

RRH: RE-EVALUATION OF *TROCHAMMINITA*

LRH: KING

A RE-EVALUATION OF THE FORAMINIFERAL GENUS *TROCHAMMINITA* (CUSHMAN  
AND BRÖNNIMANN, 1948) IN NEW ZEALAND AND A DESCRIPTION OF  
*PSEUDOTROCHAMMINITA MALCOLMI* (NEW GENUS, NEW SPECIES)

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## ABSTRACT

Salt-marsh foraminiferal assemblages serve as a key proxy for reconstructing sea level on multi-decadal to multi-millennial timescales, enabling reconstruction of sea level to potentially within 5 to 15-cm precision. The genus *Trochamminita*, common in salt-marsh environments, has proven unclear in recent decades with regard to the number of species represented within it. Because different species may possess different preferred elevations relative to sea level, it is important that the number of taxa be elucidated, to ensure future sea-level reconstructions using foraminifera are as precise as possible. Here, using new specimens identified from Pauatahanui Inlet, southern North Island of New Zealand, and Aramoana salt marsh, southern South Island, the agglutinated species *Trochamminita irregularis* is recognised as likely distinct from *Trochamminita salsa*, and a new species, *Pseudotrochamminita malcolmi* (n. gen., n. sp.), is named, having been identified in earlier studies either as specimens of *T. irregularis*, or of the unrelated species *Polysaccamina ipohalina*. *Trochamminita irregularis* and *Ps. malcolmi* differ from one another in chamber morphology, apertural morphology and number, chamber texture, geographical distribution, and optimal heights relative to sea level.

## INTRODUCTION

The reconstruction of past relative sea levels using intertidal foraminifera has proven particularly useful in our understanding of the magnitude and drivers of relative sea-level change (e.g., Phleger, 1970; Gehrels, 1999; Gehrels et al., 2008; Hayward et al., 2008; Hawkes et al., 2010; Grenfell et al., 2012, Kemp et al., 2013). The tests (shells) produced by these protists provide a key means of deriving high-resolution sea-level reconstructions, often to a sub-tentimetre resolution, due to the differing vertical ranges of different species, relative to sea level (e.g., Scott & Medioli, 1978, 1980; Southall et al., 2006; Callard et al., 2011). As anthropogenic climate change continues to drive accelerations in global mean sea-level rise (e.g., Nerem et al., 2018; Frederikse et al., 2020), the use of foraminifera to reconstruct past sea levels will become increasingly important in the production of sea-level reconstructions (Kaminski et al., 2020; King et al., 2020).

*Trochammina* (Cushman & Brönnimann, 1948) is a genus of salt-marsh-dwelling foraminifera which often dominate the upper parts of low-salinity salt marshes (e.g., Hayward et al., 1999; Callard et al., 2011), and is therefore an important taxon for the reconstruction of sea-level using foraminiferal assemblages. However, there is little agreement regarding whether the two recognised members of the genus should be treated as two species or as one with high intraspecific variability. As one form has been documented possessing a wider vertical range than the other (Callard et al., 2011), it is important that the taxonomy be resolved in order to ensure the highest precision of transfer functions reconstructing past relative sea level. Here, an

attempt is made to resolve the taxonomy of the genus on the basis of new observations from two salt marshes in New Zealand.

#### A HISTORY OF THE OBSERVATIONS AND TAXONOMY OF THE GENUS *TROCHAMMINITA*

*Trochamminita* is a genus of salt-marsh dwelling foraminifera which was first described by Cushman & Brönnimann (1948). The type species, *Trochamminita irregularis*, was described from Trinidad as planispiral in “the early stages,” with globular, chitinous chambers, a proportionally small, single, rounded aperture (which is slit-shaped in the younger chambers) with a raised border, and a coarsely arenaceous agglutinated wall. Cushman & Brönnimann (1948) assigned the species to the family Trochamminidae in the order Lituolida. Whilst *T. irregularis* remains the type species for the genus, a second species was also identified by these authors earlier in the same paper, although they assigned it to the genus *Labrospira* (Höglund, 1947), in the family Lituolidae (de Blainville, 1825). This species (then *Labrospira salsa*) was described by Cushman & Brönnimann (1948) as being a close-coiled, planispiral species with 6–7 chambers per whorl, possessing a single, raised aperture, and smoothly polished chamber walls dominated by arenaceous sediments. Both of these species were identified from the “inshore” brackish-water muds of an unidentified mangrove swamp, later identified by Saunders (1957) as Maracas Bay River, on the west coast of Trinidad.

