Taxonomy and biogeography of living species of the Family Notorotaliidae (*Notorotalia, Parrellina, Porosorotalia, Buccella, Cristatavultus*)

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ABSTRACT: DNA sequencing shows that species of the genera *Notorotalia, Porosorotalia* and *Buccella* form a distinct branch (Notorotaliidae) of Rotaloidea, and cluster as sister to Elphidiidae. In this review we report on the sequencing of three species of *Buccella* (from the Arctic Ocean, Patagonia and Chile) and one each of *Notorotalia* (New Zealand) and *Porosorotalia* (Chile). This information has been combined with all the morphological descriptive information on species of these genera plus the genera *Cristatavultus* and *Parrellina* to provide a global synthesis of living species of the Notorotaliidae.

We recognize 11 species of the southern hemisphere genus *Notorotalia*, which has a centre of diversity around New Zealand (8 species). A second southern-hemisphere-restricted genus, restricted to eastern Australia is *Parrellina* (3 species) although specimens (possibly introduced) have been recorded from the Mediterranean Sea. *Cristatavultus* has a single species, with a tropical west Pacific distribution. We synonymize *Cribrorotalia* under *Porosorotalia*, which has a disjunct distribution with one species in the northwest Pacific and a second around the southern parts of South America. *Buccella* is the most diverse and widespread genus (16 species recognized) with its greatest abundance in the Arctic Ocean and around subantarctic-temperate South America. Five species of *Buccella* live in a belt along the west coast of central America, from USA to Peru, with some spillage into the Caribbean Sea and Gulf of Mexico. Two new species of *Buccella* are recognized: *B. dejardini* (from South Georgia) and *Buccella* n. sp. A (from Chile).

Keywords: Benthic foraminifera; molecular and morphological taxonomy; biogeography; Buccella; Notorotaliidae

INTRODUCTION

The application of DNA sequencing has shown that the foraminiferal genus *Buccella* belongs in the family Notorotaliidae that branches as sister to elphidiids s.l. (Holzmann and Pawlowski 2017). Reliable recognition of species within the genus *Buccella* has always been elusive (e.g., Calvo-Marcilese and Langer 2012). Here the sequencing of three separate phylotypes within *Buccella* provides a first step towards determining morphological features that may be reliably used to distinguish taxa and features that are more variable within a species.

With the increase in recent decades in the publication of numerous high-quality images of many species and now the availability on-line of images of some of the types of early described species, we have taken the opportunity to provide a review of the taxonomy and biogeography of *Buccella* species together with the other species in the family Notorotaliidae and present here altogether for ease of reference.

Previous studies on the taxonomy of *Notorotalia*, *Parrellina*, *Porosorotalia* and *Cristatavultus*

Notorotalia is a Southern Hemisphere taxon. The first recognized species was living *Rotalia clathrata*, described by Brady (1884) from Challenger Expedition stations off Australia, New Zealand and Patagonia. Parr (1950) split this into two species, one from Australia (*clathrata*) and one from Patagonia (*patagonica*). Parr (1950) also described a third species based on fragmentary Recent tests from the Kerguelen Islands (*kerguelensis*). Finlay (1939) noted that *clathrata* was quite different from *Rotalia* and proposed the new genus *Notorotalia* for it and other species (fossil and Recent) from the Southern Hemisphere.

Hornibrook (1961) went further and proposed a new subfamily Notorotaliinae and two new genera, *Discorotalia* and *Cribrorotalia*, for related species that have compressed discoidal tests (former) and thick-shelled, strongly biconvex tests with beaded ornament (*Cribrorotalia*) and were only known in the fossil record in New Zealand. Unbeknown to Hornibrook, three years earlier Voloshinova (1958) had proposed the Eocene-Pleistocene genus Porosorotalia for a species in eastern Russia that had the same generic characters as Hornibrook's Cribrorotalia. Realising this, Loeblich and Tappan (1964) placed Cribrorotalia as a junior synonym of Porosorotalia. Hornibrook (in Hofker 1969) maintained that the internal structure of the umbilical plug differed between the two, but this is not apparent in all the generic descriptions (e.g., Loeblich and Tappan 1987). There was sufficient doubt for Loeblich and Tappan (1987) to recognise the genera as separate with a Southern hemisphere Cribrorotalia and Northern Hemisphere Porosorotalia both within the Notorotaliinae. Since the 1960s, both these latter two genera have been recognised to have one living species each, with Cribrorotalia meridionalis off South America and Porosorotalia makiyamai off Japan.

Hornibrook (1961) also included in the Notorotaliinae the planispiral genus *Parrellina*, that was otherwise similar to the other notorotaliine genera and had been proposed by Parr (1950) using the junior homonym name *Elphidioides* that was replaced as *Parrellina* by Thalmann (1951).

Vella (1957) was the first to undertake detailed studies on numerous Neogene specimens of the genus *Notorotalia* correcting and improving on the precision of some of the earlier descriptions of Brady (1884), Chapman (1941), Heron-Allen and Earland (1932), Finlay (1939) and Parr (1950). As a result, Vella (1957) described and named six new species from the New Zealand Neogene and six new living species.

Hofker (1969) undertook the most in-depth review undertaken so far of the internal structures and taxonomic validity of the genera *Notorotalia, Cribrorotalia, Discorotalia* and *Parrellina.* He concluded that all belonged together in the subfamily Notorotaliinae and that the superficially similar Northern Hemisphere genera *Polystomellina* and *Faujasina* are sufficiently different to be excluded and should be considered to be trochospiral *Elphidium.* He considered that the Notorotaliinae had its origins in the New Zealand region in the Eocene. Hornibrook (1996) undertook a detailed review of these taxa in New Zealand's Eocene and Oligocene strata and proposed that Notorotaliinae be raised to family level and described ten new species of *Notorotalia* and one new species of *Cribrorotalia.*

The genus *Cristatavultus* was proposed by Loeblich and Tappan (1994) and placed in the family Elphidiidae, partly because they thought it was planispirally coiled. Hayward et al. (1997) showed that the genus was partly trochospiral and placed it within the subfamily Notorotaliinae because of the similarity of its costate ornament to *Notorotalia* and the presence of costae extending over the apertural face of the last chamber – a feature that helps distinguish most species of Notorotaliidae from those in the Elphidiidae.

Previous studies on the taxonomy of Buccella

Prior to the 1950s, species of this genus were placed in the broad genera *Rotalina* and *Eponides*. Then Andersen (1952) proposed the genus *Buccella* to include species that had "multiple apertures on the ventral side of the test". At the same time, he reviewed the specimens of *Eponides* with multiple ventral apertures that were in the Cushman collection and shifted nine taxa into the new genus *Buccella* with *Eponides hannai* Phleger and Parker 1951, the genotype. He also proposed three new spe-

cies of *Buccella* and revised the descriptions of several of the existing ones.

Voloshinova (1960) followed this with a review of the Neogene species of Buccella on the northeast Pacific coast of Siberia. She, and several colleagues within her review, proposed a further 13 new fossil species or infraspecies, several of which were recognized as still living in the region. The abundant Buccella around the coast of South America were proving difficult to identify, so Theyer (1966) undertook a numerical taxonomic review and concluded that there were basically two common species with one restricted to the Pacific coast north of 42°S and the other occurring on the Atlantic coast around the southern tip and up the Pacific coast as far as 42°S. In the most recent study to focus on the taxonomy of Buccella, Calvo-Marcilese and Langer (2012) studied the morphology of a large population in Bahia Blanca Estuary, Argentina, and showed major morphological changes during ontogeny from juvenile to adult and suggested that a number of described species in the South American region correlated with one of these stages. As a result, they concluded that the earliest named species B. peruviana was the senior synonym and combined the two species that had been recognized by Theyer (1966).

Previous molecular studies on the Notorotaliidae

Notorotaliidae were part of a study of phylogenetic relationships in rotaliid foraminifera based on SSU and LSU rRNA genes (Holzmann and Pawlowski 2017). They were included in the superfamily Rotaloidea together with sequenced representatives of four other families (Elphidiellidae, Ammoniidae, Elphidiidae and Haynesinidae). Notorotaliidae are a monophyletic clade strongly supported by bootstrap values (94%) and branch as sister to Elphidiidae s.l. (94%BV) (Holzmann and Pawlowski 2017). Four notorotaliid species had been sequenced, identified as Notorotalia zelandica, Cribrorotalia sp. (herein = Porosorotalia meridionalis), B. peruviana (herein = B. alvarezii) and B. frigida (herein = new species). The current study presents additional molecular and morphological data of notorotaliid species to that examined by Holzmann and Pawlowski (2017) and also includes a newly investigated species, Buccella tenerrima.

MATERIALS and METHODS

Sample collection for molecular studies

For new sequencing studies presented here, specimens were acquired by surface sediment sampling intertidally, or by dredge or grab subtidally. The sediment was sieved over a 125 or 250 mesh and distributed in Petri dishes filled with seawater. Living specimens showing extended pseudopodes were isolated under a binocular microscope, cleaned with a brush, transferred to micropaleontological slides and dried at ambient temperature. Buccella tenerrima specimens were acquired from multiple corer surface samples on the lower shelf (station 32 at 220 m water depth) during Polarstern expedition PS92 in 2016. As sampling followed a carbon export event (phytoplankton bloom), specimens were identified by their green cytoplasm staining. Scanning electron microscope (SEM) images were taken for almost all specimens before extraction.

Specimen repositories and catalogue numbers

All sequenced specimens were destroyed during DNA extraction, although SEM images of most were captured prior to destruction. Non-sequenced specimens imaged by SEM are



TEXT-FIGURE 1

PhyML phylogenetic tree based on the 3'end fragment of the SSU rRNA gene, showing the evolutionary relationships of 83 rotalioid foraminiferal sequences belonging to Notorotaliidae, Ammoniidae, Haynesinidae and Elphidiidae. The tree is unrooted. Notorotaliid specimens are identified by their isolate numbers (1st), clone numbers (2nd) and accession numbers (3d). The remaining rotalioid foraminifera are identified by their accession numbers. Numbers at nodes indicate bootstrap values (BV). Only BV>70% are shown.

3rd

mostly held in the collections of Maria Holzmann and GNS Science, Lower Hutt, New Zealand (figured specimens on stubs prefixed by BWH, figured specimens on slides prefixed by FP, faunal samples prefixed by F) or Auckland Museum, New Zealand (figured specimens prefixed by AK, faunal samples prefixed by L). Some faunal samples used are held in the collections of the University of Auckland, New Zealand (prefixed by AU) or Auckland Museum (prefixed by AK). A few imaged specimens are housed in the Cushman Collection, Smithsonian Institute, Washington DC (prefixed by CC or USNM PAL). Other SEM images loaned to the authors for use in providing additional locality records have the specimens held in the collections of the individuals acknowledged in the text. Type specimens of the new species described here have been lodged in the Geneva Natural History Museum (prefixed by MHNG-INVE). Isolate numbers are always labelled as isolates. Genbank accession numbers are in the format of two capital letters followed by six numerals (Appendix 1).

DNA extraction, amplification, cloning and sequencing

Sixteen foraminiferal specimens were extracted individually using guanidine lysis buffer (Pawlowski 2000). Semi-nested PCR amplification was carried out for the 18S barcoding fragment of foraminifera (Pawlowski and Holzmann 2014) using primers s14F3 (acgcamgtgtgaaacttg)-sB (tgatccttctgcaggttcacctac) for the first and primers s14F1 (aagggcaccacaagaacgc)-sB for the second amplification. For Buccella tenerrima, reverse primer s20r (gacggcggtgtgtacaa) was used instead of sB. Thirty-five and 25 cycles were performed for the first and the second PCR, with an annealing temperature of 50°C and 52°C, respectively. The amplified PCR products were purified using the High Pure PCR Cleanup Micro Kit (Roche Diagnostics). The obtained PCR products were cloned with the TOPO TA Cloning Kit (Invitrogen) following the manufacturer's instructions and transformed into competent E. coli. Sequencing reactions were performed using the BigDye Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems) and analyzed on a 3130XL Genetic Analyzer (Applied Biosystems). The newly acquired sequences were deposited in the EMBL/GenBank database. Isolate and accession numbers are specified in Appendix 1.

Phylogenetic analysis

The obtained sequences were added to an existing database using the Muscle automatic alignment option, as implemented in SeaView vs. 4.3.3. (Gouy et al. 2010). The alignment contains 83 sequences with 1126 sites used for analysis. The phylogenetic tree was constructed using maximum likelihood phylogeny (PhyML 3.0) as implemented in ATGC:PhyML (Guindon et al. 2010). An automatic model selection by SMS (Lefort et al. 2017) based on Akaike Information Criterion (AIC) was used, resulting in a GTR+G+I substitution model being selected for the analysis. The initial trees are based on BioNJ. Bootstrap values (BV's) are based on 100 replicates.

Taxonomic study

We reviewed as many publications as we could find (see references) that provided high quality figured specimens of Recent species of Notorotaliidae. These records and our subsequent re-identification of them (where necessary) are listed by region in Appendix 2. A key to help identify the 33 species that we recognize is presented after the taxonomy section. We reviewed the type figures and descriptions of all 64 Late Pleistocene-Recent described and named species or infraspecies attributed to the genera *Notorotalia* (11 species), *Cribrorotalia* (1 species), *Cristatavultus* (1 species), *Porosorotalia* (1 species), *Parrellina* (4 species) and *Buccella* (46 species or infraspecies) in the World Register of Marine Species (Hayward et al. 2021). The descriptions and figures of 12 of these named species (Appendix 3) were considered to be insufficient to confidently recognize the species and distinguish them from others. Future studies and detailed SEM photographs of their primary types or topotypes (or sequencing of morphologically comparable topotypes) may allow some of these species to be recognized as additional species or as senior synonyms of species recognized in this study. A further 14 named species are here considered to be junior subjective synonyms of earlier described and named species (Appendix 4).

MOLECULAR PHYLOGENY

The Family Notorotaliidae is highly supported (100%BV) and consists of two sister clades (text-fig. 1). One clade contains *N. zelandica* (100%BV) branching next to *P. meridionalis* (99%BV). The clade is well supported (82%BV). The second clade is not supported by bootstrap values and contains *Buccella* sp. A (82%BV) branching at the base of *B. tenerrima* (100% BV) and *B. alvarezii* (90% BV). Notorotaliidae branches next to a clade containing *Ammonia* spp. (100%BV), *Haynesina germanica* (100%BV) and *Elphidium* spp. (98%BV).

ECOLOGICAL DISTRIBUTION

Species of the genus *Buccella* inhabit a wide range of marine environments from the polar Arctic Ocean to the tropical Caribbean Sea and east Pacific. One species, *Buccella* n.sp. A has been collected alive intertidally, but most of them appear to be subtidal. Most live on the floor of the open ocean or in deeper parts of open bays. *Buccella* are particularly abundant (often dominant) at shelf depths (0–200 m) in the cold waters of the Arctic Ocean and beneath the cold polar currents that flow north along both coasts of South America and south down the west coast of North America.

In the Arctic Ocean and along the northern shores of North America, *Buccella frigida* mostly lives at inner shelf depths (0–50 m depth) and may comprise up to 30% of the benthic foraminiferal fauna (e.g., Buzas 1965). Two other species living in the Arctic Ocean, *B. floriformis* and *B. tenerrima*, are common constituents of faunas at shelf to mid bathyal depths (down to ~1000 m). The Arctic species, *B. floriformis* and *B. tenerrima*, thrive in high organic carbon flux environments (JW pers. obs.).

Two smaller species, *B. angulata* and *B. troitzkyi*, live at inner-mid shelf depths (20–100 m) on either side of the North Pacific Ocean. The five species we recognize that occur along the west coast of central America, between USA and Peru (*Buccella compactiformis, B. discors, B. hannai, B. plana, B. pulpitoensis*) all live in the open ocean at inner- to mid-shelf depths (0–100 m) and occasionally down to 200 m (McCulloch 1977).

The two most common species around the southern half of South America, *Buccella alvarezii* and *B. peruviana*, live abundantly at inner shelf to uppermost bathyal depths (0–400 m) and are often the most common species in the benthic foraminiferal fauna. They are almost always present in seafloor sediment, particularly sandier, off the coast (e.g., Boltovskoy 1976; Bernasconi and Cusminski 2015) but also may be abundant subtidally in shallow sheltered inlets and bays (e.g., Calvo-Marcilese and Langer 2012). In the Atlantic part of the Southern



TEXT-FIGURE 2

Geographic distribution of the five genera in the family Notorotaliidae.

Ocean, the rare species *B. depressa*, has been recorded living at inner shelf depths (8–20 m) at the Falkland Islands and *B. dejardini* is common living at 200–350 m water depth off South Georgia (Dejardin et al. 2018).

All species of Notorotalia live in normal marine salinity (~35 psu) below low tide level (subtidal). Around New Zealand the majority of species are common at inner shelf depths (0-50 m) off both exposed and somewhat sheltered coasts (e.g., Hayward et al. 1999), with several species (e.g., N. finlayi, N. hornibrooki) having their greatest abundance (up to 30% relative abundance of benthic foraminifera) in quieter, deeper parts (10-40 m) of enclosed inlets. Notorotalia zelandica is characteristic of more exposed, current-swept sandy substrates. This latter species, along with N. aucklandica and N. depressa has a living depth range extending down into the upper bathyal (~400-600 m). Around New Zealand, a single species, N. profunda, has a much deeper depth range extending from mid shelf to lower bathyal (50-1300 m) with its greatest relative abundance (5-10% of benthic foraminifera) at outer shelf-uppermost bathyal depths (100-400 m) (Hayward et al. 2010). The Australian and South American species (N. clathrata, N. patagonica) mostly live at mid-outer shelf depths (50-200 m).

The three species of the Australian genus *Parrellina* have similar ecological distribution patterns. They are most common at inner shelf depths (0–50 m) in normal marine salinity (~35 psu) in the slight shelter around the open mouths of harbours, bays and estuaries (e.g., Albani 1968a, 1978, Yassini and Jones 1995). All three may sometimes also live at slightly deeper shelf depths (50–100 m). The two species of *Porosorotalia* on opposite sides of the Pacific, and in different hemispheres, both

live in the open sea at near normal marine salinity (\sim 32–35 psu) at deep inner to mid shelf depths (\sim 20–100 m). The single species of *Cristatavultus* lives in normal marine salinity at inner shelf depths (0-50 m) on the sandy slopes of coral reefs.

