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Checklist, assemblage composition, and biogeographic assessment of Recent benthic foraminifera (Protista, Rhizaria) from São Vincente, Cape Verdes

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Abstract

We describe for the first time subtropical intertidal foraminiferal assemblages from beach sands on São Vincente, Cape Verdes. Sixty-five benthic foraminiferal species were recognised, representing 47 genera, 31 families, and 8 superfamilies. Endemic species were not recognised. The new checklist largely extends an earlier record of nine benthic foraminiferal species from fossil carbonate sands on the island. *Bolivina striatula*, *Rosalina vilardeboana* and *Millettiana milletti* dominated the living (rose Bengal stained) fauna, while *Elphidium crispum*, *Amphistegina gibbosa*, *Quinqueloculina seminulum*, *Ammonia tepida*, *Triloculina rotunda* and *Glabratella patelliformis* dominated the dead assemblages. The living fauna lacks species typical for coarse-grained substrates. Instead, there were species that had a planktonic stage in their life cycle. The living fauna therefore received a substantial contribution of floating species and propagules that may have endured a long transport by surface ocean currents. The dead assemblages largely differed from the living fauna and contained redeposited tests deriving from a rhodolith-mollusc carbonate facies at <20 m water depth. A comparison of the Recent foraminiferal inventory with other areas identified the Caribbean and Mediterranean as the most likely source regions. They have also been constrained as origin points for littoral to subtidal macroorganisms on other Cape Verdean islands. Micro-and macrofaunal evidences assigned the Cape Verde Current and North Equatorial Current as the main trajectories for faunal immigrations. The contribution from the NW African coast was rather low, a pattern that cannot be explained by the currently available information.

Key words: Benthic foraminifera, biogeographic patterns, Eastern Atlantic, taxonomy, catalogues

Introduction

The species inventory of oceanic islands, their evolution and their connectivity has been the subject of scientific research for decades (McArthur & Wilson 1967, and references therein). Earlier studies focused on immigration, evolution, and extinction controlling the species richness. Later studies investigated the role of isolation, size and age of the islands in balancing the ratio of endemic and immigrated taxa (e.g. Whittaker & Fernándes-Palacios 2007; Whittaker *et al.* 2008). Shallow-water organisms living on and around the islands came into focus of recent investigations (e.g. Hachich *et al.* 2015; Cunha *et al.* 2017; Pinheiro *et al.* 2017). They suggested that gene flow, i.e. connectivity, and island age were important for the biogeographical distribution of species. Furthermore, Pleistocene sea-level changes were considered a critical variable in the evolution and dispersal of marine organisms on and between oceanic islands (Ávila *et al.* 2018).

Benthic foraminifera are millimetre to sub-millimetre sized, shell-bearing unicellular organisms living in all marine environments. Foraminifera are well adapted to their habitat, have short generation times, and their tests are readily preserved in the sediment after reproduction. Benthic foraminifera are therefore considered as sensitive indicators for the prevailing environmental conditions for today and the geological past (Murray 2006 and references therein). Global warming and sea-level rise is expected to profoundly change the assemblage structure of intertidal and near-shore foraminiferal communities in the near future (Schmidt *et al.* 2011; Weinmann & Goldstein 2016; Müller-Navarra *et al.* 2017). In order to constrain their resilience, to assess and monitor the impact of Global Change on near-coastal ecosystems in the future, baseline studies

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and surveys of Recent foraminiferal distributions are needed with appropriate spatial coverage on an ocean-wide scale (Murray 2013).

Benthic foraminifera on oceanic islands and sea mounds are of particular importance Since these spots provide stepping stones for long-range species dispersal (e.g. Heinz *et al.* 2004). Unfortunately, the island faunas have scarcely been investigated (e.g. Murray & Smart 1994; Javaux & Scott 2003; Lübbers & Schönfeld 2018). In many places, the only records date back to the HMS Challenger expedition in the late 19th century (Di Bella *et al.* 2015).

The goal of the present paper is to explore the intertidal benthic foraminiferal inventory of the Cape Verdean island São Vincente, which has not been described to date. We hypothize that a distance of >500 km between the Cape Verde archipelago and Western Africa is sufficient to act as an effective zoogeographic barrier for small, near-shore benthic foraminifera, similar to the Eastern Pacific Barrier for symbiont-bearing larger foraminifera (Förderer *et al.* 2018). Once the hypothesis is rejected, the species inventory is to be described and migration pathways are to be delineated, in particular, to which possible source regions the species associations show the highest similarities.

Geography and geology. The Cape Verdes archipelago is located in the subtropical eastern North Atlantic around 17°N 24°W, and 570 to 870 km off the western African coast of Senegal. The islands are situated on the western edge of the 3000 to 3500 m deep Cape Verde Rise that has been built up by hotspot volcanism since the latest Oligocene (Torres *et al.* 2002; Ramalho 2011). The formation of the island São Vicente started more than 9 Ma ago. The island emerged during the first eruptive phase between 6.5 and 4.5 Ma. A second growth phase between 4.5 and 3.1 Ma, and minor recent volcanism around 0.3 Ma augmented and stabilised the island (Holm *et al.* 2008; Ancochea *et al.* 2010). In contrast to other Cape Verde islands, São Vicente has undergone no significant uplift since its origin (Ramalho *et al.* 2010). The volcanic edifice was prone to mass wasting by a huge land slide during the Pliocene (Ancochea *et al.* 2010) and by coastal erosion today. High cliffs are common all around the island. Beach sands and late Quaternary sediments have accumulated in only a few places (Ramalho *et al.* 2013: there Fig. 10).

Eolian sand sheets, Recent and fossil dunes are common on the Cape Verdian islands (e.g. Samrock *et al.* 2018). The dunes show northeastward dipping stoss slopes and steep southwestwards dipping leeward slip faces indicating the direction of the prevailing trade wind. The sands are mainly composed of marine carbonate debris from mollusks, corals, echinoderms, foraminifera and coralline red algae. Rhodoliths, i.e. fragments of red algae, account for the vast majority of bioclasts (74–96 %), while foraminifera are reported to contribute only 1–5 % to the sand-sized components. Lithic grains, e.g. basalts, were a minor constituent with 5–10 % of the eolian sands (Johnson *et al.* 2013).

Oceanographical setting. The hydrography in the vicinity of the Cape Verdes is influenced by different surface currents at the southeastern limb of the North Atlantic subtropical gyre. The southward-flowing Canary Current (CC), including the Canary Upwelling Current (CUC), transports cool North Atlantic Central water from the Azores along the African coast. The CC deviates from the coast off Cape Blanc at 21°N (Mittelstaedt 1991), turns westwards and passes into the North Equatorial Current (NEC) flowing to the north of the Cape Verdes (Fernandes *et al.* 2005). A small, anticlockwise circulating gyre is centred to the southwest of the Archipelago and named Guinea Dome (GD) (Siedler *et al.* 1992). To the south of the GD, the North Equatorial Counter Current prevails and carries warm South Atlantic Central Waters from offshore Brazil eastwards (NECC) (Richardson & Walsh 1986). A northern limb of the NECC turns northwards off the African shelf edge forming the the Cape Verde Current (CVC) (Pelegrí & Peña-Izquierdo 2015). The CVC merges the NEC in a ENE-WSW running Cape Verde Frontal Zone, which touches the northern isles of the Cape Verde Archipelago (Zenk *et al.* 1991; Arístegui *et al.* 2009). This convergence zone is an effective barrier between the North Atlantic and South Atlantic surface water circulation cells. The current systems show a pronounced seasonality, notably an intensification of the NECC and CVC and a northward displacement of the NEC during late summer and fall. This is related to seasonal migrations of the Intertropical Convergence Zone and the resulting variations in trade wind intensity (Stramma & Siedler 1988; Siedler *et al.* 1992). This seasonality is also mirrored in surface water temperatures around the island São Vicente as recorded by the Cape Verde Ocean Observatory mooring station. The temperatures showed minimum values of 21.5–22.5°C in March and a maximum of 26–27.5°C in September. However, the surface water salinity of 36.5 units was rather stable (Fiedler 2012).

Previous foraminiferal studies. Living intertidal or near-shore foraminifera had not been studied at or around São Vicente and other Cape Verdian islands to date. The majority of Recent foraminiferal studies in this region focused on sampling transects and grids on the West African continental slope and shelf, estuaries and lagoons (Haake 1980; Debenay 1990; Schiebel 1992; Debenay & Redois 1997; Jorissen *et al.* 1998; Redois & Debenay 1999; Reymond *et al.* 2014). Lutze (1980) reported the bathyal benthic foraminiferal fauna of three stations from 3568 to 1948 m water depth on the outer Cape Verde Rise, close to the eastern islands of the archipelago. Brady (1984) figured seven benthic foraminiferal species from HMS Challenger stations 352 and 352A, of which five commonly occurred in shallow waters. The deployments were assigned to a water depth of 11 fathoms (20 m), close to São Vicente (Jones 1994). In fact, station coordinates and hydrographic measurements taken on board HMS Challenger locate this sample on the continental slope off Guinea-Bissau and at >550 m depth (Burbage 2009).

Fossil benthic foraminifera were reported among other biogenic components in petrographic studies of Quaternary sediments from Cape Verdian islands (Torres & Soares 1946, Johnson *et al.* 2013). Nine species were recognised in carbonate sands from São Vincente, of which two were extinct.

Material and methods

Surface sediment samples were taken by opportunity on an excursion to São Vicente during the HOSST Cape Verde Summer School at Mindelo in May and June 2018. The sample locations were chosen according to accessibility and wetness of the sediment surface. In particular : a shallow lagoon behind the breakwater wall at Baia das Gatas, the landward slope of the beach bar in a runnel at Sao Pedro, and the top of the swash zone on the beach of Calhau were sampled. Sampling was done close to the actual water level. The uppermost 1–2 cm of the surface sediment was scraped off with a spoon, transferred into 100 ml PVC (Kautex®) bottles, and immediately preserved and stained with a solution of 2 g rose Bengal in 1 l alcohol (40 %, vodka) (Lutze & Altenbach 1991; Schönfeld 2012: there p. 58). The preservative was exchanged two weeks later in order to rise the ethanol concentration to >90 % for long-term storage (Schönfeld *et al.* 2012). Global Positioning System (GPS) coordinates and sampling time were retrieved from a mobile phone and noted on the vials (Appendix Table 1). The hights of the samples were obtained from the tide curve for Porto Grande at Mindelo (16.8667°N, 24.9833°W), as calculated by the web application of Xtide for the respective sampling day (http://tides.mobilegeographics.com/locations/5064.html) following Rashid (2015). They were consequently referred to the mean tidal level (MTL) at Mindelo.

The foraminiferal samples were prepared and analysed following the procedures described by Schönfeld *et al*. (2013), and Lübbers & Schönfeld (2018). The volume of the samples ranged from 54 to 77 cm^3. The residues 63–2000 µm were split using a HAVER RT 6,5 sample splitter to facilitate microscopic work. One sixteenth was wet picked for rose Bengal stained foraminifera that were alive at the time of sampling. This split was dried and further subdivided with an Otto microsplitter to an aliquot that contained approximately 100–300 unstained (dead) foraminiferal tests. These subsamples were dry picked. The specimens from the living fauna and dead assemblages were sorted by species in separate Plummer cell slides, fixed with glue, and counted. Once rose Bengal stained specimens were not found in the 1/16 split, the remaining 15/16 were treated with a sodium polytungstate solution of 2.303 g cm^{-3} density to recover all foraminifera from the sample (Parent *et al.* 2018). The float ate and deposited parts of the sample were washed with tap water to remove remaining polytungstate and dried at 50 °C. The floatate was carefully examined for living foraminifera and added to the deposited part of the sample again after picking.

Benthic foraminiferal morphotypes may include different genotypes (OTUs) that are depicted by subtle morphological characters (e.g.Darling *et al*., 2016). Once these characters are disclosed, they may be used to discriminate morphotypes representing a single OTU (Roberts *et al*. 2016; Kucera *et al*. 2017; Richirt *et al.* 2019). We therefore attempted to discern the species up to a comprehensible level, in particular miliolids that were previously lumped as ”*Quinqueloculina* spp.”. Species were determined by using both taxonomic literature and online data bases (Ellis and Messina 1940; WoRMS Editorial Board 2018). Literature from all ocean basins was considered, since organisms in a submillimeter size range tend to have a more cosmopolitan rather than endemic distribution (e.g. Fenchel & Finlay, 2004). Preference was given to literature providing high-quality images and accurate taxonomic references for the respective taxon. Once the holotype figure was ambiguous, we gathered all accessible information. For instance, we approached the Smithonian collections at Washington DC, USA, for supplementary type images, and examined reference slides with living foraminifera (rose Bengal stained, plankton catchments) from well investigated areas (southern Portugal, Gulf of Cadiz, Puerto Rico) (Schönfeld 1997, 2002; Kucera *et al.* 2017). In the literature, foraminiferal species were often reported with several different genus names. We have chosen that genus which has not been amended later, which was in best agreement with the morphological characters of the species, or which has been validated by recent genetic investigations. A genus is regarded as monophyletic group comprising at least two different species. The use of monospecific genera (e.g. *Lobatula*) was therefore avoided in the present study. Images were taken with a Keyence VHX-700 FD digital microscope at the Institute of Geosciences, Christian-Albrechts University Kiel, and with a Zeiss LEO 1455VP Scanning Electron Microscope (SEM) at the Institute for Geology, University of Hamburg. Due to the explorative character of the present study, we documented as many species as possible.