Saunders (1957) emended the above descriptions of both species, reassigning *L. salsa* to the genus *Trochamminita*, noting that both species may possess multiple apertures, invariably prominently lipped. Once again, *T. salsa* was defined as planispiral and possessing typically polished walls of arenaceous grains in fine cement. *Trochamminita irregularis* was differentiated

from *T. salsa* by its planispiral to slightly trochospiral first “stage,” followed by irregularly positioned and shaped chambers with rougher surfaces and coarser walls.

Saunders (1957) assigned both species to the same genus *Trochamminita* on the basis that they only differed in the habit/direction of chamber growth and wall texture, then argued that *L. salsa* could not belong to the genus *Cribrostomoides* (Cushman, 1910) of which *Labrospira* was at that time considered synonymous on the basis of their multiple apertures, resulting in the movement of the genus from the family Trochamminidae to Lituolidae. *Labrospira*'s synonymy with *Cribrostomoides* was considered erroneous by Loeblich & Tappan (1987) due to the tendency for *Labrospira* to have a more evolute and planispiral test than *Cribrostomoides*, with coarser material and only a single aperture as opposed to the row of openings observed in *Cribrostomoides*. They also lack the characteristic streptospiral coiling with repeated axial modification distinctive of *Cribrostomoides* (Jones et al., 1993). *Trochamminita* along with many other then-Lituolid genera were moved into the family Haplophragmoididae (Maync, 1952) by Podobina (1978) and were formally recognised as such by Loeblich & Tappan (1987). In the absence of genetic work, the genus has remained classified within Haplophragmoididae ever since.

The recognition of two species within *Trochamminita* (according to Saunders, 1957), was generally accepted until Hayward & Hollis (1994) argued that the textural differences that formed the dominant means of separating the two species (*T. salsa* and *T. irregularis*) were too subtle to be of practical value and concluded that the two species were synonymous. In a study of marshes in southern Chile (Jennings et al., 1995) and an unpublished thesis examining specimens from New Zealand salt marshes (Figueira, 2012) it was argued that the two forms (*T. salsa* and

*T. irregularis*) had the same preferred elevational ranges, and that the differences between the species were due solely to intraspecific variability among specimens of *T. salsa*.

All studies using foraminifera to derive relative sea-level reconstructions published since 1994 in New Zealand have retained this synonymy and treated both species as the same. However, assessing the suitability of salt-marsh foraminifera to reconstruct sea-levels in Tasmania, Callard et al. (2011) argued against the synonymy of the two species. Callard et al. (2011) showed in both of their transects that whilst *T. salsa (sensu stricto)* dominates the upper salt-marsh, *T. irregularis* (which was noted to have rougher and less oval-shaped chambers) was found throughout the entirety of the marsh, a trend also observed in other southeast Australian marshes (S. Williams, personal communication, 2020), albeit not those studied by Lal et al. (2020) in which both *Trochammina* species were absent. Following this work, the World Foraminiferal Database presently treat both species as valid (Hayward et al., 2020a), though they still include images of *T. irregularis (sensu Callard et al., 2011)* listed as images of *T. salsa*. Callard et al. (2011) also noted a preference for specimens of *T. irregularis* to possess only a single aperture, whilst specimens of *T. salsa* more typically possess two apertures. They also noted apparent differences in the geographic distribution of *T. salsa* and *T. irregularis*, with *T. irregularis* alone being documented from the coast of Oregon where *T. salsa* appears to be absent (Hawkes et al., 2010). Intriguingly, specimens described as belonging to *T. salsa* have been observed in tidal marshes from northern Portugal by Fatela & Moreno (2019), which appear to have the irregular growth pattern of *T. irregularis* yet also possess the smooth texture characteristic of *T. salsa*. Similarly, specimens from Iceland described as belonging to *T. irregularis* also possess this smooth texture atypical of *T. irregularis* populations further south (Lübbers & Schönfeld, 2018). These specimens likely belong to *T. irregularis*, reflecting

intraspecific textural variability, or they could belong to an undescribed cryptic species or subspecies limited to high latitudes in the Northern Hemisphere. However, such textural differences are insufficient to make this claim definitively, and DNA analyses of different populations would be required to test this.