BIOGEOGRAPHY

The family Notorotaliidae has a mostly antitropical (bipolar and bitemperate) distribution (text-fig. 2) with *Notorotalia* and *Parrellina* being essentially Southern Hemisphere-restricted, and *Buccella*, *Cristatavultus* and *Porosorotalia* occurring in both hemispheres. Only *Buccella* and *Cristatavultus* have a continuous distribution through the tropical and subtropical zones and then only on either side of the American continents (*Buccella*) or in the west Pacific (*Cristatavultus*). Most of the coast of Africa and the southern coast of Asia are devoid of notorotaliids.

Buccella occurs throughout the Arctic Ocean but seems to be absent from around the coast of Antarctica. The southeastern coast of South America has sometimes been referred to as the *Buccella* or Argentine zoogeographical province (Boltovskoy 1976) because of its abundance there, whereas New Zealand could be referred to as the *Notorotalia* province for a similar reason. *Buccella* is the most diverse genus with 16 species recognized by us in this study. Six species are restricted to the subantarctic or temperate zones around South America (text-fig. 3) with four of these, *B. depressa*, *B. dejardini*, *B. viejoensis* and *B.* n.sp. A, being rare with each only known from 1–2 areas or collections. This might be a collection bias or also based on misidentification such as in the case of *Buccella* n.sp. A that was originally identified as *B. frigida*. The remaining two species are more common and widespread with *B. peruviana* restricted to the Pacific coasts of Ecuador to Chile (north of 42°S) and *B. alvarezii* restricted to the Atlantic coast from Brazil to Argentina around the tip and up the Pacific coast of Patagonia to 42°S.

Five species of Buccella are recognized from around the coast of central America, mostly in the east Pacific. Two of these, B. *plana* and *B. pulpitoensis*, are rare and only recorded from 1–2 localities in the east Pacific. The other three are more widespread. Buccella discors occurs in low numbers right along the east Pacific coast of central and North America from northern Peru to Oregon (text-fig. 3). Buccella compactiformis has a slightly more southern distribution than B. discors, extending from the Gulf of California (Mexico) to Lima (southern Peru) and sneaking into the Caribbean (?introduced through the Panama Canal) on the coast of Panama. The most widespread central American species is B. hannai which also appears to occur rather sporadically and in low numbers from North Carolina (eastern USA) to the Gulf of Mexico (Texas) and along the east Pacific coast between the Gulf of California and Ecuador (text-fig. 3).

Five species of *Buccella* live in the polar to temperate zones of the Northern Hemisphere (text-figs. 4–5). Two species appear to be rare with few records: *B. angulata* has only been recorded from the Pacific coast of the USA states of California and Washington; *B. troitzkyi* was described from the Pleistocene of the Arctic coast of Siberia but its Holocene records are from the northwest Pacific coasts of Japan and South Korea. *Buccella floriformis* has few, but widespread, verified records from the Atlantic and Pacific coasts of Canada and from the Barents Sea on the Arctic Coast of western Russia.

The genus *Porosorotalia* also occurs in both hemispheres, but with a disjunct distribution. One living species, *P. makiyamai*, occurs in the northeast Pacific, around the coasts of Japan and China (text-fig. 5), and another, *P. meridionalis*, has a wide-spread distribution along the coast of much of southern South America, from northern Peru to northern Argentina (text-fig. 3).

Notorotalia is a diverse Southern Hemisphere-restricted genus with the centre of diversity around the islands of New Zealand, where eight endemic morphospecies are recognized. Three other species are known - each endemic to their region (text-fig. 2). Notorotalia clathrata is endemic to southern Australia where it occurs along more than 3000 km of coast from northern New South Wales to southeastern Western Australia, including around Tasmania (text-fig. 6). Notorotalia patagonica is endemic to Argentina where it occurs right along its South Atlantic coast, as well as at the Falkland Islands offshore (text-fig. 3). The rare species N. kerguelenensis has only been recorded from around the Kerguelen Islands in the Southern Ocean. Around New Zealand (text-fig. 6), three species, N. depressa, N. finlavi and N. hornibrooki, occur throughout the islands. N. profunda and N. zelandica occur around both main islands in the subtropical and temperate zones. The other three species are restricted to one climate zone each: N. olsoni to the subtropical northeast North Island, N. inornata to the temperate South I. and southern North I., and N. aucklandica to the subantarctic and Stewart islands.

The genus *Parrellina* is endemic to eastern Australia (text-fig. 6) except for several records of *P. verriculata* from the Mediterranean Sea (text-fig. 4), where it may have been introduced many years ago by shipping. Of the three species of *Parrellina*

we recognize, two (*P. imperatrix* and *P. verriculata*), occur from Townsville (northern Queensland) all the way south to Hobart (southern Tasmania). The third species, *P. papillosa*, is more restricted and is only recorded along the coast of New South Wales and from Lord Howe Island in the Tasman Sea. The single species of *Cristatavultus* has a tropical west Pacific distribution extending from Tonga in the south to the southern islands of Japan (21°S to 26°N).

TAXONOMY

Morphological terminology follows that defined by Hottinger (2006) with many of the more commonly used descriptive terms, used for the test profile, peripheral angle, sutures and ornament REPLACE labelled in text-figure 6. Synonyms have only been included iwith 7 available images are definitive or sequences with corresponding images are available, unless stated otherwise in the discussion. Descriptions of each species (where provided) are based on images of the types (where available and detailed) supplemented by all available SEM images given in the synonym list and list of sequenced and additional specimens examined.

Order ROTALIIDA Delage and Hérouard 1896 Superfamily ROTALIOIDEA Ehrenberg 1839

Family **NOTOROTALIIDAE** Hornibrook 1961, p. 129, emend. Hornibrook 1996

Diagnosis: Test usually trochospiral; in *Parrellina* planispiral; costate ornament extends over the apertural face of the last chamber; vertical umbilical canals and an intraseptal canal system with branching canals leading to insignificant sutural pores in *Notorotalia, Porosorotalia* and *Parrellina*. Multiple ventral apertures in *Buccella, Notorotalia* and *Porosorotalia*. Middle Eocene–Recent.

Constituent genera: Notorotalia (Eocene-Recent), Buccella (Oligocene-Recent), Cristatavultus (Recent), Discorotalia (Oligocene-Miocene), Parrellina (Oligocene-Recent), Porosorotalia (Eocene-Recent), Cristatavultus.

Taxonomic discussion: Following detailed study of the internal structure of the type species of the genera *Notorotalia, Cribrorotalia, Discorotalia,* and *Parrellina*, Hofker (1969) concluded that this group is similar to the Elphidiidae but differ from them in having "relatively reduced retral processes without porous outer walls, ending in elongate massive poreless costae at right angles to the sutures."

Following phylogenetic analysis of many sequenced phylotypes, Holzmann and Pawlowski (2017) were the first to transfer the genus *Buccella* in with *Cribrorotalia* and *Notorotalia* in the family Notorotaliidae. This genetically-supported placement is followed here.

Genus *Buccella* Andersen 1952 *Buccella* ANDERSEN 1952, p. 143. *Mesorotalia* MCCULLOCH 1977, p. 426.

Type species: Eponides hannai Phleger and Parker 1951

Diagnosis: Test trochospiral, planoconvex to lenticular; periphery rounded to keeled; spiral side with 2–4 whorls in adults, 5–12 chambers per whorl; spiral side sutures variably thickened, oblique and curved back towards periphery; umbilical side sutures radial and incised; umbilicus and part or all of incised umbilical sutures covered by tubercles with one or more



TEXT-FIGURE 3

Verified geographic distribution of species of *Buccella*, *Notorotalia* and *Porosorotalia* around central and South America, based on specimen images in references in the synonym lists under each species in the taxonomy section. Hollow symbols are location of sequenced specimens.

secondary apertures on the side of each suture near the periphery; low arched, primary aperture interiomarginal, midway between umbilicus and periphery, maybe partly covered by tubercles and only visible from the chamber interior.

Age range and geographic distribution: Oligocene to Holocene, cosmopolitan.

Taxonomic discussion: Mesorotalia was synonymized to *Buccella* by Loeblich and Tappan (1987). *Buccella* differs from *Pseudoeponides* by the lack of secondary sutural openings on the spiral side and by the well-developed tubercles in the umbilicus and along the sutures on the umbilical side. *Buccella* differs from *Ammonia* by the presence of the well-developed umbilical and sutural tubercles and presence of secondary sutural apertures on the umbilical side.

Key features of recognized living species of Buccella:

Buccella alvarezii: Test small-medium size (0.2–0.45 mm); peripheral profile acutely rounded early, becoming keeled in adults; 7–9 chambers per adult whorl; spiral side sutures strongly oblique; umbilical side sutures deeply incised, moderately wide and filled with a wide band of dense pustules which also fill its moderate-sized umbilicus. Southwest Atlantic Ocean, southernmost southeast Pacific Ocean.

Buccella angulata: Test small (up to 0.2 mm); 5–6 chambers per adult whorl; profile rounded angular but not keeled; chambers slightly inflated on the umbilical side; pustules down full length of radial sutures on umbilical side. Northeast Pacific Ocean.

Buccella compactiformis: Tests medium to large (0.3–0.6 mm); narrow keel; numerous chambers (9–12) in adult whorl; umbilical chambers mostly covered in pustules; umbilicus small. Equatorial east Pacific Ocean, Caribbean Sea.

Buccella depressa: Test medium size (0.4–0.6 mm); 7–9 chambers per adult whorl; peripheral profile broadly rounded; tubercles in umbilicus and deeply depressed radial sutures. Falkland Islands.

Buccella discors: Test medium size (0.35–0.6 mm); narrow keel; 6–8 chambers in adult whorl; small tubercle-filled umbilicus and narrow, deeply incised, radial sutures on umbilical side with single row of small beads on each side separated by feather-like grooves. East Pacific Ocean.

Buccella dejardini n.sp.: Test large (up to ~ 0.8 mm); 8–10 chambers per adult whorl; strong peripheral keel; mix of two distinct sizes of rounded tubercles and pustules in the umbilical region; dense pustules fill the rest of the sutures. South Georgia.

Buccella floriformis: Test small (0.1–0.25 mm); 5–7 chambers in adult whorl; thin-walled translucent; periphery acutely-angled and keeled in juveniles and adults; tubercles cover the umbilicus, radial sutures and umbilical ends of early chambers. Arctic Ocean, North Pacific Ocean.

Buccella frigida: Test medium size (adults \sim 0.2–0.5 mm); 5–7 chambers per adult whorl; peripheral profile broadly rounded; tubercles in umbilicus and radial sutures. Arctic Ocean, North Sea, North Atlantic Ocean, North Pacific Ocean.

Buccella hannai: Test medium size (0.3–0.45 mm); narrow, peripheral keel in adults; 7–9 chambers per adult whorl; outline

lobulate; sutures on spiral side limbate and raided. Equatorial east Pacific Ocean, Gulf of Mexico, northeast Atlantic Ocean.

Buccella peruviana: Test medium size (~0.5 mm); peripheral profile acute with narrow keel; 9–12 chambers per adult whorl; spiral side sutures strongly oblique; umbilical side sutures narrow usually with a narrow band of pustules along each. Southeast Pacific Ocean.

Buccella plana: Test medium size (~0.4 mm); numerous (10–12) chambers in adult whorl; biconvex to lenticular with wide rounded keel; small umbilicus filled with small tubercles; tubercles lacking from radial sutures or chamber surfaces. Peru.

Buccella pulpitoensis: Test small (~0.3 mm); ~8 chambers per adult whorl; plano-convex with high domed spiral side; acutely rounded periphery; raised, limbate sutures on early part of spiral side; radial sutures on spiral side perpendicular to periphery and not oblique; wide umbilicus and short straight radial sutures filled with tubercles. Equatorial east Pacific Ocean.

Buccella tenerrima: Test medium-large (0.4–0.6 mm); 6–9 chambers in adult whorl; periphery acutely rounded to keeled in adult; wide band of tubercles down radial sutures and over small umbilicus and umbilical ends of mots chambers. Arctic Ocean, North Sea, North Pacific Ocean.

Buccella troitzkyi: Test small (0.2–0.4 mm); 5–6 chambers per adult whorl; acutely rounded periphery; umbilical ends of chambers extend into umbilicus; radial sutures on umbilical side partly closed by thick calcite, partly open at peripheral end around secondary apertures; small umbilicus and radial sutures filled with tubercles. Arctic Ocean, northwest Pacific Ocean.

Buccella viejoensis: Test of medium size (~0.45 mm); 9–10 chambers per adult whorl; acute, limbate periphery, weakly lobulate throughout. Opaque, secondary shell conceals chambers of earliest whorl on spiral side and has dark, narrow lines resembling curved radial sutures extend over it; wide umbilicus (0.25–0.35 diameter of test) and incised radial sutures filled with dense tubercles. Southeast Pacific Ocean.

Buccella n. sp. A: Test medium size (~0.4 mm); 7–10 chambers per adult whorl; strong peripheral keel; large, rounded tubercles fill wide umbilicus and become progressively smaller in the incised sutures towards and around the periphery; a row of tubercles runs down the sutural sides of each chamber on the umbilical side. Chile.

Buccella alvarezii (d'Orbigny 1839) Plate 1, figures 1–11; text-fig. 3

- Pulvinulina alvarezii D'ORBIGNY 1839, pl. 1, fig. 21, pl. 2, figs. 1–2 [Argentina, Patagonia, San Blas; Falkland Islands; Chile, Cape Horn].– HERON-ALLEN and EARLAND 1932, pl. XV, figs. 26–36 [Falkland Islands].
- *Pulvinulina peruviana* (d'Orbigny).– HERON-ALLEN and EARLAND 1932, pl. XV, figs. 37–39 [Falkland Islands].
- Buccella peruviana (d'Orbigny).- FIGUEROA et al. 2005, figs. 9a-b [Chile, off Melinka, 400-3000 m].- CALVO-MARCILESE and LANGER 2012, fig. 2A-O [Argentina, Bahia Blanca estuary].-RODRIGUES et al. 2013, fig. 3.5 [South Brazil, off Laguna, 180 m (p.c. P. Eichler 2021)].- BERNASCONI et al. 2018, figs. 3.1-3.2 [Argentina, 39-41°S, inner-mid shelf, 11-70 m].- MARQUEZ 2019, fig. 3.8 [Argentina, Pampa coastal plain, Holocene].- EICHLER et al. 2019, pl. 1.9 [South Brazil, off Laguna, 180 m (p.c. P. Eichler 2021)].
- Eponides peruviana ssp. campsi BOLTOVSKOY 1954, pl. 17, figs. 6–8 [Argentina, Gulf of San Jorge].



TEXT-FIGURE 4

DELETE

Verified geographic distribution of species of Buccella, Parrellina, and Porosorotalia around the northern half of the Northern Hemisphere, based on specimen images in references in the synonym lists under each species in the taxonomy section.

- Buccella peruviana campsi (Boltovskoy).-BOLTOVSKOY 1959, pl. 4,
- 4 figured specimens [Argentina, Malvin Current]. Buccella peruviana f. typica (d'Orbigny) transitional to f. campsi (Boltovskoy).– BOLTOVSKOY et al. 1980, pl. 4, figs. 6, 11, 17 [Ar-
- gentina entire coast; Uruguay] Buccella peruviana f. campsi (Boltovskoy).– BOLTOVSKOY et al. 1980, pl. 4, figs. 7, 8, 12, 13, 18, 19 [Argentina entire coast; Uruguay; mid shelf].– ALPERIN et al. 2011, fig. 2.2 [Argentina, shelf, 40–42°S, 40–100 m depth].–MARQUEZ and FERRERO 2011, fig. 9.5 [Argentina, Buenos Aires, Mar Chiquita Lagoon, Holocene].
- *Buccella peruviana f. frigida* (Cushman).– BOLTOVSKOY et al. 1980, pl. 4, figs. 9, 14, 15, 20–22 [Argentina entire coast south to Ushuaia; Uruguay; inner shelf]
- Buccella frigida (Cushman).- THEYER 1966, plate, figs. 16-30 [Brazil, Playa Tramandai; Chile, Isla Talcan; Argentina, Golfo San Jorge].– JONES 1994, pl. 105, figs. 8a–c [Argentina, Magellan Strait].– FERNANDEZ and ZAPATA 2010, figs. 3G–H [Chile, Quillaipe Inlet]
- Pulyinulina karsteni (Reuss).—BRADY 1884, pl. 105, figs. 8a-c [Argen-tina, Magellan Strait].—HERON-ALLEN and EARLAND 1932, pl. XV, figs. 26-36 [Falkland Islands].

Eponides peruvianus campsi BOLTOVSKOY 1954, pl. 17, figs. 6–8 [Argentina, Gulf San Jorge].

Buccella sp. 2. DEJARDIN et al. 2018, figs. 14.11, 14.12 [South Georgia]

Unpublished images: Two images from Patricia Eichler [Brazil, off Praia de Iporanga, 5 m; off Laguna, 180 m]; *Buccella* 3 SG18, images of one specimen collected by Wojciech Majewski [South Georgia].

Sequenced specimens: isolates 6299, 6300, 6301, Argentina, Ushuaia Harbour; isolate 20675, UK, Falkland Islands, Goose Green, Choiseul Sound, intertidal. These are effectively topotypes as they come from the type region with no type locality specified.

Type locality: Not designated but localities mentioned were Argentina, Patagonia, San Blas; Falkland Islands; Chile, Cape Horn.

Brief description: Tests small-medium size (0.2–0.45 mm diameter), spiro-convex to biconvex-lenticular in adults; periphery acutely rounded in juveniles becoming angular with a moderately well-developed keel in adults; periphery subcircular to weakly lobulate. Spiral side with 5 (juveniles)–9 (adult) chambers per whorl and up to 3 whorls in adults; sutures slightly curved. Umbilical side with radial sutures slightly curved; umbilicus filled with dense pustules, radial sutures have a wide band of pustules down each; chambers have a distinctive truncated triangular shape as a result of the wide umbilicus, especially in adult specimens.

Molecular characteristics: Buccella alvarezii (90%BV) branch as sister to *B. tenerrima* (100%BV). The branching is not supported by bootstrap values. The partial 18S sequences of *B. alvarezii* contain between 923 and 935 nucleotides, the GC content ranges from 38.1% to 39.5%. The overall mean genetic distance is 0.012.

Taxonomic discussion: Calvo-Marcilese and Langer (2012) showed the ontogenetic change in test morphology from rounded peripheries and 5 chambers in juveniles to keeled peripheries and 8-9 chambers in adults. Our sequenced specimens from the Falkland Islands and Patagonia are adolescent tests with angled and keeled peripheries identical to adult B. alvarezii and the type illustration of d'Orbigny 1839. Calvo-Marcilese and Langer (2012) called this species B. peruviana in contrast to Theyer (1966) who undertook numerous morphological measurements of specimens from both coasts of South America and concluded, like us, that this species from the Atlantic coast and southern tip of South America is morphologically distinct from *B. peruviana* which has its type locality in Peru. Theyer (1966) called this species B. frigida, which is a distinctly different morphospecies restricted to the northern hemisphere. B. alvarezii is distinguished from B. peruviana by its fewer chambers per adult whorl (7-9 versus 9-12) and by having wide, incised radial sutures on the umbilical side, with wide bands of dense pustules along each.