Regional species occurrences were compiled by also considering literature without images but with taxonomic references, provided the species names‘ lists were given with the author and publication year. Google®, Bing® and Mac OS X Spotlight search functions were used to retrieve notes on the occurrence of each species.

Grainsize distribution and coarse fraction composition were analysed by using remaining aliquots from the sample residues. They were dry sieved with ISO 3310-1 certified sieves with a mesh sizes of 125, 150, 250, 355, 500, and 1000 µm. The size fraction >2000 µm was considered as well. Coarse fraction analysis was performed by applying the protocol of Sarnthein (1971). The subfractions were weighed and further subdivided with an Otto microsplitter. Between 103 and 265 grains were identified and counted under a stereo-microscope from each subfraction. Only three major groups of components were considered, i.e. volcanic grains, biodetritic grains and foraminifera (e.g. Wolf & Thiede 1991). Therefore, the accuracy of the census is deemed acceptable (van der Plas & Tobi 1965 Fatela & Taborda 2002). The composition of the sand-sized fraction >63 µm was calculated by combining the proportion of individual components with the weight of the subfractions examined. The weighed proportions were added for each component, and percentages were calculated in reference to the sum of all subfraction weights (Sarnthein 1971).

Results

Composition of the coarse-grained fraction. The grain-size distributions revealed that the deposits were pure medium to coarse sands. The grains were well rounded, the surfaces were smooth, and the carbonate grains appeared as having been polished. Some of these carbonate grains showed a layered and punctuated internal structure of translucent and opaque material resembling the reticulate structure of coralline red algae. Spines of regular echinoids, coral fragments, gastropod shells and fragments, bivalve shells and debris, fragments of balanid plates, bryozoans and benthic foraminifera could be identified in the size fractions >500 µm. Judging only from the aspect of the grains‘ surface, rhodoliths could not be distinguished with certainty from strongly bioeroded or encrusted shell debris of molluscs. The biogenic components were therefore summarized as undifferentiated bioclasts. Their proportion ranged from 78–92 %. Benthic foraminifera were rather rare with 1–3 % (Appendix Table 1). The foraminiferal tests were mostly well or moderately preserved. Only a few species showed a moderately to poor preservation. SEM images revealed that in particular tests of *Amphistegina gibbosa* have been bioeroded by filamentous microborings (e.g. Young & Nelson, 1988; Günther, 1990).

The terrigenous fraction comprised basalts, single mafic minerals, altered or silicified pumice of light green and brown colour, dark volcanic glass particles, and ash charts. Light coloured charts were common at Calhau only. They may derive from the young strombolian volcanic cones at Calhau and Bahia das Gatas (Ancochea *et al.* 2010; Ricardo Ramalho, pers. comm. 6th December 2018). The proportion of the volcanic particles ranged from 7–19 % of the coarse fraction (Appendix Table 1). These figures are in good agreement with point counting data on thin sections of Pleistocene dune sands on other Cape Verdian islands (Johnson *et al.* 2013).

Foraminiferal check lists. Sixty-five benthic foraminiferal species were recorded in the present study, of which 42 species were recorded in the living fauna and 52 species in the dead assemblages (Appendix Table 2). They belonged to 47 genera, 31 families and 8 superfamilies.

The genus *Quinqueloculina* and *Bolivina,* with 10 and 5 different species, was rather diverse. *Elphidium* showed 3 species, while *Lepidodeuterammina* showed 2 and *Peneroplis* showed 3 species. All other genera were represented by a single species. Endemic species were not recognised. These figures rejected our initial hypothesis; a distance of >500 km between the Cape Verdes and Western Africa is not an effective zoogeographic barrier for near-shore benthic foraminifera.

Fifty-seven fossil benthic foraminiferal species were recognised on the Cape Verdian islands (Torres & Soares 1946). Ten of these species were extinct (Appendix Table 3). From the nine species recorded on São Vincente by the authors, only *Elphidium cripsum* was found in the present study.

Taxonomy

The suprageneric foraminiferal classification as proposed by Pawlowski *et al*. (2013) and Holzmann & Pawlowski (2017) was applied in the present study. If a certain genus or a family was not rooted in the tree of gene sequences by the authors, it was affiliated to the respective family or superfamily after the classification scheme of Loeblich and Tappan (1988). Species are listed in alphabetical order under the respective genera. The type reference, as retrieved from the Ellis and Messina (1940) catalogue, and at least one reference to a high-quality image in a recent publication is given for each species. References to the specimens images in this paper are given in square brackets after the type reference.

Phylum Foraminifera d'Orbigny 1826

Class Tubothalamea Pawlowsk, Holzmann & Tyska 2013

Order Miliolida Delage & Hérouard 1896

Superfamily Cornuspiracea Schultze 1854

Family Cornuspiridae Schultze 1854

Genus *Cornuspira* Schultze 1854

Cornuspira involvens (Reuss) = *Operculina involvens* Reuss 1850, p. 370, pl. 46, figs. 20a, 20b [Plate 1, Fig. 3]. Cimmermann & Langer (1991), p. 25, pl. 15, figs. 4–7. Spezzaferri *et al.* (2015), p. 59, pl. 6, fig. 7. Müller-Navarra *et al.* (2016), p. 74, fig. 3.6.

Family Fischerinidae Millett 1898

Genus *Wiesnerella* Cushman 1933a

Wiesnerella auriculata (Egger) = *Planispira auriculata* Egger 1893, p. 245, pl. 3, figs. 13–15. Revets (2000), p. 371, pl. 2, fig 31. Sanchez (2010), p. 155, pl. 2, fig. 16. Milker & Schmiedl (2012), p. 46, fig. 12.4.

Family Ophthalmidiidae Wiesner 1920

Genus *Spirophthalmidium* Cushman 1927

Spirophthalmidium sp. 1 Cimerman & Langer 1991, p. 26, pl. 17, figs. 8–10 [Plate 2, Fig. 3]. Milker & Schmiedl (2012), p. 47, fig. 12.12.

Superfamily Miliolacea Ehrenberg 1839

Family Spiroloculinidae Wiesner 1920

Genus *Adelosina* d'Orbigny 1826

Adelosina carinata-striata Wiesner 1923, p. 77, pl. 14, figs. 190–191 [Plate 1, Fig. 19]. Cimerman & Langer (1991), p. 28, pl. 20, figs. 1–4. "*Quinqueloculina carinatastriata*" Bouchet *et al.* (2007), p. p. 205, pl. 1, figs. 1–6. Yokes *et al.* (2014), fig. 7.1. Note: this species was common in the Mediterranean and recently has invaded the Atlantic coast of Europe (Bouchet *et al.* 2007).

Genus *Spiroloculina* d'Orbigny 1826

Spiroloculina scrobiculata Cushman 1921, p. 406, pl. 81, fig. 1 [Plate 1, Fig. 2, Plate 5, Fig. 13]. Loeblich & Tappan (1994), p. 44, pl. 67, figs. 10–17. Szarek (2001), p. 102, pl. 11, fig. 16. Note: the costae are faint and anastomosing. They are developed around the whole chambers and not only on the outer side as in *Spiroloculina antillarum* d'Orbigny 1839b.

Family Hauerinidae Schwager 1876

Genus *Cycloforina* Łuczkowska 1972

Cycloforina rugosa (d'Orbigny) = *Quinqueloculina rugosa* d'Orbigny 1826, p. 302, no. 24. Cimerman & Langer (1991), p. 33, pl. 28, fig. 3, 4. Hanagata & Nobuhara (2015), p. 21, fig. 8.4.

Cycloforina tenuicollis (Wiesner) = *Miliolina tenuicollis* Wiesner 1923, p. 44, 48, pl. 6, fig. 66. Cimerman & Langer (1991), p. 33, pl. 28, figs. 5–6. "*Cycloforina*? *tenuicollis*" Milker & Schmidl (2012), p. 54, fig. 14.8. Note: this species has been recorded only in the Mediterranean to date.

Genus *Quinqueloculina* d'Orbigny 1826

Quinqueloculina auberiana d'Orbigny 1839b, p. 193, pl. 12, figs. 1–3 [Plate 1, Fig. 8]. Cimerman & Langer (1991), p. 36, pl. 32, figs. 8, 9. Milker & Schmiedl (2012), p. 56, figs. 15.1, 2. Hanagata & Nobuhara (2015), p. 21, figs. 8.7–8.8.

Quinqueloculina bosciana d'Orbigny 1839b, p. 191, pl. 11, figs. 22–24 [Plate 1, Figs. 4, 5]. Van Hengstum & Scott (2011), p. 224, fig. 12.16. Milker & Schmidl (2012), p. 56, fig. 15.7–9. Weinmann & Goldstein (2016), fig. 3D. Note: This species is very similar to *Quinqueloculina laevigata* and may also be mistaken with *Quinqueloculina oblonga*. Earlier chambers of *Quinqueloculina bosciana* are oblique to the longitudinal axis of the test. The top of the last chamber forms a low collar around the aperture.

Quinqueloculina disparilis d'Orbigny 1826, p. 302, no. 21 [Plate 1, Fig. 14, 15]. Cimerman & Langer (1991), p. 36, pl. 33, figs. 1–4. Milker & Schmiedl (2012), p. 56, figs. 15.10–12. Non "*Adelosina disparilis*" Sanchez (2010), p. 156, pl. 2, fig. 4.

Quinqueloculina eburnea (d'Orbigny) = *Triloculina eburnea* d'Orbigny 1839b, p. 180, pl. 10, figs 21–23 [Plate 2, Fig. 9]. Thissen (2015), p. 46, pl. 7, figs. 1–3. "*Pseudolachnalella eburnea*" Chen & Lin (2017), fig. 2.3. "*Affinetrina eburnea*" Poignant (2019), pl. 2, figs. 11–12.

Quinqueloculina laevigata d'Orbigny 1826, p. 143, pl. 3, figs. 31–33 [Plate 1, Figs. 9–12]. Carvalho & Chermont (1952), p. 82, pl. 1, figs. 3a–c. Cimerman & Langer (1991), p. 37, pl. 33, figs. 8–11. Milker & Schmiedl (2012), p. 58, figs. 15.13–15. "*Pseudotriloculina laevigata*" Yokes *et al.* (2014), figs. 8.8a, b. "? *Adelosina laevigata*" Laut *et al.* (2017), p. 137, pl. 1, fig. M. Note: this species is more slender than *Quinqueloculina seminulum* and the outline is rounded triangular.

Quinqueloculina lamarckiana d'Orbigny 1839b, p. 189, pl. 11, figs. 14, 15 [Plate 1, Fig. 7]. Bock (1971), p. 19, pl. 6, figs. 7–9. Jones (1994), p. 21, pl. 5, fig. 12. Javaux & Scott (2003), p. 20, figs. 4.12, 4.13.

Quinqueloculina lata Terquem 1876, p. 82, pl. 11, fig. 8a–c [Plate 1, Fig. 16]. Le Campion (1968), p. 247, pl. 22, figs. 3a–c. non Sanchez (2010), p. 157, pl. 2, fig. 6. Milker & Schmiedl (2012), p. 58, fig. 15.16.

Quinqueloculina parvula Schlumberger 1894, p. 255, pl. 3, figs. 8–9 [Plate 1, Figs. 17–18]. Cimerman & Langer (1991), p. 37, pl. 34, figs. 6–8. Milker & Schmidl (2012), p. 59, figs. 15.25–27. Frontalini *et al.* (2015), fig. 5a, b. Note: the rough surface, inflated chambers, and a rim borderung the aperture are distinctive characters of this species.

Quinqueloculina seminulum (Linné) = *Serpula seminula* Linné 1758, p. 786 [Plate 1, Fig. 13, Plate 5, Fig. 12]. Jones (1994), p. 21, pl. 5, fig. 6. Reymond *et al.* (2014), pl. 1, figs. 17, 18. "*Quinqueloculina seminula*" Raposo *et al.* (2016), p. 11, fig. 3.b. Laut *et al.* (2017), p. 137, pl. 5, fig. I. Note: this species shows a large morphological variety as noted by Haake (1980: p. 8). The tests are always elongated-ovate in lateral view and subrounded-triangular in peripheral view.

Quinqueloculina stelligera Schlumberger 1893, p. 68, pl. 2, figs. 58, 59 [Plate 1, Fig. 6, Plate 5, Fig. 11]. Cimerman & Langer (1991), p. 38, pl. 34, figs. 13–15. Mendes *et al.* (2012), p. 38, figs. 2.5a–c. Milker & Schmiedl (2012), p. 59, figs. 16.1–4. Note: the elongated O-shaped outline in lateral view and acute costae on the peripheral chamber margins are diagnostic features of this species.

Genus *Miliolinella* Wiesner 1931

Miliolinella webbiana (d'Orbigny) = *Triloculina webbiana* d'Orbigny 1839c, p. 140, pl. 3, figs. 13–15 [Plate 2, Fig. 1]. *"Triloculina webbiana"* Vénec-Peyré (1984), pl. 4, fig. 5. Cimerman & Langer (1991), p. 42, pl. 39, figs. 1–3. Yokes *et al.* (2014), Fig. 8.7.