*Trochamminita* can be considered a “Lazarus taxon,” as microfossils belonging to a species morphologically identical to the modern *T. irregularis* have been observed from palaeo-marsh coal horizons (analogous to modern upper salt marshes) of Upper Carboniferous age in Nova Scotia, Canada (Thibaudeau, 1993). This is followed by a paucity in their fossil record of over 300 million years with all other records being Quaternary in age (Hayward et al., 1999). The specimens observed by Thibaudeau (1993) confirm that the genus has been a specialist of upper salt-marsh soil environments since at least this time, and the low preservation potential of these environments in the long-term geological record partially explains the gap in the fossil record. The gap may also be the result of the fact that Palaeozoic to Mesozoic coal biostratigraphic studies typically examine microflora (pollen and spores) rather than foraminifera, even in paralic palaeoenvironments where marsh foraminiferal assemblages should theoretically be present (e.g., Ettensohn & Peppers, 1979; Ogala, 2010; Jerrett et al., 2011; Pendleton, 2012). So, foraminifera while present, are missed, creating artificial gaps in the fossil record. The tendency for Palaeozoic foraminifera to be examined in thin-section (e.g., BouDagher-Fadel, 2008) may also be a contributing factor in the *Trochamminita* fossil record gap, with the species being missed due to a lack of specimens with a clear 3D morphology.

## NEW OBSERVATIONS

At Pauatahanui Inlet, southern North Island, New Zealand, and Aramoana salt marsh, southern South Island, New Zealand (Fig. 1), ongoing work by the author to use foraminiferal assemblages to reconstruct sea level has resulted in new insights that may aid in resolving much of the uncertainty regarding the taxonomy of *Trochammina*. Both *T. salsa* and *T. irregularis*, as described in the aforementioned literature, are observed at both sites. However, in the four transects surveyed (Fig. 1), “*T. irregularis*” specimens are observed which possess notable morphological differences at different heights along the salt marsh and do not conform to the ranges relative to sea level that were described by Callard et al. (2011).

At Pauatahanui, rough-chambered *T. irregularis* specimens (Figs. 2a–c) are observed only in the upper part of the salt marsh, disappearing altogether at elevations lower than 0.48 m above the New Zealand Vertical Datum (NZVD2016). Below this height, specimens resembling *T. irregularis* (*sensu* Callard et al., 2011) but differing in several key aspects (Fig. 3) continue to be found in samples with vertical ranges extending down into the sandy intertidal flat (Fig. 4). At Aramoana, the two forms display distinctly more vertical overlap, though again this second form resembling *T. irregularis* appears in greatest abundance in the lower part of the marsh.

These specimens, referred to in this section as *T. irregularis* Type B, resemble *T. irregularis* (*sensu stricto*) greatly, having chitinous chambers which become irregular in orientation after the first whorl as well as having pronounced apertural lips (Figs. 3a–c). However, they differ in several key aspects that cannot be ignored. For example, they almost invariably use argillaceous material to build their tests, even when they are present in the sandy tidal flat environment, distinguishing them from *T. irregularis* and *T. salsa* which consistently prefer coarser material.



Specimens of this previously undescribed form also possess proportionally far larger, more pronounced apertural lips than *T. irregularis*, and invariably possess only a singular aperture, whilst specimens of *T. irregularis* at these sites show no tendency towards any number of apertures, unlike the description of Callard et al. (2011). Chambers of *T. irregularis* Type B are also considerably flatter in morphology than those of *T. irregularis (sensu stricto)*, with flattening being parallel to the direction of coiling in the planispiral section, more closely resembling those of the irregular form of the closely related species *Cribrostomoides jeffreysi* (see plate 35 of Brady, 1884). However, *C. jeffreysi* prefers far deeper water and uses far coarser grains to create its tests (see Hayward et al., 1999). Furthermore, this new form cannot be classified as part of *Cribrostomoides*, as their diagnostic tooth-like processes are not observed in the apertures of any Type B specimens, nor do any such specimens display the characteristic alternating streptospiral coiling pattern of *Cribrostomoides* described by Jones et al. (1993). Tests of Type B are also typically much more elongate in morphology than *T. irregularis (sensu stricto)* at this site, which combined with their aperture morphology often gives them a close superficial resemblance to the unrelated monoserial to irregular taxon *Polysaccamina ipohalina* (Fig. 5). *Polysaccamina ipohalina* has likely often been confused with *T. irregularis* (see Adams, 1979, who could not confidently distinguish between the two species) because both species possess globular, chitinous agglutinated chambers with irregular chamber orientation and both are dominant in the upper salt marsh environment. At both marshes studied, *Po. ipohalina* are restricted to a narrow vertical zone in the uppermost salt marsh, overlapping minimally with *T. irregularis* Type B, supporting the notion that *T. irregularis* Type B do not represent intraspecific variability among *Po. ipohalina*, which can be distinguished from all *Trochamminita* species and *T. irregularis* Type B by its lack of a planispiral section (see Scott,