Geographic distribution: South America – Argentina; Brazil; southern Chile (south of 41.5°S); Uruguay. South Atlantic – Falkland Islands; South Georgia.

Ecological distribution: In the South Atlantic, this species lives on the continental shelf up the east coast of Argentina, Uruguay and Brazil under the influence of the cold, southern-sourced Malvinas Current (Boltovskoy et al. 1980; Eichler et al. 2019).

It has been recorded commonly at 40–1000 m water depth but sometimes even outside these depth limits.

Etymology: Probably named for José Ignacio Álvarez Thomas a famous South American military commander and politician of the early 19th century.

Buccella angulata Uchio 1960

Plate 1, figures 12–17; text-fig. 4

Buccella angulata UCHIO 1960, pl. 9, figs. 1–3 [USA, California, 110 m]

Buccella angulata Uchio.– SNYDER et al. 1990, pl. 4, figs. 3a–c [USA, Washington shelf].

No sequenced specimens.

Type photo images: USNM MO 626806, holotype, 3 views (Smithsonian USNM collection images on the web).

Type locality: United States, California, San Diego, off Point Loma, 106 m, Recent.

Brief description: Tests small (up to 0.2 mm diameter), biconvex-lenticular in adults with umbilical side more convex than spiral side; periphery acutely angled lacking a keel; peripheral outline slightly lobulate. Spiral side tightly coiled, with 5, rarely 6 chambers per adulty whorl; sutures slightly oblique, curved. Umbilical side with radial sutures relatively narrow, slightly curved; small umbilicus and sutures covered in dense pustules, most of chamber surfaces unornamented. Low arched, interiomarginal aperture.

Taxonomic discussion: This rarely recorded, small species is similar in size and shape to *B. troitzkyi*. It differs in having chambers more inflated on the umbilical side and having pustules extending the full length of the radial sutures on the umbilical side. Sequencing is required to test whether this species is a distinct taxon as we suspect.

Geographic distribution: Northeast Pacific – USA: California, Washington.

Ecological distribution: Comprises $\sim 5\%$ of fauna at 30–60 m depth off San Diego (Uchio 1960). Mostly occurs at deep inner – mid shelf depths (30–100 m) off the Pacific coast of USA.

Etymology: Named for the angular profile of the test.

Buccella compactiformis McCulloch 1977 Plate 1, figures 18–23; text-fig. 3

- *Buccella compactiformis* McCULLOCH 1977, pl. 144, figs. 5a–5c [Mexico, San Francisquito Bay].
- Buccella cf. peruviana (d'Orbigny).- McCULLOCH 1977, pl. 144, figs. 7a-c, 9a-c; pl. 145, figs. 2a-c [Mexico, Pond Island, 120–170 m; Peru, Lobos de Afuera, 45 m].
- Buccella viejoensis McCulloch.– McCULLOCH 1977, pl. 145, figs. 1a–c [Ecuador, La Plata Island, 20 m]
- *Buccella peruviana resupina* McCULLOCH 1977, pl. 145, figs. 7a–c [Peru, San Juan Bay, 60–80 m]
- Buccella caledoniana McCULLOCH 1981, pl. 58, figs. 11a-c [Caribbean Sea, Panama, Caledonia Bay, 22 m]

No sequenced specimens.

Type locality: Mexico, San Francisquito Bay, 32 m, Recent.

Brief description: Tests medium to large size (0.3–0.6 mm diameter), biconvex-lenticular in adults; periphery acutely angled



TEXT-FIGURE 5

Verified geographic distribution of species of *Buccella tenerrima* and *Porosorotalia makiyamai* in the northern half of the Northern Hemisphere, based on specimen images in references in the synonym lists under each species in the taxonomy section. Hollow symbols are location of sequenced specimens.

with narrow keel in adults; peripheral outline circular to weakly lobulate in last chambers. Spiral side tightly coiled, with 8 (juveniles)–12 (adult) chambers per whorl and up to 3.5 whorls in adults; sutures short, straight to slightly curved. Umbilical side with radial sutures relatively narrow, straight to slightly curved; small umbilicus and sutures covered in dense tubercles, most of chamber surfaces covered in pustules except for peripheral parts of the last few chambers.

Taxonomic discussion: This species is distinguished from *B. alvarezii* by the greater number of chambers per adult whorl (10–12) compared to 7–9, the smaller umbilicus and the pustules over most of the umbilical chambers. It differs from *B. peruviana* by the pustules over most of the chambers and its smaller umbilicus. Adult specimens of this species are distinguished from all others by the greater number of chambers.

Geographic distribution: East Pacific – Ecuador; Mexico; Peru. Caribbean Sea – Panama.

Ecological distribution: Recorded by McCulloch (1977, 1981) from 20–170 m depth in normal marine conditions in open deep-water bays.

Etymology: Presumably named for its compact form.

Buccella dejardini Hayward and Holzmann **n. sp.** Plate 2, figures 1–9; text-fig. 3

- Buccella peruviana (d'Orbigny).– FERNÁNDEZ 2010, pl. 3, fig. 32–33 [Chile, Contaco Estuary].– FERNÁNDEZ and ZAPATA 2010, fig. 31 [Chile, Quillaipe Inlet].
- *Buccella* sp. 1 DEJARDIN et al. 2018, figs. 14.14–16 [South Georgia, shelf, 253 m].

No sequenced specimens.

Holotype: MHNG-INVE-0138919, deposited in the Geneva Natural History Museum, SG20 (Plate 2, figs. 1–3).

Paratypes: MHNG-INVE-0138920, deposited in the Geneva Natural History Museum, SG18, from 54° 10.783' S, 36° 39.979' W, 102 m depth; MHNG-INVE-0138921, SG 27, from 54° 09.372' S, 36° 38.426' W, 136 m depth (Plate 2, fig. 4–6).

Type locality: South Georgia, Stromness Bay, 54° 13.586' S, 36° 25.234' W, 106 m depth (SG20).

Brief description: Test large (up to ~ 0.8 mm diameter); biconvex-lenticular profile with a strong keel in adults; outline circular, sometimes slightly lobulate in the last few chambers.

Spiral side low convex with 8–10 chambers in adult whorls and about 3.5 whorls in the adult test; radial sutures narrow, flush, straight to slightly curved, and moderately oblique to the periphery; spiral sutures somewhat limbate but also flush. Umbilical side with weakly curved, incised radial sutures separating smooth, slightly inflated chambers; secondary calcite fills over these sutures between earlier chambers of the whorl; umbilicus and incised sutures are filled with dense pustules that are mixed with less numerous, larger tubercles in the umbilical region. Apertures not visible beneath the dense cover of pustules that extend part way up the apertural face of the last chamber.

Taxonomic discussion: This species resembles the common eastern South American species *Buccella alvarezii* from which it differs by the two distinct sizes of tubercles and pustules in the umbilical region. This new species differs from *Buccella* n.sp. A by its larger size, the lack of the row of tubercles down each side of the chambers on the umbilical side and by the progression from large to small tubercles from the umbilicus to the periphery.

Geographic distribution: Southeast Pacific – Southern Chile. Southern Ocean – South Georgia.

Ecological distribution: Recorded as occurring commonly at 200–350 m water depths off South Georgia at infaunal sediment depths of 2–8 cm by Dejardin et al. (2018) and from 100–140 m depth in the same region (WM pers. obs.). Also recorded and illustrated from the intertidal of Contaco Estuary, southern Chile (Fernández 2010).

Etymology: Named for Rowan Dejardin, who first recognized this species as being undescribed.

Buccella depressa Andersen 1952 Plate 1, figures 24–29; text-fig. 3

Buccella depressa ANDERSEN 1952, pl. 1, figs. 7a-c, 8 [Falkland Islands]

No sequenced specimens.

Type locality: Falkland Islands, Port William, 16-20 m depth.

Type photo images: USNM PR 833, holotype (Smithsonian USNM collection images on the web).

Brief description: Test medium size (0.4–0.6 mm diameter); biconvex, periphery lobulate, rounded. Spiral side finely perforate with slightly curved, oblique sutures; 7–9 chambers per adult whorl, 2.5–3 whorls on adults. Umbilical side more

coarsely perforate than spiral side, radial sutures deeply depressed, chambers inflated, umbilicus, and sutures partly filled with tubercles.

Taxonomic discussion: This species is distinguished from many other Recent species by its rounded rather than acute angled periphery. It is most similar to *B. frigida*, which also has a rounded periphery, but differs in having more chambers per whorl, a more depressed umbilicus and more incised sutures on the umbilical side with less granular covering, and less limbate spiral-side sutures. Sequencing is required to test whether this is indeed a separate species from its northern counterpart *B. frigida*.

Geographic distribution: Only known at present from South Atlantic – Falkland Islands.

Ecological distribution: Recorded from 8–20 m depth in a moderately sheltered bay at the Falkland Islands.

Etymology: Presumably named for its depressed profile.

Buccella discors McCulloch 1977 Plate 2, figures 10–15; text-fig. 3

- Buccella discors McCULLOCH 1977, pl. 144, figs. 1a-c, 3a-c; pl. 145, figs. 3a-c, 5a-c [Mexico, Gulf of California, 65 m; Peru, Lobos de Afuera, 45 m]
- *Buccella oregonensis* (Cushman, Stewart and Stewart).– McCULLOCH 1977, pl. 143, figs. 11a–c [USA, Oregon, Sunset Bay, shallow water] NOT *B. oregonensis* of Cushman, Stewart and Stewart (1947).
- Buccella tenerrimiformis McCULLOCH 1977, pl. 145, figs. 4a-c [Co-lombia, 36 m]
- Buccella cf. angulata Uchio.– McCULLOCH 1977, pl. 143, figs. 10a–c [California, Port San Luis Obispo, 16 m]

Buccella tenerrima (Bandy).–BARBIERI 2001, pl. 1, figs. 16–17 [Mexico, Gulf of California, Colorado River delta, intertidal mud flats]

No sequenced specimens.

Type locality: Mexico, Gulf of California, 65 m.

Brief description: Test of medium size (0.35–0.6 mm diameter); biconvex to planoconvex with slightly more convex spiral side; periphery acutely angled and sharply keeled in adult. Spiral side with 6–8 chambers per whorl, tightly coiled with oblique weakly curved sutures. Umbilical side with smooth triangular, only weakly inflated chambers separated by straight radial sutures; umbilicus small and filled with fine tubercles extending slightly over the umbilical ends of chambers; radial sutures extremely narrow and deeply incised, bordered on each side by a single row of small granular beads separated by feather-like grooves. Secondary postero-sutural low arched apertures on side of each radial suture.

Taxonomic discussion: This species is distinguished from all other Recent species of *Buccella* by the single row of granular beads along each side of the extremely narrow straight radial sutures on the umbilical side and by the small granular umbilical area.

Geographic distribution: East Pacific – Colombia; Mexico; Peru; USA: California, Oregon.

Ecological distribution: McCulloch (1977) records this species off the west coast of central America at 6–180 m water depth.

Etymology: Named for the Latin "discors" meaning at variance or inconsistent as McCulloch (1977) states that the spiral side is



TEXT-FIGURE 6

Verified geographic distribution of species of *Notorotalia, Parrellina* and *Cristatavultus* around the southwest Pacific based on specimen images in references in the synonym lists under each species in the taxonomy section. Hollow symbols are location of sequenced specimens. texturally like *Gyroidina* but the umbilical features place it in the genus *Buccella*.

Buccella floriformis Voloshinova 1960 Plate 2, figures 16–21; text-fig. 4

Buccella floriformis VOLOSHINOVA 1960, p. 270, pl. 1, figs. 1–5 [Russia, Sea of Okhotsk, Katangli, Miocene]

- *Buccella hannai* (Phleger and Parker) var. *arctica* VOLOSHINOVA 1960, p. 286, pl. 8, figs. 2–4 [Barents Sea, Quaternary].
- *Buccella arctica* Voloshinova. RODRIGUÉS et al. 1993, pl. 2, figs. 13–14 [Canada, Gulf of St Lawrence, Late Quaternary]
- *Buccella hannai* (Phleger and Parker).– RIVEIROS and PATTERSON 2008, figs. 13.4a–c [Canada, British Columbia, Seymour Inlet].

No sequenced specimens.

Type locality: Northwest Pacific, Russia, Sea of Okhotsk, Sakahalin Island, Katangli, upper Miocene.

Brief description: Tests small (0.1–0.25 mm diameter), planoconvex to biconvex-lenticular; periphery acutely angled with a well-developed keel in both juveniles and adults; peripheral outline weakly lobulate. Spiral side low convex to flat; sutures slightly limbate, oriented strongly oblique to periphery; 5–7 chambers per adult whorl, 2–3 whorls in adult tests. Umbilical side flat to convex; slightly inflated chambers separated by depressed, very slightly curved radial sutures; sutures, moderately small umbilicus and umbilical ends of most chambers covered with small, rounded tubercles; small arched secondary apertures sometimes visible on anterior side of radial suture near the periphery.

Taxonomic discussion: This species is morphologically similar to *B. tenerrima* from which it differs by its much smaller, thinner and translucent test, a smaller proloculus and fewer whorls in the adult test.

Geographic distribution: Arctic Ocean – Russia: Barents Sea. North Atlantic Ocean – Canada: Quebec. North Pacific – Canada: British Columbia; Russia: Sea of Okhotsk.

Ecological distribution: Lives infaunally down to 4 cm depth at shelf to mid bathyal depths (shallower than 1000 m, but most commonly on the continental shelf) on the edge of the Arctic Ocean (JW pers. obs.).

Etymology: Named from the Latin word "flori" meaning flower as its shape suggests a flower-like form.

Buccella frigida (Cushman 1922) Plate 3, figures 1–12; text-fig. 4

Pulvinulina repanda var karsteni (Reuss).–PARKER and JONES 1865, pl. 14, figs. 14–15, 17 [Arctic Ocean].

Pulvinulina frigida CUSHMAN 1922, p. 144.

Buccella frigida (Cushman).- ANDERSEN 1952, figs. 4–6 [Canada, Hudson Bay and south down Atlantic coast to Maryland].-LOEBLICH and TAPPAN 1953, pl. 22, figs. 2a–c, 3a–c [USA, Alaska, Point Barrow, 42 m; Canada, Nunavut, Baffin Island; Greenland].- TODD and LOW 1961, pl. 1, figs. 24–25 [USA, Massachusetts, Martha's Vineyard].-BUZAS 1965, pl. 4, figs. 3a–b [USA, New York, Long Island Sound].- KNUDSEN 1971, pl. 8, figs. 12–14 [Denmark, Lokken, Pleistocene].- HAYNES 1973, figs. 42.1–42.5 [UK, Wales, Cardigan Bay].- TOOD and LOW 1981, figs. 127 a–c [northeast USA].-FEYLING-HANSSEN et al. 1983, pl. 2, figs. 4–6 [Greenland, Plio-Pleistocene].- NOMURA and SETO 1992, figs. 16.7a–b [Japan, Honshu, Lake Nakanoumi],- AUSTIN and SEJRUP 1994, pl.2, fig. 5 [Norway, Syslakvag].- RIVEIROS and PATTERSON 2008, figs. 13.3a–c [Canada, British Columbia, Seymour Inlet].- LEI and LI 2016, figs. 54a–I [China, Bohai Sea, Yellow Sea, intertidal to 80 m].– NESBITT and MARTIN 2021, web image [USA, Washington, Puget Sound].

- *Eponides frigida* var. *calida* CUSHMAN and COLE 1930, pl. 13, figs. 13a–c [USA, Maryland, Pleistocene].–CUSHMAN 1931, pl. 10, figs. 3a–c, 4a–c [USA, Massachusetts, Buzzards Bay].
- *Buccella calida* (Cushman and Cole).– RODRIGUES et al. 1993, pl. 2, figs. 5, 6 [Canada, Gulf of St Lawrence, Gaspe Peninsula, Late Quaternary]
- Buccella inusitata Andersen.– LEI and LI 2016, figs. 53a–I [China, Yellow Sea, South China Sea].
- Buccella hannai arctica Voloshinova.– GUDINA 1969, pl. 8, figs. 5–6 [Russia, Siberia, Pleistocene].
- Buccella depressa Andersen.– RIVEIROS and PATTERSON 2008, figs. 13.2a–b [Canada, British Columbia, Seymour Inlet].
- Aubignya sp. KORSUN et al. 2014, figs. 9.9-13 [Russia, White Sea].

No sequenced specimens.

Type locality: Canada, Hudson Bay, between Black Whale and Olaska Harbors, 20 m depth. Recent.

Type photo images: USNM 3032, lectotype [Andersen 1952, figs. 6a–c]; USNM CC3031, paralectotype (Smithsonian USNM collection images on the web).

Brief description: Test of moderate size (0.3–0.5 mm diameter), biconvex; periphery slightly lobular and broadly to acutely rounded without a keel. Spiral side smooth with narrow, slightly curved and limbate, oblique sutures; adults with 2.5 to 3 whorls, 5–7 chambers per adult whorl. Umbilical side finely perforate, radial sutures slightly depressed and curved; umbilicus, sutures and basal margin of last chamber covered with tubercles.

Taxonomic discussion: This species is somewhat variable and characterised by its size, robust test and broadly to acutely rounded periphery. When living under permanent ice-cover in the Arctic Ocean, specimens of this species are generally much smaller than those in areas with greater food supply (JW pers. obs.). *Buccella frigida* is most similar to *B. depressa* but the former has a thicker coat of tubercles, fewer chambers per whorl and smaller test (Andersen 1952). *Buccella frigida* lacks the lenticular profile and peripheral keel possessed by adult *B. alvarezii* (Calvo-Marcilese and Langer 2012) and *B. tenerrima*. Juvenile *B. alvarezii* have similar morphologies to adult *B. frigida*, which led Theyer (1966) to identify his eastern South American populations as *B. frigida*. In the Arctic juvenile *B. tenerrima* are commonly misidentified as *B. frigida* because they have not yet developed their adult profile and keel.

Geographic distribution: Arctic Ocean – Canada; Greenland; Norway; Russia: White Sea; USA: Alaska. North Sea – Denmark. North Atlantic Ocean – Canada: Quebec; UK: Wales; USA: Maryland, Massachusetts. North Pacific Ocean – Canada: British Columbia; China; Japan.

