Atypical, high-diversity assemblages of foraminifera in a mangrove estuary from Northern Brazil

Nisan Sariaslan, Martin R. Langer

Institute für Geowissenschaften, Paläontologie, Universität Bonn, Bonn, 53115, Germany

Correspondence to: Martin R. Langer (martin.langer@uni-bonn.de)

Abstract. Mangrove forests are extremely productive ecosystems, sources and sinks of organic carbon, and provide essential services both to the marine environment and people. We have studied the composition and species richness of mod[illegible] benthic foraminiferal assemblages from mangrove swamps along the Mamanguape River in Paraíba, northern Brazil. Sampling points for foraminifera were selected to acquire information on the composition of foraminiferal assemblages from dense mangrove stands collected along a river transect. Almost 100 species of benthic foraminifera were identified within the shallow mangrove habitats. The large number of identified mangrove taxa is the highest recorded so far for true mangrove habitats. The high species richness rivals shallow-water assemblages recorded from nearby offshore and reef environments and indicates that a particularly large number of species is capable to grow and flourish under conditions of multiple stressors. Numerical analysis of the faunal assemblages shows that specific taxa, which were previously known to be uncommon in mangrove environments, are abundant in the Mamanguape River estuary. The atypical foraminiferal fauna found in the Mamanguape River Estuary resembles shallow-water offshore assemblages, is characterized by high percent abundances of perforate and miliolid taxa and contains only a very few of the otherwise typical and numerically abundant agglutinated mangrove taxa. The unusual structure of the assemblages recorded provide insight of what combination of environmental variables controls their composition and novel perspectives to reconstruct past mangrove environments. Distribution, diversity and species-specific analysis will provide guidance on the use of Brazilian mangrove foraminifera as indicators for the strength of tidal activity, pollution and anoxia in coastal waters and sea-level reconstructions.

1. Introduction

Mangrove ecosystems around the world play an important role in protecting biodiversity, preserving shorelines and regulating carbon cycling. They respond actively to coastal processes and sediment input, and are considered one of the best geological indicators for the detection of modifications in coastal zone dynamics (Cunha-Lignon et al., 2009). Brazil is home to approximately 15% of the world's total mangal forest areas but the release of effluents and untreated wastewater pose threats to ecosystems and marine biotas. Nearly 6700 km (90%) of the whole 7400 km of Brazil coastline hosts mangrove forests. The Mamanguape River Estuary is the second largest estuary in the northeastern State of Paraíba (Brazil) covering a mangrove swamp area of more than 57 square kilometres (Bezerra et al., 2012).

Mangrove ecosystems, are subject to a suit of disturbances that vary in their intrinsic nature (e.g., geological, physical, chemical, biological) in time and space. Inhabiting the interface between land and sea at low latitudes, these ecosystems occupy a harsh environment, are subject to daily tidal changes, temperature and salinity variations, and varying degrees of anoxia. Mangrove forests and their inhabitants are therefore rather robust and highly tolerant to life in their saline environments within warm, subtropical and tropical seascapes (Alongi, 2008). In addition to the natural fluctuations, anthropogenic activities also affect these ecosystems. The estuaries of the north-eastern Ecoregion are among the most affected by the human occupation processes in Brazil and need actions that guide an integrated management to maintain ecosystem sustainability. Nearby cities to the Mamanguape River Estuary have a total of nearly 40.000 inhabitants (Instituto Brasileiro de Geografia e Estatistica, 2019), and extensive sugarcane and shrimp aquaculture fields place environmental pressure on the mangrove ecosystem. The synergistic effects of multiple stressors may cause broad-scale changes in estuarine and coastal ecosystems impacting the abundance, species richness and distribution of functionally important taxa. The interactions of multiple stressors are likely to increase as climate change and anthropogenic pressures will alter the delivery of freshwater and associated nutrients and pollutants to estuarine and coastal ecosystems (Scavia et al., 2002; Paerl et al., 2006; Gillanders et al., 2011; Schiedek et al., 2008). Understanding the response of benthic communities to key stressors is vital for managing mangrove environments and the first step towards setting ecologically relevant limits.

Foraminifera in tropical mangrove environments of South America and the islands nearby have been studied since the late 1940's in Trinidad (Cushman and Brönnimann, 1948a, b; Wilson et al., 2008), the Gulf of Paria (Todd and Brönnimann, 1957), Bahia (Zaninetti et al., 1979; Hiltermann et al., 1981; Eichler et al., 2015; Laut et al., 2016), Rio de Janeiro (Brönnimann et al., 1981; Debenay et al., 2001; Barbosa et al., 2005; Laut et al., 2016; Martins et al., 2016; Gasparini and Vilela, 2017; Belart et al., 2019), Columbia (Boltovskoy and Hincapié de Martínez, 1983), Puerto Rico (Culver, 1990), French Guiana (Debenay et al., 2002; Debenay et al., 2004), Santa Catarina (Laut et al., 2016), Sao Paulo (Eichler et al., 2007; Passos et al., 2017; Eichler et al., 2019), and Rio Grande do Sul (Laut et al., 2016; Damasio et al., 2020; Semensatto et al., 2009). Most foraminifera [illegible]nblages studied from true mangrove settings were previously reported to be dominated by agglutinated species in a low-diversity ensemble (e.g. Boltovskoy 1984; Culver, 1990; Debenay, 1990; Murray, 1991; Brönnimann et al., 1992 and references therein). However, we were persuaded to perform an in-depth investigation of our samples, upon observing highly diverse and calcareous-dominated assemblages in our preliminary results. The objectives of the present study were i. to provide a detailed documentation on the structure and species richness of foraminiferal assemblages in mangroves of the Mamanguape River Estuary of northern Brazil, ii. to understand the driving forces contributing to the unusual composition and high diversity of these assemblages, and iii. to discuss implications for interpreting the fossil record of foraminiferal mangrove assemblages.

2. Regional Setting

The Mamanguape River Estuary System is located on the coast of the Paraíba State in northeastern Brazil and bound by latitudes 6°43'02" S to 6°51'54" S and longitudes 35°07'46" W to 34°54'04" W (Fig. 1). It is situated in an incised river valley, formed along a graben structure and oriented perpendicular to the coastline (Bezerra et al., 2001). The Mamanguape River Estuary belongs to the Northeastern Marine Ecoregion (NEME; Spalding et al., 2007), covers an area of ~658 km^2, and is characterized by different rainfall regimes with varying rates of precipitation and duration during the wet and dry periods. As a result, a pronounced environmental variability among NEME estuaries is observed, where the highest reported pH (9.5) was recorded in the Mamanguape River (Lana and Angelo, 2018; see Table 3.1).

Radiocarbon dates collected from core sample material provide evidence that the inundation of the estuary occurred over the last 6000 years, and more abruptly within the last 1000 years (Alvez, 2015). The dissolved oxygen levels in the estuary are controlled by a balance between the deoxygenation caused by the intense vegetation and tidal cycles, and the oxygenation brought by bioturbating organisms. It is likely that hypoxia are a common condition of intertidal Mamanguape mangrove environments due to the mineralisation of a large amount of organic matter produced by mangrove trees, responsible for a high consumption of oxygen by bacteria (Alongi et al., 2004), but also due to the exchange of porewater between sediments and the water column, known as “tidal pumping” (Li et al., 2009; Gleeson et al., 2013; Call et al., 2015; Leopold et al., 2017). According to Nordi et al. (2009), the tidal cycle is semi-diurnal on the northeastern coast of Brazil, producing two floods and two ebbs per day, with a tidal range of approximately 2.8 m (Paludo and Klonowski, 1999). The estuary is heavily bioturbated by macrofaunal organisms such as oligochaetes, polychaetes, gastropods, bivalves and shipworms. In addition, crabs and fish are diverse and abundant, and are part of the vibrant ecosystem found in the estuary (Leonel et al., 2002; Nascimento et al., 2016; Van der Linden et al., 2017). Thus, sediments of the Mamanguape River Estuary are heterogenous in terms of their oxygen content; they rapidly become anoxic below the sediment surface, but bioturbation results in localized oxygenation of sediments around macrofaunal burrows (see also Langer et al., 1990).