Genus *Sigmamiliolinella* Zheng 1988

Sigmamiliolinella australis (Parr) = *Quinqueloculina australis* Parr 1932, p. 7, pl. 1, fig. 8 [Plate 2, Fig. 6]. Jones (1994), p. 21, pl. 5, figs. 10–11. Loeblich & Tappan (1994), p. 58, pl. 100, figs. 1–3.

Genus *Triloculina* d'Orbigny 1826

Triloculina rotunda d'Orbigny in Schlumberger 1893, p. 64, pl. 1, figs. 48–50 [Plate 2, Fig. 2, Plate 5, Figs. 8–10]. Bock (1971), p. 27, pl. 11, figs. 8–10. Sanchez (2010), p. 159, pl. 2, fig. 14. *"Triloculina asymetrica"* Thissen (2015), p. 50, pl. 8, figs. 4–6.

Genus *Subedentostomina* McCulloch 1981

Subedentostomina sp. 1 Cimerman & Langer 1991, p. 48, pl. 46, fig. 9 [Plate 2, Fig. 4].

Genus *Parrina* Cushman 1931

Parrina bradyi (Millett) = *Nubecularia bradyi* Millett 1898, p. 261, pl. 5, figs 6a, b [Plate 2, Fig. 5]. Jones (1994), p. 17, pl. 1, figs. 5–8. Loeblich & Tappan (1994), p. 59, pl. 64, figs. 1–3, pl. 105, figs. 1–10. Dias *et al.* (2010), Fig. 2.9.

Family Peneroplidae Schulze 1854

Genus *Peneroplis* de Montfort 1808

Peneroplis carinatus d'Orbigny 1839a, p. 33, pl. 3, figs. 7, 8 [Plate 2, Fig. 13, Plate 5, Fig. 4]. Wright & Hay (1971), p. 33, pl. 13, fig. 9. Javaux & Scott (2003), p. 17, figs. 3.10 and 3.11. Araujo & Machado (2008), p. 38, pl. 1, figs. 10, 11. "*Laevipeneroplis carinatus*" Sanchez (2010), p. 160, p. 1, fig. 6. Note: the markedly lower chamber height, a higher number of chambers, and the closed umbilicus discriminates this species from *Peneroplis proteus*.

Peneroplis pertusus (Forskål) = *Nautilus pertusus* Forskål 1775, p. 125, no. 65 [Plate 2, Fig. 8, Plate 5, Figs. 6,7]. Cushman (1930b), p. 35, pl. 12, figs. 3–6. Bock (1971), p. 34, pl. 13, fig. 10. Jones (1994), p. 29, pl. 13, figs. 16–17, 23. Mouanga (2017), p. 211, pl. 10, figs. 18–19. Note: One specimen of the dead assemblage from Baia das Gatas has developed a rectilinear stage similar to *Coscinospira arietina* (Batsch 1791). The aperture constitutes a series of pores in the depression on the apertural face of the last chamber, some are bordered by a lip, which is a diagnistic feature of *Peneroplis*.

Peneroplis proteus d'Orbigny = *Peneroplis protea* d'Orbigny 1839b, p. 60, pl. 7, figs. 7–11. Cushman (1930b), p. 37, pl. 13, figs. 1–17. Bock (1971), p. 34, pl. 13, fig. 11. Jones (1994), p. 29, pl. 14, figs. 3, 4.

Family Soritidae Ehrenberg 1839

Genus *Amphisorus* Ehrenberg 1839

Amphisorus hemprichii Ehrenberg 1839, p. 130, pl. 3, fig. 3. Cushman (1930a), p. 51, pl. 18, figs. 5–7. Jones (1994), p. 30, pl. 16, fig. 7. Caruso & Cosentino (2014), fig. 4.11, figs. 5.12–16. Chen & Lin (2017), fig. 2.5.

Genus *Sorites* Ehrenberg 1839

Sorites marginalis (Lamarck) = *Orbulites marginalis* Lamarck 1816, p. 196 [Plate 2, Fig. 7]. Müller-Merz & Lee (1976), fig. 1. "*Parasorites marginalis*" Jones (1994), p. 30, pl. 15, figs. 1–5, 5. Javaux & Scott (2003), p. 22, fig. 5.5. Araujo & Machado (2008), p. 38, pl. 2, fig. 1. Note: *Amphisorus hemprichii* Ehrenberg 1839 of authors. *Sorites marginalis* has later been designated as type species for the genus *Sorites* (Loeblich & Tappan 1988: p. 382). *Sorites marginalis* has been designated as type species for the genus *Sorites* (Loeblich & Tappan 1964: p. C496). The coiling direction of the initial spire is the same as in the younger part of the test of *Sorites marginalis*. The spiral part is, however, detached in the similar species *Broeckina orbitoloides* (Hofker 1930). The latter also shows a complete encirculation of chambers younger than 19 (e.g. Hallock & Peebles 1993, pl. 2, fig. 5), which happens later in *Sorites marginalis*.

Order Spirillinida Hohenegger & Piller 1975)

Family Spirillinidae Reuss & Fritsch 1861

Genus *Spirillina* Ehrenberg 1843

Spirillina vivipara Ehrenberg 1843, p. 422, pl. 3, sec. 7, fig. 41 [Plate 4, Fig. 11]. Parker (1954), p. 522, pl. 8, figs. 15, 16. Bock (1971), p. 55, pl. 20, fig. 4. Forster (2013), p. 175, pl. 5, fig. 5.

Class Globothalamea Pawlowski, Holzmann & Tyska 2013

Order Rotaliida Delage & Hérouard 1896

Superfamily Discorboidea Ehrenberg 1838

Family Discorbidae Ehrenberg 1838

Genus *Neoeponides* Reiss 1960

Neoeponides auberii (d'Orbigny) = *Rosalina auberii* d'Orbigny 1839b, p. 94, pl. 4, figs. 5–8. Jones (1994), p. 94, pl. 87, fig. 8. „*Rotorbis auberi*" Loeblich & Tappan (1994), p. 137, pl. 278, figs. 1–11. "*Rotorbis auberi*" Nobes & Uthicke (2014), p. 24, figs. 26a–26f. "*Neoeponides auberi"* Hanagata & Nobuhara (2015), p. 95, figs. 29.1, 29.2.

Family Rosalinidae Reiss 1963

Genus *Rosalina* d'Orbigny 1826

Rosalina vilardeboana d'Orbigny 1839a, p. 44, pl. 6, figs. 13–15 [Plate 3, Figs. 7–9, Plate 6, Figs. 1–5]. Cimerman & Langer (1991), p. 67, pl. 72, figs. 1–2. Jones (1994), p. 93, pl. 86, figs. 9a–c. Debenay *et al.* (2001), pl. 5, figs. 6,11. Note: the flattened test, wide umbilicus, and the short, triangular to comma-shaped umbilical flabs extending from the last chambers discriminate this species from other *Rosalina* species. The earlier chambers on the spiral side may be brown to orange-coloured.

Genus *Tretomphalus* Möbius 1880

Tretomphalus bulloides (d'Orbigny) = *Rosalina bulloides* d'Orbigny 1839b, p. 98, pl. 3, figs. 2–5. "*Cymbaloporetta bulloides*" Rückert-Hilbig (1983), p. 46, pl. 2, figs. 1–6, pl. 5, figs. 1–6. Loeblich & Tappan (1988), p. 262, pl. 612, figs. 1–11. "*Cymbaloporetta bulloides*" Thissen (2015), p. 88, pl. 18, figs. 1–4. Note: the designation of this species to the genus *Tretomphalus* has been validated by Loeblich & Tappan (1988: p. 263) and is followed herein.

Genus *Neoconorbina* Hofker 1951

Neoconorbina terquemi (Rzehak) = *Discorbina terquemi* Rzehak 1888, p. 228 [Plate 3, Figs. 10–13]. Jorissen (1987), p. 40, pl. 3, figs. 3, 4. Jones (1994), p. 94, pl. 88, figs. 5–8. Debenay *et al.* (2001), pl. 5, figs. 7, 8. Javaux & Scott (2003), p. 16, figs. 3.7, 3.8.

Superfamily Rotalioidea Ehrenberg 1839

Family Elphidiidae Galloway 1933

Genus *Elphidium* Montfort 1808

Elphidium crispum (Linné) = *Nautilus crispus* Linnaeus 1758, p. 709 [Plate 4, Figs. 7–9, Plate 5, Fig. 5]. Milker & Schmidl (2012), p. 120, figs. 27.13–14. Reymond *et al.* (2014), pl. 4, fig. 9. Nobes & Uthicke (2014), figs. 28 l-r.

Elphidium excavatum (Terquem) = *Polystomella excavata* Terquem 1875, p. 429, pl. 2, figs. 2a, 2b. "*Cribroelphidium* sp." Redois & Debenay (1999), pl. 1, figs. 5a, 5b. "*Elphidium excavatum* forma *selseyensis*" Poignant *et al.* (2000), p. 399, pl. 1, figs. 7, 11. Camacho *et al.* (2015), p. 26, fig. 5.11. "*Elphidium selseyense*", genotype S5, Darling *et al.* (2016), fig. 4E.

Elphidium margaritaceum (Cushman) = *Elphidium advenum* (Cushman) var. *margaritaceum* Cushman (1930b), p. 25, pl. 10, figs. 3a, 3b. Voorthuysen (1973), p. 45, pl. 4, figs 7a, b. Cimerman & Langer (1991), p. 79, pl. 92, figs. 4–6.

Family Ammoniidae Saidova 1981

Genus *Ammonia* Brünnich 1771

Ammonia tepida (Cushman) = *Rotalia beccarii* var. *tepida* Cushman 1926, p. 79, pl. 1 [Plate 3, Figs. 15, 16, Plate 6, Figs. 12, 13]. Hayward *et al.* (2004), p. 264, pl. 2–4, fig. T. Laut *et al.* (2016), pl. 2, figs. G, H. "Phylotype T1". Richirt *et al.* (2019), p. 83, fig. 7. Note: The specimens are in good agreement with the locotypes figured by Hayward *et al.* (2003). They also have raised sutures on the spiral side. An umbilical plug may be developed in adult specimens, which otherwise is a characteristic feature of *Ammonia parkinsoniana*. The specimens from São Vincente have a much lower number of chambers in the last whorl with 6–8 as compared to *A. parkinsoniana* that usually has 10 chambers.

Family Haynesinidae (Mikhalevic 2013)

Genus *Haynesina* Banner and Culver 1978

Haynesina depressula (Walker & Jacob) = *Nautilus depressulus* Walker & Jacob 1798, p. 641, pl. 14, fig. 33 [Plate 3, Fig. 14]. "*Nonion depressulus*" Haake (1962), p. 40, pl. 3, figs. 1, 2. "*Nonion depressulus*" Horton & Edwards (2006), pl. 4, figs 22a, b. "*Haynesina depressula*" Camacho *et al.* (2015), p. 25, fig. 5.8. "*Haynesina depressula*" genotype S17, Darling *et al.* (2016), figs. 3.G, 4.Q. Note: the assignment of this species to the genus *Haynesina* is due to its close genetic similarity and monophyletic relationship with *Haynesina germanica* (Ehrenberg 1839).

Superfamily Glabratelloidea Loeblich & Tappan 1964

Family Glabratellidae Loeblich & Tappan 1964

Genus *Glabratella* Dorreen 1948

Glabratella patelliformis (Brady) = *Discorbina patelliformis* Brady 1884, p. 647, pl. 88, fig. 3, pl. 89, fig. 1 [Plate 3, Figs. 1, 2, Plate 6, Figs. 9–11]. Abu-Zied *et al.* (2011), p. 362, figs. 9.1, 2. Ernst *et al.* (2011), p. 112, fig. 4.40, 4.41. Milker & Schmidl (2012), p. 102, fig. 23.16–17.

Superfamily Serioidea Holzmann & Pawlowski 2017

Family Uvigerinidae Haeckel 1894

Genus *Trifarina* Cushman 1923

Trifarina bella (Phleger & Parker) = ”*Angulogerina bella*” Phleger & Parker 1951, p. 12, pl. 6, figs. 7, 8 [Plate 2, Figs. 22–24]. ”*Angulogerina bella*” Parker (1954), p. 521, pl. 8, fig. 7. ”*Angulogerina bella*” Platon *et al.* (2005), p. 268, pl. 2, figs. 18, 19. Note: this species has only been recorded in the Gulf of Mexico, off Puerto Rico (”*Angulogerina angulosa”* by Schmucker 2000), and off the western coast of Central America to date.

Family Bolivinitidae Cushman 1927

Genus *Bolivina* d'Orbigny 1839a

Bolivina plicatella Cushman 1930a, p. 46, pl. 8, Fig. 10 [Plate 2, Figs. 25, 26]. Mehrnusch (1993), figs. 22–27. Milker & Schmiedl (2012), p. 80, fig. 19.21. Fenero *et al.* (2013), pl. 1, fig. 2a–b.

Bolivina striatula Cushman 1922a, p. 27, pl. 3, fig. 10 [Plate 2, Figs. 14–17, Plate 6, Figs. 6–8]. Smith (1963), p. A19, pl. 30, figs. 9, 10. Martins & Gomes (2004), p. 100, fig. 2.57. Abu-Zied *et al.* (2008), p. 65, pl. 1, fig. 30. Raposo *et al.* (2016), p. 4, fig. 3E.