Ecological distribution: One of us (JW pers. obs.) has observed that *B. frigida* only lives at inner shelf depths (0-50 m) around the edge of the Arctic Ocean. It comprises 20-30% of faunas at 15–25 m depth in Long Island Sound (Buzas 1965).

Etymology: Named from the Latin "frigida" meaning cold, with reference to its Arctic type locality.

Buccella hannai (Phleger and Parker 1951) Plate 2, figures 22–27; text-fig. 3

Eponides hannai PHLEGER and PARKER 1951, pl. 10, figs. 11–14 [USA, Texas, off Galveston, 35–65 m]



TEXT-FIGURE 7 Terminology used in the description of the tests and ornament of Notorotaliidae tests in this review.

- Buccella hannai (Phleger and Parker).– ANDERSEN 1952, figs. 3a–c [[USA, Texas, off Galveston, 35 m; Louisiana, Mississippi River South Pass].– AKERS 1971, p. 150 [USA, North Carolina, Beaufort].– LOEBLICH and TAPPAN 1987, pl. 726, figs. 14–16 [Gulf of Mexico, Holocene, holotype].–COLLINS 2010, 3 figures [PPP 1660, Panama, upper Miocene]
- *Buccella sinulata* McCULLOCH 1977, pl. 144, figs. 4a–c [Mexico, Tenacatita Bay, 100 m; also recorded from Costa Rica, Ecuador, Colombia and Peru, 2–100 m]

No sequenced specimens.

Type locality: Gulf of Mexico northwest, 35 m depth, Holocene.

Brief description: Test of moderate size (0.3–0.45 mm diameter), planoconvex to biconvex; periphery distinctly lobulate, acutely angled and keeled in adults. Spiral side smooth, finely perforate, usually high convex with curved and limbate sutures; 7–9 chambers in last whorl. Umbilical side more coarsely perforate, flat to low convex, radial sutures depressed slightly curved back towards periphery, tubercles cover umbilicus, sutures and basal portion of last chamber or chambers. Secondary apertures low arched to slit-like at peripheral end of each radial suture on the umbilical side.

Taxonomic discussion: This species is distinguished from all others by the raised limbate sutures on the spiral side. Juvenile specimens may have a more rounded angular peripheral profile with a keel developing in adults. This species appears to be rare in modern seas and is mostly recorded from Miocene and Pliocene strata.

Geographic distribution: Pacific coast of central America – Colombia; Costa Rico; Ecuador; Mexico; Peru. Gulf of Mexico – USA: Texas. North Atlantic – USA: North Carolina.

Ecological distribution: Recorded as living at inner-mid shelf depths (0–100 m) in the northwest Gulf of Mexico (Phleger and Parker 1951) and off the west coast of central America.

Etymology: Named for esteemed American oil geologist Marcus A. Hanna (1898–1978) who assisted in the research programme on the recent sediments and foraminifera of the northwest Gulf of Mexico.

Buccella peruviana (d'Orbigny 1839) Plate 3, figures 13–17; text-fig. 3

Rotalina peruviana D'ORBIGNY 1839, pl. 2, figs. 3–5 [not designated, listed localities from Ecuador, Peru and Chile].

Buccella peruviana (d'Orbigny).– THEYER 1966, pl. 1, figs. 1–15 [Chile–Valparaiso, Golfo de Arauco, Mehuin, Mejillones, and Chiloe Isla].– ZAPATA et al. 1995, pl. 2, figs. 1–3 [Chile south].

Buccella peruviana f. typica (d'Orbigny).– BOLTOVSKOY et al. 1980, pl. 4, figs. 5, 10, 16 [Chile]

Unpublished specimens examined: 19 specimens [MZUC 1818, 1820, Chile offshore between 34 and 42°S, 12–240 m depth].

No sequenced specimens.

Type locality: Peru, Callao, near the Lorenzo Island (Boltovskoy et al. 1980).

Brief description: Tests of medium size (adults ~0.5 mm diameter), variable spiro-convex to biconvex-lenticular in adults; periphery acute with narrow keel, even in juveniles; periphery circular to weakly lobulate. Spiral side with 6–8 chambers per

whorl in juveniles and 9–12 chambers per whorl in adults; up to 3 whorls in adults; radial sutures straight to slightly curved. Umbilical side often with a flat or concave umbilical region; radial sutures straight to slightly curved; moderately wide umbilicus filled with dense tubercles; radial sutures narrow, incised, often with a narrow band of pustules along each.

Taxonomic discussion: Our observations on all figured and unfigured specimens available to us indicate that there are two distinct common species of Buccella around the southern half of South America – B. alvarezii and B. peruviana. This is in agreement with Theyer (1966) who undertook quantitative measurements on hundreds of specimens around both coasts, although he incorrectly identified the southern and eastern species as the Northern hemisphere-restricted *B. frigida*. It is also consistent with the observations of Boltovskoy et al. (1980) who recognized a South Pacific population (peruviana f. typica) with more chambers per whorl (9-11) and more strongly-developed keel than South Atlantic and Patagonian populations (which they called peruviana f. campsi and f. frigida). We distinguish B. peruviana from the South Atlantic species B. alvarezii, by its narrower bands of sutural pustules on the umbilical side and by the generally greater number of chambers in adult whorls (9-12 versus 7-9). The hypothesis that *B. peruviana* is a separate species from B. alvarezii needs to be tested with molecular sequencing of live material from Chile or Peru, but we are confident that Theyer (1966), Boltovskoy et al. (1980) and ourselves are correct in recognising two geographically separate taxa.

Geographic distribution: South America – Central and north Chile (north of 42°S); Peru; Ecuador.

Ecological distribution: Specimens live in open, normal marine salinity waters in a wide bathymetric range from inner shelf to uppermost bathyal (10–400 m) and possibly deeper.

Etymology: Meaning from Peru, its type locality.

Buccella plana McCulloch 1977 Plate 3, figures 18–20; text-fig. 3

Buccella plana McCULLOCH 1977, pl. 141, figs. 8a–c [Peru, Lobos de Afuera Islands]

No sequenced specimens.

Type locality: Peru, Lobos de Afuera Islands, 50-60 m, Recent.

Brief description: Tests of medium size (~0.4 mm diameter); biconvex-lenticular in adults; periphery acute with rounded limbate keel in adults; peripheral outline circular to weakly lobulate in last chambers. Spiral side 10–12 chambers per whorl in adult and 2.5–3 whorls in adults; sutures short, straight to slightly curved. Umbilical side with narrow radial sutures relatively narrow, straight to slightly curved; small umbilicus covered in dense tubercles, sutures and chamber surfaces lack any tubercles or pustules.

Taxonomic discussion: This species is most similar to *B. compactiformis* from which it differs by the lack of pustules or tubercles on the umbilical chambers or in the radial sutures and by the wide limbate periphery rather than a narrow keel. Sequencing is needed to confirm this species belongs in this genus.

Geographic distribution: This rare species is only known from the type locality off Peru.

Ecological distribution: Only recorded from 50–60 m water depth, at the type locality.

Etymology: Named from the Latin "plana" meaning level or flat, presumably because of the relative lack of ornament on this species.

Buccella pulpitoensis McCulloch 1977 Plate 3, figures 21–23; text-fig. 3

Buccella pulpitoensis McCULLOCH 1977, pl. 144, figs. 6a–c [Mexico, Gulf of California]

No sequenced specimens.

Type locality: Mexico, Gulf of California, off Pulpito Rock, 36 m, Recent.

Brief description: Test small (~0.3 mm); planoconvex with high domed spiral side; periphery acutely rounded, probably lacking a keel; outline moderately lobulate. Spiral side with ~8 inflated chambers per whorl; straight to weakly curved sutures, perpendicular to the periphery; early spiral side sutures raised and prominent becoming depressed towards periphery. Umbilical side flat with finely perforate to smooth, slightly inflated, bluntly triangular chambers separated by straight, depressed radial sutures; umbilicus wide and filled with fine tubercles as are the radial sutures.

Taxonomic discussion: We have retained this rarely-recorded morphotype as a distinct species but its validity needs to be tested by sequencing to be confident it is not a variant of a more common species. This morphospecies is distinguished by its raised sutures in the middle of the spiral side, in common with *B. hannai.* It lacks the sharp keel of *B. hannai* which also does not have a dorso-convex profile like this species. *Buccella pulpitoensis* also differs from most others by the radial sutures on the spiral side being perpendicular to the periphery.

Geographic distribution: Pacific west coast of central America – Costa Rico; Mexico.

Ecological distribution: McCulloch (1977) records this rare species off the west coast of central America at 20–40 m water depth.

Etymology: Named for the type locality Pulpito Rock, Mexico.

Buccella tenerrima (Bandy 1950) Plate 4, figures 1–17; text-fig. 5

- Rotalia tenerrima BANDY 1950, pl. 42, figs. 3a–c [USA, Oregon, Cape Blanco, Pleistocene].–KNUDSEN 1971, pl. 8, figs. 15–17 [Denmark, Lokken, Pleistocene].– WOLLENBURG 1992, pl. 20, fig. 7 [Arctic Ocean, Nansen Basin].–McCORMICK et al. 1994, pl. 3, fig. 5 [USA, California, Tomales Bay].–LLOYD 2006, pl. 2, figs. d–e [Greenland, Disko Bugt]; RIVEIROS and PATTERSON 2008, figs. 13.6a–c [Canada, British Columbia, Seymour Inlet].
- Buccella cf. tenerrima (Bandy).– McCULLOCH 1977, pl. 132, figs. 8a–c [USA, Alaska, Point Barrow, 60 m]
- Buccella inusitata ANDERSEN 1952, figs. 10a-c, 11a-c [USA, Washington, Straits of Juan de Fuca, Dallas bank].- LOEBLICH and TAPPAN 1953, pl. 22, figs. 1a-c [USA, Alaska, Point Barrow; Canada, Nunavut, Baffin Island; Greenland].- GUDINA 1969, pl. 8, fig. 7 [Russia, Siberia, Pleistocene].- SHCHEDRINA and LUKINA 1984, pl. 14, figs. 77a-c, 78a-c [northwest Pacific Ocean].
- Buccella cf. inusitata Andersen. McCULLOCH 1977, pl. 141, figs. 7a–c, pl. 143, figs. 7a–c, 9a–c [USA, Alaska, Wrangell; California, Albion River estuary and Bodega Bay].

- Buccella frigida (Cushman).- GUDINA 1969, pl. 8, fig. 4 [Russia, Siberia, Pleistocene].- MURRAY 1971, pl. 53, figs. 1–5 [British Isles from English Channel northwards].- JONES 1994, pl. 105, figs. 9a–c [Canada, Ellesmere Island, Cape Frazer].- TSUJIMOTO et al. 2006, figs. 5.2a-b [Japan, Osaka Bay].- SPEZZAFERI et al. 2015, pl. 36, figs. 1a–c [Norway].- SKIRBEKK et al. 2016, figs. 3C–D [Norway, Svalbard].- LIMOGES et al. 2018, pl. 4, figs. 1–2 [Greenland, Independence Fjord].- HESEMANN 2021, FEU-1005741 [Fram Strait].- HESEMANN 2021, FEU-100576–7, 100595–6 [Russia, Laptev Sea].
- *Buccella* cf. *frigida* (Cushman).– McCULLOCH 1977, pl. 143, figs. 5–6 [USA, Alaska, Wrangell, 4 m].
- Buccella frigida s.l. BARTELS 2017, fig. 10a [Norway, Svalbard, Recent]
- Buccella frigida ssp. biconvexa Shchedrina in SHCHEDRINA and LUKINA 1984, pl. 15, figs. 80a-c [northwest Pacific Ocean].
- Pulvinulina karsteni (Reuss).- BRADY 1884, pl. 105, figs. 9a-c [Canada, Ellesmere Island, Cape Frazer]
- Buccella cf. bella Bandy and Arnal.- McCULLOCH 1977, pl. 143, figs. 4a-c [USA, Alaska, Wrangell, 4 m]
- Mesorotalia fastidiosa McCULLOCH 1977, pl. 123, figs. 5a-c [USA, Alaska, Chukchi Sea, Holocene, holotype only]
- Buccella fastidiosa (McCulloch 1977).- LOEBLICH and TAPPAN 1987, pl. 726, figs. 14-16 [USA, Alaska, Chukchi Sea, holotype].

Buccella daidokoensis McCULLOCH 1977, pl. 146, figs.4a-c [Korea, Daido Ko, 20 m]

Buccella differens McCulloch Form A.- McCULLOCH 1981, pl. 58, figs. 9a-c [Sweden, Gothenburg]

Buccella differens McCulloch Form B.– McCULLOCH 1981, pl. 58, figs. 10a–c [Norway, Ballestrand, 16 m]

Buccella radiata Shchedrina in SHCHEDRINA and LUKINA 1984, pl. 15, figs. 81a-c [northwest Pacific Ocean].

Buccella sp. TODD and LOW 1981, fig. 127 a-c [northeast USA].

Sequenced specimens: isolates 19383, 19384, Arctic Ocean, 312 m. These are not topotypes as they were collected thousands of kilometres from the fossil type locality.

Unpublished images: Three specimens from Maria Holzmann [Arctic Ocean, north of Svalbard, 195 m, Recent]

Type locality: USA, Oregon, Cape Blanco, Pleistocene.

Type photo images: PAL237397 holotype (Smithsonian USNM collection images on the web).

Brief description: Test of medium-large size (0.3-0.6 mm diameter), planoconvex to biconvex-lenticular; periphery acutely rounded in juveniles becoming acutely angled with a well-developed keel in adults; peripheral outline subcircular to weakly lobulate. Spiral side convex, smooth, finely perforate; sutures slightly limbate oriented strongly oblique to periphery; 6-9 chambers per adult whorl, 3-3.5 whorls in adult tests. Umbilical side flat to convex, more coarsely perforate than spiral side; slightly inflated chambers separated by depressed radial, very slightly curved sutures; sutures, small umbilicus and umbilical ends of most chambers covered with small, rounded tubercles; in adults the sutures widen and are more depressed towards the periphery where they are densely lined with rounded tubercles perforated by a number of small irregularly-shaped openings; as a result the adult chambers develop a rectangular appearance on the umbilical side.

Molecular characteristics: Buccella tenerrima (100%BV) branches at the base of *B. alvarezii* (90%BV). The branching is not supported by bootstrap values. The partial 18S sequences of *B. tenerrima* contain between 762 and 766 nucleotides, the GC content ranges from 41.1% to 41.5%. The overall mean genetic distance is 0.010.

Taxonomic discussion: Buccella tenerrima is characterised by its acutely-angled periphery becoming weakly keeled in adults and its moderate size in adult specimens; the pattern of rounded tubercles forming a wide band along the length of the sutures on the umbilical side widening at the peripheral end in adults and the presence of one or more bosses in the umbilicus among tubercles. This species is morphologically identical to *B. inusitata* Andersen with its type locality in the same region. Although not mentioned in the description, the holotype image of *B. inusitata* (CC64503 in Smithsonian image library) also possesses a rounded boss in the umbilicus the same as in the image of the holotype of *B. tenerrima*. This species is morphologically similar to *B. floriformis*, from which *B. tenerrima* differs by its larger size and the additional calcite on the central part of the spiral side giving the sutures a distinctive whitish appearance.

Buccella tenerrima is morphologically similar to *B. alvarezii*, a widespread and common species around the coast of South America, that has been shown to have considerable morphological changes during ontogeny (Calvo-Marcilese and Langer 2012). *Buccella tenerrima* is very similar to *B. alvarezii* from which it differs by having a wider band of tubercles along the sutures, more extensive cover of tubercles around the umbilicus and less depressed sutures. It can be also distinguished from *B. peruviana* by the latter's species more numerous chambers and narrower radial sutures on the umbilical side.

Geographic distribution: Arctic Ocean – Canada; Greenland; Norway, Russia: Barents Sea, Laptev Sea; USA: Alaska. North Atlantic Ocean – Canada: Quebec; United Kingdom: England as far south as English Channel. North Sea – Denmark; Sweden. North Pacific Ocean – Canada: British Columbia; Japan; Korea; Russia; USA: Alaska, California, Oregon, Washington.

Ecological distribution: Lives infaunally (at depths down to 4 cm) at shelf and bathyal depths (0–1400 m) in seasonally ice-free areas of the Arctic Ocean with large adult specimens usually only found at shelf depths (JW pers. obs.).

Etymology: From the Latin "tenerrima" meaning delicate shell.

Buccella troitzkyi Gudina 1969

Plate 3, figures 24-29; text-fig. 4

Buccella troitzkyi GUDINA 1969, pl. 9, figs. 1–3 [Russia, Siberia, Pleistocene].

Buccella frigida (Cushman).– AKIMOTO et al. 2002, pl. 63, figs. 2a–c [Japan, Kyushu, Shimabara Bay].– TAKATA et al. 2016, figs. 4.3a–c [South Korea, Nakdong River Delta, Holocene]

Buccella inusitata Andersen.– AKIMOTO et al. 2002, pl.63, figs, 1a–c [Japan, Kyushu, Shimabara Bay]

No sequenced specimens.

Type locality: Russia, north Yenisei River Plain, Pleistocene.

Brief description: Test small (0.25–0.4 mm in diameter); unequally biconvex profile; periphery acutely rounded, sometimes thickened; weakly to strongly lobular in outline. Spiral side often flat or low convex; 5.5–7 chambers per adult whorl; sutures narrow, oblique to periphery, slightly curved; Umbilical side with slightly inflated chambers, especially the last; umbilical area small, often partly filled by folium of last chamber; radial sutures depressed partly covered by secondary shell between earlier chambers with a wider depression towards the periphery containing a secondary sutural aperture; umbilicus and depressed sutural areas filled with dense rounded pustules. *Taxonomic discussion:* This species is distinguished by its narrow sutures on the spiral side, its acutely rounded, sometimes limbate peripheral profile, and the presence of secondary calcite growing over the umbilical end of radial sutures with a sutural depression near the periphery.

Geographic distribution: Arctic Ocean – Russia. North Pacific Ocean – Japan; South Korea.

Ecological distribution: Recorded in short cores from 20–50 m water depth in Shimabara Bay, Japan (Akimoto et al. 2002).

Etymology: Named after S.L. Troitzky, Russian expert on the Pleistocene of Siberia.

Buccella viejoensis McCulloch 1977 Plate 4, figures 18–23; text-fig. 3

Buccella viejoensis McCULLOCH 1977, pl. 144, figs. 10a–c, 11a–c [Peru, Independencia Bay, 24 m; Peru, Sechrua, Callao; Peru, San Juan Bay, 6–40 m; Ecuador, La Plata Island, 20 m; Mexico, Gulf of California, 12–100 m;]

No specimens sequenced.