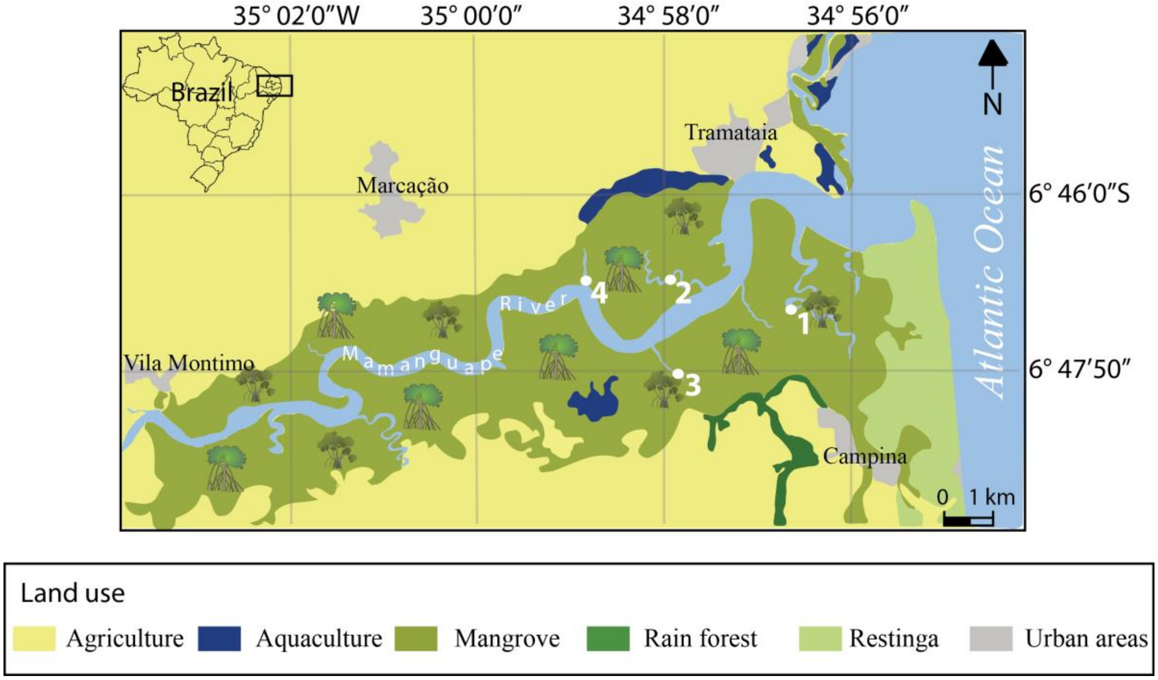

Figure 1. Map of the Mamanguape River Estuary with location of sample sites (modified from Dolbeth et al., 2016).

3. Material and Methods

Sediment samples were collected from the top 2 cm in September 2006 along the Mamanguape River Estuary (Fig. 1). This time of the year falls within the dry season (August to November; Debenay et al., 2004) and the year 2006 is considered a “very dry” year and the driest between 2002 and 2006 (dos Santos et al., 2015). The sampling sites selected are located along the main and tributary mangrove channels and are scattered along a 2 km traverse upstream (Fig. 2). Sampling was conducted within dense mangrove stands and in distance to the channels (>10m) to avoid potentially allochthonous species transported by currents along the channel. Sampling points are located directly around the roots within the mangrove trees and the sediments collected are composed of organic-rich mud and silt. The samples were washed over 63 µm sieves, dried at room temperature and a total of ~ 1352 foraminifera specimens were picked from these samples (Table 1). All specimens were identified to species level, illustrated by SEM, and arranged into plates using Adobe Illustrator CS5 (Figures 3–9). The total number of individuals was then counted for each species (Table 1), and their abundance and distribution patterns were analysed.

As a measure of diversity, species richness was determined for each sample and is illustrated by the Fisher α diversity index (Fig. 2, Table 2; Fisher et al., 1943; Murray, 1973). To this end, the total number of individuals has been plotted against the total number of species via the PAST software, to compare the foraminiferal assemblage diversity/species richness in regard to the sampled locations. In addition, the Shannon diversity index (*H*), was calculated to characterize species diversity in foraminiferal communities. The Shannon's index accounts for both abundance and evenness of the species present. The proportion of species *i* relative to the total number of species (p_i) is calculated, and then multiplied by the natural logarithm of this proportion ($\ln p_i$). The resulting product is summed across species, and multiplied by -1:

$$H=-\sum_{J=1}^{S} p_j ln(p_j)$$

Species richness and Fisher α diversity values were then compared to other mangrove studies from around the world to place our study in perspective. Lastly, the foraminiferal fauna was documented on plates (Figures 3–9). All specimens are deposited in the micropaleontological collection at the Institute of Geosciences, University of Bonn (Germany).

4. Results

4.1 Composition of foraminiferal assemblages

A total of 1352 benthic foraminifera specimens belonging to 93 species and 53 genera, including perforate-hyaline, porcelaneous and agglutinated taxa were recovered from the samples collected in the Mamanguape estuary (Fig. 1 and Table 1). The foraminiferal tests obtained were found to be particularly well preserved, with even the most fragile forms in good condition, lacking signs of dissolution, abrasion or breakage. Many specimens were found to contain pyrite framboids inside their tests, a feature considered to be indicative of anoxic conditions in the surrounding sediment (Fig. 9, 22–23). Perforate-hyaline foraminifera comprise 34 genera (64% of the total assemblage) and 53 species (57% of the total assemblage), porcelaneous types account for 14 genera (26%) and 33 species (35%), and agglutinated taxa are represented by 5 genera (9%) and 7 species (8%). Percent abundances of wall structural types (agglutinated, perforate-hyaline, porcelaneous) do not show any significant variation among the sampling sites. Hyaline-perforate foraminifera range between 72 and 75%, porcelaneous foraminifera constitute 23 to 27 %, and agglutinated species contribute only 1 or 2 % to the total assemblage at each site (Table 2). The total number of benthic foraminifera species increases slightly from sample site 1 near the mouth of the estuary (65 species) towards the innermost sample site 4, where 70 species were recorded.

Table 1: Alphabetical list, abundance of all species of foraminifera identified and total abundances specimens, genera and species in the samples from the Mamanguape River Estuary.

Species	Sample 1	Sample 2	Sample 3	Sample 4
Abditodentrix rhomboidalis	2	2	2	4
Adelosina milletti	3	4	2	3
Ammonia advena	2	3	3	1
Ammonia veneta	23	11	11	20
Amphistegina lessonii	1	1		
Amphistegina radiata	1			
Angulogerina cf. *A. occidentalis*	2	7	5	7
Anomalinulla glabrata	1	2		
Anomalinulla sp. 1	25	17	18	17
Arenoparella mexicana				1
Articulina alticostata				1
Astrononion gallowayi	2	1		
Bigenerina sp. 1	1	2	2	1
Bolivina brevior	2		1	
Bolivina densipunctata	4	3		
Bolivina ordinaria	9	9	2	2
Bolivina striatula	4	5	1	7
Bolivina sp. 1		2		
Bolivina variabilis	1	1		7
Bolivina cf. B. variabilis	6	6	13	10
Buliminella elegantissima	1		1	
Cassidelina sp. 1	2	2	1	2
Cornuspira involvens	5	5	3	1
Cornuspira planorbis			1	1
Cribroelphidium mirum	2	6	12	5
Cushmanina bricei			1	2
Discorbis williamsoni	1			1
Discorbitina pustulata		1	1	2
Edentostomina sp. 1	2	3	2	3
Elphidium sagrum		2	3	3
Elongobula parallela	4	10	9	7
Eoponidella pulchella	4	1		
Fischerina sp. 1	1			
Fissurina sp. 2	2	1	2	1
Fissurina bispinata			1	
Fissurina colomboensis	1	2	2	3
Fissurina semimarginata		2	1	2
Fissurina ? sp. 1	1			
Glabratella carinata	2	4	2	3
Glabratella mirabilis	2	1	1	2
Globocassidulina crassa	2	2	5	4
Globocassidulina rossensis	2	4	3	
Hauerina atlantica				1
Inaequalina sp. 1				1
Laevipeneroplis bradyi				1

Lagena tenuis				1
Loxostomina costulata	5	1	1	
Miliolinella webbiana		1	2	3
Miliolinella sp. 1	1		1	1
Mychostomina revertens				1
Neoconorbina radiatogranulata		1	1	2
Neoconorbina sp. 1	3	3	4	4
Neoconorbina terquemi		5	1	1
Nonionoides grateloupii	8	5	2	4
Orbitina carinata	12	25	30	22
Pararotalia cananeiaensis	81	76	75	71
Procerolagena oceanica				1
Pseudolachlanella eburnea	1	2	2	3
Pseudolachlanella bermudezi	9	6	6	12
Pseudotriloculina sp. 1	4	2	3	2
Pseudotriloculina sp. 2	2	2	1	2
Pseudotriloculina sp. 3	2	1	2	3
Quinqueloculina cf. *Q. bosciana*	5	5	2	3
Quinqueloculina cf. *Q. carinatastriata*	3	3	3	3
Quinqueloculina cuvierina	10	8	16	15
Quinqueloculina moynensis	19	22	15	17
Quinqueloculina poeyana	1			
Quinqueloculina cf. *Q. rebeccae*	1	1		
Quinqueloculina samoaensis	3	5	4	4
Quinqueloculina tantabiddyensis	1	1		
Quinqueloculina sp. 1	2		1	2
Quinqueloculina quinquecarinata	1		1	1
Quinqueloculina sp. 2			3	2
Quinqueloculina sp.3	2	2	3	3
Quinqueloculina sp. 4		1		
Quinqueloculina cf. *Q. compta*		1	1	2
Quinqueloculina cf. *Q. zhengi*	1			
Rosalina sp. 1		2	2	1
Rosalina sp. 2	15	14	8	11
Rosalina bradyi		7		1
Rotaliammina trumbulli	2		1	
Rotorbis auberii	4	5		3
Sagrina pulchella		1	3	3
Sigmoilinita costata	2		2	1
Sigmavirgulina tortuosa	1	3	6	2
Svratkina acuta	2	1	1	2
Siphonina reticulata	4	3	4	5
Spirillina grosseperforata			1	1
Textularia sp. 1		1	2	1
Textularia sp. 2		2	1	1
Textularia cf. *T. semialata*		1		
Trochammina inflata	1		1	
Wiesnerella auriculata	4	5	5	
Total number of specimens	**335**	**346**	**328**	**343**
Number of genera	**40**	**38**	**38**	**44**
Number of species	**65**	**66**	**66**	**70**

Table 2. Sample site information including geographical position, salinity (Medeiros et al., 2018), number of species, Fisher **α**, Shannon's H', dominance (SID), **Evenness** e^H/S, and percent abundances of agglutinated, miliolid and perforate specimens, and the five most abundant species.

