldstein	1999	CBF	<i>Ammonia tepida</i> , <i>Chilostomella</i> sp., <i>Triloculina oblonga</i>
	DeLaca et al.	2002	SWF	<i>Notodendrodes hyalinosphaira</i>
	Bowser et al.	2002	SWF	<i>Astrammmina triangularis</i>
	Habura et al.	2006	ABF	<i>Miliammmina fusca</i>
	Altin et al.	2009	SWF	<i>Niveus flexilis</i>
	Altin et al.	2013	SWF	<i>Psammophaga sapela</i>
Pores	Angell	1967b	CBF	<i>Rosalina floridana</i>
	Berthold	1976	CBF	<i>Patellina corrugate</i>
	Leutenegger and Hansen	1979	CBF	<i>Bolivina</i> spp.
	Heeger	1990	CBF	<i>Cibicidoides wuellerstorfi</i>
Reticulopods (microtubule) / ectoplasm	Wohlfarth-Bottermann	1961	SWF	<i>Allogromia laticollaris</i>
	Angell	1967a	CBF	<i>Rosalina floridana</i>
	Lengsfeld	1969b	SWF	<i>Allogromia laticollaris</i>
	Marszalek	1969	SWF	<i>Iridia diaphana</i>
	Schwab and Schwab-Stey	1972	SWF	<i>Allogromia laticollaris</i>
	Schwab and Schwab-Stey	1973	SWF	<i>Myxotheca arenilega</i>
	Hauser and Schwab	1974	SWF	<i>Allogromia laticollaris</i>
	McGee-Russell	1974	SWF	<i>Allogromia</i>
	Nyholm and Nyholm	1975a	SWF	<i>Cylindrogullmia alba</i>
	Nyholm and Nyholm	1975b	SWF	<i>Cylindrogullmia alba</i>
	Alexander and Banner	1984	CBF	<i>Haynesina germanica</i>
	Travis and Allen	1981	SWF	<i>Allogromia laticollaris</i>
	Travis et al.	1983	SWF	<i>Allogromia laticollaris</i>
	Koury et al.	1985	SWF	<i>Allogromia</i> sp., Strain NF
	Bowser and	1985	SWF	<i>Allogromia</i> sp., Strain NF

		Rieder			
		Koonce and Schliwa	1985	SWF	<i>Reticulomyxa filose</i>
		Koonce and Schliwa	1986	SWF	<i>Reticulomyxa</i>
		Rieder et al.	1985	SWF	<i>Astrammia rara</i>
		Bowser et al.	1986	SWF	<i>Astrammia rara</i>
		Euteneuer et al.	1986	SWF	<i>Reticulomyxa</i>
		Koonce et al.	1986b	SWF	<i>Reticulomyxa</i>
		Koonce et al.	1986a	SWF	<i>Reticulomyxa</i>
		Rupp et al.	1986	SWF	<i>Allogromia</i> sp., Strain NF
		Travis and Bowser	1986	SWF	<i>Allogromia</i> sp., Strain NF
		Kachar et al.	1987	SWF	<i>Allogromia laticollaris</i>
		Bowser et al.	1988	SWF	<i>Allogromia</i> sp., Strain NF
		Hauser and Lindenblatt	1989	SWF	<i>Reticulomyxa filose</i>
		Jensen et al.	1990	SWF	<i>Allogromia laticollaris</i> , <i>Allogromia</i> sp.