Type locality: Peru, Independencia Bay, Viejo Island east side, 24 m depth.

Brief description: Tests of medium size (\sim 0.4–0.45 mm diameter), spiro-convex to biconvex-lenticular in adults; periphery acute with narrow keel or narrow limbate fringe; periphery weakly lobulate throughout. Spiral side with \sim 9–10 chambers per whorl and 2.5–3 whorls in adults; sutures curved backwards; polished opaque, secondary shell conceals chambers of earliest whorl; dark, narrow lines resembling curved radial sutures extend over secondary shell from proloculus to last coil of spiral suture. Umbilical side with radial sutures straight to slightly curved; wide umbilicus (0.25–0.35 diameter of test) and wide, incised radial sutures filled with dense tubercles, chambers often have a truncated triangular shape as a result of the wide umbilicus, especially in adult specimens.

Taxonomic discussion: This species resembles *B. alvarezii* in its appearance on the umbilical side, with 9–10 truncated chambers per whorl, a large umbilicus filled with small tubercles and wide, incised, radial sutures similarly filled with dense tubercles. It differs significantly on the spiral side which has thick secondary shell obscuring the early whorls and dark, narrow lines resembling curved, radial sutures extending over the polished secondary shell. This feature is unique within *Buccella*.

Geographic distribution: East and southeast Pacific – Ecuador; Mexico; Peru.

Ecological distribution: Recorded from moderate shelter in normal marine salinity environments at 6–100 m water depth (McCulloch 1977).

Etymology: Named for the type locality.

Buccella n. sp. A

Plate 4, figures 24–27; text-fig. 3

Buccella peruviana (d'Orbigny).- HOLZMANN and PAWLOWSKI 2017, pl. 1, figs. 11–12 [Chile, Bahia de Concepcion].

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Sequenced specimens: isolates 17572, 17573, 17574, 17575, 17576, 17577, Chile, Bahia de Concepcion, intertidal.

Brief description: Test of small-medium size (up to ~0.4 mm in diameter); test biconvex-lenticular; peripheral profile acutely angled with a relatively strong rounded keel; outline circular sometimes slightly lobular in the last few chambers. Spiral side with limbate, slightly raised sutures; radial sutures straight to slightly curved and slightly oblique to periphery; 7-10 chambers per adult whorl; central region with smooth secondary calcite. Umbilical side with straight, deeply-incised, radial sutures between flat, smooth-topped chambers; umbilicus and entire sutures extending all way to periphery covered in rounded tubercles; larger rounded tubercles occur in the umbilical area, becoming smaller towards the periphery; in adults, fine tubercles may extend around the peripheral edge of the chambers along the side of the keel; the edges of many of the chambers have a line of small tubercles parallel to the sutures; pustules cover the apertural face of the last chamber; weak radiating grooves may be present at the periphery where the radial suture ends; the apertures are obscured by the tubercles.

Molecular characteristics: Buccella n. sp. A (82%BV) branch at the base of *B. tenerrima* (100%BV) and B. alvarezii (90% BV). The partial 18S sequences of *Buccella* sp. A contain between 890 and 906 nucleotides, the GC content ranges from 40.9% to 41.7%. The overall mean genetic distance is 0.010.

Taxonomic discussion: This species is morphologically-similar to the widespread South American species *B. alvarezii*, from which it differs by the far more extensive development of tubercles with larger tubercles in the umbilical area and tubercles along the edges of early chambers in the final whorl on the umbilical side. This species has not been described because we lack any specimens to designate as primary types. The illustrated specimens that were sequenced were destroyed during DNA extraction.

Geographic distribution: Only recorded from the southeast Pacific – Chile.

Ecological distribution: Only recorded from Bahia de Concepcion, where it was collected live at intertidal depths.

Genus *Cristatavultus* Loeblich & Tappan 1994 *Type species: Elphidium pacificum* Collins 1958

Diagnosis: Test inflated, irregularly trochospiral; crisp irregular or wavy, often anastomosing, ribs extending over chambers roughly parallel to the periphery, but no radial ribs along or parallel the sutures; sutural fossettes present; fine ribs extend over apertural face; aperture semi-circular at the base of the apertural face.

Age range and geographic distribution: Only recorded from the Recent; tropical west Pacific and southwest Pacific distribution.

Cristatavultus pacificus (Collins 1958) Plate 4, figures 27-28; text-fig. 6

- *Elphidium pacificum* COLLINS 1958, p1. 5, fig. 13 [Australia, Queensland, Great Barrier Reef].
- Parrellina pacifica (Collins).- HATTA and UJIIE 1992, pl. 49, figs. 8a-b, pl. 50, figs. 1 a-c [Japan, Ryukyus Islands].
- *Elphidium millettiforme* McCULLOCH 1977, p1. 97, fig. 12 [Philippine Islands].
- Polystomella milletti (Heron-Allen & Earland).- CUSHMAN 1924, p1. 16, figs. 8–9 [Samoa].
- Elphidium milletti (Heron-Allen & Earland). CUSHMAN 1933, pl. 11, figs, 8a-b [Tonga, Vavau Passage; Fiji, Nairai, 25 m]. – CUSHMAN

1939, pl.16, figs. 22a-b [Tonga, Vavau Passage].- ALBANI 1968b, fig. 156 [Australia, New South Wales].

- *Cristatavultus pacificus* (Collins).– LOEBLICH and TAPPAN 1994, pl. 377, figs. 7–8, pl. 378, figs. 1–3.
- Cristatavultus milletti (Heron-Allen & Earland).- LOEBLICH & TAPPAN 1994, pl. 377, figs. 1-6 [Australia, Northern Territory].
- *Cristatavultatus pacificus* (Collins).– HAYWARD et al. 1997, pl. 17, figs. 14–16, pl. 18, figs. 1–3 [Australia, Queensland; Fiji; Samoa; Tonga; Vanuatu].– DEBENAY 2012, p. 219 [New Caledonia].

Type locality: Not designated, but Collins (1958) material is from 600 m depth in Trinity Opening, off the Great Barrier Reef, Queensland, Recent.

Brief description: Test medium to large size, slightly trochospiral; outline lobulate; profile ovate, with involute side nearly flat and evolute side convex; periphery broadly rounded; 7–9 strongly inflated chambers in adult whorl; sutures deeply impressed to channelised, radial; no radial or sutural ribs; numerous, narrow, fine, irregular, transverse riblets ornament the later chambers, and develop into an anastomosing network of crisp, sharp ridges on earlier chambers; apertural face ornamented with narrow, fine riblets radiating outwards from around the aperture; aperture a large semi-circular opening located at the base of the apertural face; coarsely perforate wall texture. Greatest diameter 0.8-1.0 mm; width/thickness ratio 3.2-3.6.

Taxonomic discussion: This species has for many years been confused with *Elphidium milletti* from the west Indian Ocean. Close examination shows the two species to be quite distinct and that *E. milletti* is planispiral and not trochospiral, lacks the single aperture of *Cristatavultus* and is best left in the genus *Elphidium* rather than placed in this genus as proposed by Loeblich and Tappan (1994).

Geographic distribution: Tropical West Pacific – Australia: Northern Territory, Queensland; Fiji; Japan: Ryukyus Islands; New Caledonia; Philippines; Samoa; Tonga; Vanuatu.

Ecologic distribution: C. pacificus lives in normal marine salinity at inner shelf depths on the sandy slopes of coral reefs around the tropical shores of Queensland and many Pacific islands. Small numbers of specimens, including the holotype, have come from greater depths and are inferred to have been transported downslope following their death.

Etymology: Name refers to this species' distribution in the Pacific Ocean.

Genus Notorotalia Finlay 1939

Type species: Notorotalia zelandica Finlay 1939, p. 517.

Diagnosis: Lenticular test with acute, often keeled, peripheral profile; possess a combination of both sutural and intersutural ribs of varied development on both sides; the terminal or apertural face is ornamented with wavy ridges; possess a line of tiny cribrate apertures along the base of the terminal face located in clefts between the sculptural ridges (Vella 1957).

Age range and geographic distribution: Middle Eocene–Recent, Southern Hemisphere temperate to subantarctic zones.

Fossil species: Thirty-eight species currently recognized -35 from New Zealand, 4 from Australia and 1 from South America (Hayward et al. 2021). Several occur in more than one region.

Key features of recognized living species of Notorotalia:

Notorotalia aucklandica: Test large (up to 1.2 mm); spiral side convex, domed; central region of umbilical surface deeply concave; 12–14 chambers in adult whorls; sutural ribs well developed, intersutural ribs extend from suture to suture in early chambers, but not in later chambers. Southern New Zealand.

Notorotalia clathrata: Test large (up to 1.5 mm); biconvex with acute, keeled periphery; 10–11 chambers in adult whorls; strongly raised sutural ribs on both spiral and umbilical sides. Southern Australia.

Notorotalia depressa: Test moderate to large (up to 0.8 mm); compressed, almost parallel-sided; 10–12 chambers in adult whorls; umbilical surface with flattened or gently concave umbilical area; sutural ribs well-developed, intersutural ribs thin and usually not reaching anterior sutural rib. New Zealand.

Notorotalia finlayi: Test small to moderate size (up to 0.7 mm); planoconvex; 11–13 chambers in adult whorls; sutural ribs well-developed on spiral side, intersutural ribs strong but dying out before reaching anterior sutural rib on spiral side. New Zealand.

Notorotalia hornibrooki: Test small to moderate size (up to 0.6 mm); compact and biconvex, typically more convex spiral side; 8–9 chambers in adult whorls; umbilical sutural ribs strong, gently curved and only slightly oblique to periphery; spiral side often lacks sculpture. New Zealand.

Notorotalia inornata: Test large (up to 0.8 mm); biconvex; 11–12 chambers in adult whorl; sutural ribs fade out towards periphery, intersutural ribs truncated at or before middle of each chamber; smooth thin callus deposit on spiral side. New Zealand.

Notorotalia kerguelenensis: Test of moderately small size (up to 0.6 mm); depressed biconvex, 9–10 chambers in adult whorls; periphery acutely angled with narrow keel. Spiral side with sutures between chambers depressed and slightly curved; sutural and intersutural ribs narrow and moderately developed; intersutural ribs widely spaced and extend across full width of chambers; a semi-reticulate pattern of ribs develops over early whorls. Umbilical side with moderately weak to discontinuous radial ribs and similar intersutural ribs to the spiral side. Kerguelen Islands.

Notorotalia olsoni: Test large (up to 1 mm), planoconvex; 10–11 chambers per adult whorls; sutural ribs weak on umbilical surface, difficult to discern on spiral surface; intersutural ribs fine, dense; spiral surface lacking callus, dense ribbing producing reticulate appearance. Northern New Zealand.

Notorotalia patagonica: Test moderately small (up to 0.6 mm diameter); low biconvex; 8–10 chambers per adult whorls; sutural and intersutural ribs of equal moderate strength on both sides; areas of weakly-developed reticulate ribbing occurs in centre of the test on both sides. South America.

Notorotalia profunda: Test small (up to 0.5 mm); biconvex, usually more convex on the umbilical side; 6–8 chambers per adult whorls, compact; sutures oblique, curved; sutural ribs weak or absent; sculpture weakly reticulate on spiral side. New Zealand.

Notorotalia zelandica: Test large (up to 1.5 mm); biconvex, with centre of umbilical side somewhat flattened; 12–14 chambers per adult whorls; prominent callus knob on spiral side; sutural ribs weak, intersutural ribs extend from suture to suture. New Zealand.

Notorotalia aucklandica Vella 1957 Plata 5. figuras 1. 4: taxt fig. 6

Plate 5, figures 1–4; text-fig. 6

Notorotalia aucklandica VELLA 1957, p.57, pl. 3, figs. 39–43 [New Zealand, Auckland Islands]; HAYWARD et al. 1999, pl. 16, figs. 13–15 [New Zealand – subantarctic islands].–HAYWARD et al. 2007, pl. 1, figs. 17–19 [New Zealand, Auckland and Campbell islands].– HAYWARD et al. 2010, pl. 25, figs. 1–3 [New Zealand – Stewart, Auckland and Campbell Islands]

Type locality: Auckland Islands, Musgrave Peninsula, 12 m, Recent.

Brief description: Large size (up to 1.2 mm diameter); periphery acute with a weak keel, 12–14 chambers/whorl, biconvex to planoconvex with high-domed spiral side. Umbilical side convex to flat with deeply concave central region. Sutural side with sutural ribs well developed and gently curved, intersutural ribs extend from suture to suture in early chambers, but not in later chambers.

Geographic distribution: Endemic to southern New Zealand, $47-53^{\circ}$ S.

Ecological distribution: Common in exposed and moderately sheltered, fully marine, shelf environments at 0–200 m depth.

Etymology: Named for the Auckland Islands in Subantarctic New Zealand. where it was described from.

Notorotalia clathrata (Brady 1884) Plate 5, figures 5–10; text-fig. 6

Rotalia clathrata BRADY 1884, pl. 107, figs. 8a–c, NOT fig. 9 [Australia, Victoria, Bass Strait].

- Notorotalia clathrata (Brady).- YASSINI and JONES 1995, figs. 1059–1061 [Australia, New South Wales]; HAYWARD et al. 1999, fig. 152 A-C [Australia, Bass Strait, 77 m].- ALBANI et al. 2001, 5 figures [Australia: Western Australia (southeast coast), South Australia, Victoria, New South Wales, Tasmania]
- Polystomellina clathrata (Brady).– JONES 1994, pl. 197, figs. 8a–c [Australia, Bass Strait].
- Notorotalia decurrens CHAPMAN 1941, pl. 8, figs. 7a–b [southeast Australia Victoria, 100–1000 m water depth]

Type locality: Australia, Victoria, Bass Strait, east Moncoeur Island, 75–80 m depth, Recent (Lectotype nominated by Finlay 1939).

Brief description: Test large (up to 1.5 mm); biconvex with acute, keeled periphery. Sutural side high domed to convex, 10–11 chambers per adult whorl with strongly raised sutural ribs but much weaker intersutural ribs not always connecting between sutural ribs. Umbilical side with very strong, raised, sutural ribs that narrow towards, and often don't reach, the periphery; intersutural ribs weaker but may stretch over entire chamber; umbilical area partly filled with several irregular short costae.

Taxonomic discussion: Examination of the type figures and short description of *N. decurrens* Chapman 1941 indicates that it has the same characteristic strong sutural ribs on the umbilical side as in *N. clathrata* and its morphology lies within the vari-

ability of the latter species. It also has the same geographic distribution. Jones (1994) was unaware of Hofker's (1969) detailed studies that clearly show that *Polystomellina* is a trochospiral elphidiid and not a notorotaliid.

Geographic distribution: Australia: New South Wales, South Australia, Tasmania, Victoria, Western Australia.

Ecological distribution: Shelf depths.

Etymology: From the Latin word "clathratus", meaning latticed, with reference to the rib ornament.

Notorotalia depressa Vella 1957 Plate 5, figures 11–13; text-fig. 6

Notorotalia depressa VELLA 1957, pl. 1, figs.13, 19, 20 [New Zealand, Cook Strait].– HAYWARD et al. 1999, pl. 16, figs. 16–18.– HAY-WARD et al. 2010, pl. 25, figs. 4–6 [New Zealand, North, South, Stewart and Auckland Islands]

Type locality: New Zealand, Cook Strait, 25 m depth, Recent.

Brief description: Test moderate to large (up to 0.8 mm diameter), compressed and almost parallel–sided; both spiral and umbilical sides slightly convex but umbilical side with a flattened or gently concave umbilical area. Spiral side with 10–12 chambers in adult whorl; sutural ribs well developed, straight to slightly curved. Umbilical side with moderately curved sutural ribs with thin intersutural ribs, which do not usually reach the anterior suture.

Geographic distribution: Endemic to New Zealand, 34-51°S.

Ecological distribution: Widespread and common (up to 15% of faunas) in exposed and moderately sheltered, fully marine, shelf depths (0–200 m, most commonly 20–70 m).

Etymology: Named for the depressed or flattened nature of the test in profile view compared with other *Notorotalia* species.

Notorotalia finlayi Vella 1957

Plate 5, figures 14–19; text-fig. 6

Notorotalia finlayi VELLA 1957, pl. 1, figs. 4, 5, 9, 10 [New Zealand, Cook Strait, 6–180 m].– HAYWARD et al. 1999, pl. 16, figs. 19–21 [New Zealand, North, South, Stewart and Auckland Islands]

Type locality: New Zealand, North Island, Wairarapa, Whang-aehu Valley, lower Pleistocene.

Brief description: Test small to medium-sized (up to 0.7 mm); planoconvex with spiral side flat to gently convex and umbilical side convex but distinctly concave in the umbilical area. Spiral side with 11–13 chambers per adult whorl. On both spiral and umbilical sides, the sutural ribs are well-developed, with intersutural ribs strong at posterior end but dying out before reaching the anterior sutural rib. Sutural pores usually developed at posterior margin of the chambers.

Geographic distribution: Endemic to New Zealand, 34–51°S.

Ecological distribution: Widespread in low numbers in exposed and moderately sheltered, fully marine, inner- and mid-shelf depths (0–100 m). Its greatest abundance (up to 30% of faunas) occurs in the quieter, deeper parts (10–40 m) of enclosed inlets in central and southern New Zealand. *Etymology*: Named for the founder of New Zealand foraminiferal research – the late Dr Harold J. Finlay.

Notorotalia hornibrooki Hayward, Grenfell, Reid and Hayward 1999

Plate 5, figures 20–22; text-fig. 6

Notorotalia clathrata (Brady).- VELLA 1957, p.47 [New Zealand, Cook Strait].

Notorotalia hornibrooki HAYWARD et al. 1999, pl. 16, figs. 31–33 [New Zealand, North, South, Stewart, Chatham and Auckland Islands].

Type locality: New Zealand, Wanganui Bight, 86 m, Recent.

Brief description: Test of small to moderate size compact and biconvex, 8–9 chambers per whorl; acute periphery and rounded keel. Often more convex on the spiral side which also commonly lacks sculpture.

Geographic distribution: Endemic to New Zealand, 34-51°S.

Ecological distribution: Widespread and common in exposed and moderately sheltered, fully marine, inner-shelf environments. Its greatest abundance's (up to 25% of foraminiferal faunas) are in the sheltered shallows of enclosed, fully marine bays.

Etymology: Named for the "Father of New Zealand foraminiferal biostratigraphy" – the late Dr Norcott deB. Hornibrook,

Notorotalia inornata Vella 1957

Plate 5, figures 23–25; text-fig. 6

- Notorotalia inornata VELLA 1957, pl. 2, fig. 29, pl. 3, figs. 36–38 [New Zealand, Cook Strait, 170–350 m; Queen Charlotte Sound, 6–8 m].– HAYWARD et al. 1999, pl. 16, figs. 22–24 [New Zealand, southern North, South, Stewart and Auckland Islands]
- non Notorotalia inornata Vella 1957.– LOEBLICH and TAPPAN 1994, p. 170, pl. 387, figs. 4–6.