	Sample 1	**Sample 2**	**Sample 3**	**Sample 4**
Longitude Latitude	6°46'59.61"S 34°56'40.83"W	6°46'57.84"S 34°57'54.95"W	6°47'57.89"S 34°57'49.94"W	6°46'55.93"S 34°58'55.04"W
Salinity ‰	32 ± 3.9	30.3 ± 3.9	28.3 ± 3.0	28.7 ±3 .1
Fisher α	24.04	24.19	24.89	26.6
Shannon H	3.324	3.439	3.345	3.484
Dominance D	0.08149	0.0696	0.07689	0.06473
Evenness e^H/S	0.4271	0.4721	0.4297	0.4656
Agglutinated %	1.19	1.73	2.13	1.17
Porcelaneous %	24.78	23.12	23.78	26.53
Hyaline-perforate %	74.02	75.14	73.17	72.30
Ammonia veneta %	7.46	3.18	3.35	5.83
Anomalinulla sp. 1 %	7,4[illegible]	4,91	5,49	4,96
Orbitina carinata	3,5[illegible]	7,22	13,16	6,41
Pararotalia cananeiaensis %	24,18	21,97	22,87	20,70
Quinqueloculina moynensis %	5,67	6,36	4,57	4,96

4.2. Species richness and diversity

Species richness values vary between 65-70 among the sample sites (Table 1). The highest value (70 species) was recorded at site 4 and the lowest at site 1 (65 species). Fisher α values range between 24.04–26.60 (Tbl. 2 and Fig. 3), with highest values at site 4 and lowest at site 1. As a general trend, species richness and Fisher α values were found to increase from the sampling sites closer to the ocean towards the inner parts of the estuary with highest values at site 4 (Table 1 and Fig. 2). Dominance, Evenness and Shannon index values recorded revealed only minor variability and were found to be comparatively uniform across all sample sites analysed (Table 2).

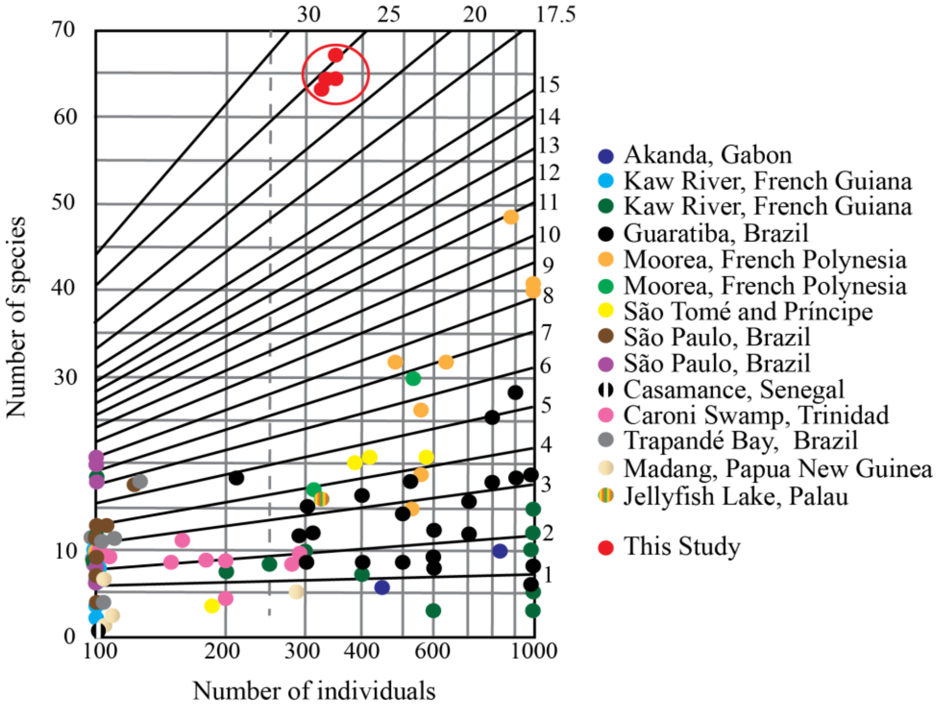

Figure 2: Fisher [illegible]versity index graph for foraminiferal samples from the Mamanguape River Estuary in comparison to total assemblages reported in previous mangrove studies [data from Brönnimann et al., 1981 (Guaratiba, Brazil); Rouvillois, 1982 (Casamance, Senegal); Lipps and Langer, 1999 (Jellyfish Lake, Palau); Debenay et al., 2002, 2004 (Kaw River, French Guiana); Langer and Lipps, 2003 (Madang, Papua New Guinea); Langer and Lipps, 2006 (Moorea, French Polynesia); Wilson et al., 2008 (Trinidad); Fajemila et al., 2015 (Moorea, French Polynesia); Langer et al., 2016 (Akanda, Gabon); Fajemila and Langer, 2017 (Sao Tome and Principe); Eichler, 2018 (Sao Paulo, Brazil); Semensatto, 2009 (Trapande Bay, Brazil)].

4.3. Distribution patterns

Samples were found to have a comparatively uniform composition, without much difference in species richness, species diversity and community structure. The assemblages analysed from each sampling site show a striking dominance of *Pararotalia cananeiaensis* (20.7–24.2% of the total assemblages). The second most abundant taxon is *Orbitina carinata*, a hyaline-perforate species with highest percent abundances in distance from the mouth of the estuary. *Ammonia veneta* and *Anomalinulla* sp. 1 are also abundant in all our samples, constituting 3.2–7.5% and 4.9–7.5% of the total assemblages, respectively. The porcelaneous species *Quinqueloculina moynensis* constitutes between 4.57–6.36% to the total assemblage at individual sites. Species of the genus *Quinqueloculina* are represented in the assemblages by a highly diverse group and constitute 15 species. Among the 93 species recorded, a total of 40 species were present at all four sampling sites including the five most abundant species (*P. cananeiaensis*, *A. veneta*, *A.*[illegible], *O. carinata* and *Q. moynensis*).

Occurrence records of a few species display preferences for particular sites in the estuary. Among these, *Angulogerina* cf. *A. occidentalis*, *Cribroelphidium mirum*, and *Elongobula parallela* are particularly abundant at site 2, 3 and 4, which correspond to the inner reaches of the estuary. Species recorded exclusively at sites located near the mouth region of the estuary (sites 1 and 2) include *Anomalinulla glabrata*, *Bolivina densipunctata*, *Bolivina variabilis*, *Eoponidella pulchella*, *Fischerina* sp. 1, *Fissurina*? sp. 1, *Quinqueloculina poeyana*, *Q.* cf. *Q. rebeccae*, and *Q. tantabiddyensis*. Amphisteginid foraminifera, although present in low abundances, are also restricted to sample site 1 and 2.

5. Discussion

Analyses of foraminiferal assemblages from the Mamanguape mangrove estuary revealed highly diverse, particularly species-rich and structurally complex biotas of benthic taxa. With a total of 93 taxa, species richness exceeds previous species counts and was found to be the highest among all true mangrove environments studied so far (see below and Fig[illegible]. In addition, our samples yielded unusual assemblages heavily dominated by calcareous taxa, lacking agglutinated specimens to a great degree, as reflected by the dominance of perforate-hyaline taxa that contribute between 72.3–75.1% to the total population. Porcelaneous miliolids, representatives of shallow marine environments, constitute the second most abundant group with an abundance of 23,8–26,5%. Agglutinated species, which are typically dominant in mangrove environments (Murray, 1991), contribute only 1.7–2.1% to total assemblages (Table

2). Species richness values recorded range between 65 and 70 at individual sites, whereas the average species richness was found to be generally much lower in other studies (Fig. 2; Debenay, 1990, 2001; Murray, 2006 and references therein). The atypical composition and highly diverse Mamanguape assemblages raise the question which driving forces are decisive for the development of such unusual mangrove biotas. Because such assemblages rather resemble foraminiferal faunas from shallow coastal settings and are difficult to relate to mangrove habitats, potential implications for the interpretation of the fossil record are considered.

As outlined above and illustrated in the Fisher α diagram (Fig. 2), the Mamanguape foraminiferal assemblages were found to deviate from usual foraminiferal mangrove biotas in species-richness, in the composition of wall-structural types, the presence of abundant hyaline-perforate and porcelaneous miliolid taxa, and in particularly low abundances of agglutinated species. While Fisher α value recordings from previous mangrove studies ranged between 0.3 and 11, the Mamanguape faunas ranged between 24.4 and 26.6 (Fig. 2). The higher numbers are mainly due to the presence of both porcelaneous-miliolid and hyaline-perforate taxa and are more similar to values commonly encountered in coastal nearshore environments, at the seaward end of river estuaries, or in tropical lagoon or back-reef settings, where foraminiferal diversity is much higher than in mangroves (Saunders, 1958; Halicz et al., 1984; Debenay et al., 2000; Langer and Lipps, 2003; Thissen and Langer, 2017; Langer et al., 2013; Fajemila et al., 2020a).