Bolivina subspinescens Cushman 1922b, p. 48, pl. 7, fig. 5 [Plate 2, Fig. 19]. Bock (1971), p. 47, pl. 17, fig. 4. Seiler (1975), p. 62, pl. 1, fig. 10. Schiebel (1992), p. 34, pl. 1, fig. 7. Milker & Schmiedl (2012), p. 81, fig. 19.24.

Bolivina tongi Cushman, 1929, p. 93, pl. 13, figs. 29 a, b [Plate 2, Fig. 18]. Schiebel (1992), p. 34, pl. 1, figs. 10 a, b. Phipps (2012), p. 81, fig. 8.5. Note: the test is rather thick-walled as compared to other *Bolivina* species, and the chamber walls are slightly opaque. The species-specific marginal costae may be indistinct or even missing in juvenile specimens.

Bolivina variabilis (Williamson) = *Textularia variabilis* Williamson 1858, p. 76, pl. 6, figs. 162, 163 [Plate 2, Figs. 27–30]. Sellier de Civrieux (1976), p. 26, pl. 24, figs. 1–9. Martins & Gomes (2004), p. 102, fig. 2.58 A–D. Kucera *et al.* (2017), Figure 7, Lineage 1.

Family Cassidulinidae d'Orbigny 1839b

Genus *Cassidulina* d'Orbigny 1826

Cassidulina minuta Cushman 1933b, p. 92, pl. 10, fig. 3 [Plate 3, Fig. 3]. Lutze (1974), p. 39, pl. 10, figs. 147–148. Boltovskoy *et al.* (1980), p. 22, pl. 7, figs. 7–11. Schiebel (1992), p. 40, pl. 2, fig. 12. Erdem & Schönfeld (2017), p. 18, fig. 7.15.

Family Turrilinidae Cushman 1927

Genus *Floresina* Revets 1990

Floresina paralleliformis (McCulloch) = *Buliminella parallelliformis* McCulloch 1977, p. 241, pl. 103, fig. 26 [Plate 2, Figs. 20, 21, Plate 6, Figs. 14, 15]. Revets (1990), p. 160, pl. 1, figs. 7–9. Note: this species has only been recorded in the Pacific Ocean to date. A similar species, *Floresina amphiphaga*, has been described as predatory on reef-dwelling *Amphistegina gibbosa* in Florida (Hallock & Talge 1994). *Floresina amphiphaga* differs from *Floresina paralleliformis* in being stout, costate and showing more numerous grooves on the apertural face.

Superfamily "Clade 3" Holzmann & Pawlowski 2017

Family Nonionidae Schultze 1854

Genus *Nonionoides* Saidova 1975

Nonionides grateloupi (d'Orbigny) = *Nonionina grateloupi* d'Orbigny 1826, p. 294. "Nonion grateloupi" Cushman (1939), p. 21, pl. 6, figs. 1–7. "*Nonionella grateloupi*" Schiebel (1992), p. 51, pl. 5, fig. 12. Loeblich & Tappan (1994), p. 158, pl. 342, figs. 1–5. Thissen (2015), p. 95, pl. 19, fis. 21–23.

Genus *Pseudononion* Asano 1936

Pseudononion granuloumbilicatum Zheng 1979, p. 229, pl. 25, fig. 9 [Plate 4, Fig. 10]. Loeblich & Tappan (1994), p. 158, pl. 355, figs. 5–10. Note: this species been recorded only in the eastern Pacific and Timor Sea to date.

Family Epistominellidae Holzmann & Pawlowski 2017

Genus: *Epistominella* Husezima & Maruhasi 1944

Epistominella sp. Note: the specimen is very similar to the deep-water species *Epistominella exigua* (Brady 1884), but the earlier parts of the test comprise more than half of the test diameter on the dorsal side, which otherwise is a character of the shelf-dwelling species *Epistominella vitrea* Parker 1953. None-the-less, our specimen is missing the inflated chambers, depressed sutures and rounded periphery of the latter species.

Family Stainforthiidae Reiss 1963

Genus: *Stainforthia* Hofker 1956

Stainforthia fusiformis (Williamson) = *Bulimina pupoides* var. *fusiformis* Williamson 1858, p. 63, pl. 5, figs. 129, 130 [Plate 2, Fig. 12]. Gooday & Alve (2001), figs. 3, 4, pl. 1, figs. H–L, pl. 3, figs. A–J. Alve (2003), fig. 1. Murray (2003), p. 26, fig. 10.1–4.

Family Buliminellidae Hofker 1951

Genus *Buliminella* Cushman 1911

Buliminella elegantissima (d'Orbigny) = *Bulimina elegantissima* d'Orbigny 1839a, p. 51, pl. 7, figs. 13, 14 [Plate 2, Fig. 31, 32]. Höglund (1947), p. 215, pl. 18, fig. 1a, b. Barrick (1989), p. 263, fig. 3.1. Rodrigues *et al.* (2014), fig. 11.4 e.

Family Cibicididae Cushman 1927

Genus: *Cibicides* Montfort 1808

Cibicides lobatulus (Walker & Jacob) = *Nautilus lobatulus* Walker & Jacob 1798, p. 642, p. 14, fig. 36. Jones (1994), p. 97, pl. 93, fig. 1 a–c. "*Lobatula lobatula*" Martins & Gomes (2004), p. 211, fig. 2.126 A, B. Abu-Zied *et al.* (2008), pl. 3, figs. 1–2.

Family Discorbinellidae Sigal 1952

Genus *Discorbinella* Cushman & Martin 1935

Discorbinella araucana (d'Orbigny) = *Rosalina araucana* d'Orbigny 1839, p. 44, pl. 6, figs. 16–18 [Plate 3, Figs. 4, 5]. Jones (1994), p. 93, pl. 86, figs 10–11. Non "*Valvulineria araucana"* Ingle *et al.* (1980), p. 146, pl. 8, figs 9–11. Note: the presumably different species from the western Pacific, with 6 chambers per whorl, has a markedly lower number than those described by d'Orbigny, which should have 8 or more chambers.

Genus *Hanzawaia* Asano 1944

Hanzawaia bertheloti (d'Orbigny) = *Rosalina bertheloti* d'Orbigny 1839c, p. 135, pl. 1, figs. 28–29 [Plate 3, Fig. 6, Plate 4, Fig. 2]. "*Discorbinella bertheloti*" Jones (1994), p. 95, pl. 89, figs. 10–12. Non Parker (1954), p. 523, pl. 8, figs. 22,23, non Redois & Debenay (1999), pl. 2, figs. 3a, b, non Milker & Schmidl (2012), p. 104, figs. 23.29–30 (= *Hanzawaia concentrica*). Note: the species has often been mistaken with *Hanzawaia concentrica* (Cushman 1918), which is very similar in shape and chamber arrangement. The last 4 to 5 chambers of the latter species extend into triangular, axe-shaped flabs on the umbilical side, each off set from the previous, and thereby forming a rosette collar around the umbilicus. This feature is poorly developed in the present species. The flabs are only recognisable at very high microscope magnifications. Consequently, umbilical flabs neither have been mentioned nor drawn by d'Orbigny (1839). The specimens figured by Brady (1884) also show no flabs, thus mirroring the 19th century view of this species. Furthermore, d'Orbigny's *Rosalina bertheloti* is much more compressed than the holotype of *Hanzawaia concentrica* (Cushman 1918).

Family Cymbaloporidae Cushman 1927

Genus *Millettiana* Banner, Pereira & Desai 1985

Millettiana milletti (Heron-Allen & Earland) = *Cymbalopora milletti* Heron-Allen & Earland 1915, p. 689, pl. 51, figs. 32–35 [Plate 4, Figs. 4–6, Plate 6, Figs. 16, 17]. "*Cymbaloporetta milletti*" Rückert-Hilbig (1983), p. 51, pl. 6, 1–6. Jones (1994), p. 102, pl. 102, fig. 9. Loeblich & Tappan (1994), p. 153, pl. 329, figs. 1–12. Note: only microspheric specimens without a floating chamber were found in the present study. Adult specimens show a beehive-shaped outline in lateral view, and the umbilicus is surrounded by four inflated chambers. The species differs from *Cymbaloporetta squammosa* d'Orbigny 1839b by the distinct sutures that are hardly visible in the latter, and by the umbilicus, which is not covered by an umbilical disc as in *Cymbaloporetta squammosa* (e.g., Rückert-Hilbig 1983). Such an umbilical disc has not been seen in our specimens from São Vincente.

Family Bagginidae Cushman,1927

Genus *Eponides* Montfort 1808

Eponides repandus (Fichtel & Moll) = *Nautilus repandus* Fichtel & Moll 1798, p. 35, pl. 3, figs. a–d [Plate 4, Figs. 12–14]. Parker (1954), p. 529, pl. 9, figs. 27–28. Jones (1994), p. 104, pl. 104, figs. 19a–c. Note. *Eponides repandus* has been reported from many deep and shallow water carbonate environments at strong near-bottom currents (e.g. Bader 2001; Reymond *et al.* 2014).

Genus *Valvulineria* Cushman 1926

Valvulineria minuta Parker 1954, p. 527, pl. 9, figs. 4, 5, 6. Jones (1994), p. 96, pl. 91, fig. 4. Loeblich & Tappan (1994), p. 135, pl. 268, figs 1–3. Sen Gupta *et al.* (2009), p. 85, pl. 108, figs. 1–4.

Family Fursenkoinidae Loeblich & Tappan 1961

Genus *Sigmavirgulina* Loeblich & Tappan 1957

Sigmavirgulina tortuosa (Brady) = *Bulimina tortuosa* Brady 1881, p. 57. *Bolivina tortuosa*, Brady, 1884, pl. 52, figs. 31–34. Sellier de Civrieux (1976), p. 25, pl. 22, figs. 8–10, pl. 23, figs. 1–7. *Sigmavirgulina tortuosa* (Brady), Jones (1994), p. 58. Milker & Schmidl (2012), p. 93, fig. 21.12.

Family Siphoninidae Cushman 1927

Genus *Siphonina* Reuss 1850

Siphonina tubulosa Cushman 1924, p. 40, pl. 13, figs. 1, 2. Jones (1994), p. 100, pl. 96, figs. 5–7. Thissen (2015), p. 82, pl. 16, figs. 4–6. García Gallardo *et al.* (2017), fig. 7.Q.

Family Amphisteginidae Cushman 1927

Genus *Amphistegina* d'Orbigny 1826

Amphistegina gibbosa d'Orbigny 1839b, p. 120, pl. 8, figs. 1–3 [Plate 4, Figs. 15–17, Plate 5, Figs. 1–3]. Crouch & Poag (1979), p. 91, pl. 1, figs 5, 8. Eichler *et al.* (2019), fig. 1. "*Amphistegina lessonii*" Bock (1971), p. 58, pl. 21, fig. 10. Note: *Amphistegina lessonii* d'Orbigny 1826 occurs in the Pacific, and the slightly more compressed *Amphistegina gibbosa* d'Orbigny 1839b is confined to the Atlantic (Larsen 1977). *Amphistegina lessonii* is sinistrally coiled and shows 8 chambers per whorl, while *Amphistegina gibbosa* is dextrally coiled and has on average 15 chambers per whorl (Crouch & Poag 1979). In fact, 17 of 26 well preserved *Amphistegina* specimens of the dead assemblage from Sao Pedro are dextrally coiled and show 12 to 14 chambers. The Cape Verdean specimes show a high variability from plano-convex to biconvex shape, as it has been observed off Brazil (Eichler *et al.* 2019). The thickness of most tests resembles the High Light morphotype of Hallock *et al.* (1986, there Figure 4).

Order "Textulariida" Delage & Hérouard 1896

Family Trochamminidae Schwager,1877

Genus *Trochammina* Parker & Jones 1859

Trochammina squamata Jones & Parker 1860, p. 304. Schiebel (1992), p. 63, pl. 7, figs. 12a, b. "*Tritaxis challengeri*" Jones (1994), p. 46, pl. 41, figs. 3a–c. "*Tritaxis challengeri*" Szarek (2001), p. 91, pl. 7, fig. 3. Schönfeld (2002a), pl. 1, fig. 1. Dorst & Schönfeld (2015), p. 170, figs. 3.4, 4.4, 8.8, 10.2.

Genus *Rotaliammina* Cushman 1924

Rotaliammina concava (Seiglie) = *Tiphotrocha concava* Seiglie 1964, p. 500, pl. 1, figs. 4a–b, 5a–c [Plate 1, Fig. 1]. Dorst & Schönfeld (2015), p. 175, figs. 5.2, 6.2, 8.3, 10.6. Note: images of this species were sparsely provided in the literature. The specimen is very similar to those found in the Celtic Sea. It has been deformed by cytoplasm shrinking during desiccation.

Genus *Lepidodeuterammina* Brönnimann & Whittaker 1983

Lepidodeuterammina ochracea (Williamson) = *Rotalina ochracea* Williamson 1858, p. 55, pl. 4, fig. 112, pl. 5, fig. 113. Debenay *et al.* (2001), pl. 1, figs. 12, 13. Dorst & Schönfeld (2015), p. 181, fig. 3.2, 4.2, 9.4, 10.13.