1976). This previously undescribed form also should not be placed within *Labrospira* (the closely allied genus to which *T. salsa* was originally ascribed), because it lacks the typical coarse grains and slit-shaped apertures of this genus (see Hesemann, 2020a).

Therefore, this new form (Type B) cannot be considered a morphotype of *T. irregularis* or *Po. ipohalina*, differing significantly from it as previously discussed. Nor should it be considered a part of the genus *Trochamminita*, as described by Saunders (1957), owing to its invariable single aperture and argillaceous texture. The uncoiled adult phase and the general position of the apertures of specimens away from the septal face support the inclusion of this new species within the subfamily Lituolinae, in accordance with the criteria of Maync (1952), and therefore within Haplophragmoididae, in accordance with Podobina (1978) and Loeblich & Tappan (1987).

#### SYSTEMATIC DESCRIPTION

A new genus is therefore erected, likely (on the basis of the single apertures) more closely allied to *Labrospira* than *Trochamminita*, to accommodate this new form. The proposed genus name is *Pseudotrochamminita*, and the species name *malcolmi*. The taxonomy is presented in accordance with Hayward et al. (2020b) as:

Kingdom CHROMISTA (Cavalier-Smith, 1981)

Phylum FORAMINIFERA (d'Orbigny, 1826)

Class GLOBOTHALAMEA (Pawłowski et al., 2013)

Subclass TEXTULARIANA (Mikhalevich, 1980)

Order LITUOLIDA (de Blainville, 1825)

Suborder LITUOLINA (Lankester, 1885)

Superfamily LITUOLOIDEA (de Blainville, 1825)

Family HAPLOPHRAGMOIDIDAE (Maync, 1952)

Genus *Pseudotrochamminita* (new genus)

Type species: *Pseudotrochamminita malcolmi* (new species)

*Etymology.* Pseudo (from Greek “pseudos” meaning “false”), *Trochamminita* (due to the deceptively close resemblance of the genus to *Trochamminita irregularis*). The species name “*malcolmi*” is named for the late Malcolm King, who greatly encouraged the author’s interest in geology and helped in a great deal of his early fieldwork.

*Pseudotrochamminita malcolmi* n. gen, n. sp.

Figs. 3a–c

*Trochamminita irregularis* Cushman & Brönnimann, 1948. Dreher & Flocks, 2011, p. 3, fig. 2,  
(probable on the basis of low chamber number in planispiral section).

*Polysaccamina ipohalina* Scott, 1976. Moreno et al. 2014, appendix 3, pl. 2, fig. 3.

*Genus diagnosis.* *Pseudotrochamminita* (Type species: *Ps. malcolmi*, described below) can be defined by its finely agglutinated, chitinous, flattened chambers (which are flattened in the direction of the coiling of the planispiral section), invariable single aperture with a prominent lip pointing outwards into the younger chamber, and irregular chamber orientation.