The composition of our benthic foraminifera assemblages also contrasts with the ones found in previous studies on mangrove foraminifera from the southern Atlantic, where benthic foraminifera assemblages are exclusively dominated by agglutinated and hyaline-perforate species and mostly lack porcelaneous taxa (Fig. 2; Murray, 1991, 2006). Agglutinated foraminifera within the Mamanguape mangroves contribute a mere 1 to 2 % to the total assemblages, while other studies showed abundances that generally range above 40 % (Culver, 1990; Brönniman et al., 1992; Debenay and Guillou, 2002; Murray 2006).

Deviations from “typical” mangrove assemblages are also marked by the dominance and numerical abundance of *Pararotalia cananeiaensis* (Debenay et al., 2001), a taxon of a nearshore, shallow-water genus that is commonly not expected in large numbers in mangrove habitats (Geslin et al., 2002; Debenay et al., 2001). Within the Mamanguape mangroves, percent abundances of *P. cananeiaensis* were found to range between 20.1 and 24.2 %, making it the most abundant taxon of all species. Similar high abundances were recently reported by Damasio et al. (2020) from the Santos estuary (SE Brazil), where the species was reported from the bay and along the main channel but absent from the low-saline northernmost mangrove habitats. Eichler et al. (1995) reported the species from the Bay of Trapandé (Brazil) and attributed its inshore occurrence to the marine influence. Similarly, Murray et al. (1982) attributed the upstream presence of small coastal species to be indicative of an upstream transport of sediment of marine origin. Debenay et al. (2001) studied in detail the occurrence and transportation of *P. cananeiaensis* along Brazilian coasts under variable hydrodynamic conditions. They associated the presence of *P. cananeiaensis* in estuary channels with the intensity of marine intrusion into paralic systems and considered the upstream presence more likely a function of transport (allochtonous) than of *in situ* growth (see also Burone et al., 2006).

Seven different lines of evidence, however, strongly argue for an in-situ deposition of assemblages and autochthonous presence of *P. cananeiaensis*, at least within the Mamanguape estuary: i.) numerical abundances of *P. cananeiaensis*, Shannon-H, evenness, Fisher α, and Dominance index values do not vary substantially along the sampled transect and are largely uniform across the sample sites. Evidence for decreasing percent abundances upstream or features of successive filtering through the dense tributary mangrove channels is thus lacking; ii.) the Mamaguape River estuary is partially dammed by a natural sand barrier (Fig. 1) and acts as a hindrance in terms of water exchange and transport of coastal species deep into the estuary; iii.) except for two individuals, planktic foraminifera are absent, thus arguing against a large-scale transport of open-ocean taxa upstream; iv.) the preservation of taxa recovered ranges from good to excellent and includes both fragile, robust, smaller and larger species. Features of abrasion, transport or rolling over large distances were not observed; v.) the sample sites investigated all revealed a particularly high species richness of benthic foraminifera; vi.) the lack of both peneroplid and soritid foraminifera, two groups that are widely present in shallow-water nearshore biofacies in the region (Weinmann, 2009; Disaró et al., 2014), argues against a transport of species from nearshore to estuarine mangrove habitats; vii.) pyrite framboids were frequently observed within the chambers in the majority of species, reflecting the presence of anoxic conditions at the site of deposition (see Figure 9, 22–23). Pyrite formation is tightly intertwined with the presence of organic matter (Berner 1970, 1984; Thiel et al., 2019), suggesting that a.) foraminifera cell cytoplasm was present during deposition, b.) autolytic, bacterially- or prey-mediated protoplasm decay in foraminifera has been largely prevented (Murray and Bowser, 2000), and c.) foraminiferal assemblages are largely autochthonous. The time required for pyrite framboids to form the largest crystals, like the ones found in our assemblages, was previously estimated to be around 35 days (Rickard, 2019).

If a large-scale upstream transport of coastal species would indeed have taken place, a successive filtering and numerical reduction effect of coastal species through the dense mangrove stands would be expected. However, this has not been recorded in the assemblages. Instead, the number of benthic species was found to increase towards the inner parts of the estuary and the assemblages are therefore considered to be largely autochthonous.

Marine conditions supporting such diverse assemblages are manifested in high salinity values in our sampling area during both dry and wet seasons and are interpreted as the result of a longer residence time of marine waters in the estuary (Fig. 2, Dolbeth et al., 2016; Medeiros et al., 2018). Prevailing marine conditions within the dense Mamanguape mangrove estuary were also considered a major factor contributing to fish diversity in previous studies (MacDonald et al., 2008; Blaber, 2013).

The results obtained revealed unprecedentedly high species richness values and assemblages dominated by calcareous species instead of agglutinated forms, and represent an atypical example for a mangrove benthic foraminiferal fauna when compared to previous studies. While these findings may seem puzzling at first sight, they are considered to be mainly resulting from high salinity values in the upstream areas of the Mamanguape River Estuary (Table 2). The resemblance to shallow-water nearshore foraminiferal communities is both indicated by the presence of a large number of porcelaneous miliolid and hyaline-perforate species, and in the abundance of *P. cananeiaensis*. In addition, it should be noted that the low number of agglutinated specimens and species found in our assemblages is not an artefact of preservation, as samples were carefully treated and the material was picked immediately after transportation to the laboratory.

Salinity has long been recognized as a major driving force governing the species richness, composition of wall structural types and diversity of foraminiferal assemblages (Murray, 1991; Debenay et al., 1990). A distinct separation between agglutinated and calcareous taxa along a pronounced salinity gradient has recently been reported from Lagos Lagoon, where mangrove and low salinity environments are dominated by agglutinated foraminifera (Fajemila et al., 2020b). While the majority of mangrove assemblages from along the Atlantic coast of South America were reported to be dominated by agglutinated taxa, the Mamanguape mangrove estuary was found to contain abundant calcareous wall types and to be almost devoid of agglutinated taxa. Among the environmental framework conditions promoting such atypical mangrove assemblages of foraminifera, salinity stands out as a prominent control factor. Salinity recordings along the sampling traverse revealed values ranging between ~25 and 35 ‰, indicating mostly euhaline to brackish water conditions. The prevalence of marine conditions within the studied area of the Mamanguape estuary is supported by comparatively long residence times of marine waters, high tidal amplitudes, and semi-diurnal tidal flushing of the estuarine environment. The resemblance of the atypical mangrove assemblages to shallow-water nearshore biotas may thus be attributed to the intensity of marine conditions, where calcareous foraminifera dominate over agglutinated taxa (Boltovskoy, 1954; Todd and Brönnimann, 1957; Boltovskoy and Hincapié de Martínez, 1984; Scott et al., 1990; Debenay, 2001; Debenay et al., 2002; Debenay et al., 2004; Moreno et al., 2005; Eichler et al., 2007; Camacho et al., 2015; Shaw et al., 2016; Passos et al., 2017). The penetration of calcareous species into the Paraiba estuary, has also been reported from the neighbouring Paraiba estuary (Debenay et al., 2002). However, unlike the Mamanguape estuary, the Paraiba estuary receives freshwater discharge from more rivers, and invasions of marine foraminifera only occur during the dry season, and completely disappear during the rainy season (Debenay et al., 2002).

Independent of whether the foraminiferal assemblages are allochthonous or autochthonous, the atypical Mamanguape mangrove faunas raise questions concerning implications for the interpretations of the fossil record. Unlike previous studies on foraminifera from south American and many other mangroves environments around the world, where specialized agglutinated taxa dominated mangrove environments, exceptionally species-rich and diverse assemblages of foraminifera prevail within the dense mangroves at Mamanguape. Both Debenay (2000) and Woodroffe et al. (2005) demonstrated that a range of environmental factors jointly govern both the composition, distribution and preservation of foraminiferal biotas in mangrove environments. Besides salinity, these include the elevation, grain size, organic content and taphonomic processes related to low pH excursions resulting in the removal of agglutinated and calcareous taxa. Post-mortem disaggregation and taphonomic loss may thus bias the fossil record and constitute a serious constraint regarding paleoenvironmental reconstructions.