Type locality: New Zealand, Cook Strait, 350 m depth, Recent.

Brief description: Test large (up to 0.8 mm diameter); biconvex. Periphery bluntly angled often with a heavy keel. Spiral side with 11–12 chambers per adult whorl; a more or less continuous intersutural rib usually present adjacent to the periphery; early chambers have a smooth thin callus deposit. On both spiral and umbilical sides, the sutural ribs are weakly curved and intersutural ribs truncated at or before the middle of each chamber in adults.

Geographic distribution: Endemic to New Zealand, 40-51°S.

Ecological distribution: Sporadic occurrences generally in low numbers in exposed and moderately sheltered, fully marine, inner- and mid-shelf depths (0–100 m). Greatest abundance's (up to 10% of faunas) in the quieter, deeper parts (10–40 m) of enclosed inlets.

Etymology: Named for its sparse ornament – inornate.

Notorotalia kerguelenensis Parr 1950 Plate 6, figures 1–3

Notorotalia kerguelenensis PARR 1950, pl. 14, figs. 18a–c; text-figs. 8a–c [Indian Ocean, Kerguelen Island].

Type locality: Kerguelen Island, 150 m depth, Recent.

Brief description: Test of moderately small size (up to 0.6 mm diameter); depressed biconvex, almost parallel-sided; periphery acutely angled with narrow keel. Spiral side with 9–10 chambers in adult whorl; sutures between chambers depressed and slightly curved; sutural and intersutural ribs narrow and moderately developed; intersutural ribs widely spaced and extend across full width of chambers; a semi-reticulate pattern of ribs develops over early whorls. Umbilical side with moderately weak to discontinuous radial ribs and similar intersutural ribs to the spiral side.

Taxonomic discussion: Too few specimens of this species have been recorded or illustrated to be certain that is a distinct from its neighbour *N. clathrata* to the east. For the present we retain it as separate but these needs testing with sequencing and population studies.

Geographic distribution: Only three specimens have been recorded, all from the Southern Ocean's Kerguelen Islands.

Ecological distribution: recorded from 40–300 m water depth in normal marine salinity water (Parr 1950).

Etymology: Named for the location where it was described from – Kerguelen Islands.

Notorotalia olsoni Vella 1957 Plate 6, figures 4–6; text-fig. 6

Notorotalia olsoni VELLA 1957, pl. 2, figs. 23, 24 [New Zealand, Hen and Chickens Islands, 60 m].– HAYWARD et al. 1999, pl. 16, figs. 25–27 [New Zealand, northeast coast of North Island]

Type locality: New Zealand, North Island, Hen and Chickens, 60 m depth, Recent.

Brief description: Test large (up to 1 mm diameter); distinctly planoconvex with spiral side nearly flat and umbilical side roundly convex at the sides, with a slightly concave umbilical area. Spiral side with 10–11 chambers in adult whorls; spiral surface without callus deposits and dense ribbing producing a reticulate appearance. On the umbilical side the sutural ribs are very weak, nearly straight with fine dense intersutural ribs.

Geographic distribution: Endemic to New Zealand, 34-51°S.

Ecological distribution: Common in moderate numbers in exposed and moderately sheltered, fully marine, inner-shelf environments (0–50 m). Also found in low numbers at mid- and outer-shelf depths.

Etymology: Named for New Zealand molluscan paleontologist, Mr Pat Olson, who was killed in the Tangiwai lahar train disaster in 1953.

Notorotalia patagonica Parr 1950

Plate 6, figures 7-9; text-fig. 3

- Rotalia clathrata BRADY 1884 (part), pl. 107, fig. 9 (NOT 8) [Patagonia].– HERON-ALLEN and EARLAND 1932, pl. 16, figs. 1–4 [Falkland Islands].
- Notorotalia clathrata (Brady).– BOLTOVSKOY et al. 1980, pl. 23, figs. 1–3 [South America east coast from Patagonia to Buenos Aires].
- Notorotalia patagonica PARR 1950, p. 375 [Patagonia]

Polystomellina patagonica (Parr).- JONES 1994, pl. 107, figs. 9a-c [Patagonia]

Type locality: Southern Ocean, off west coast of Patagonia in 350 m water depth, recent, Challenger Station 305.

Brief description: Test small (0.3–0.55 mm diameter), planoconvex to low biconvex; periphery acutely angular and weakly keeled. Spiral side flat to low convex; 8–10 chambers per adult

PLATE 1

Recent species of the genus Buccella. Scale bar is 100 µm.

- 1–2 *Buccella alvarezii* (d'Orbigny 1839), sequenced specimen, MW834377, Falkland Islands, Goose Green, Choiseul Sound.
 - 3 *Buccella alvarezii* (d'Orbigny 1839), unsequenced specimen, republished from Argentina, Pampa coastal plain, Marquez (2019).
- 4 *Buccella alvarezii* (d'Orbigny 1839), sequenced specimen, Chile, off Melinka (44°S), 400–3000 m, republished from Figueroa et al. (2005).
- 5–11 *Buccella alvarezii* (d'Orbigny 1839), series of unsequenced specimens from juvenile to adult, Argentina, Bahia Blanca estuary, republished from Calvo-Marcilese and Langer (2012).
- 12–14 *Buccella angulata* Uchio 1960, unsequenced specimens, USA, Washington, republished from Snyder et al. (1990).

- 15–17 *Buccella angulata* Uchio 1960, holotype, USNM MO 626806, USA, California, San Diego.
- 18–20 Buccella compactiformis McCulloch 1977, holotype, AHF 2185, Mexico, San Francisquito Bay, 32 m, republished from McCulloch (1977).
- 21–23 *Buccella compactiformis* McCulloch 1977, unsequenced specimen, AHF 2189, Mexico, off Pond Island, 120–170 m, republished from McCulloch (1977).
- 24–26 Buccella depressa Andersen 1952, holotype, USNM PR 833, Falkland Islands, Port William, 16–20 m, republished from Andersen (1952).
- 27–29 *Buccella depressa* Andersen 1952, holotype, USNM PR 833, Falkland Islands, Port William, 16–20 m.



whorl; sutures oblique to periphery; sutural and intersutural ribs of equal moderate strength; intersutural ribs extend full width of chambers; and area of weakly developed reticulate ribbing occurs in centre of test over early whorl. Umbilical side low convex, sometimes with depressed umbilicus; sutural and intersutural ribs of equal, moderate strength; sutural ribs discontinuous; an umbilical area of reticulate rib ornament often present.

Taxonomic discussion: Jones (1994) was unaware of Hofker's (1969) detailed studies that clearly show that *Polystomellina* is a trochospiral elphidiid and not a notorotaliid.

Geographic distribution: South Atlantic – Argentina, 35–57°S; Falkland Islands. Southern Ocean – Argentina: Patagonia.

Ecological distribution: Shelf depths (0–350 m) in normal marine salinity (Brady 1884; Boltovskoy et al. 1980).

Etymology: From the locality it was described from – Patagonia.

Notorotalia profunda Vella 1957 Plate 6, figures 10–13; text-fig. 6

Notorotalia profunda VELLA 1957, pl. 1, figs. 6–8 [New Zealand, Lord Howe Rise, 600 m and off Greymouth, 650 m].– HAYWARD et al. 2010, pl. 25, figs. 7–9 [New Zealand off both coasts of North and northern South islands].

Type locality: Tasman Sea, Lord Howe Rise, 600 m depth, Recent.

Brief description: Test small (up to 0.5 mm diameter); stout, biconvex with an angular keeled periphery. Spiral side with 7–8 chambers in adult whorls. On both sides the intersutural ribs

strong, crisp and continuous from suture to suture, sometimes locally reticulate with secondary ribs.

Geographic distribution: Endemic to New Zealand region and Tasman Sea, 35–45°S.

Ecological distribution: A deep-water species that occurs between mid-shelf and lower bathyal depths (65-1300 m), with greatest relative abundances (5-10%) at outer shelf to upper bathyal depths (90-400 m) (Vella 1957; Hayward et al. 2010).

Etymology: Named from the Latin "profundus" meaning deep, being the deepest living species of *Notorotalia*.

Notorotalia zelandica Finlay 1939

Plate 6, figures 14-19; text-fig. 6

- Notorotalia zelandica FINLAY 1939, p. 518.– HOFKER 1969, figs. 1–10 [New Zealand, fossil].– HAYWARD et al. 1999, pl. 16, figs. 34–36 [New Zealand, North, South and Stewart islands].– LOEBLICH and TAPPAN 1987, pl. 792, figs. 1–8 [New Zealand, types].– HAYWARD et al. 2010, pl. 25, figs. 10–12 [New Zealand, North, South, Stewart islands].
- Notorotalia zelandica zelandica Finlay.- VELLA 1957, pl. 2, figs. 31, 33, 34, text-figs. 2a-e [New Zealand, East Cape, Cook Strait and Otago Heads].
- Notorotalia finlayi Vella.– HOLZMANN and PAWLOWSKI 2017, pl. 1, fig. 13 [New Zealand, Queen Charlotte Sound]

Sequenced specimens: isolates FF126, FF128, FF133, New Zealand, Marlborough, Pelorus Sound, Crail Bay; isolates 16463, 16464, 16465, 16467, 17468 17469, 17470, New Zealand, Marlborough, Queen Charlotte Sound. These are not topotypes as they were collected 150 km south of the fossil type locality.

Type locality: New Zealand, Whanganui, Castlecliff, Pleistocene.

PLATE 2

Recent species of the genus Buccella. Scale bar is 100 µm.

- 1–3 Buccella dejardini Hayward and Holzmann n.sp., MHNG-INVE-0138919, holotype, South Georgia, Stromness Bay, 106 m.
- 4-6 Buccella dejardini Hayward and Holzmann n.sp., MHNG-INVE-0138921, paratype, South Georgia, Stromness Bay, 136 m.
- 7–9 *Buccella dejardini* Hayward and Holzmann n.sp., unsequenced specimen, GC666-002, South Georgia, republished from Dejardin et al. (2018).
- 10–12 Buccella discors McCulloch 1977, holotype, AHF 2183, Mexico, Gulf of California, 65 m, republished from McCulloch (1977).
- 13–15 *Buccella discors* McCulloch 1977, unsequenced specimen, AHF 2179, USA, Oregon, Sunset Bay, shallow water, republished from McCulloch (1977).

- 16–18 Buccella floriformis Voloshinova 1960, holotype, VNIGRI 454/19, northwest Pacific, Russia, Sea of Okhotsk, Sakahalin Island, Katangli, upper Miocene, republished from Voloshinova (1960).
- 19–21 Buccella floriformis Voloshinova 1960, holotype, VNIGRI 454/12, Arctic Ocean, Barents Sea, holotype of Buccella hannai var. arctica Voloshinova 1960, republished from Voloshinova (1960)
- 22–24 *Buccella hannai* (Phleger and Parker 1951), holotype, USA, Texas, off Galveston, 35–65 m, republished from Phleger and Parker (1951).
- 25–27 *Buccella hannai* (Phleger and Parker 1951), unsequenced fossil specimen, PPP 1660, Panama, Colon, upper Miocene, republished from Collins (2010).



Brief description: Test large (up to 1.5 mm diameter); Spiral side convex with a distinct knob of callus in the centre. Umbilical side convex with flattened or slightly concave umbilical area. Spiral side with 11–12 chambers in adult whorls; a more or less continuous intersutural rib is usually present adjacent to the periphery. Umbilical side with sutural ribs gently arcuate with dense heavy intersutural ribs that usually extend from suture to suture.

Molecular characteristics: Notorotalia zelandica (100%BV) branches as sister to *P. meridionalis* (99% BV). The branching is well supported (82%BV). The partial 18S sequences of *N. zelandica* contain between 963 and 974 nucleotides, the GC content ranges from 40.1% to 41%. The overall mean genetic distance is 0.007.

Geographic distribution: Endemic to New Zealand, 34-48°S.

Ecological distribution: Widespread in moderate numbers in exposed and moderately sheltered, fully marine, inner- and mid-shelf depths. Most common around central New Zealand with its greatest abundance's (up to 10% of faunas) in exposed, sandy inner-shelf environments.

Etymology: Named for the country where it occurs – New Zealand.

Genus *Parrellina* Thalmann 1951 *Parrellina* Thalmann 1951, p. 224. *Elphidioides* Parr 1950 (non *Elphidioides* Cushman 1945), p. 373.

Type species: Polystomella imperatrix Brady 1881, p.66.

Diagnosis: Test planispiral, bilaterally symmetrical, involute to slightly evolute; sutural canal system opens into a single row of indistinct pores, quite different from the characteristic sutural

fossettes of *Elphidium*; narrow, raised, often slightly wavy sutural ribs, linked by a series of similar intersutural ribs, at times forming an anastomosing pattern of ornament; apertural face strongly ornamented all over with radiating pustules and/or fine ribs; aperture a series of large circular pores at base of apertural face.

Taxonomic discussion: We support the opinion of Hofker (1969) that this genus, characterised by its type species *P. imperatrix*, is closely linked to *Notorotalia* and has not evolved from *Elphidium*. We restrict it purely to those species having typical *Notorotalia*-like ornament, with narrow, raised, often slightly wavy sutural and intersutural ribs, radiating ribs on the apertural face and lacking the characteristic sutural fossettes and septal bridges of the Elphidiidae.

There has been considerable confusion as to the diagnostic characteristics of this genus, which have led to differing opinions as to which subfamily or family it should be placed in. We support Hornibrook (1961), Hofker (1969) and Loeblich and Tappan (1987) in placing it together with the genera *Notorotalia* and *Cribrorotalia*, at that time in the subfamily Notorotaliinae but now, following Hornibrook (1996), in the family Notorotaliidae based on the characteristics of the sutural canal system and the similarity of the rib ornament to that in the genus *Notorotalia*.

Key features of recognized living species

Parrellina imperatrix: Large test with up to five large peripheral spines. Australia.

Parrellina papillosa: Large test covered in dense, irregular tuberculose and costate ornament that obscures everything beneath. Australia.

PLATE 3

Recent species of the genus Buccella. Scale bar is 100 µm.

- 1–3 *Buccella frigida* (Cushman 1922), lectotype, CC3032, Canada, Hudson Bay, 20 m depth.
- 4-6 *Buccella frigida* (Cushman 1922), paralectotype, CC3031, Canada, Hudson Bay, 20 m depth.
- 7–9 *Buccella frigida* (Cushman 1922), unsequenced specimen, CC14213, Maryland, Wailes Bluff, Pleistocene, holotype of *Eponides frigida* var. *calida* Cushman and Cole 1930, republished from Cushman and Cole (1930).
- 10–12 Buccella frigida (Cushman 1922), unsequenced specimen, CC12952, USA, Massachusetts, Buzzards Bay, republished from Cushman (1931).
- 13–15 *Buccella peruviana* (d'Orbigny 1839), unsequenced specimen, Chile, republished from Zapata et al. (1995).

- 16 *Buccella peruviana* (d'Orbigny 1839), unsequenced specimen, Chile, Mehuin (39.5°S), republished from Theyer (1966).
- 17 Buccella peruviana (d'Orbigny 1839), unsequenced specimen, Chile, Mehuin (39.5°S), republished from Theyer (1966).
- 18–20 Buccella plana McCulloch 1977, holotype, AHF 2155, Peru, Lobos de Afuera Islands, republished from McCulloch (1977).
- 21–23 *Buccella pulpitoensis* McCulloch 1977, holotype, AHF 2186, Mexico, Gulf of California, off Pulpito Rock, 36 m, republished from McCulloch (1977).
- 24-26 Buccella troitzkyi Gudina 1969, holotype, Russia, north Yenisei River Plain, Pleistocene.
- 27–29 *Buccella troitzkyi* Gudina 1969, unsequenced specimen, KAUM-FO-324, Japan, Kyushu, Shimabara Bay, republished from Akimoto et al. (2002).



Parrellina verriculata: Large, compressed, parallel-sided test; 10–14 chambers per whorl; narrow, distinct, sometimes wavy sutural and intersutural ribs; no peripheral spines. Australia.

Present-day geographic and stratigraphic range: Australia, Oligocene-Recent.

Parrellina imperatrix (Brady 1881) Plate 6, figures 20–21; text-fig. 6

Polystomella imperatrix BRADY 1881, pl. 110, figs. 13–15 [Australia, Tasmania, Storm Bay, and New South Wales, Sydney]. *Elphidioides imperatrix* (Brady).– PARR 1950, p. 373.

- Elphidium imperatrix (Brady).- CUSHMAN 1930, pl. 17, figs. 5–9 [Australia, Tasmania, Storm Bay]; PARR 1945, p. 217.- ALBANI 1968a, pl. 9, figs. 13–14 [Australia, New South Wales, Port Hacking].- ALBANI 1968b, fig. 154 [AUSTRALIA, New South Wales].
- High Theorem 1, 1997 (1997) (191) (197) (191) (197) (191) (197) (191) (197) (191) (197) (191) (197) (191) (197) (191) (197) (191) (197) (191) (197) (191) (1

Type locality: Not given by Brady, presumably Australia, Sydney, 4–20 m, Recent.

Brief description: Test large (up to 1 mm diameter); slightly evolute; planispiral with profile strongly compressed and parallel-sided; periphery acute with narrow keel and 4–5 strong, rod-like peripheral spines per whorl. 12–17 slightly inflated

chambers in adult whorl; sutural ribs narrow, fine, slightly irregular; sutures flush to slightly depressed, curved backwards towards the periphery; 8-12 narrow, wavy or irregular, transverse ribs extend over the full width of each chamber; sutural and transverse ribs become irregular and anastomosing over the wide, flat umbilical area; numerous fine pustules cover the test wall between the ribs; apertural face ornamented with fine, pustulate riblets radiating out from the apertural area. Width/thickness ratio = 3-4.

Taxonomic discussion: Parrellina imperatrix is easily distinguished by its 4–5 long, solid spines per whorl.

Geographic distribution: Australia: Queensland, New South Wales, Victoria and Tasmania.

Ecologic distribution: Parrellina imperatrix lives around the coast of eastern Australia in normal marine salinity, mostly at inner shelf depths. It is particularly common in the open mouths of large estuaries and bays at 5–30 m depth (e.g., Albani 1968a, 1978).

Etymology: From the Latin "imperator" meaning emperor, possibly because the peripheral spines may be said to produce a crown effect.