*Pseudotrochamminita* can be distinguished from *Trochamminita* by its flattened chambers (*Trochamminita* instead has globular chambers), more pronounced apertural lip, preferred use of finer material, and invariable usage of only one aperture. It can be distinguished from *Paratrochamminoides* (Soliman, 1972) and *Trochamminoides* (Cushman, 1910) by its proportionally larger, flatter chambers, more regular chamber shape, and lack of depressed apertures (cf. Kaminski & Gradstein, 2005; Kaminski & Kuhnt, 2004; Hesemann, 2020b). The irregular position of the apertures, and circular shape of the apertures also distinguishes *Pseudotrochamminita* from *Conglophragmium* (Bermúdez & Rivero, 1963) (cf. Kaminski & Gradstein, 2005; Hesemann, 2020c). *Pseudotrochamminita* can be distinguished from *Polysaccamina* (Scott, 1976) by its more flattened chambers and the presence of a planispiral section [hence the “*Po. ipohalina*” specimen presented by Moreno et al. (2014) is here revised to represent a specimen of *Pseudotrochamminita*]. *Polysaccamina* species are also known to undergo “branching,” wherein a test will occasionally split in two or more directions of chamber growth (e.g., Scott, 1976, fig. 4c; Horton & Edwards, 2006, pl. 1, fig. 6c; Camacho et al., 2015, fig. 2.5), occasionally observed *Pseudotrochamminita* (e.g., in the holotype specimen, Fig. 3a), but no member of the Polysaccaminidae (Loeblich & Tappan, 1984) family possess any form of spiral growth pattern (Loeblich & Tappan, 1984), indicating that the two species are not likely to be closely related. *Pseudotrochamminita* can be distinguished from *Cribrostomoides* by its lack of a streptospiral growth pattern, its irregular aperture placement, its preference for using finer material to agglutinate its tests, and its lack of tooth-like aperture projections. This fine-material preference, as well as the flattened chamber morphology, also distinguishes the genus from *Labrospira*, and it should be noted that *Labrospira* more typically have long, flat apertures, unlike those of *Pseudotrochamminita* (cf. Hesemann, 2020a). The early whorls of

*Pseudotrochamminita* can at times resemble *Entzia* (Daday, 1883) due to their flattened, planispiral morphology, but *Entzia* specimens lack the irregular growth pattern, have an inconsistent aperture number and shape, often lack pronounced apertural lips, and do not develop an irregular growth phase, although morphological deformities certainly may occur (see Kaminski et al., 2020, pl. 2). The irregular growth pattern and pronounced apertural lip also distinguish the genus from the similarly uncoiled, initially planispiral genus *Ammotium* (Loeblich & Tappan, 1953), as does the broad, squared-off shape of their chambers.

*Species description.* *Pseudotrochamminita malcolmi* can be recognised by its flattened, flexible, finely-agglutinated chambers and single, lipped apertures. Specimens are typically 200–400 microns in length and begin with a planispiral section containing between 3 and 7 chambers per whorl, with sutures slightly curving towards the newer chambers and connected by a single, circular, strongly lipped aperture. No *Ps. malcolmi* specimens have been found possessing non-circular apertures, and as shown in Figs. 3a–c, the internal structure of these apertures is unornamented. After the planispiral section, chamber orientation becomes random, with the aperture present on any face of new chambers, irrespective of the direction in which those chambers are flattened (cf. Figs. 3a, b).

As is displayed in Fig. 6b, some unusual specimens display flat, chitinous platy outgrowths which extend along one side of the test and are always aligned with the orientation of chamber flattening. This is not, however, a commonly observed trait. As can be observed in Figures 3a–b and Figure 6a, chamber flattening is always approximately parallel with the direction of coiling during the initial planispiral phase (though the direction of flattening may twist somewhat), and as observed in the holotype specimen, some degree of branching may occur.

The chitin layer beneath the agglutinated test is a highly variable greenish or orange-brown colour (varying in intensity from a pale golden brown to a dark, almost blood-red, as is clear when a light is shone through the specimens (Figs. 6a–b). Their thin, fine agglutinated layer makes them highly translucent, and their surfaces tend to possess a reflective sheen (most obvious in Fig. 6a). Due to its presentation of all the diagnostic traits for the species, the specimen displayed on Fig. 3a (Specimen Paua\_2) is designated as the holotype. Occasionally, subtly rougher-textured individuals can be observed (Fig. 3b), but the flattened chamber morphology and more pronounced apertural lip indicates that such specimens still belong within *Ps. malcolmi*, and these specimens still appear “polished” under visible light.

*Comparison with similar species.* *Pseudotrochamminita malcolmi* is typically smaller than *T. irregularis* (though exceptions do exist), and has finer-grained, flattened, and more flexible chambers that are less prone to damage by cracking (unlike the globular, more brittle chambers of the true *Trochamminita* species), and possessing a distinctive, reflective outer surface. Their circular, unornamented, strongly lipped apertures distinguish them from *T. salsa*, lacking the small tooth-like projections or shape variability typical of that species, and from *T. irregularis* due to the lack of any kidney-shaped or oval-shaped apertures in any observed *Ps. malcolmi* specimens (cf. Fig. 2c, and the plates presented for *T. irregularis* by Saunders, 1957).