Mangrove ecosystems have existed at least since the Late Cretaceous and fossil evidence used for palaeoecological reconstructions is mostly based on organic remains (fruit, flowers, wood or leaves, or microfossils particularly pollen; Ellison et al., 1999) and sedimentological features (Augustinus, 1995). Sedimentation of typical fine-grained mangrove deposits results from the reduction in current velocity where tree trunks, prop roots and pneumatophores exercise a filter function and result in typical mangrove mud sediments. Within the Mamanguape estuary, the accumulation and vertical accretion of mangrove mud is a mixture of river-born clastic sediments, organic material produced by mangrove trees and associated fauna, and suspension-rich ocean floating debris penetrating mangrove swamps. In high precipitation areas and under low salinity conditions, the production of organic material is generally promoted, but reduces pH conditions within the sediment and limits carbonate availability and thus reproduction of calcareous foraminifera. On the other hand, agglutinated tests are known to resist low pH conditions and dissolution, while they are removed through oxidation-reduction reactions (Ellison and Nichols, 1976; Scott and Medioli, 1978; Boltovskoy, 1984; Goldstein, 1988 and the references therein; Thomas and Varekamp, 1991; Debenay et al., 2002; Debenay et al., 2004). However, in the absence of considerable rainfall and during the warm periods, penetration of coastal waters into the estuarine system occurs. Based on the intensity of the marine influence/tides, calcareous foraminifera start to dominate and get preserved in the otherwise brackish/freshwater realm (Boltovskoy, 1954; Todd and Brönnimann, 1957; Scott et al., 1990; Debenay 2001; Debenay et al. 2002; Debenay et al., 2004; Moreno et al., 2005; Eichler et al., 2007; Camacho et al., 2015; Shaw et al., 2016; Passos et al., 2017; Woodroffe et al. 2005). Normally, salinity tends to be higher in the downstream areas in estuaries, yet the upstream areas of the Mamanguape are characterized by high salinity (Table. 2), indicative of a consistent influence of oceanic waters penetrating even further upstream of the sampling sites.

6. Conclusions

Mangrove environments of the Mamanguape River estuary are home to diverse assemblages of benthic foraminifera including 33 porcelaneous, 53 hyaline-perforate and 7 agglutinated species and represent an extraordinary ecosystem characterized by atypical, highly diverse and species-rich benthic foraminiferal biotas. The atypical population structure features prominent components of hyaline-perforate and miliolid-porcelaneous benthic foraminifera and are unprecedented in the previous mangrove studies. The assemblages resemble coastal nearshore biotas that are traditionally not classified as mangrove foraminiferal faunas and are here considered to be the result of highly saline ocean waters consistently penetrating deep into the estuary and promoting the presence of compositionally diverse and species-rich biotas. When preserved in the fossil record, such assemblages are not readily related to mangrove ecosystems and would most likely be interpreted as a coastal, nearshore shallow-water environment. Our findings thus have implications for inferring environmental conditions of past mangrove ecosystems. Salinity was found to be the main controlling factor structuring benthic foraminiferal assemblages, where both the comparatively long residence time of marine waters and the low fresh-water inflow support prevailing euhaline to brackish water conditions and the presence of calcareous dominated, species-rich foraminiferal assemblages.

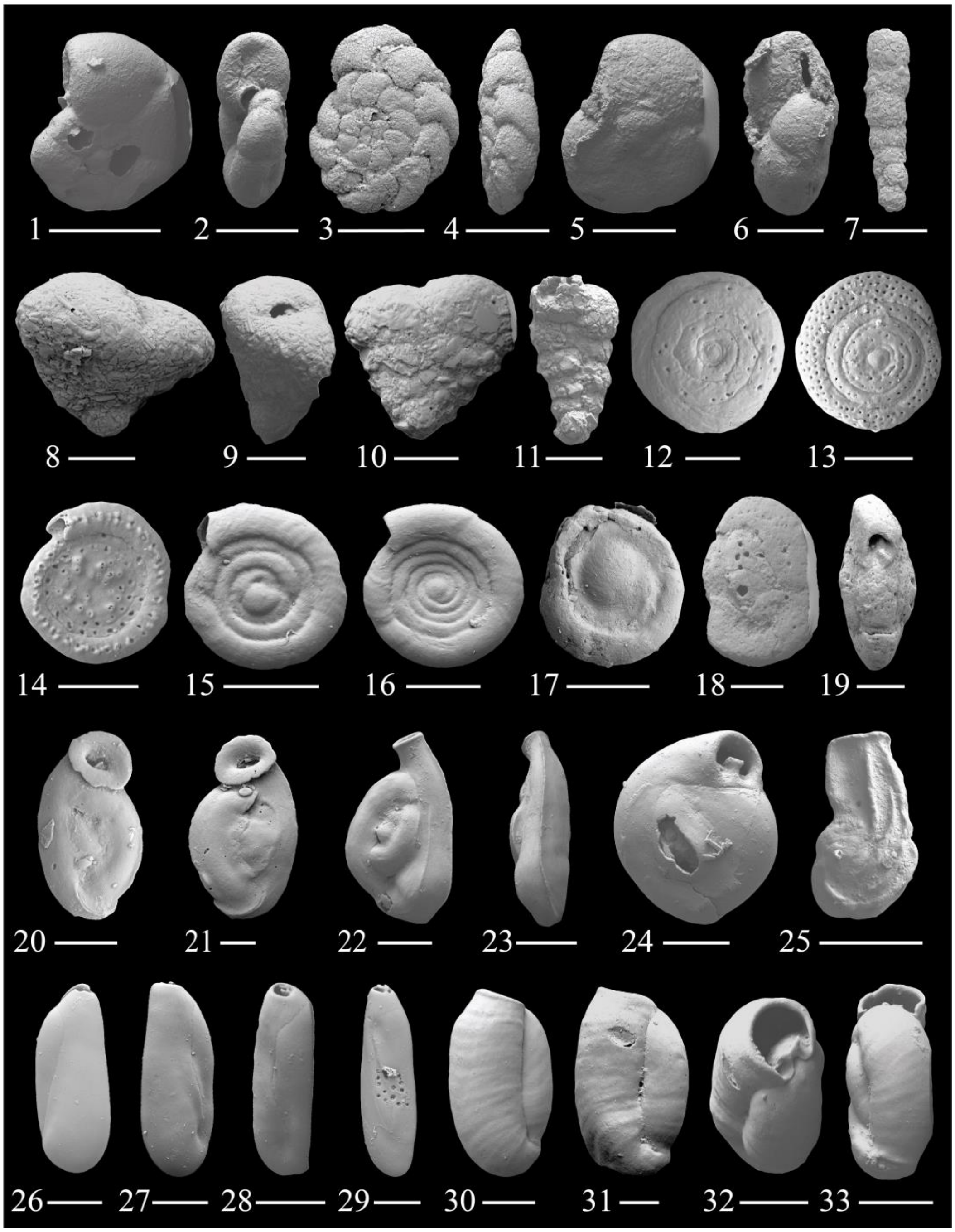

Figure 3. 1–2. *Trochammina inflata* (Montagu, 1808); 3–4. Rotaliammina trumbulli Seiglie, 1977; 5–6. *Arenoparrella mexicana* (Kornfeld, 1931); 7. *Bigenerina* sp. 1; 8–9. *Textularia* sp. 1; 10. Textularia cf. *T. semialata Cushman, 1913*; 11. *Textularia* sp. 2; 12. *Mychostomina revertens* (Rhumbler, 1906); 13–14. *Spirillina grosseperforata* Zheng, 1979; 15–16. *Cornuspira involvens* Reuss, 1850; 17. Cornuspira planorbis Schultze, 1854; 18–19. *Fischerina* sp. 1; 20–21. *Wiesnerella auriculata* (Egger, 1893); 22–23. *Edentostomina* sp. 1; 24. *Adelosina milletti* (Wiesner, 1911); 25. *Articulina alticostata* Cushman, 1944; 26–27. *Pseudotriloculina* sp. 1; 28–29. *Pseudotriloculina* sp. 2; 30–33. *Pseudotriloculina* sp. 3. Scale bar is 100 μm and 50 μm for Figs. 8-14, 17-19, 21-24, 26-29.