Lepidodeuterammina sinuosa (Brönnimann) = *Asterotrochammina sinuosa* Brönnimann 1978, p. 6, fig. 3, pl. 2, figs. 1, 2, 6–8. "*Deuterammina (Lepidodeuterammina) sinuosa"* Dorst & Schönfeld (2015), p. 183, Fig. 3.1, 4.1, 9.3, 10.14.

Class Incertae sedis Pawlowski, Holzmann & Tyska 2013

Superfamily Nodosariacea Ehrenberg 1838

Order Lagenida Delage & Hérouard 1896

Family Polymorphinidae d'Orbigny 1839b

Genus *Guttulina* d'Orbigny 1839a

Guttulina communis (d'Orbigny) = *Polymorphina (Guttuline) communis* d'Orbigny 1826, p. 266, pl. 12, figs. 1–4. Jones (1994), p. 84, pl. 72, figs. 19–20, pl. 73, fig. 1.

Foraminiferal assemblages

Living (rose Bengal-stained) benthic foraminifera were common in the sample from Baia das Gatas. The samples from Calhau and São Pedro were barren of living foraminifera. The population density at Baia das Gatas, with 478 individuals per 10 cm^3, was well in the range of standing stocks on sand substrates in the lower intertidal zone under warm climatic conditions (ca. 100–1000 individuals per 10 cm^3; e.g. Culver & Horton 2005). The abundance of empty tests of the dead assemblage varied from 29 to 298 specimens per gram of sediment (Appendix Table 2). At Baia das Gatas, their concentration per volume, i.e. 2160 specimens per 10 cm^3, outnumbered the concentration of living specimens by a factor of 4.5, which is in reasonable agreement with literature data (1:4 to 1:6, Scott & Medioli 1980).

Bolivina striatula, *Rosalina vilardeboana* and *Millettiana milletti* dominated the living fauna with 24, 15 and 13 % respectively. *Ammonia tepida*, *Quinqueloculina bosciana* and *Quinqueloculina laevigata* were common with 4–3 %. The remaining 36 species of the living fauna were rather rare with <3 %. Only 22 of 42 living species were also recorded in the dead assemblage.

Quinqueloculina seminulum, *Ammonia tepida*, *Triloculina rotunda* and *Glabratella patelliformis* dominated the dead assemblage at Baia das Gatas with 13–9 %. *Quinqueloculina lamarckiana*, *Millettiana milletti*, *Peneroplis carinatus* and *Quinqueloculina lata* were common with 5–3 %, and the remaining 42 species were rare with <3 %. It has to be noted that only two of the eight frequent or common species from the dead assemblage were also frequent in the living fauna.

Elphidium crispum, *Amphistegina gibbosa* and *Glabratella patelliformis* dominated the dead assemblages with 50–8 % at São Pedro and Calhau. *Eponides repandus*, *Neoeponides auberii*, *Cibicides lobatulus* and *Peneroplis proteus* were common with 11–2 %. From these common species, only *Glabratella patelliformis* was found living at Baia das Gatas.

The Fisher alpha diversity index of the living fauna and dead assemblage at Baia das Gatas of 15.06 and 16.96 respectively was very similar, depicting rich and highly diverse foraminiferal assemblages at this site. The Fisher alpha index was substantially lower at São Pedro and Calhau with 1.75 and 1.95 (Appendix Table 2).

Discussion

Composition of the living foraminiferal fauna. Beach sands in subtropical environments have been considered as barren of living benthic foraminifera (Pamela Hallock, St. Petersburg, USA, pers. comm.), which might explain why we did not record living foraminifera at Sao Pedro and Calhau. However, early studies on the microhabitat depth of near-shore foraminifera in intertidal sands demonstrated that they live deeper in the sediment than usually sampled (Richter 1964a,b; Giese 1991; Langer *et al.* 1989). Own observations from Esteiro Ancão backbarrier sands, Ria Formosa, Portugal, at warm climatic conditions and high salinities, revealed that living benthic foraminifera were with 1–4 individuals per 10 cm^3 indeed very rare in the uppermost 1–2 cm of beach sands above MTL. It is therefore conceivable that the abundance maximum of living foraminifera was encountered at Baia das Gatas but missed at the other sampling locations.

The living fauna at Baia das Gatas did not resemble littoral faunas at temperate to warm climatic conditions in the Atlantic. Typical species for coarse-grained substrates, for instance *Asterigerinata mamilla* (Williamson 1858), *Haynesina depressula* or *Cibicides lobatulus*, were missing. Arenaceous species were underrepresented when compared to West African sites (e.g. Debenay 1990). On the contrary, such a high proportion as 28 % *Bolivina* spp. was not observed in intertidal settings elsewhere in the tropics or subtropics (e.g. Laut *et al.* 2017). Only the proportion of *Ammonia tepida* and *Quinqueloculina* spp. was in the expected range. Therefore, the fauna may be considered as being incomplete.

The life cycle and ecology of frequent and some rare species deserves attention in this respect. *Millettiana milletti* matures to a planktonic stage before reproduction (Rückert-Hilbig, 1983). However, specimens with a globular floating chamber were not observed in the living fauna from Baia das Gatas. The tychopelagic life mode of *Bolivina variabilis* is well constrained (Darling *et al.* 2009). However, other *Bolivina* spp. tend to float under environmental disturbance as well (Kucera *et al.* 2017; Glock *et al*. 2019). They were widely dispersed off NW Africa (Lutze 1980). *Trifarina bella* was recorded in plankton catchments south of Puerto Rico during certain days at high numbers (Schmucker 2000; Anna Jentzen, Kiel, and own unpubl. data). Even though recent studies revealed that foraminiferal propagules are of local or regional rather than of remote origin (Weinmann & Goldstein 2017; Weinmann *et al.* 2019), it is reasonable to assume that either floating propagules or the capability of a transient planktonic lifestyle were important for sustaining the benthic foraminiferal population at São Vincente.

Generation of the dead assemblages. The living fauna forms the dead assemblage over the course of many generations (Murray 1982). Species proportions and abundances may differ from the living fauna due to bias inferred by dissolution, bioerosion and lateral transport (e.g. Murray *et al.* 1982; Schröder 1988; Berkely *et al.* 2009). The living fauna may be subjected to a strong seasonal and interannual variability in species proportions and population densities (e.g. Murray & Alve 2000; Bouchet *et al.* 2007). None-the-less, common and frequent taxa of both, living fauna and dead assemblage should be the same.

At Baia das Gatas, only *Millettiana milletti* and *Ammonia tepida* are common or frequent in the living fauna and dead assemblage. However, about half of the living species were found in the dead assemblage as well. The missing species do not have delicate, fragile tests that easily could be destroyed (Kotler *et al.* 1982). Population densities in high-energy, near-shore sands are usually low because most species can not stand the permanent redeposition of their substrate (e.g. Langer *et al.* 1989; Humphreys *et al.* 2018). Only a few attached species may persevere. Such specialists, e.g. Trochamminidae, were rare in both assemblages at Baia das Gatas. A possible seasonal variability of the living fauna at Baia das Gatas is difficult to constrain since. The seasonality on São Vincente is characterised by changes in trade wind intensity. During sampling in late May and early June, the trades were on the decline but still strong. On the other hand, the difference in dead foraminiferal assemblage composition between samples from the windward locations Baia das Gatas and Calhau was higher than between the latter and the leeward sample from São Pedro.

The most plausible explanation for the difference between living and dead assemblages is that the dead assemblage received a substantial amount of redeposited tests. For instance, the frequent species *Elphidium crispum* is a symbiont-bearing, epifaunal species living in shallow, subtidal waters in temperate to tropical environments (Leutenegger 1984; Lee & Lee 1989; Parker & Gischler 2015). *Peneroplis proteus* is frequent in tropical shallow waters where moderate redeposition prevails (Wilson & Wilson 2011). *Amphistegina gibbosa* prefers coral reef rubble as substrate (Eichler *et al*. 2019, and references therein). *Eponides repandus* is adapted to high energy environments as well and prefers coarse sands and gravels (Edwards 1982). Empty tests of these species were probably taken up by wave turbulences in subtidal, shallow waters and were transported on the shore by surf action. The similarity of the dead assemblages from all three sampling sites, and the good agreement of the coarse fraction composition with literature data from fossil sands in other areas, suggest that this redepositional process is extensively prevailing around the Cape Verdian islands, in that beach sands are augmented by shallow water rhodolith-mollusc carbonate production sites.

Comparison of checklists. In fossil carbonate sands from São Vincente, nine benthic foraminiferal species were recognised (Appendix Table 3; Torres & Soares 1946). Two of them date back to the late Pliocene (*Faujasina carinata*) and Bajocian (*Epistomina regularis*), whereas the maximum depositional age of these sands is late Pleistocene (0.33 million years; Ramaldo *et al.* 2010). The identification of foraminiferal species by thin section analyses has been proven suitable for investigations of the internal structures of large, shallow-water benthic foraminifera, as well as for assessments of the planktonic foraminiferal inventory of limestones from the late Paleozoic to Neogene (e.g. Wernli *et al.* 1997; BouDagher-Fadel 2008; Asis *et al.* 2018). The determination of modern foraminifera by thin section examination is difficult however, in particular once test shape, apertural characteristics, and surface structures are diagnostic features. Misidentifications are likely. Therefore, the comparison of the 1946 checklist with data of the present study is not a straightforward way to accomplish the Recent benthic foraminiferal inventory of Cape Verdian islands.

Source regions and trajectories. The Cape Verdian archipelago is separated from the African continent by more than 500 km of a 3000 m deep ocean. As endemic species were not recognised, any Recent littoral or near-shore foraminifera must have been transported to the islands. A long-range transport of propagules by ocean currents or adult individuals by transocean rafting, a medium-range displacement by ichtyochory, and the introduction of alien species by marine traffic or migratory birds have been invoked as dispersal mechanisms for benthic foraminifera (McGann *et al.* 2000; Alve & Goldstein 2003; Riedel *et al.* 2011; Polovodova Asteman & Schönfeld 2016; Guy-Haim *et al.* 2017; Finger 2018). Indeed, source regions of the displaced species have to be identified first before migration routes are delineated and transport mechanisms are constrained (Lübbers & Schönfeld 2018).

We explored data from Bahia Reefs, Brazil, the Caribbean region, Bermuda, the Algarve coast of the Gulf of Cadiz, the Mediterranean, Gran Canaria and, more importantly, West Africa for benthic foraminiferal species co-occurring with São Vincente (Appendix Table 2, and references therein). The numbers of foraminiferal species in common with the potential source regions ranged from 28–59 %. Between 2–8 % of the species encountered on São Vincente were assigned to a single source region. None-the-less, 11 % of the species were not recorded in the tropical to temperate northern Atlantic to date and may derive from remote areas, e.g. eastern Pacific or Indian Ocean. The highest proportion of >50 % co-occurrences as well as the highest single-source region matches were with the Mediterranean and Caribbean regions (Figure 2). The adjacent NW African margin showed a markedly lower similarity with 44 % co-occurrences.

These far-reaching relationships are corroborated by data on shallow-water macrofauna from Cape Verdean islands. The barnacle *Chthamalus stellatus* (Poli 1791) dominated the epizoan fauna on intertidal rocky shores. This species is common in the Mediterranean, western Europe, and Atlantic Islands, but absent from West Africa. The Cape Verdean corals and algae came from the Caribbean and eastern America (Morri *et al.* 2000). Three of 13 new records of marine invertebrates on the Cape Verde an islands derive from the Caribbean and Mediterranean, and only one species came from West Africa (Wirtz 2009). From nine keyhole limpet species of the genus *Diodora*, five derive from the western Atlantic and one from the Mediterranean, whereas two came from the Pacific and one is endemic (Cunha *et al.* 2017). All authors emphasized the role of ocean currents as dispersal vectors, and the latter also considered the durability and resilience of larval stages as being crucial for their survival during long-distance transport. Evidences for invasions of alien species transported by marine traffic or fishing gear were not reported to date.

São Vincente is bathed by surface currents coming from the Canary Islands or Brazil, depending on the seasonal position of the CVFZ (Fig. 1). It is conceivable that these currents have brought propagules or floating specimens of meroplanktonic foraminifera to the Cape Verdes. The composition of the living fauna at Baia das Gatas suggests that the latter are of particular importance as contributors. It remains enigmatic, however, why the relationship to West Africa is so sparsely developed, even though the CVC follows the African shelf break over a long distance (Fig. 1). One may speculate that coastal upwelling creates an effective border that inhibits the off-shore proliferation of propagules of near-shore foraminifers in this area.