		Travis and Bowser	1990	SWF	<i>Allogromia laticollaris</i>
		Travis and Bowser	1991	SWF, CBF	<i>Allogromia</i> spp., <i>Spiroloculina hyaline</i>
		Golz and Hauser	1994	SWF	<i>Allogromia laticollaris</i>
		Welnhofner and Travis	1996	SWF	<i>Allogromia laticollaris</i>
		Goldstein	1999	CBF	<i>Spiroloculina hyaline</i>
		Bowser and Travis	2000	SWF	<i>Allogromia laticollaris</i> , <i>Allogromia</i> sp., Strain NF
		Travis et al.	2002	SWF	<i>Allogromia laticollaris</i>
		Habura et al.	2005	CBF, ABF	<i>Ammonia tepida</i> , <i>Miliammina fusca</i>
Specific organelles	Nucleus	Dahlgren	1967a, b	SWF, CBF	<i>Ovammia opaca</i> , <i>Hippocrepinella alba</i> , <i>Globobulimina turgida</i>
		Lena	1972	SWF	<i>Allogromia flexibilis</i>

		Schwab	1972	SWF	<i>Allogromia laticollaris</i>
		Schwab and Schwab-Stey	1979b	SWF	<i>Kibisidytes</i> sp.
		Schwab and Schwab-Stey	1979a	SWF	<i>Allogromia laticollaris</i>
		Heeger	1990	CBF	<i>Quinqueloculina seminula, Miliolinella vigilax</i>
		Goldstein	1997	CBF, SWF	<i>Ammonia tepida, Triloculina oblonga, Cribrothalammina alba</i>
		Raikov et al.	1998	CBF	<i>Elphidium ponticum</i>
	Mitochondria	Hedley and Wakefield	1968	SWF	<i>Boderia turneri</i>
		Heeger	1990	CBF, ABF	<i>Quinqueloculina</i> sp., <i>Ammotium cassis</i>
		Bernhard	2000	CBF	<i>Buliminella tenuata</i>
	Peroxisomes and endoplasmic reticulum	Hruban and Rechcigl	1969	CBF	<i>Rosalina leei</i>
		Heeger	1990	ABF, CBF	<i>Ammotium cassis, Triloculina rotunda, Pyrgo murrhina, Cibicides lobatulus</i>
		Bernhard and Reimers	1991	CBF	<i>Nonionella stella, Chilistomella ovoidea</i>
		Bernhard and Alve	1996	CBF	<i>Stainforthia fusiformis</i>
		Bernhard and Sen Gupta	1999	CBF	<i>Buliminella tenuata</i>
		Bernhard et al.	2001	CBF	<i>Buliminella tenuata, Globobulimina</i> sp.
		Bernhard and Bowser	2008	CBF	<i>Nonionella stella, Buliminella tenuata, Buliminella elegantissima</i>
		Bernhard et al.	2010b	CBF	<i>Buliminella tenuata</i>
		Bernhard et al.	2010a	CBF	<i>Bolivina pacifica</i>
		Bernhard et al.	2012a	CBF	<i>Buliminella tenuata</i>
		Tsuchiya et al.	2015	CBF	<i>Virgulinella fragilis</i>
	Sequestered chloroplasts	Lopez	1979	CBF	<i>Elphidim williamsoni</i>
		Lee and McEnery	1983	CBF	<i>Elphidim williamsoni</i>

	Lee et al.	1988	CBF	<i>Elphidium crispum</i>
	Cedhagen	1991	CBF	<i>Nonionella labradorica</i>
	Bernhard and Alve	1996	CBF	<i>Bulimina marginata, Stainforthia fusiformis</i>
	Bernhard and Sen Gupta	1999	CBF	<i>Nonionella stella</i>
	Bernhard and Bowser	1999	CBF	<i>Nonionella stella, Elphidium sp.</i>
	Correia and Lee	2002	CBF	<i>Elphidium excavatum</i>
	Grzymiski et al.	2002	CBF	<i>Nonionella stella</i>
	Bernhard	2003	CBF	<i>Virgulinea fragilis</i>
	Goldstein et al.	2004	CBF	<i>Haynesina germanica</i>
	Goldstein et al.	2010	SWF	<i>Xiphophaga minuta</i>