Parrellina papillosa (Cushman 1936) Plate 6, figures 22–23; text-fig. 6

Elphidium papillosum CUSHMAN 1936, pl. 14, fig. 12 [Australia, New South Wales, off Wollongong].

Parrellina papillosa (Cushman).– ALBANI 1978, fig. 9G [Australia, New South Wales, Broken Bay].– ALBANI and YASSINI 1993, figs. 88–89, 92–93 [Australia].– YASSINI and JONES 1995, figs. 1063–5 [Australia, New South Wales].– HAYWARD et al. 1997, pl. 18, figs. 13–14 [Australia, New South Wales, Bermegui shelf, 89 m].–

PLATE 4

Recent species of the genus Buccella and Cristatavultus. Scale bar is 100 µm.

- 1–3 Buccella tenerrima (Bandy 1950), holotype, USNM PAL 237397, USA, Oregon, Cape Blanco, Pleistocene.
- 4-6 Buccella tenerrima (Bandy 1950), unsequenced specimen, CC 64503, USA, Washington, Straits of Juan de Fuca, Dallas bank, holotype of Buccella inusitata Andersen 1952.
- 7-9 Buccella tenerrima (Bandy 1950), unsequenced specimen, Arctic Ocean, north of Svalbard, 195 m depth.
- Buccella tenerrima (Bandy 1950), unsequenced specimen, Greenland, Disko Bugt, republished from Lloyd (2006).
- 11 *Buccella tenerrima* (Bandy 1950), unsequenced specimen, Norway, Svalbard, republished from Bartels (2017).
- 12–14 Buccella tenerrima (Bandy 1950), unsequenced specimen, USNM P2102, USA, Alaska, Point Barrow, republished from Loeblich and Tappan (1953).

- 15–17 Buccella tenerrima (Bandy 1950), unsequenced specimen, AHF 2173, USA, Alaska, off Wrangell, republished from McCulloch (1977).
- 18–20 Buccella viejoensis McCulloch (1977), holotype, AHF2191, Peru, Independencia Bay, Viejo Island, 24 m, republished from McCulloch (1977).
- 21–23 *Buccella viejoensis* McCulloch (1977), paratype, AHF2190, Peru, Independencia Bay, Viejo Island, 24 m, republished from McCulloch (1977).
- 24–25 *Buccella* n. sp. A, isolate 17572, LN873746, Chile, Bahia de Concepcion, intertidal.
 - 26 *Buccella* n. sp. A, isolate 17576, LN873747, Chile, Bahia de Concepcion, intertidal.
- 27–28 *Cristatavultus pacificus* (Collins 1958), unsequenced specimen, FP4412, F201642, Samoa, Apia.



ALBANI et al. 2001, 2 figures [Australia, New South Wales].– SWITZER et al. 2011, figs. 6.18–19 [Australia, New South Wales, Old Punt Bay, Holocene].

Parrellina verriculata (Brady).– HOFKER 1969, figs. 77–78 [Australia, Victoria, off Tamboon].

Type locality: Australia, New South Wales, 25 km east of Wollongong, 200 m, Recent.

Brief description: Test large (1–1.5 mm diameter); outline smoothly circular; profile moderately compressed with flat sides; periphery broadly rounded with no keel. Non-inflated chambers, sutures and flat umbilical area completely obscured by ornament; ornament of numerous, close-spaced beads often fused together in twos or threes to form short wavy or worm-like irregular costae; beads around the periphery on the early part of the whorl are stronger and more regularly circular; apertural face ornamented with numerous, wavy, radiating riblets and pustules; chamber walls not visible. Width/thickness ratio = 2.0-2.5.

Taxonomic discussion: The shape, ornament style and apertural face characters all suggest that this species is most appropriately placed in the genus *Parrellina*, even though it lacks the typical narrow, wavy sutural and intersutural ribs. *Parrellina papillosa* is readily distinguished from all others by its dense ornament that obscures all chambers and sutures.

Hofker (1969) studied the internal structure of all three living *Parrellina* species and concluded that it was identical in *P. papillosa* and *P. verriculata* and suggested that these were possibly different generations of the one species. We retain the distinction of the two species here, awaiting DNA testing one day of Hofker's (1969) suggestion.

Geographic distribution – Australia: New South Wales, Lord Howe Island.

Ecologic distribution: Parrellina papillosa lives in normal marine salinity at inner shelf depths and possibly deeper, especially in the open entrance to large harbours or bays (e.g., Albani 1978).

PLATE 5 Recent species of the genus *Notorotalia*. Scale bar is 100 μm.

- 1–2 Notorotalia aucklandica Vella 1957, topotype, BWH131/7, F2001002, 12 m, New Zealand, Auckland Islands.
- 3-4 *Notorotalia aucklandica* Vella 1957, unsequenced topotype, BWH131/8, F2001002, 12 m, New Zealand, Auckland Islands.
 - 5 *Notorotalia clathrata* (Brady 1884), unsequenced near topotype, BWH133/1, Australia, Bass Strait, 22 m.
- 6-8 *Notorotalia clathrata* (Brady 1884), holotype, Australia, Bass Strait, 80 m, republished from Brady (1884).
- 9–10 Notorotalia clathrata (Brady 1884), unsequenced near topotype, BWH133/2, Australia, Bass Strait, 22 m.
 - 11 Notorotalia depressa Vella 1957, paratype, BWH132/23, F201217, New Zealand, Cook Strait, 22 m.
 - 12 Notorotalia depressa Vella 1957, paratype, BWH132/22, F201217, New Zealand, Cook Strait, 22 m.
 - 13 Notorotalia depressa Vella 1957, unsequenced specimen, AK131698, L629, New Zealand, Queen Charlotte Sound, 11 m.
- 14–15 *Notorotalia finlayi* Vella 1957, paratype, BWH133/5, F8230, New Zealand, Wairarapa, Pleistocene.

- 16 Notorotalia finlayi Vella 1957, unsequenced specimen, BWH121/13, L624, New Zealand, Queen Charlotte Sound, 18 m.
- 17 Notorotalia finlayi Vella 1957, unsequenced specimen, BWH121/14, L624, New Zealand, Queen Charlotte Sound, 18 m.
- 18 Notorotalia finlayi Vella 1957, unsequenced specimen, BWH121/12, L624, New Zealand, Queen Charlotte Sound, 18 m.
- Notorotalia finlayi Vella 1957, paratype, BWH133/6, F8230, New Zealand, Wairarapa, Pleistocene.
- 20 *Notorotalia hornibrooki* Hayward, Grenfell, Reid and Hayward 1999, paratype, TF1662/2, F201253, New Zealand, off Greymouth, 596 m.
- 21–22 *Notorotalia hornibrooki* Hayward, Grenfell, Reid and Hayward 1999, holotype, TF1662/1, F201253, New Zealand, off Greymouth, 596 m.
 - 23 *Notorotalia inornata* Vella 1957, unsequenced autotype, BWH133/8, F201283, New Zealand, Queen Charlotte Sound, Rellings Bay, 5 m.
 - 24 *Notorotalia inornata* Vella 1957, unsequenced autotype, BWH133/7, F201283, New Zealand, Queen Charlotte Sound, Rellings Bay, 5 m.
 - 25 Notorotalia inornata Vella 1957, unsequenced specimen, BWH121/18, F202280, New Zealand, Stewart Island, Port Pegasus, 2.5 m.



Etymology: Named for its papillose surface ornament.

Parrellina verriculata (Brady 1881)

Plate 6, figures 24–27; text-figs. 4, 6

- Polystomella verriculata BRADY 1881, p. 66.– BRADY 1884, pl. 110, fig. 12 [Australia, Bass Strait, 75–80 m].– CHAPMAN 1907, pl. 10, fig. 10 [Australia, Victoria].– CUSHMAN 1939, pl. 17, fig. 13 [Australia, Bass Strait].
- *Elphidium jenseni* (Cushman).– YASSINI and JONES 1988, pl. 17, nos. 7–8 [Australia, New South Wales, Lake Illawarra].
- *Elphidioides verriculatus* (Brady).– PARR 1950, pl. 15, fig. 17 [Australia, northeast Tasmania].
- Parrellina verriculata (Brady).- ALBANI and YASSINI 1993, figs. 97–102, 105 [Australia]; HOFKER 1969, figs. 74–76, 79–85 [Australia, Victoria, off Tamboon].- SGARELLA and MONCHARMONT ZEI 1993., pl. 21, fig. 7 [Italy, Bay of Naples].- LOEBLICH and TAPPAN 1994, pl. 386, figs. 11–12 [Australia, Northern Australia, Sahul Sea].- YASSINI and JONES 1995, figs. 1014, 1041, 1062 [Australia, New South Wales].- HAYWARD et al. 1997, pl. 19, figs. 1–3 [Australia, Tasmania, Derwent Estuary; New South Wales, Nonabeca].- ALBANI et al. 2001, 4 figures [Australia, Queensland (Townsville) to Tasmania (Hobart) and Victoria (Melbourne)].- SWITZER et al. 2011, figs. 6.20–21 [Australia, New South Wales, Old Punt Bay, Holocene].- HESEMANN 2021, FEU-1002934–5 [Croatia, Paski Channel, 70–80 m].

Type locality: Not stated, but probably the site of Brady's figured specimen in Bass Strait, Challenger Station 162, 80 m, Recent.

Brief description: Test large (up to 1 mm diameter), involute; profile strongly compressed and parallel-sided; periphery broadly rounded with or without a narrow irregular keel. 11-14 non-inflated chambers in adult whorl; sutural ribs narrow, fine, slightly wavy; sutures flush, curved backwards towards the periphery; 8-10 narrow, wavy or straight, transverse ribs extend over the full width of each chamber, linking up with the sutural ribs on both sides; sutural and transverse ribs are more irregular and anastomosing over the earlier chambers in the whorl and may form a strong regular reticulate pattern over the later or more adult chambers; flat umbilical area filled with several small wavy ribs or tubercles; numerous pustules may cover the test wall between the ribs; apertural face ornamented with narrow, fine riblets radiating outwards from the apertural area. Width/thickness ratio = 3.2-3.6.

Taxonomic discussion: Parrellina verriculata is distinguished from *Parrellina imperatrix,* mainly by the lack of peripheral spines.

PLATE 6

Recent species of the genera Notorotalia and Parrellina. Scale bar is 100 µm.

- 1–3 *Notorotalia kerguelenensis* Parr 1950, holotype, Kerguelen Island, 150 m depth, republished from Parr (1950).
- 4-5 Notorotalia olsoni Vella 1957, paratype, BWH133/10, F201408, New Zealand, hen and Chickens Islands, 55m.
- 6 *Notorotalia olsoni* Vella 1957, paratype, BWH133/9, F201408, New Zealand, hen and Chickens Islands, 55m.
- 7–9 *Notorotalia patagonica* Parr 1950, holotype, Southern Ocean, off Patagonia, 350 m, republished from Brady (1884).
- Notorotalia profunda Vella 1957, unsequenced specimen, BWH142/24, F201289, New Zealand, West Coast, off Greymouth, 610 m.
- 11–13 Notorotalia profunda Vella 1957, unsequenced specimen, BWH142/27, F202394, New Zealand, Chatham Rise, 721 m.
- 14–15 Notorotalia zelandica Finlay 1939, sequenced specimen, isolate 17468, LN873845, New Zealand, Queen Charlotte Sound.
 - 16 Notorotalia zelandica Finlay 1939, sequenced specimen, isolate 17469, New Zealand, Queen Charlotte Sound.

- 17 *Notorotalia zelandica* Finlay 1939, unsequenced specimen, BWH121/10, L637, New Zealand, Queen Charlotte Sound, 37 m.
- 18–19 Notorotalia zelandica Finlay 1939, unsequenced specimen, BWH121/11, L637, New Zealand, Queen Charlotte Sound, 37 m.
- 20–21 *Parrellina imperatrix* (Brady 1881), unsequenced specimen, FP4417, F201595, Australia, Queensland, Claremont Lighthouse.
 - 22 Parrellina papillosa (Cushman 1936), unsequenced specimen, FP4420, Australia, New South Wales, Bermegui Shelf, 89 m.
 - 23 Parrellina papillosa (Cushman 1936), unsequenced specimen, FP4419, Australia, New South Wales, Bermegui Shelf, 89 m.
 - 24 *Parrellina verriculata* (Brady 1881), unsequenced specimen, FEU 1002934, Croatia, Adriatic Sea, Paski Channel, 70–80 m, republished from Hesemann (2021).
 - 25 *Parrellina verriculata* (Brady 1881), unsequenced specimen, FEU 1002935, Croatia, Adriatic Sea, Paski Channel, 70–80 m, republished from Hesemann (2021).
- 26–27 *Parrellina verriculata* (Brady 1881), unsequenced specimen, FP4421, F201332, Australia, Tasmania, Derwent River estuary.



Geographic distribution: Australia: New South Wales, Queensland, Tasmania, Victoria. Mediterranean Sea: Croatia; Italy, possibly introduced.

Ecologic distribution: Parrellina verriculata lives in normal marine salinity at inner shelf depths and possibly deeper, especially in the open entrance to large harbours or bays (e.g., Collins 1974).

Etymology: From the Latin "verriculum" meaning fishing net, probably relating to the surface rib ornament.

Genus *Porosorotalia* Voloshinova 1958 *Porosorotalia* Voloshinova 1958 *Cribrorotalia* Hornibrook 1961 (type species *Notorotalia tainuia*)

Type species: Notorotalia clarki Voloshinova 1952 in Voloshinova and Dain 1952, p. 167

Diagnosis: Biconvex, lenticular test with acute, often keeled, peripheral profile; usually possessing a prominent umbilical plug containing a labyrinth of anastomosing canals; sutural pores well developed on umbilical side; sutures, umbilicus and often chambers on the umbilical side ornamented with beads and tubercles often coalescing to form sutural ribs; ornament usually much weaker on the spiral side; aperture consists of one or two rows of pores in the terminal face.

Age range and geographic distribution: Late Eocene to Recent; northwest Pacific, South Pacific and southwest Atlantic temperate and subantarctic zones.

Key features of recognized living species of Porosorotalia:

Porosorotalia makiyamai: Test moderately large (0.5–0.7 mm); subequal, inflated biconvex, with limbate acutely rounded periphery; 9–10 chambers per adult whorl; limbate to weakly raised sutures on spiral side; umbilical side covered in dense pustules with tubercles and short ribs confined to central part of umbilical side. Northeast Pacific.

Porosorotalia meridionalis: Test moderately large (up to 0.9 mm); biconvex, with acute keeled periphery; 10–12 chambers per adult whorl; weakly raised or ribbed sutures on spiral side; umbilical side with umbilical tubercles and sutural ribs and tubercles extending most of way to periphery. South America.

Fossil species: Twenty species recognized – 10 from New Zealand, 5 from South America, 5 from northwest Pacific and 2 from Australia (Hayward et al. 2021). Several occur in more than one region.

Porosorotalia makiyamai (Chiji 1961) Plate 7, figures 6–14; text-fig. 5

Buccella makiyamai CHIJI 1961, pl. 1, figs. 13–15, text-figs. 2a-c [Ja-

- pan, Toyama Prefecture, Himi, Pleistocene]. Eponides schreibersii (Reuss).- MORISHIMA and CHIJI 1952, pl. 2,
- figs. 6a–c [Japan, Hokkaido, Akkeshi Bay] Porosorotalia makiyamai (Chiji).– AKIMOTO et al.2002, pl. 70, figs.
- 5a-c [Japan, Kyushu, Shimabara Bay].- KANEKO et al. 2018, figs. 5.5a-c [Japan, Urawa, Sataima City, Pleistocene].- NAKAGAWA and NAKAMURA 2019, pl. 1, figs. 9a-b [Japan, Fukui Prefecture, Wakasa-Wan]

Buccella inculta HE, HU and WANG 1965, pl. 8, figs. 2a–c [China, Shanghai, Quaternary].– LEI and LI 2016, figs. 55a–I [China, Yellow Sea, 51 m]

Type locality; Japan, Toyama Prefecture, Himi, Pleistocene.

Brief description: Test moderately large test (0.5–0.7 mm diameter); subequally biconvex, inflated lenticular test, with acutely rounded to weakly keeled periphery with rounded limbate peripheral band in adults. Spiral side with 9–10 chambers in adult whorl; sutures limbate to weakly raised, curved and oblique to periphery. Umbilical side with weakly curved radial sutures slightly depressed towards the periphery; small umbilicus closed with tubercles; rounded tubercles or short ribs extend part of the way along the radial sutures from the umbilical area; chamber surfaces completely covered in pustules. Interiomarginal low slit aperture; supplementary apertures at the outer margin of the sutures near the periphery.

Geographic distribution: Northwest Pacific – China; Japan. Pleistocene – China; Japan; Korea; Russia.

Ecological distribution: Occurs at 20–40 m water depth in Shimabara Bay (Akimoto et al. 2002).

Etymology: Named for Japanese paleontologist, the late Professor Jiro Makiyama.

Porosorotalia meridionalis (Cushman and Kellett 1929) Plate 7, figures 1–5; text-fig. 3

Eponides meridionalis CUSHMAN and KELLETT 1929, pl. 4, figs. 4, 6 [Chile, Corral and Lota; Peru, Pimentel]

- *Cribrorotalia meridionalis* (Cushman and Kellett).– BOLTOVSKOY et al. 1980, pl. 9, figs. 18–20 [Argentina, entire coast].– MARCHANT 1993, pl. 1, figs. 8a–b [Chile, Scholl Bay].– MALUMIAN and SCARPA 2005, pl. 4, figs. T, U [Peru, Chile, Argentina].– FERNÁNDEZ 2010, pl. 3, fig. 34 [Chile, Contaco Estuary].– SPISKE et al. 2013, figs. 5d.4–6 [Peru, Vila Vila].
- *Cribrorotalia* sp. HOLZMANN and PAWLOWSKI 2017, pl. 1, figs. 9–10 [Chile, Bahia de Concepcion].

Sequenced specimens: isolates 17611, 17612, 17613, 17615, 17616, Chile, Bahia de Concepcion, intertidal. These are not topotypes as they were collected 200 km north of the type locality.

Unpublished specimens examined: 3 specimens (MZUC 32726, Chile, Punta Negra, 30 m depth).

Type locality: Chile, off Corral, Recent.

Brief description: Large test (0.4–0.9 mm diameter); biconvex, lenticular test with rounded periphery in juveniles becoming acute and keeled in adults. Spiral side with 10–12 chambers in adult whorl; limbate, weakly curved sutural ribs. Umbilical side with beaded sutures; umbilicus with tubercles and much of the chamber surface covered in pustules.