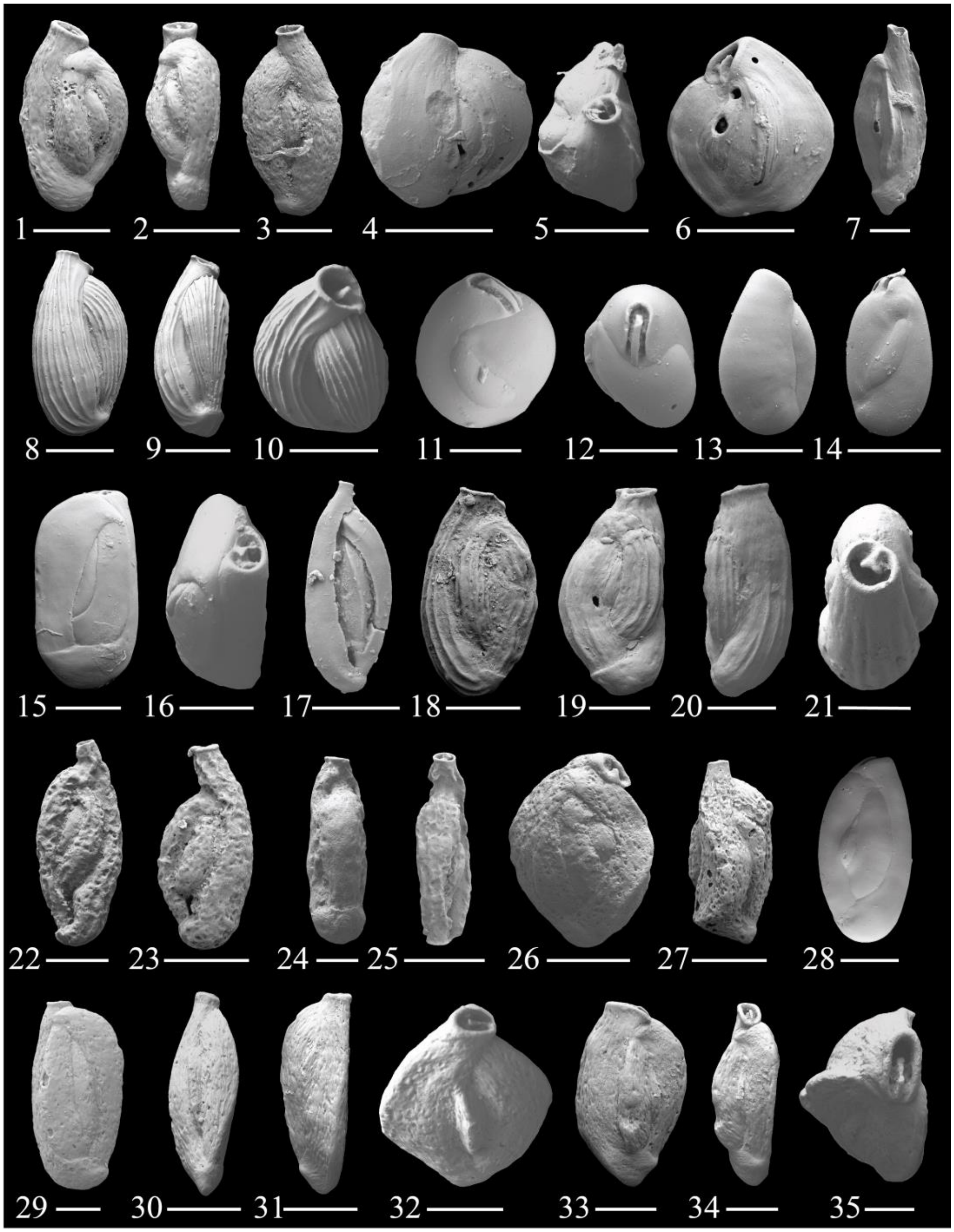

Figure 4. 1–3. *Quinqueloculina* cf. *Q. compta* Cushman, 1947; 4–6. *Quinqueloculina cuvierina* (d'Orbigny, 1839); 7. *Quinqueloculina* cf. *Q. zhengi* Parker, 2009; 8–10. *Quinqueloculina poeyana* d'Orbigny, 1839; 11–12. *Pseudolachlanella eburnea* (d'Orbigny, 1839); 13–14. *Pseudolachlanella bermudezi* (Acosta, 1940); 15–16. *Quinqueloculina moynensis* Collins, 1953; 17. *Quinqueloculina quinquecarinata* Collins, 1958; 18–21. *Quinqueloculina* cf. *Q. rebeccae* Vella, 1957; 22–25. *Sigmoilinita costata* Schlumberger, 1839; 26–27. *Quinqueloculina samoensis* Cushman, 1924; 28. *Quinqueloculina tantabiddyensis* Parker, 2009; 29. *Quinqueloculina* sp. 2; 30–32. *Quinqueloculina* sp. 1; 33–35. *Quinqueloculina* sp. 4. Scale bar is 100 μm and 50 μm for Figs.11-12, 16, 21, 24, 26, 29, 30-31, 33.

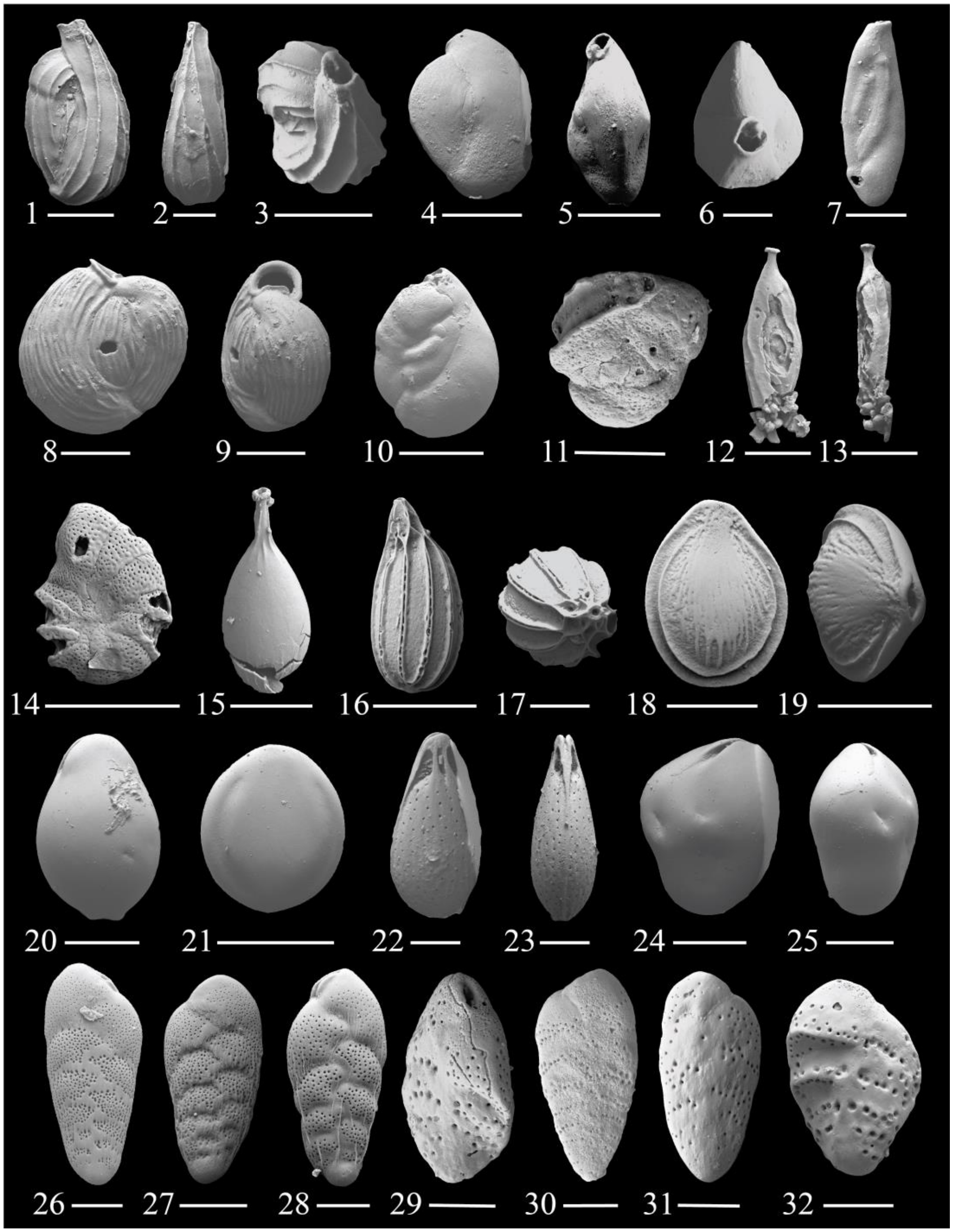

Figure 5. 1–3. *Quinqueloculina* cf. *Q. carinatastriata* Wiesner, 1923; 4–6. *Quinqueloculina* sp. 3; 7. *Quinqueloculina* cf. *Q. bosciana* d'Orbigny, 1839; 8-9. *Miliolinella webbiana* d'Orbingy, 1839; 10. *Miliolinella* sp. 1; 11. *Hauerina atlantica* Cushman, 1946; 12–13. *Inaequalina* sp. 1; 14. *Laevipeneroplis bradyi* Cushman, 1930; 15. *Procerolagena oceanica* (Albani, 1974); 16–17. *Cushmanina bricei* McCulloch, 1981; 18–19. *Fissurina colomboensis* McCulloch, 1977; 20. *Fissurina bispinata* Ujiié, 1963; 21. *Fissurina* sp. 2; 22–23. *Fissurina semimarginata* Reuss, 1870; 24–25. *Fissurina*? sp. 1; 26–28. *Bolivina densipunctata* Sellier de Civrieux, 1976; 29–32. *Bolivina ordinaria* Phleger and Parker, 1952. Scale bar is 100 *μm* and 50 *μm* for Figs. 2, 6-7, 17, 20, 22-25, 26, 28-32.