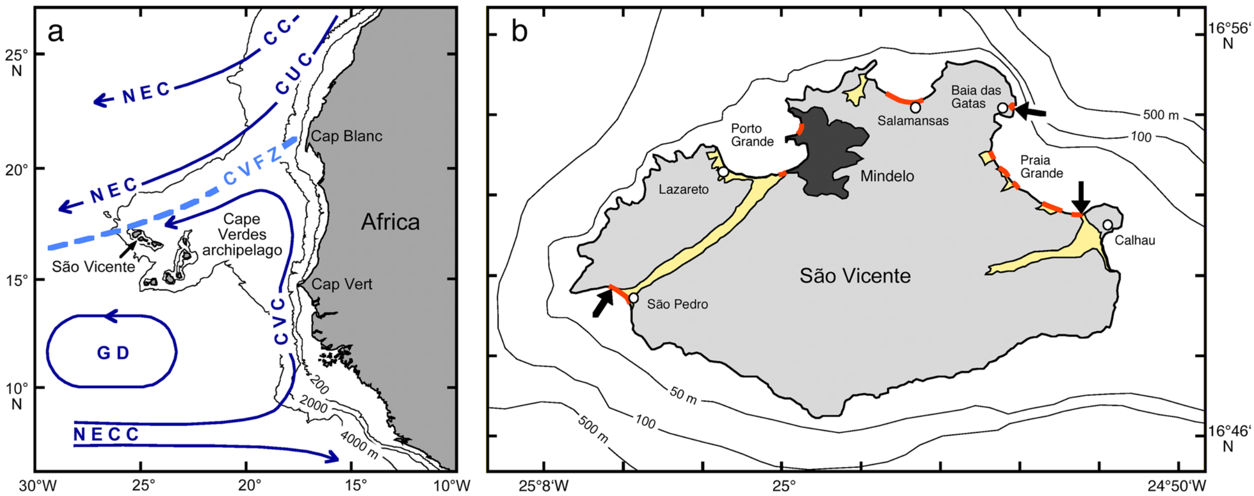

FIGURE 1. Map with location of (a) the Cape Verde Archipelago and (b) sampling sites on São Vincente. CC: Canary Current, CUC: Canary Upwelling Current, CVC: Cape Verde Current, CVFZ: Cape Verde Frontal Zone, GD: Guinea Dome, NEC: North Equatorial Current, NECC: North Equatorial Counter Current (modified after Fiedler, 2012; Fernandes *et al.* 2015; Pelegrí & Peña-Izquierdo, 2015). Depth contours in (a) were given for the continental margin only. Colours and symbols in (b): light grey: volcanic or volcanoclastic rocks, yellow: sedimentary deposits (redrawn after Ancochea *et al.* 2010), orange: beach sands, dark grey and circles: urban areas and villages (after satellite images and observations during the geological excursion), arrows: sampling sites. The geographical coordinates are given in Appendix Table 1.

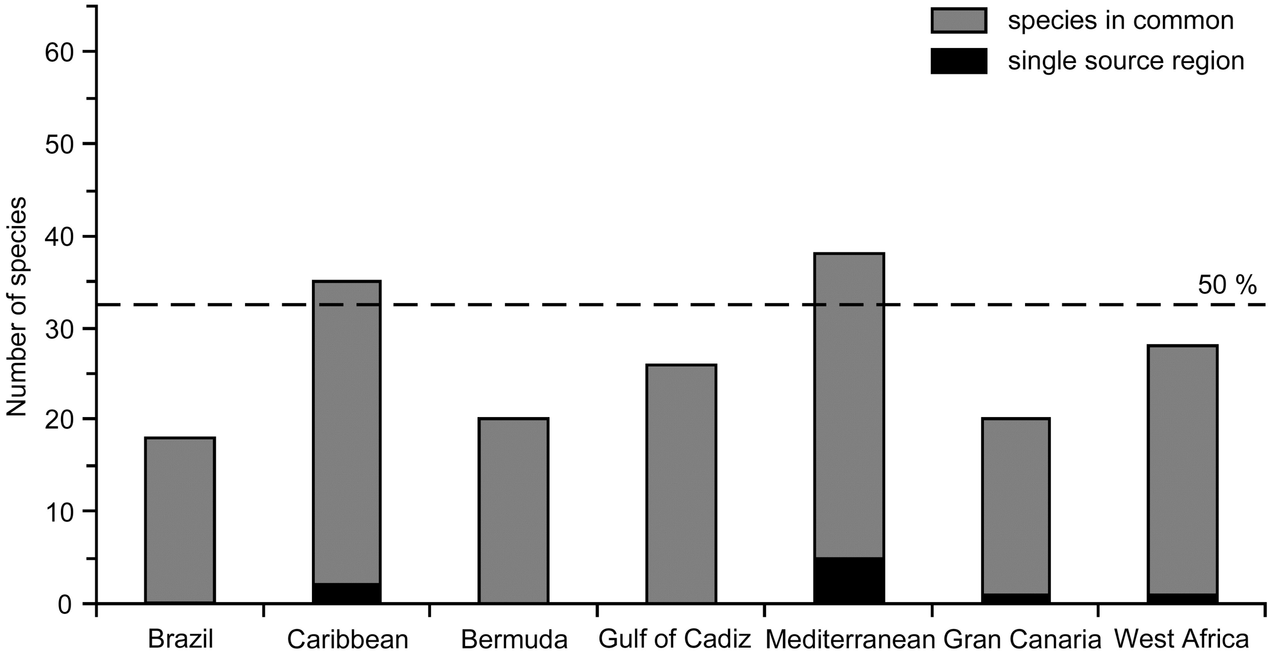

FIGURE 2. Species in common with source regions in the tropical to temperate North Atlantic. See Appendix Table 2 for references.

Conclusions

Sandgrain composition and dead benthic foraminiferal assemblages corroborated earlier evidences from petrographic studies that the beach sands from São Vincente had derived from a subtidal rhodolith-mollusc carbonate facies off shore. The maximum depth can be constrained to approximately 20 m because coralline algae were absent below (Morri *et al.* 2000). The preferred depth range of *Amphistegina gibbosa* is 14–40 m due to the specific light demands of their symbionts, even though the species may be found as shallow as 10 m on patch reefs, and as deep as 100 m on carbonate shelf sediments (e.g. Hallock *et al*. 1986; Martin & Liddell 1988; Hallock 1999). The sandgrain composition indicated that the sublittoral carbonate environments were highly detritus productive in comparison to the extensive coastal erosion of volcanic rocks at the cliffs around the island. The good agreement in the composition of bioclasts and benthic foraminiferal constituents in Recent beach deposits and fossil eolian sands revealed that the near-shore environmental conditions at São Vincente have not substantially changed since at least 330 thousand years.

The comparison of benthic foraminiferal checklists from Cape Verdian fossil sands and Recent dead foraminiferal assemblages from São Vincente revealed several misidentifications of foraminiferal species in thin sections. The island had not yet emerged from the sea at times when the respective species had lived. Even though thin section analyses provide reliable data on larger shallow-water foraminifera from Carboniferous to Miocene limestones, in particular once the internal structures are diagnostic, the technique should not be applied to Pleistocene and Recent sediments.

The living fauna at Baia das Gatas was missing typical species for coarse-grained substrates under warm climatic conditions. The proportion of arenaceous species was also rather low. Instead, species that either had a planktonic stage in their life cycle (*Millettiana milletti*), were tychopelagic (*Bolivina variabilis*), or had the ability to float (*Trifarina bella*, *Bolivina* spp.) were common. The living fauna was therefore augmented by a substantial contribution of floating species and propagules that may stand a long, transocean transport by surface ocean currents.

On the remote Marshall and Mariana Islands in the Pacific Ocean, 84 % of Recent foraminiferal species were common on other islands as well, 6 % were endemic, and 10 % were of unknown origin, i.e. derived from remote areas (Cushman *et al.* 1954; Todd 1966). These figures are in good agreement with our data from São Vincente where 11 % of the species came from remote areas. Todd (1957) speculated that reef-dwelling foraminifera probably have a planktonic stage facilitating their dissemination by ocean currents. Even though propagules of reef-dwelling foraminifera have not been caught neither individuals were raised from open ocean surface water samples, our results from Cape Verde corroborate the conclusions of these early, complementary studies from the Pacific.

A comparison with checklists from other regions in the tropical to temperate North Atlantic depicted the Caribbean and Mediterranean as probable source regions. The same processes and source regions have been described for littoral to subtidal macroorganisms on other Cape Verdian islands. The combined micro-and macrofaunal evidences identified both CVC and NEC as main trajectories for faunal immigrations. However, t he contribution from the NW African coast was considered to be rather low. The available information does not offer a plausible explanation for this. Perhaps coastal upwelling or other oceanographic processes on the West African shelf create effective barriers that inhibit an off-shore proliferation of foraminiferal propagules.

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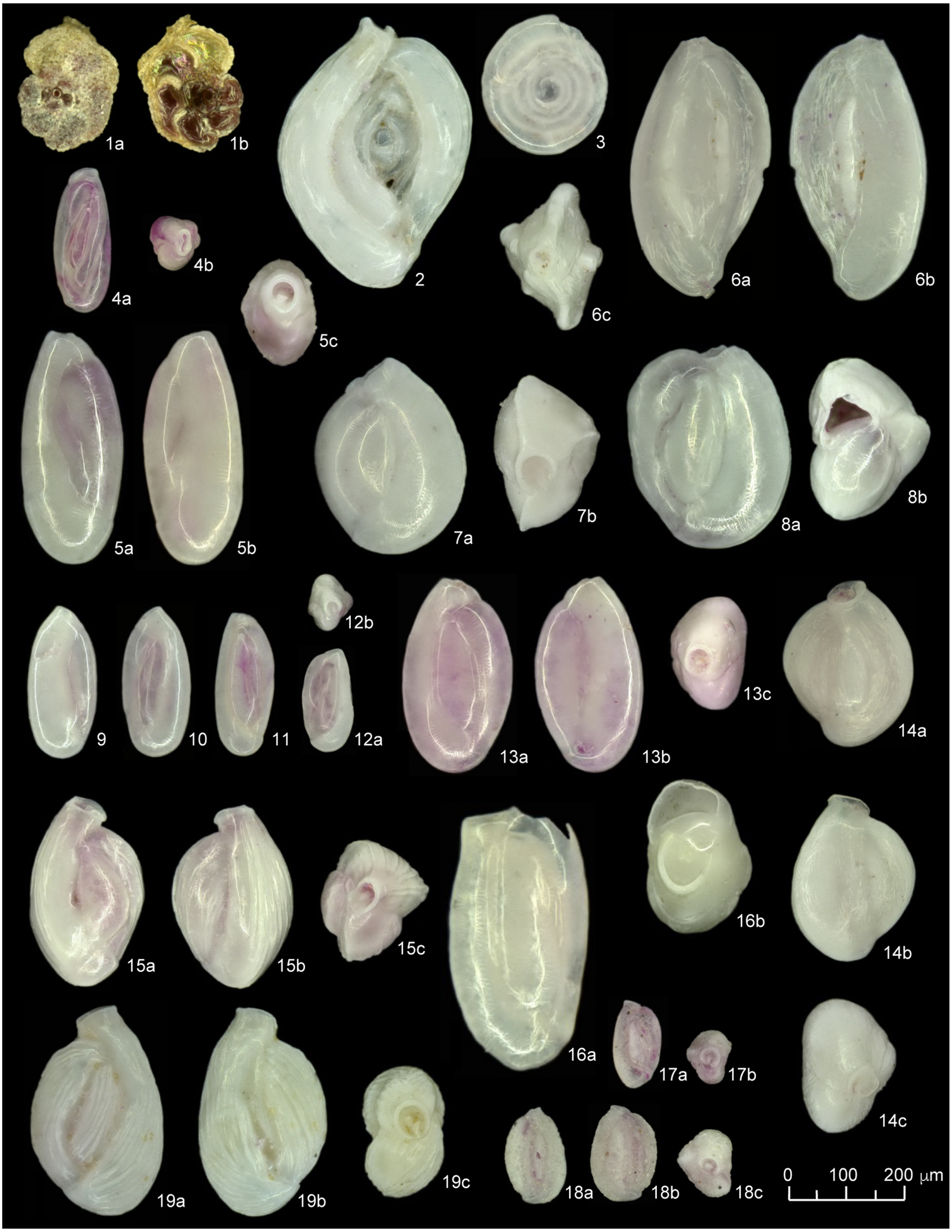

Plate 1. Living (rose-Bengal stained) foraminifera from Baia das Gatas, São Vincente, unless otherwise stated. 1: Rotaliammina concava, a dorsal, b ventral side. 2: Spiroloculina scrobiculata (dead specimen). 3: Cornuspira involvens (dead specimen). 4–5: Quinqueloculina bosciana. 6: Quinqueloculina stelligera (dead specimen). 7: Quinqueloculina lamarckiana (dead specimen). 8: Quinqueloculina auberiana. 9–12: Quinqueloculina laevigata. 13: Quinqueloculina seminulum. 14, 15: Quinqueloculina disparilis. 16: Quinqueloculina lata (dead specimen, damaged). 17–18: Quinqueloculina parvula. 19: Adelosina carinata-striata (dead specimen).

Plate 2. Living (rose-Bengal stained) foraminifera from Baia das Gatas, São Vincente, unless otherwise stated (continuation). 1: Miliolinella webbiana (dead specimen). 2: Triloculina rotunda. 3: Spirophthalmidium sp. 1. 4: Subedentostomina sp. 1. 5: Parrina bradyi (dead specimen). 6: Sigmamiliolinella australis (dead specimen). 7: Sorites marginalis (dead specimen). 8: Peneroplis pertusus (dead specimen). 9: Quinqueloculina eburnea (dead specimen). 10, 11: Guttulina communis. 12: Stainforthia fusiformis. 13: Peneroplis carinatus, a lateral, b side view. 14–17: Bolivina striatula. 18: Bolivina tongi. 19: Bolivina subspinescens. 20, 21: Floresina paralleliformis. 22: Trifarina bella. 23, 24: Trifarina bella, plankton tow, Puerto Rico. 25, 26: Bolivina plicatella. 27, 30: Bolivina variabilis. 28, 29: Bolivina variabilis, plankton tow, Puerto Rico (Kucera et al. 2017). 31, 32: Buliminella elegantissima.