Molecular characteristics: Porosorotalia meridionalis (99% BV) branches as sister to *N. zelandica* (100%BV). The branching is well supported (82% BV). The partial 18S sequences of *P. meridionalis* contain between 941 and 954 nucleotides, the GC content ranges from 37.2% to 38.2%. The overall mean genetic distance is 0.008.

Geographic distribution: South Atlantic (rare) – Argentina (35–57°S). Southeast Pacific (frequent) – Chile; Peru.

Ecological distribution: Inner to mid shelf depths (0–100 m).

Etymology: From the word "meridionalis", meaning southern.



PLATE 7 Recent species of the genus *Porosorotalia*. Scale bar is 100 μm.

- 1 *Porosorotalia meridionalis* (Cushman and Kellett 1929), isolate 17616, sequenced specimen, Chile, Bahia de Concepcion, intertidal.
- 2 *Porosorotalia meridionalis* (Cushman and Kellett 1929), isolate 17614, sequenced specimen, Chile, Bahia de Concepcion, intertidal.
- 3–5 *Porosorotalia meridionalis* (Cushman and Kellett 1929), Argentina, Ushuaia, republished from Boltovskoy et al. (1980).
- 6-8 *Porosorotalia makiyamai* (Chiji 1961), paratype, Japan, Tyama Prefecture, Himi City, Pleistocene, republished from Chiji (1961).
- 9–11 *Porosorotalia makiyamai* (Chiji 1961), unsequenced specimen, KAUM-FO-365, Japan, Kyushu, Shimabara Bay, Recent, republished from Akimoto et al. (2002).
- 12–14 *Porosorotalia makiyamai* (Chiji 1961), unsequenced specimen, sample UR22 Japan, Urawa, Sataima City, Kioroshi Formation, Pleistocene, republished from Kaneko et al. (2018).

KEY TO MORPHOLOGICAL IDENTIFICATION OF LIVING SPECIES OF NOTOROTALIIDAE Based on general features and those more clearly seen in SEM images, without the need to dissect out internal structural features.

1a.	Test planispiral	Parrellina 2
1b.	Test trochospiral	4
2a.	Possess large peripheral spines	Parrellina imperatrix
2b.	Possess no peripheral spines	3
3a.	Thick, dense tuberculose and costate ornament covers entire test	Parrellina papillosa
3b.	Lacks thick ornament; possess crisp, narrow rib ornament	Parrellina verriculata
4a. 4b.	Possess radial ribs on umbilical side; lack dense pustular mass in umbilicus and sutures on umbilical Lack radial ribs on umbilical side; possess dense pustular mass in umbilicus and sutures on umbilical	side 5 side Buccella 17
5a. 5b.	Spiral side ornament weak or lacking; radial sutural ribs and beads on umbilical side Possess ribbed ornament on both sides	Porosorotalia 6 7
6a. 6b.	Periphery acutely rounded to weakly keeled, limbate; short sutural ribs and tubercles confined to central portion of umbilical side Periphery acutely keeled; sutural ribs and tubercles extend all the way to periphery on umbilical side	P. makiyamai P. meridionalis
7a.	Solid sutural and intersutural ribs present on both sides	Notorotalia 8
7b.	Sutural ribs lacking; intersutural ribs high, irregular and forming anastomosing pattern centrally	Cristatavultus pacificus
8a.	Umbilical side has strongly-raised, radial sutural ribs	Notorotalia clathrata
8b.	Intersutural ribs on umbilical side no stronger than intersutural ribs	9
9a.	Intersutural ribs do not extend from suture to suture	10
9b.	Intersutural ribs, in early chambers at least, extend from suture to suture	12
10a	Test large, intersutural ribs truncated at or before middle of each chamber	N. inornata
10b	Test small to moderate size; intersutural ribs extend over most of each chamber	11
11a.	Test moderate-large size, almost parallel sided, compressed; intersutural ribs thin	N. depressa
11b	Test small to moderate size, planoconvex; intersutural ribs strong	N. finlayi
12a	Test small to moderate size, compact, <10 chambers/whorl	13
12b	Test large, >10 chambers/whorl	16
13a	Reticulate rib ornament developed in central area of both sides	14
13b	Reticulate rib ornament absent from umbilical side	15
14a	Tightly coiled, spiral side sutures strongly oblique to periphery (sutural angle with periphery <45°)	Notorotalia patagonica
14b	Loosely coiled, spiral side sutures weakly oblique to periphery (sutural angle with periphery >60°) No	otorotalia kerguelenensis
15a 15b	Test with 8–9 chambers/whorl; more convex on spiral side; umbilical sutural ribs strong; spiral side often lacks sculpture. Test with 6–8 chambers/whorl; usually more convex on umbilical side; sutural	N. hornibrooki
16a 16b	Prominent callus knob on spiral side; test biconvex, but umbilical side flattened; sutural ribs weak but intersutural ribs always extend from suture to suture. Lacks callus knob	N. profunda N. zelandica 17
17a 17b	Central region of umbilical surface deeply concave, sutural ribs well developed, intersutural ribs extend across chamber in early chambers but not later Test planoconvex, sutural ribs very weak on umbilical side, fine dense intersutural ribs which on the spiral surface produces a reticulate appearance	N. aucklandica N. olsoni
18a	Peripheral profile rounded, lacking a keel in adult tests	19
18b	Peripheral profile acute and keeled or limbate, at least in adult tests	23

	19a. Adult test of medium size, >0.3 mm diameter; broadly rounded periphery 19b. Adult test small, <0.3 mm diameter; periphery rounded to acutely rounded	20 21	
	20a. 5–7 chambers per adult whorl; tubercles cover all of sutures and umbilicus 20b. 7–9 chambers per adult whorl; tubercles cover part of sutures and umbilicus	B. frigida B. depressa	
	21a. 7–8 chambers per adult whorl; umbilicus wide; spiral side high-domed21b. 5–6 chambers per adult whorl; periphery acutely rounded	B. pulpitoensis 22	
	22a. Radial sutures on umbilical side extend all way to periphery22b. Radial sutures on umbilical side partially closed by secondary calcite between early chambers; sutural depressions near periphery	B. angulata B. troitzkyi	
	23a. Numerous chambers (9–12) per adult whorl 23b. Fewer chambers (<9) per adult whorl	24 28	
	24a. Tubercles generally absent from radial sutures on umbilical side 24b. Dense tubercles fill umbilicus and radial sutures on umbilical side	25 26	
	25a. Tiny umbilical area25b. Moderate-sized umbilical area filled with dense tubercles	B. plana B. peruviana	
	26a. Opaque secondary shell obscures early coils on spiral side; dark narrow lines resemble curved radial sutures extending from proloculus to last coil of spiral suture26b. Lacks opaque secondary shell and pseudosutures on spiral side	B. viejoensis 27	
	27a. Surface of chambers on umbilical side unornamented27b. Pustular ornament extends over most of chambers on umbilical sideB	B. tenerrima . compactiformis	
	28a. Test small (<0.3 mm), chambers few (5–7) per adult whorl 28b. Test medium size (>0.35 mm), 6–8 chambers per adult whorl	B. floriformis 29	
	29a. Spiral side with raised sutural costae 29b. Lacks sutural costae	B. hannai 30	
nsert pace	30a. Radial sutures on umbilical side narrow with <mark>ar</mark> ow of small pustules on each side 30b. Radial sutures moderately wide and filled with tubercles or pustules	B. discors 31	
	31a. Umbilical area of tubercles 0.15–0.25 diameter of test31b. Umbilical area of tubercles 0.3–0.4 diameter of test	32 33	
to deeply	 32a. Tubercles confined deeply incised umbilicus and relatively narrow radial sutures on umbilical side; no sutural depressions near periphery 32b. Tubercles may extend over umbilical ends of chambers; sutural depressions develop near periphery in adults 	replac with B. <u>peruviana</u> alvare B. tenerrima	ce ezii
	 33a. Umbilical area with large tubercles becoming smaller towards periphery; row of tubercles down each side of radial sutures 33b. Umbilical area with mix of two sizes of tubercles and pustules: 	<i>B</i> . n.sp. A	
	lacks row of tubercles down each side of radial sutures	B. dejardini	

insert space

CREDIT AUTHORSHIP STATEMENT

B.W. Hayward: Field collecting; morphotaxonomic research; writing; plate and figure preparation; MS preparation.

M. Holzmann: Field collecting; sequencing; SEM imaging; phylogenetic analysis; writing.

- J. Pawlowski: Field collecting; funding research.
- J. Wollenburg: Field collecting; imaging.

W. Majewski: Field collecting.

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APPENDIX 1

Sequenced specimens, isolate numbers, GENBANK accession numbers and sampling localities. Specimens in bold type have been investigated for the current study.

Organism	Isolate	Accession number	Sampling site
Notorotaliidae			
Buccella alvarezii	6299	ON087238	Argentina, Ushuaia port
Buccella alvarezii	6300	ON087239, LN873743, LN873744	Argentina, Ushuaia port
Buccella alvarezii	6301	ON087240, ON087241, LN873745	Argentina, Ushuaia port
Buccella alvarezii	20675	ON087242, ON087243	Falkland Islands
Buccella n. sp. A	17572	ON087224, LN873746	Chile: Bahia de Concepcion
<i>Buccella</i> n. sp. A	17573	ON087225, ON087226	Chile, Bahia de Concepcion
<i>Buccella</i> n. sp. A	17574	ON087227, ON087228, ON087229	Chile, Bahia de Concepcion
<i>Buccella</i> n. sp. A	17575	ON087230, ON087231, ON087232	Chile, Bahia de Concepcion
Buccella n. sp. A	17576	ON087233, ON087234, LN873747	Chile, Bahia de Concepcion
Buccella n. sp. A	17577	ON087235, ON087236, ON087237	Chile, Bahia de Concepcion
Buccella tenerrima	19383	ON087244, ON087245, ON087246	Svalbard: N 81° 9' 38", E 20° 0' 76"
Buccella tenerrima	19384	ON087247, ON087248	Svalbard: N 81° 9' 38", E 20° 0' 76"
Porosorotalia meridionalis	17611	LN873784, ON087263, ON087264	Chile, Bahia de Concepcion
Porosorotalia meridionalis	17612	ON087265, LN873785	Chile, Bahia de Concepcion
Porosorotalia meridionalis	17613	LN851685, LN851711	Chile, Bahia de Concepcion
Porosorotalia meridionalis	17615	ON087266, ON087267, ON087268	Chile, Bahia de Concepcion
Porosorotalia meridionalis	17616	ON087269, ON087270	Chile, Bahia de Concepcion
Notorotalia zelandica	16463	ON087249, ON087250	New Zealand, Q. Charlotte Sound
Notorotalia zelandica	16464	ON087251, ON087252, ON087253	New Zealand, Q. Charlotte Sound
Notorotalia zelandica	16465	LN873843, LN873844, ON087254	New Zealand, Q. Charlotte Sound
Notorotalia zelandica	16467	ON087255, ON087256	New Zealand, Q. Charlotte Sound
Notorotalia zelandica	17468	LN873845, LN873846	New Zealand, Q. Charlotte Sound
Notorotalia zelandica	17469	ON087257, ON087258, ON087259	New Zealand, Q. Charlotte Sound
Notorotalia zelandica	17470	ON087260, ON087261, ON087262	New Zealand, Q. Charlotte Sound
Notorotalia zelandica	FF126	LN851687, ON087271	New Zealand, Crail Bay
Notorotalia zelandica	FF128	ON087272, ON087273, ON087274	New Zealand, Crail Bay
Notorotalia zelandica	FF133	ON087275, LN873842	New Zealand, Crail Bay
Ammoniidae			
Ammonia confertitesta	130	AJ409970	China, Yalu Jiang
Ammonia confertitesta	132	FR839691	China, Yalu Jiang
Ammonia veneta	641	FR754381	Cuba, Playa Bailen
Ammonia veneta	642	FR754383	Cuba, Playa Bailen
Haynesinidae			
Haynesina germanica	c1	AF190720	Germany, Wadden Sea
Haynesina germanica	c4	AF190723	Germany, Wadden Sea
Elphidiids			
Elphidium aculeatum	A53	HM213822, HM213823	France, Trébeurden
Elphidium margaritaceum	A13	HM213824	France, Trébeurden
Elphidium margaritaceum	A108	HM213826	France, Roscoff
Elphidium williamsoni	10017	HM213827, HM213828	Russia, White Sea, Umba

APPENDIX 2 Records of Recent Notorotaliidae by region and country

Pacific Ocean

Southwest Pacific Australia – Cristatavultus pacificus, Notorotalia clathrata, Parrellina imperatrix, P. papillosa, P. verriculata Fiji – Cristatavultus pacificus New Caledonia – Cristatavultus pacificus New Zealand Notorotalia aucklandica, N. depressa, N. finlayi, N. hornibrooki, N. inornata, N. olsoni, N. profunda, N. zelandica Samoa – Cristatavultus pacificus Tonga – Cristatavultus pacificus Vanuatu – Cristatavultus pacificus

Northwest Pacific China – Buccella frigida, Porosorotalia makiyamai Japan – Buccella frigida, B. tenerrima, B. troitzkyi, Cristatavultus pacificus, Porosorotalia makiyamai Malaysia – Cristatavultus pacificus Philippines – Cristatavultus pacificus South Korea – Buccella tenerrima, B. troitzkyi Russia – Buccella tenerrima

Northeast Pacific Canada – Buccella frigida, B. tenerrima USA – Buccella angulata, B. discors, B. tenerrima

East Pacific

Colombia – Buccella discors, B. hannai Costa Rico – Buccella hannai, B. pulpitoensis Ecuador – Buccella compactiformis, B. hannai, B. peruviana Mexico – Buccella compactiformis, B. discors, B. hannai, B. pulpitoensis

Southeast Pacific

Chile – Buccella alvarezii, B. dejardini, B. peruviana, B. viejoensis, B. n.sp. A, Porosorotalia meridionalis Peru – Buccella compactiformis, B. discors, B. hannai, B. peruviana, B. plana, Porosorotalia meridionalis Indian Ocean Kerguelen Islands – Notorotalia kerguelenensis

Atlantic Ocean

Southwest Atlantic Argentina – Buccella alvarezii, Notorotalia patagonica, Porosorotalia meridionalis Brazil – Buccella alvarezii Falkland Islands – Buccella depressa, B. alvarezii, Notorotalia patagonica South Georgia – Buccella alvarezii, B. dejardini Uruguay – Buccella alvarezii Caribbean–Gulf of Mexico Panama – Buccella compactiformis USA – Buccella hannai

Northwest Atlantic Canada – Buccella floriformis, B. frigida, B. tenerrima USA – Buccella frigida, B. hannai

Northeast Atlantic United Kingdom – Buccella frigida, B. tenerrima

Arctic Ocean Canada – Buccella floriformis, B. frigida, B. tenerrima Greenland – Buccella frigida, B. tenerrima Norway – Buccella frigida, B. tenerrima Russia – Buccella floriformis, B. frigida, B. tenerrima, B. troitzkyi USA – Buccella frigida, B. tenerrima

North Sea Denmark – *Buccella frigida*, *B. tenerrima* Sweden – *Buccella tenerrima*

Mediterranean Sea Croatia – Parrellina papillosa Italy – Parrellina papillosa

APPENDIX 3

Described species of Recent Notorotaliidae of indeterminate status (descriptions and type illustrations insufficiently precise, type not seen). They require molecular sequencing to determine their status as distinct species or as synonyms.

Buccella afureraensis McCulloch 1977, Peru.Buccella antarctica McCulloch 1977, Antarctica.Buccella hannai ssp. oris Levchuk 1979, northwest Pacific Ocean.Buccella antarctica Saidova 1975.Buccella limpida Levchuk 1979, northwest Pacific Ocean.Buccella bollii Bermúdez and Seiglie, 1963, Venezuela.Buccella parviformis McCulloch 1977, Monaco.Buccella caridadae Bermúdez and Seiglie, 1963, Venezuela.Buccella santacruzensis McCulloch 1977, California.Buccella consagensis McCulloch 1977, Mexico.Buccella tunicata He, Hu and Wang 1965, China.

APPENDIX 4

List of genera and species of Recent Notorotaliidae considered to be subjective junior synonyms of other genera and species in this study or not to belong in the Notorotaliidae.

Buccella caledoniana McCulloch 1981, junior synonym of Buccella compactiformis McCulloch 1977

Buccella daidokoensis McCulloch 1977, junior synonym of Buccella tenerrima (Bandy 1950)

Buccella frigida var. *calida* (Cushman and Cole 1930), junior synonym of *Eponides frigida* (Cushman 1922) [*Eponides frigida* var. *calida* Cushman and Cole 1930]

Buccella frigida ssp. biconvexa Shchedrina 1984, junior synonym of Buccella tenerrima (Bandy 1950)

Buccella granulata Di Napoli Allianta 1952. This species has morphological features in common with *Buccella pustulosa* that are not found in any true *Buccella*. Sequencing has shown that *B. pustulosa* does not belong in either the Notorotaliidae or Elphidiidae. Therefore, this species probably requires a new genus.

Buccella hannai (Phleger and Parker) var. *arctica* Voloshinova 1960, junior synonym of *Buccella floriformis* Voloshinova 1960

Buccella inculta Ho, Hu and Wang 1965, junior synonym of Porosorotalia makiyamai (Chiji 1961)

Buccella inusitata Andersen 1952, junior synonym of Buccella tenerrima (Bandy 1950)

Buccella peruviana campsi (Boltovskoy1954), junior synonym of *Buccella peruviana* (d'Orbigny 1839) [*Eponides peruviana* ssp. *campsi* Boltovskoy 1954]

Buccella peruviana resupina McCulloch 1977, junior synonym of Buccella compactiformis McCulloch 1977

Buccella pustulosa Albani and Serandrei-Barbero 1982, specimens of this species from New Zealand are shown by sequencing not to belong in the Notorotaliidae nor Ammoniidae. Their morphology has elements of both these families but its DNA shows it is unrelated to either and belongs in a different family and genus.

Buccella radiata Shchedrina 1984, junior synonym of *Buccella tenerrima* (Bandy 1950)

Buccella sinulata McCulloch 1977, junior synonym of *Buccella hannai* (Phleger and Parker 1951)

Buccella tenerrimiformis McCulloch 1977, junior synonym of *Buccella discors* McCulloch 1977.

Cribrorotalia Hornibrook 1961, junior synonym of Porosorotalia Voloshinova 1958

Mesorotalia McCulloch 1977, junior synonym of Buccella Andersen 1952

Mesorotalia fastidiosa McCulloch 1977, junior synonym of Buccella tenerrima (Bandy 1950)

Parrellina sharkiana Albani and Yassini 1993, to Elphidium sharkiana (Albani and Yassini 1993).