	Bernhard et al.	2012a	CBF	<i>Bolivina argentea</i>
	Tsuchiya et al.	2015	CBF	<i>Virgulinea fragilis</i>
	Cesbron et al.	2017	CBF	<i>Haynesina germanica</i>
	Goldstein and Richardson	in press	CBF	<i>Haynesina germanica</i>
	Jauffrais et al.	in press	CBF	<i>Elphidium aff. E. crispum, Elphidium oceanense, Elphidium selseyense, Haynesina, germanica, Planoglabratella opercularis</i>
Endobionts / ectobionts	Bernhard	1993	CBF	<i>Globocassidulina cf. G. biora</i>
	Richardson and Rützler	1999	ABF	<i>Spiculidendron corallicum</i>
	Bernhard and Sen Gupta	1999	CBF	<i>Buliminella tenuata</i>
	Bernhard et al.	2000	CBF	<i>Buliminella tenuata</i>
	Bernhard	2003	CBF	<i>Virgulinea fragilis</i>
	Bernhard et al.	2006	SWF	Clade L allogromiid
	Bernhard et al.	2010a	CBF	<i>Bolivina pacifica</i>
	Bernhard et al.	2010b	CBF	<i>Uvigerina pacifica, Globobulimina pacifica</i>
	Martin et al.	2010	CBF	<i>Buliminella tenuata</i>
	Bernhard et al.	2012a	CBF	<i>Fursenkoina cornuta, Buliminella tenuata</i>
	Bernhard et al.	2012b	SWF	Clade L allogromiid

	Tsuchiya et al.	2015	CBF	<i>Virgulinea fragilis</i>
	Bernhard et al.	2017	CBF, SWF	<i>Ammonia</i> sp., <i>Bolivina pacifica</i> , <i>Bulimina mexicana</i> , <i>Buliminella tenuata</i> , <i>Cibicides wuellerstorfi</i> , <i>Globobulimina affinis</i> , <i>G. pacifica</i> , <i>Saccamminid</i> , <i>Uvigerina peregrina</i> , <i>Virgulinea fragilis</i>
Organelles linked to nutrition	Lengsfeld	1969c	SWF	<i>Allogromia laticollaris</i>
	Bowser et al.	1985	SWF	<i>Allogromia</i> sp., Strain NF
	Heeger	1990	SWF	<i>Quinqueloculina seminula</i> , <i>Ammonium cassis</i> , <i>Miliolinella vigilax</i> , <i>Rosalina globularis</i> ,
				<i>Melonis zaandami</i> , <i>Cibicides refulgens</i> , <i>Pyrgo murrhina</i> , <i>Triloculina</i> sp., <i>Triloculina rotunda</i>
	Goldstein and Corliss	1994	CBF	<i>Ammonia beccarii</i> forma <i>tepida</i> , <i>Globobulimina pacifica</i> , <i>Uvigerina pacifica</i>
	Goldstein	1999	CBF, SWF	<i>Globobulimina pacifica</i> , <i>Cribrothalammina alba</i>
	LeKieffre et al.	2017	CBF	<i>Ammonia</i> sp.
Cytoplasm / organelles linked to reproduction	Schwab	1969	SWF	<i>Allogromia laticollaris</i>
	Schwab	1970	SWF	<i>Allogromia laticollaris</i>
	Angell	1971	SWF	<i>Myxotheca</i> sp.
	Cesana	1972	SWF	<i>Iridia lucida</i>
	Mc Enery and Lee	1976	SWF	<i>Allogromia laticollaris</i>
	Schwab	1976	SWF	<i>Allogromia laticollaris</i>
	Arnold	1982	SWF	<i>Psammophaga simplora</i>
	Arnold	1984	SWF	<i>Psammophaga simplora</i>
	Bowser et al.	1984	SWF	<i>Allogromia</i> sp., Strain NF
	Goldstein	1988	SWF	<i>Saccamina alba</i>
	Goldstein and Barker	1990	SWF	<i>Cribrothalammina alba</i>
	Lee et al.	1991	SWF	<i>Allogromia</i> sp.
	Goldstein and Moodley	1993	CBF	<i>Ammonia beccarii</i> forma <i>tepida</i>
	Pawlowski et al.	1995	ABF	<i>Trochammina</i> sp.