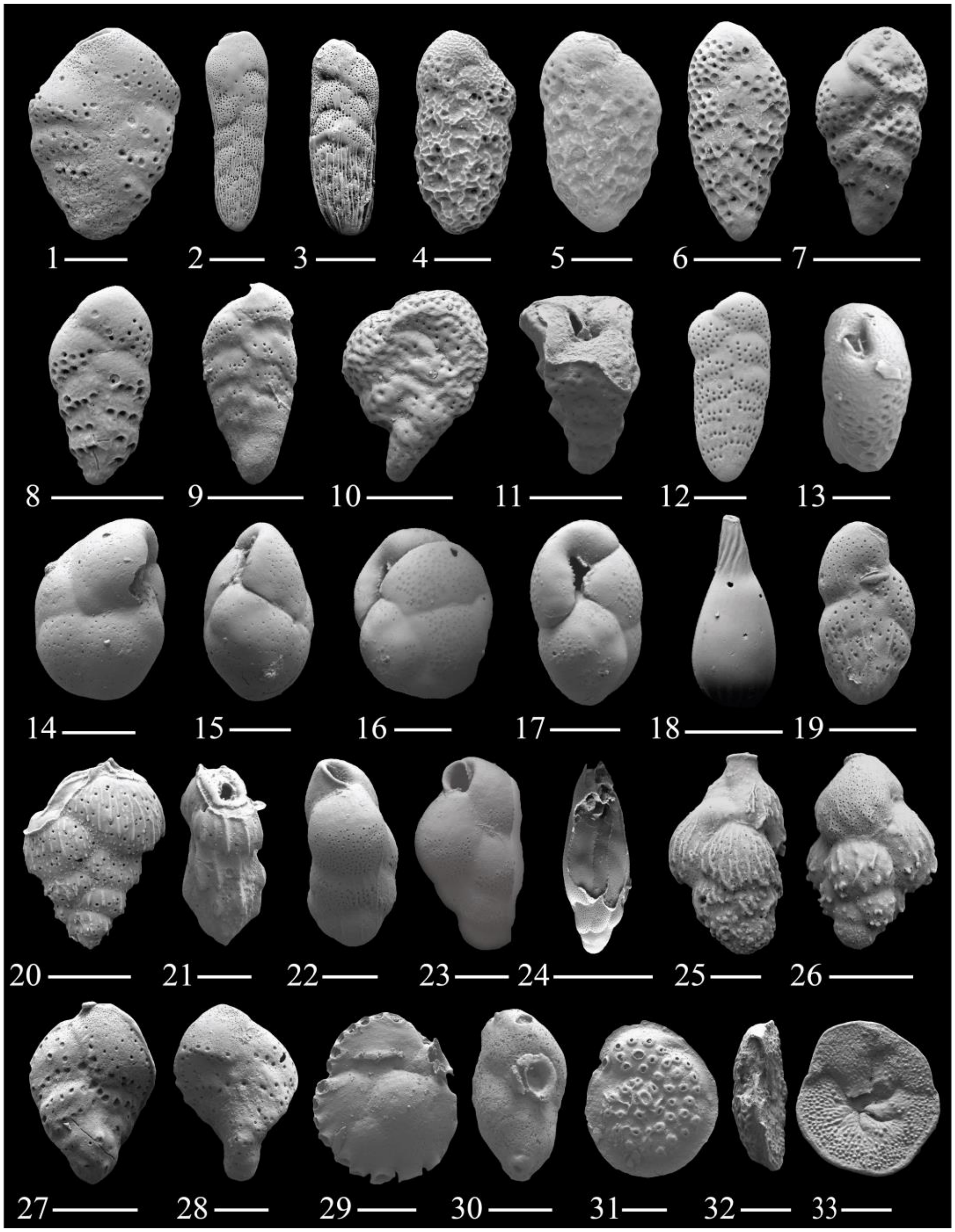

Figure 6. 1. *Bolivina ordinaria* Phleger and Parker, 1952; 2–3. *Bolivina striatula* Cushman, 1922; 4–5. *Bolivina variabilis* Williamson, 1858; 6–8. *Bolivina* cf. *B. variabilis* (Williamson, 1858); 9. *Bolivina* sp. 1; 10–11. *Abditodentrix rhomboidalis* (Millett, 1899); 12–13. *Bolivina brevior* Cushman, 1925; 14–15. Globocassidulina rossensis Kennett, 1967; 16–17. *Globocassidulina crassa* (d'Orbigny, 1839); 18. *Lagena tenuis*; 19. *Loxostomina costulata* (Cushman, 1922); 20–21. Sagrina pulchella d'Orbigny, 1839; 22–23. *Cassidelina* sp. 1; 24. *Buliminella elegantissima* (d'Orbigny, 1839); 25–26. *Angulogerina* cf. *A. occidentalis* (Cushman, 1923); 27–28. *Sigmavirgulina tortuosa* (Brady, 1881); 29–30. *Siphonina reticulata* (Czjzek, 1848); 31–33. *Discorbitina pustulata* (Heron-Allen and Earland, 1913). Scale bar is 100 μm and 50 μm for Figs. 1, 4-5, 12-17, 21-23, 25-26, 28-33.

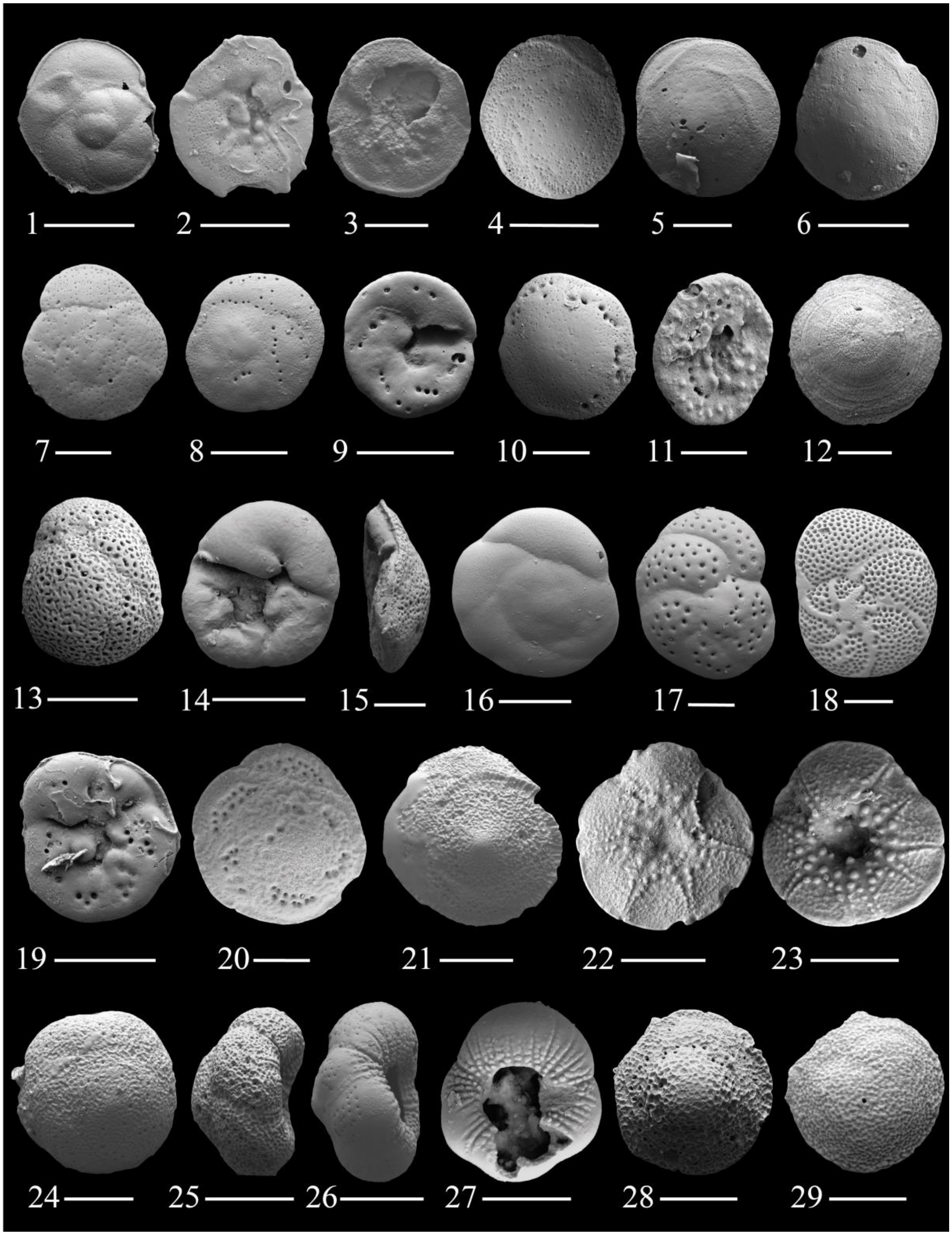

Figure 7. 1–3. *Orbitina carinata* Sellier de Civrieux, 1977; 4–6. *Rotorbis auberii* (d'Orbigny, 1839); 7–9. *Neoconorbina* sp. 1; 10–11. *Neoconorbina radiatogranulata* Parker, 2009; 12. *Neoconorbina terquemi* (Rzehak, 1888); 13–15. *Rosalina bradyi* (Cushman, 1915); 16. *Rosalina* sp. 1; 17–19. *Rosalina* sp. 2; 20–23. *Glabratella carinata* Seiglie and Bermúdez, 1965; 24–27. *Glabratella mirabilis* Seiglie and Bermúdez, 1965; 28–29. *Glabratella carinata* Seiglie and Bermúdez, 1965. Scale bar is 100 μm and 50 μm for Figs. 3-5, 7, 10-12, 14-15, 17, 20-29.