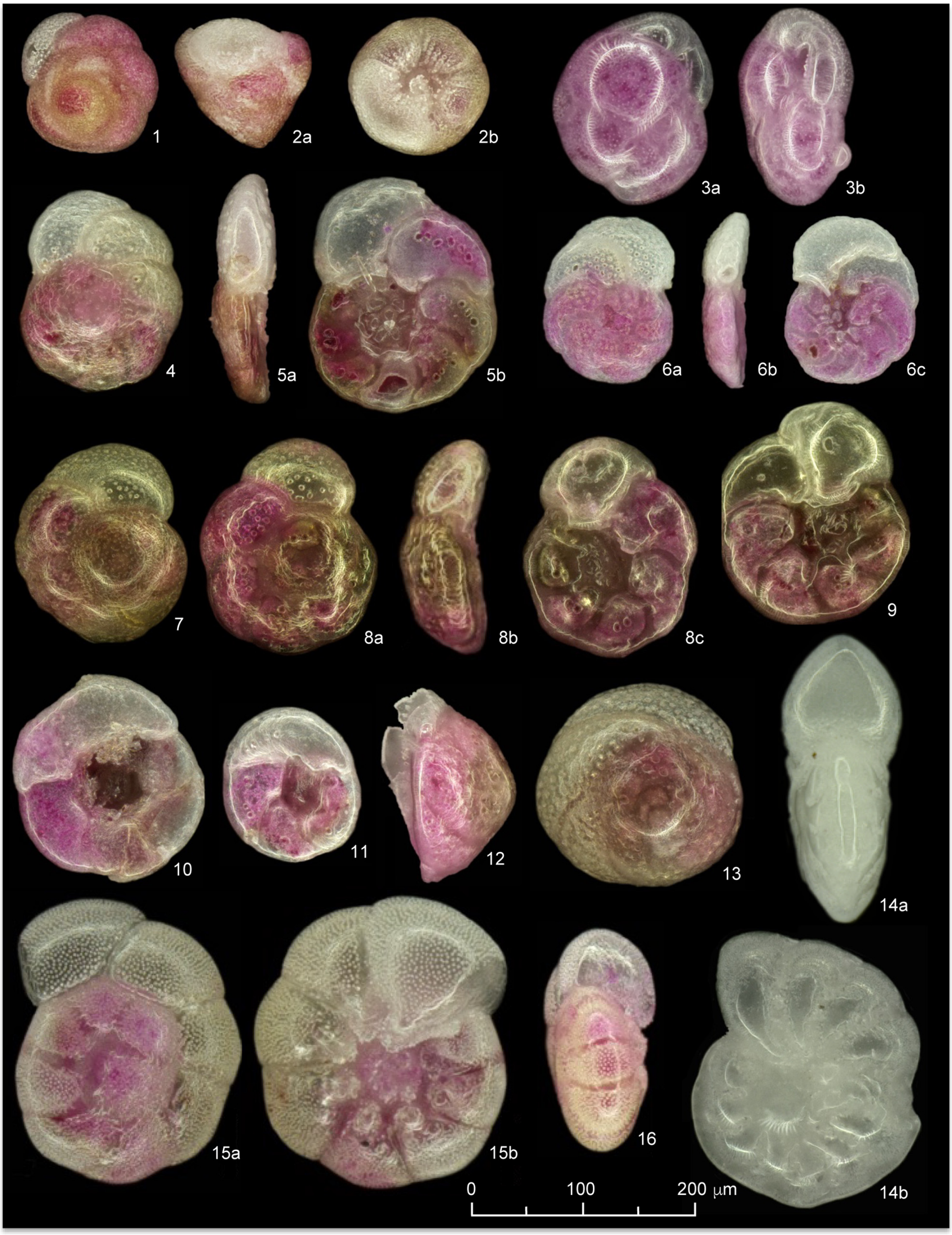

Plate 3. Living (rose-Bengal stained) foraminifera from Baia das Gatas, São Vincente, unless otherwise stated (continuation). 1, 2: Glabratella patelliformis. 3: Cassidulina minuta. 4, 5: Discorbinella araucana, 4 dorsal, 5a side view, 5b ventral view. 6: Hanzawaia bertheloti, a dorsal, b side view, c ventral view. 7–9: Rosalina vilardeboana 7, 8a dorsal, 8b side view, 8c, 9 ventral view. 10–13: Neoconorbina terquemi 10, 11 ventral, 12 side view, 13 dorsal view. 14: Nonion depressulum, a side view, b lateral view (dead specimen). 15, 16: Ammonia tepida, 15a dorsal, 15b ventral, 16 side view.

Plate 4. Living (rose-Bengal stained) foraminifera from Baia das Gatas, São Vincente, unless otherwise stated (continuation). 1: Hanzawaia concentrica, ventral view (southern Portugal, Station SO7515KG) (Schönfeld, 1997). 2: Hanzawaia bertheloti, ventral view (note different scale). 3: Hanzawaia rhodiensis, ventral view (Gulf of Cadiz, Station M39008-4) (Schönfeld, 2002). 4–6: Millettiana milletti, 4 ventral, 5 side view, 6 dorsal view. 7–9: Elphidium crispum, 7 side view (dead specimen, Sao Pedro), 8 lateral view (dead specimen, Sao Pedro), 9 lateral view (dead specimen). 10: Pseudononion granuloumbilicatum, a dorsal, b side view, c ventral view. 11: Spirillina vivipara (dead specimen). 12–14: Eponides repandus 12 ventral, 13 side view, 14 dorsal view (dead specimens, Sao Pedro). 15–17: Amphistegina gibbosa, 15 dorsal, 16 side view, 17 ventral view (dead specimens).

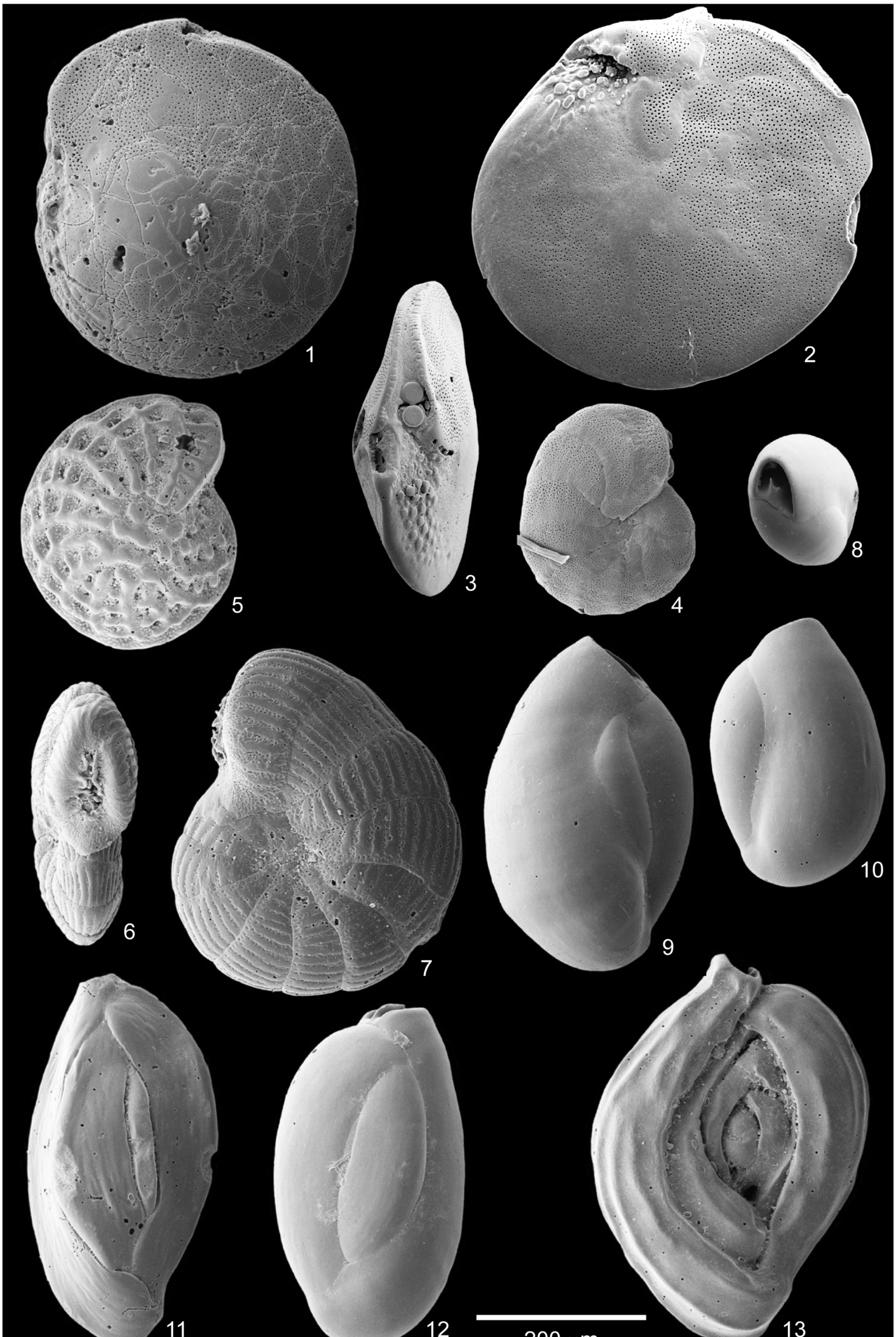

Plate 5. SEM images of dead foraminifera from Baia das Gatas, São Vincente, unless otherwise stated. 1–3: Amphistegina gibbosa, 1 dorsal view, 2 side view (Sao Pedro, note that the aperture was plugged by diatom frustrules), 3 ventral view. 4: Peneroplis carinatus (living specimen, lateral view, with detached paintbrush bristle; same specimen as Plate 2, Fig. 13). 5: Elphidium crispum, lateral view. 6, 7: Peneroplis pertusus, 6 side view, 7 lateral view (same specimen as Plate 2, Fig. 8). 8–10: Triloculina rotunda. 11: Quinqueloculina stelligera (same specimen as Plate 1, Fig. 6). 12: Quinqueloculina seminulum (living specimen). 13: Spiroloculina scrobiculata (same specimen as Plate 1, Fig. 2).

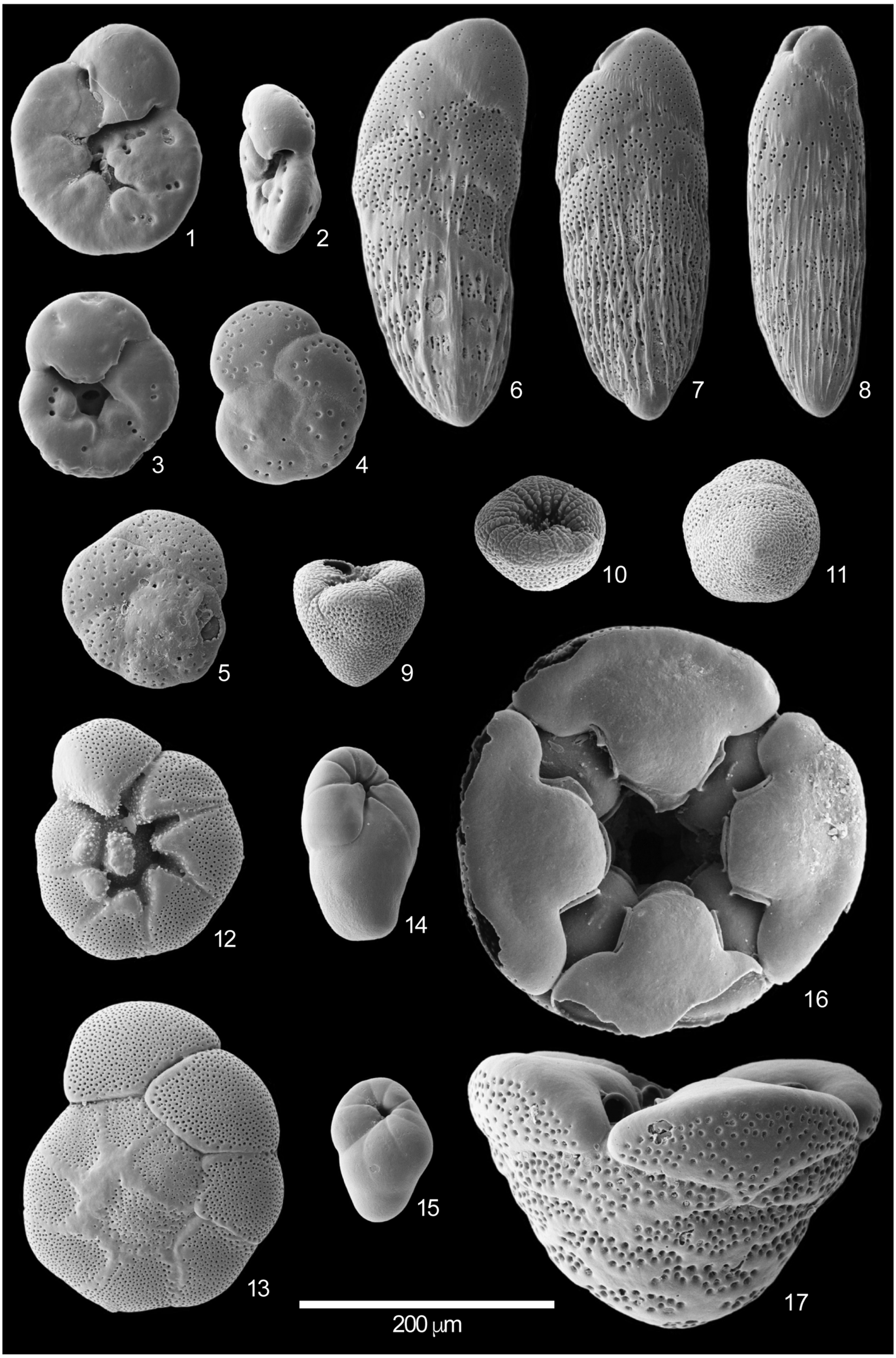

Plate 6. SEM images of living (rose-Bengal stained) foraminifera from Baia das Gatas, São Vincente, unless otherwise stated. 1–5: Rosalina vilardeboana, 1, 3 ventral view, 2 side view, 4, 5 dorsal view. 6–8: Bolivina striatula. 9–11: Glabratella patelliformis, 9 side view, 10 ventral view, 11 dorsal view. 12, 13: Ammonia tepida, 12 ventral view, 13 dorsal view (same specimen as Plate 3, Fig. 16). 14, 15: Floresina paralleliformis (14, same specimen as Plate 2, Fig. 21). 16, 17: Millettiana milletti, 16 ventral, 17 side view (same specimens as Plate 4, Figs. 4, 5).