When damaged, unlike *Trochamminita* specimens which are rigid enough to hold their shape (Figs. 2c–d), *Ps. malcolmi* chambers typically lose their shape and collapse (Fig. 3a). This is likely due to differing structural properties of their tests from those of *Trochamminita*, and possibly associated with differences in the form of chitin used by this species from that used by *Trochamminita*.

*Polysaccammina ipohalina* (Scott, 1976) is extremely similar to *Ps. malcolmi*, and at Aramoana the two species share part of their habitat ranges. Both species possess irregular chamber orientations, have flexible, chitinous chambers, and circular apertures (e.g., Javaux & Scott, 2003, fig. 6.8). Furthermore, because *Po. ipohalina* specimens are prone to collapse, they can closely resemble the life morphology of *Ps. malcolmi*. However, live and fresh specimens of *Ps. malcolmi* invariably possess much more flattened chambers than live specimens of *Po. ipohalina* and display the presence of a planispiral section. *Polysaccammina ipohalina* has never been observed possessing anything other than a monoserial to irregular chamber arrangement, as observed in the holotype and paratypes (Scott, 1976, figs. 4a–c; photographed in Jett, 2020) and all subsequent observations of the species (e.g., Scott et al., 1991; Javaux & Scott, 2003). *Polysaccammina ipohalina* also shows a more inconsistent texture than is observed in *Ps. malcolmi* (see Fig. 5 and Jett, 2020, for examples of variability in *Po. ipohalina* surface texture), and *Po. ipohalina* sometimes incorporates much larger pieces of material (including shards of wood) into their tests, as observed in Figure 5a. The apertures of *Po. ipohalina* are sometimes strongly lipped, as observed in Figure 5b, as well as in Javaux & Scott (2003; fig. 6.8), but unlike *Ps. malcolmi*, an apertural lip is not always present in *Po. ipohalina*, with apertures often simply being slightly raised from the chamber (e.g., Scott, 1976, pl. 2.1).

Figure 3c displays a specimen of *Ps. malcolmi* which has atypically twisted and grown in a linear manner similar to *Po. ipohalina* after its planispiral section, though the aforementioned criteria confirm it as a specimen of *Ps. malcolmi*. Furthermore, the approximately-consistent direction of chamber flattening parallel to the initial planispiral whorl confirms that flattening is simply part of the chamber morphology of *Ps. malcolmi*, rather than representing chamber collapse in specimens of *Po. ipohalina* (further supported by the differences in vertical range

observed between the two species in Figure 4 and the fact that *Po. ipohalina* chambers tend to collapse in on themselves, rather than to flatten, as observed in Figure 5b).

Unlike true *Trochamminita* specimens and *Po. ipohalina*, all of which are predominantly found in the uppermost marsh at both sites, at Pauatahanui, *Ps. malcolmi* is most abundant in the lower part of the salt marsh down to the upper tidal flat. At Aramoana salt marsh, southern New Zealand, *Ps. malcolmi* can be found in low abundances across the entire marsh and in the upper tidal flat, but it is at its highest abundance (21% of the total foraminiferal assemblage) in the low-marsh environment vegetated by *Salicornia quinqueflora* and *Samolus repens*.

At Pauatahanui and Aramoana, *T. salsa* and *T. irregularis* can be found living (stained by rose Bengal) at soil depths of up to 13 cm, however they are most abundant by far in the uppermost 2 cm beneath the soil surface. By contrast, *Ps. malcolmi* have not been observed living at depths of more than 4 cm beneath the surface of the substrate, possibly indicating that they are less tolerant to reduced oxygen than *Trochamminita*.

The presence of *Ps. malcolmi* in Tasmania is also confirmed, as some specimens described as belonging to *T. irregularis* from this location bear a strong similarity to those ascribed here to *Ps. malcolmi* in New Zealand (S. Williams, personal communication, 2019; Fig. 7). Inclusion of this newly described species within *T. irregularis* in previous studies in Tasmania might partially explain findings of Callard et al. (2011) that *T. irregularis* has a wider vertical range than *T. salsa* and that *T. irregularis* has a preference towards the possession of one aperture (not a trait observed in New Zealand *T. irregularis* specimens). The absence of *Ps. malcolmi* from Oregon would also explain why *T. irregularis* was documented as present in the upper marsh only by Hawkes et al. (2010). However, it is recommended that genetic work be performed on different *Trochamminita* populations to assess whether these regional differences in preferred habitat



relate to the presence of geographically limited cryptic species that closely resemble *T. irregularis* (*sensu stricto*).