	Goldstein	1997	CBF,	<i>Ammonia tepida</i> , <i>Triloculina oblonga</i> , <i>Cribrothalammina alba</i>

			SWF	
	Raikov et al.	1998	CBF	<i>Elphidium ponticum</i>
	Goldstein et al.	2010	SWF	<i>Xiphophaga minuta</i>
	Altin et al.	2009	SWF	<i>Niveus flexilis</i>
	Altin et al.	2013	SWF	<i>Psammophaga sapela</i>
Cellular response to specific environmental conditions	Leutenegger and Hansen	1979	CBF	<i>Bolivina</i> spp.
	Bernhard and Reimers	1991	CBF	<i>Nonionella stella</i> , <i>Chilostomella ovoidea</i>
	Bernhard	1993	CBF	<i>Globocassidulina</i> cf. <i>G. biora</i> , <i>Cassidulinoidea porrectus</i>
	Bernhard	1996	CBF	<i>Buliminella tenuata</i>
	Sen Gupta et al.	1997	CBF	<i>Gavelinopsis translucens</i> , <i>Cassidulina neocarinata</i>
	Bernhard and Sen Gupta	1999	CBF	<i>Buliminella tenuata</i>
	Bernhard et al.	2010a	CBF	<i>Uvigerina peregrina</i> , <i>Buliminella tenuata</i> , <i>Bulimina Mexicana</i>
	Risgaard-Petersen et al.	2006	CBF	<i>Globobulimina pseudospinescens</i>
	Koho et al.	in press	CBF	<i>Ammonia</i> spp.
Cellular response to experimental conditions	Bernhard and Alve	1996	CBF	<i>Bulimina marginata</i> , <i>Stainforthia fusiformis</i>
	Morvan et al.	2004	CBF	<i>Ammonia tepida</i>
	Lecadre and Debenay	2006	CBF	<i>Ammonia tepida</i>
	Bernhard et al.	2012a	CBF	<i>Bolivina argentea</i> , <i>Fursenkoina cornuta</i> , <i>Buliminella tenuata</i>
	Nomaki et al.	2014	CBF	<i>Ammonia beccarii</i>
	Frontalini et al.	2015	CBF	<i>Ammonia parkinsoniana</i>
	Frontalini et al.	2016	CBF	<i>Ammonia parkinsoniana</i>
	Nomaki et al.	2016	CBF	<i>Ammonia</i> sp.
	LeKieffre et al.	2017	CBF	<i>Ammonia</i> sp.
	Frontalini et al.	submitted	CBF	<i>Pseudotriloculina rotunda</i> , <i>Ammonia parkinsoniana</i>
Koho et al.	in press	CBF	<i>Ammonia</i> spp.	
Other methodologies combined with TEM	Bernhard et al.	2010a	CBF	<i>Uvigerina peregrina</i> , <i>Buliminella tenuata</i> , <i>Bulimina Mexicana</i>
	Martin et al.	2010	CBF	<i>Uvigerina peregrina</i> , <i>Buliminella tenuata</i> , <i>Bulimina Mexicana</i>

	Bernhard and Richardson	2014	CBF	Unknown
	Nomaki et al.	2015	CBF	<i>Uvigerina akitaensis</i> , <i>Globobulimina affinis</i>
	Nomaki et al.	2016	CBF	<i>Ammonia</i> sp.
	LeKieffre et al.	2017	CBF	<i>Ammonia</i> sp.
	Goldstein and Richardson	in press	CBF	<i>Haynesina germanica</i>
	Nomaki et al.	in press	CBF, ABF	<i>Ammonia</i> sp., <i>Buliminella tenuata</i> , Biserial agglutinated species, <i>Haynesina germanica</i> , <i>Nonionellina labradorica</i>
Other topics	Hruban and Rechcigl	1969	SWF	<i>Iridia lucida</i> , <i>Shepherdella taeniformis</i>
	Heeger	1988, 1990	CBF	<i>Elphidium excavatum clavatum</i>
	Rützler and Richardson	1996	ABF	<i>Spiculidendron corallicum</i> .
	Goldstein et al.	2010	SWF	<i>Xiphophaga minuta</i>