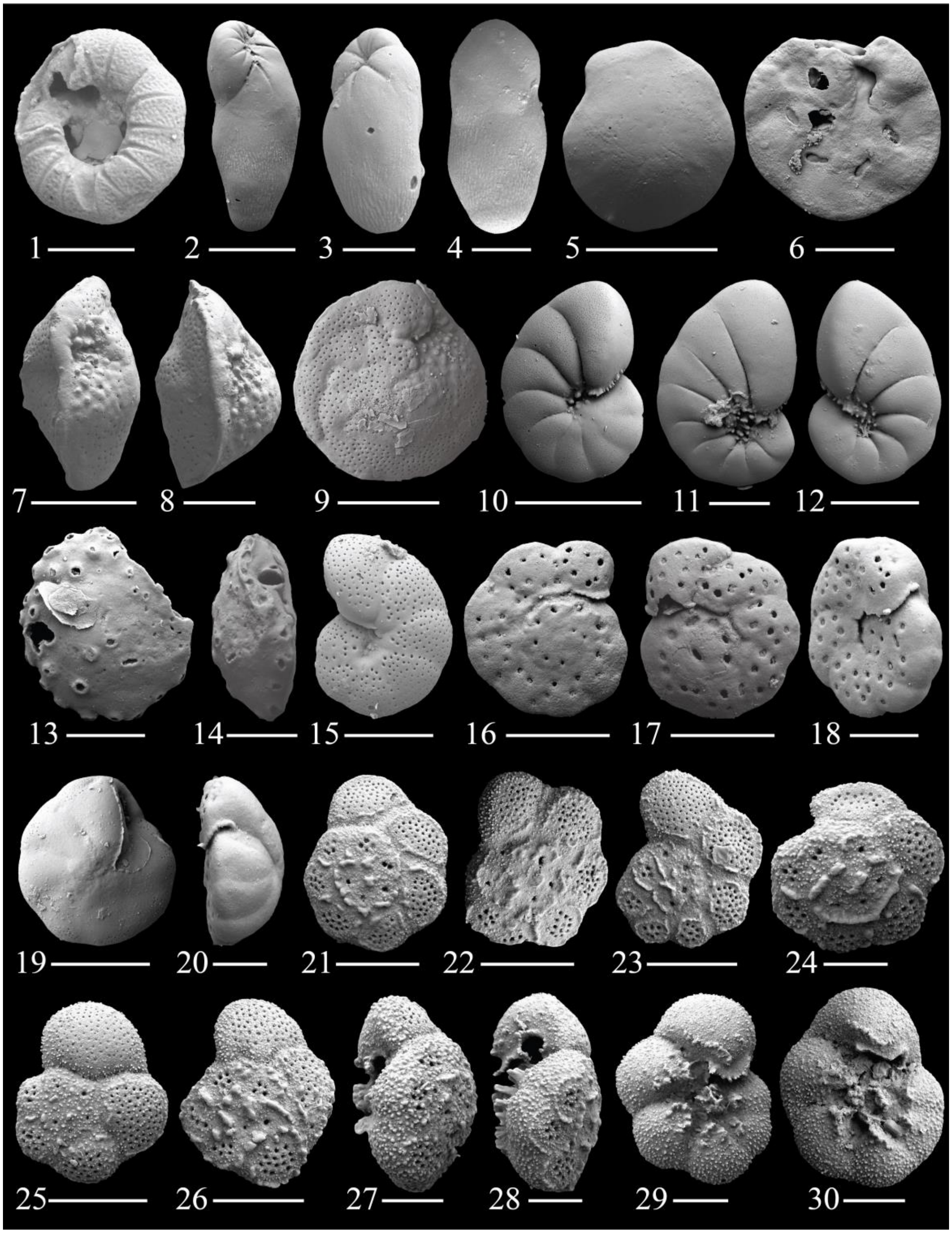

Figure 8. 1. Glabratella mirabilis Seiglie and Bermúdez; 2–4. *Elongobula parallela* (Cushman and Parker, 1931); 5–6. *Eoponidella pulchella* (Parker, 1952; 7–8. *Amphistegina lessonii* (d‘Orbingy, 1826); 9. *Amphistegina radiata* (Fichtel and Moll, 1892); 10–12. *Nonionides grateloupii* (d‘Orbingy, 1826); 13–14. *Svratkina acuta* (Sidebottom, 1918); 15. *Anomalinulla glabrata* (Cushman, 1924); 16–20. *Anomalinulla* sp 1.; 21–30. *Pararotalia cananeiaensis* Debenay, Duleba, Bonetti De Melo e Souza & Eichler, 2001. Scale bar is 100 μm and 50 μm for Figs.1, 3-4, 6-9, 13-14, 18-20, 24, 27-30.

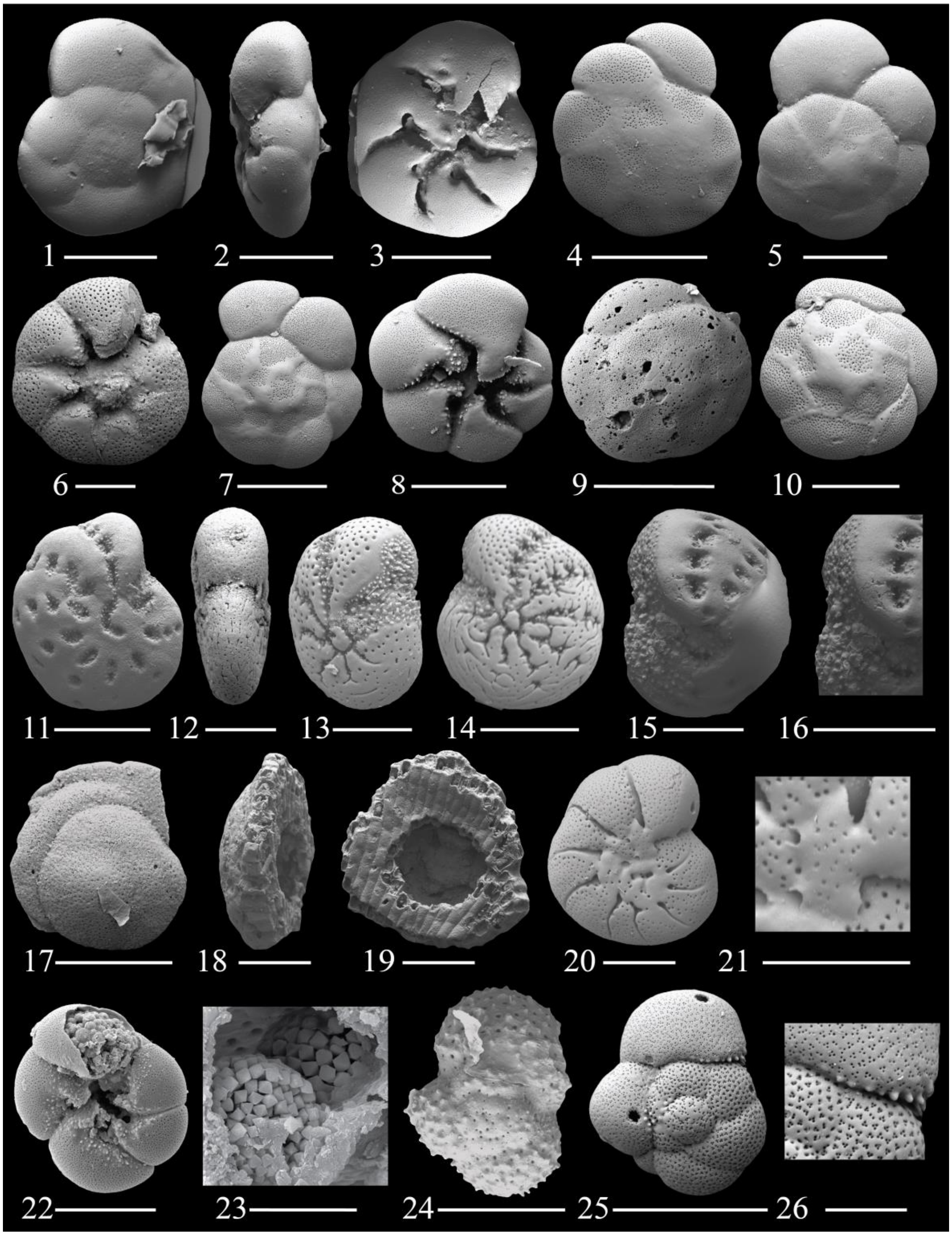

Figure 9. 1–3. *Ammonia advena* Cushman, 1922; 4–10. *Ammonia veneta* (Schultze, 1854)*;* 11–14. *Cribroelphidium mirum* Langer and Schmidt-Sinns, 2007; 15–16. *Elphidium sagrum* (d'Orbingy, 1839); 17–19. *Discorbis willamsoni* Chapman and Parr, 1932; 20-21. *Astrononion* gallowayi Loeblich and Tappan, 1953; 22–23. Pyrite framboids found in our specimens, 24. *Globigerinoides* sp. 1; 25–26. *Globigerinoides* sp. 2. Scale bar is 100 μm, 50 μm for Figs. 6, 13, 15-16, 18-20, 25 μm for Figs. 21, 26, and 10 μm for Fig. 23.

Author Contribution

ML conceptualized the study and collected the material. NS and ML analyzed the data, prepared and wrote the manuscript.

Declaration of competing interest

The authors declare that they have no conflict of interest.

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