APPENDIX TABLE 1. Grain size and coarse fraction analyses (Sarnthein, 1971) of beach sands from Sao Vincente.

Locality:	Baia das Gatas		Sao Pedro		Calhau	
Sample coordinates, Latitude:	16°54.27'N		16°49.60'N		16°51.60'N	
Longitude:	24°54.30'W		25°3.95'W		24°52.57'W	
Height (m MTL):	-0.36		+0.23		+0.35	
size fraction:	Weight (g)	cumul. %	Weight (g)	cumul. %	Weight (g)	cumul. %
63–125 µm	0.1294	2.9	0.0013	0.0	0.0016	0.0
125–150 µm	0.0972	5.1	0.0029	0.1	0.0184	0.3
150–250 µm	0.4304	14.7	0.1433	5.1	2.3868	36.8
250–355 µm	0.3891	23.5	1.2618	48.4	3.7681	94.5
355–500 µm	0.4617	33.8	1.4403	97.9	0.3441	99.7
500–1000 µm	1.5062	67.6	0.0608	100.0	0.0185	100
1000–2000 µm	0.9212	88.2	-	-	-	-
>2000 µm	0.5242	100	-	-	-	-
Total (g)	4.4594		2.9104		6.5375	
Components:	Grain and weight %		Grain and weight %		Grain and weight %	
Balanid plates and fragments	0.9		-		-	
Bivalve shells and fragments	3.1		-		-	
Bryozoan fragments	0.7		-		-	
Coral fragments	4.0		-		-	
Foraminifera	0.6		0.02		2.5	
Gastropod shells and fragments	3.1		-		-	
Ostracods	0.1		-		-	
Serpulid tubes and fragments	0.4		-		-	
Spines of regular echinoids	5.5		-		-	
Sponge needles	0.0		-		-	
Bioclasts, undifferentiated	74.2		84.3		78.4	
Volcanic glass and ash charts, dark and white	0.3		7.1		16.4	
Volcanic rock fragments, undifferentiated	7.1		8.6		2.6	
Foraminifera	0.6		0.0		2.5	
Biogenic carbonate	92.0		84.3		78.4	
Volcanites	7.4		15.7		19.0	

APPENDIX TABLE 2. Sampling point coordinates, heights, foraminiferal census data and species‘ occurrences in adjacent source regions

Locality:	Baia das Gatas	Baia das Gatas	São Pedro	Calhau								
Sample coordinates, Latitude:	16°54.27’N	16°54.27’N	16°49.60’N	16°51.60’N								
Longitude:	24°54.30’W	24°54.30’W	25°3.95’W	24°52.57’W								
Height (m MTL):	-0.36	-0.36	+0.23	+0.35								
Sampling day and time:	2-6-2018 17:00	2-6-2018 17:00	30-5-2018 10:30	1-6-2018 11:00	Source region:							
Size fraction:	63-2000 µm	63-2000 µm	63-2000 µm	63-2000 µm	Mediterranean	Gulf of Cadiz	Gran Canaria	West Africa	Bermuda	Brazil	Caribbean	other
Species	living	dead	dead	dead	(1)	(2)	(3)	(4)	(5)	(6)	(7)	
Adelosina carinata-striata		4			X						X	
Ammonia tepida	10	34			X	X		X	X		X	
Amphisorus hemprichii		1			(i)		X				X	
Amphistegina gibbosa		8	85	22					X	X	X	
Bolivina plicatella	4	1			X							
Bolivina striatula	55	5			X	X		X			X	
Bolivina subspinescens	1				X			X			X	
Bolivina tongi	1	2				X		X				
Bolivina variabilis	4				X	X		X	X		X	
Buliminella elegantissima	3	1				X	X	X	X		X	
Cassidulina minuta	2					X		X			X	
Cibicides lobatulus		4	3	4	X	X	X	X	X	X	X	
Cornuspira involvens		2			X	X	X	X			X	
Cycloforina rugosa		1			X							
Cycloforina tenuicollis	1				X							
Discorbinella araucana	6										X	
Elphidium crispum		8	49	49	X	X	X	X			X	
Elphidium excavatum	1					X		X			X	
Elphidium margaritaceum	1				X							
Epistominella sp.		1										
Eponides repandus		3	8	13	X		X	X	X	X	X	
Floresina paralleliformis	5	4										X
Glabratella patelliformis	6	29	14	24	X		X	X				

......*continued on the next page*

APPENDIX TABLE 2. (Continued)

Guttulina communis	2					X	X	X			X	
Hanzawaia bertheloti	2	3			(non)			(non)		X	X	
Haynesina depressula		3			X	X			X		X	
Lepidodeuterammina ochracea	1			1		X		X	X		X	
Lepidodeuterammina sinuosa	2											X
Miliolinella webbiana		2			X		X					
Millettiana milletti	29	10										X
Neoconorbina terquemi	5	3			X	X	X	X				
Neoeponides auberii		5	8				X					
Nonionides grateloupi	1				X	X	X	X	X	X	X	
Parrina bradyi		2			X						X	
Peneroplis carinatus	1	10							X	X	X	
Peneroplis pertusus		7			X		X		X	X	X	
Peneroplis proteus			1	2					X	X	X	
Pseudononion granuloumbilicatum	1	1										X
Quinqueloculina auberiana	1				X			X			X	
Quinqueloculina bosciana	10	5			X					X	X	
Quinqueloculina disparilis	3	1			X	X		X		X		
Quinqueloculina eburnea		4			X				X			
Quinqueloculina laevigata	7				X	X		X	X	X	X	
Quinqueloculina lamarckiana		16		2			X	X	X	X	X	
Quinqueloculina lata	4	10			X	X	X	X		X		
Quinqueloculina parvula	4	3			X	X						
Quinqueloculina seminulum	6	39			X	X	X	X	X	X	X	
Quinqueloculina stelligera		7			X	X						
Rosalina vilardeboana	35	7			X	X	X					
Rotaliammina concava	2											X
Sigmamiliolinella australis		2										X
Sigmavirgulina tortuosa		3	1		X			X		X		
Siphonina tubulosa		1						X				
Sorites marginalis		1								X	X	

......continued on the next page

APPENDIX TABLE 2. (Continued)

Spirillina vivipara	3	3			X	X	X		X		X	
Spiroloculina scrobiculata		4										X
Spirophthalmidium sp. 1	2	2			X				X			
Stainforthia fusiformis	1				X	X					X*	
Subedentostomina sp. 1	1				X							
Tretomphalus bulloides		3			X						X	
Trifarina bella	1										X	
Triloculina rotunda	2	30					X		X	X	X	
Trochammina squamata	1					X		X				
Valvulineria minuta		1			X			X				
Wiesnerella auriculata	1	1			X	X	X	X	X	X	X	
others, indet. spp.	2	9	-	-								
Total:	230	306	169	117	38	26	20	28	20	18	35	7
Species no.:	42	50	8	8	5**		1**	1**			2**	
Sample volume (cm^3):	77	77	73	54								
Split (n):	0.0625	0.0156	0.0625	0.00039								
Split weight (g):	3.9418	1.3658	5.9109	0.3925								
Population density (Ind./10 cm^3):	478	-	-	-								
Abundance (Ind./g sediment):	-	224	29	298								
Fisher alpha:	15.06	16.96	1.75	1.95								

(i) invasive species

(non) misidentification verified by image

* identified by metabarcoding (Moss *et al.* 2016)

** species with single source region (bold X)

(1) Cimerman & Langer (1991), Milker & Schmiedl (2012), Caruso & Cosentino (2014), Jorissen *et al.* (2018), and others.

(2) Ria Formosa lagoon, Algarve coast, Portugal (own data).

(3) Sanchez (2010).

(4) Debenay (1990), Schiebel (1992), Redois & Debenay (1999), Reymond *et al.* (2014).

(5) Javaux & Scott (2003).

(6) Araujo & Machado (2008), Eichler *et al*. (2019).

(7) Todd & Brönniman (1957), Bermudez & Seglie (1963), Bock (1971), Gaby & Sen Gupta (1985), Bouchet *et al*. (2007), Moss *et al*. (2016), Laut *et al.* (2017), own data.

APPENDIX TABLE 3. Benthic foraminiferal species from Recent and fossil carbonate sands from Cape Verde islands (Torres & Soares, 1946). The type references can be found in the Ellis and Messina (1940) catalogue or WORMS Editorial Board (2018). They are not included in the reference list. § species recorded on São Vincente, * extinct species.

Amphistegina hauerina d'Orbigny, 1846*
Amphistegina lessonii d'Orbigny in Guérin-Méneville, 1832
Amphistegina mammilla (Fichtel & Moll, 1798)*
Amphistegina parisiensis Terquem, 1882*
Amphistegina vulgaris d'Orbigny in Deshayes, 1830*
Amphistegina sp. §
Anomalina amonoides (Reuss, 1844)*
Anomalina balthica (Schröter, 1783) = *Hyalinea balthica*
Anomalina sp.
Anomalinella rostrata (Brady, 1881)
Archaias aduncus (Fichtel & Moll, 1798) = *Archaias angulatus*
Archaias spirans Montfort, 1808 = *Archaias angulatus*
Bigenerina nodosaria d'Orbigny, 1826
Biloculina bulloides d'Orbigny, 1826 = *Pyrgo bulloides*
Biloculina depressa d'Orbigny, 1826 = *Pyrgo depressa*
Biloculina ringens (Lamarck, 1804) = P*yrgo ringens*
Biloculina sp. §
Bolivina aenariensis (Costa, 1856)
Bolivina robusta (Brady 1881)
Cancris auricula (Fichtel & Moll, 1798) §
Cibicides concentrica (Cushman, 1918) = *Hanzawaia concentrica*
Cibicides lobatula (Walker & Jacob, 1798)
Cibicides sp.
Discorbina opercularis (d'Orbigny, 1839) = *Planoglabratella opercularis*
Elphidium crispus (Linné, 1758) = *Elphidium crispum* §
Elphidium macellus (Fichtel & Moll, 1798) = *Elphidium macellum*
Elphidium sp. §
Eponides sp.
Epistomina regularis Terquem, 1883 § *
Faujasina carinata (d'Orbigny, 1839) § *
Gyroidina soldanii (d'Orbigny, 1826)
Lagena ornata (Williamson, 1858) = *Fissurina ornata*
Lepidocyclina canellei Lemoine & Douville 1904*
Miliolina (Quinqueloculina) seminulum (Linné, 1758) = *Quinqueloculina seminulum*
Miliolina (Triloculina) valvularis (Reuss, 1851) = *Miliolinella valvularis*
Miliolina sp.
Miliolina trigonula (Lamarck, 1804) = *Triloculina trigonula*
Myogypsina irregularis (Deshayes, 1838)*
Nautilus adunco (Fichtel & Moll, 1798) = *Archaias angulatus*
Orbiculina compressa (D'Orbigny, 1839) = *Cyclorbiculina compressa*
Operculina complanata (Defrance in Blainville, 1822)
Orbitolites marginalis Lamarck, 1816 = *Sorites marginalis*
Patellina sp.
Peneroplis planatus (Fichtel & Moll, 1798)
Planorbulina sp.
Polymorphina variata Jones Parker & Brady 1866*
Quinqueloculina striata d'Orbigny in Guérin-Méneville, 1832
Rotalia beccarii (Linné, 1758) = Ammonia beccarii
Rosalina opercularis Orbigny 1839

Sorites orbiculus (Forsskål in Niebuhr, 1775)
Textularia agglutinans (d'Orbigny, 1839)
Textularia gibbosa ('Orbigny, 1826)
Textularia sp. §
Triloculina oblonga (Montagu, 1803)
Triloculina trigonula (Lamarck, 1804) §
Trochammina nitida Brady, 1881 = *Polystomammina nitida*
Truncatulina rostrata Brady, 1881 = *Anomalinella rostrata*