*Type locality.* Pauatahanui Salt Marsh, New Zealand.

*Type specimens.* Holotype: TF 1678, Paratypes: TF 1679 and TF 1680. National Palaeontological Collection. Microfossils, GNS Science, Lower Hutt, New Zealand.

*Recorded stratigraphic range.* Recent.

*Occurrence.* Recorded in this study from New Zealand (North and South Islands) and Tasmania, as well as in Portugal (Moreno et al., 2014), and possibly Louisiana, USA (Dreher & Flocks, 2011).

*Trochamminita irregularis* Cushman & Brönnimann, 1948

Figs. 2a–c

*Trochamminita irregularis* Cushman & Brönnimann, 1948. (Cushman & Brönnimann, 1948, p. 17, pl. 4, figs. 1–3; Saunders, 1957, p. 14, pl. 2, figs. 2–8; Loeblich & Tappan, 1987, p. 76, pl. 51, Figs. 1–6; Hayward, 1993, p. 85, fig. 5I; Hayward & Triggs, 1994, p. 114, pl. 1, fig. 3; Dreher, 2006, p. 97 pl. II, figs. 8a–9b; Hawkes et al., 2010, p. 133, pl. 1, figs. 3a–3b; Callard et al., 2011, p. 125, pl. 1, Figs. 11–15; Dreher & Flocks, 2011, p. 4, fig. 7; Milker et al., 2015a, p. 5, pl. 1, fig. 11; Fürstenberg et al., 2017, p. 334, fig. 2, part 18; Laut et al., 2017, p. 136, pl. 6J; Semensatto, 2020, p. 5, pl. 3, fig. 41); ?Lübbers & Schönfeld, 2018, p. 388, pl. 1, figs. 4a–f?. Type Locality: Maracas Bay River, Trinidad.

*Trochamminita salsa* Cushman & Brönnimann, 1948. (Hayward & Hollis, 1994, p. 206, pl. 2, figs. 13–15; Hollis et al., 1995, p. 199, figs. 3a–3c; Jennings et al., 1995, p. 119, pl. 1,

figs. 1, 9–17; Hayward et al., 1999, p. 84, pl 1, figs. 30–32; Figueira et al., 2012, p. 209, figs. 2N–S; Hayward, 2014, p. 305, fig. 5, part 14, ?Fatela & Moreno, 2019, figs. 1–3, 5–7?; Hayward et al. 2020c, images 1–3).

## DIAGNOSIS

*Trochamminita irregularis* (now perhaps best described as *T. irregularis sensu stricto*) is restricted to the upper salt-marsh environment and shares its elevational range with *T. salsa* almost exactly (at apparently all New Zealand salt marshes, though seemingly not in Tasmania). This species has an irregular number and shape of apertures, typically between one and six (and most commonly between one and three; Figs. 2a–b), and these are projected into the younger chambers by a prominent apertural lip in approximately 80% of specimens (with apertural lips being absent in approximately 20% of observed specimens; see for example Figure 2b). Texturally, chambers are usually rougher in appearance and lack the polished texture observed in *T. salsa* (with Figure 2c displaying a particularly coarse-grained, rough-textured specimen). However, such polished textures may be apparent in young chambers, rendering the two species difficult, and at times impossible to distinguish, in particular with young specimens. Chambers are generally globular in shape (though become quite variable after growth direction becomes irregular). New Zealand specimens display no obvious partition in chamber inflation between *T. irregularis* and *T. salsa*, counter the observations from Tasmania by Callard et al. (2011). It is strongly recommended that genetic work be performed to confirm whether the two currently recognised *Trochamminita* species should be considered representative of variability within the same species, rather than fully distinct. Until then, due to the difference in geographic ranges (cf. Hawkes et al., 2010), apparent differences in vertical ranges at some sites (Callard et al., 2011), and the clear morphological differences between mature specimens (cf. Figs. 2a–c; d–e), it is

proposed that the two forms be considered separate. *Trochamminita irregularis* is initially planispiral, though chamber orientation often becomes random after one to four whorls. A notable exception to this trend is observed in Figure 2d, in which a specimen has remained planispiral throughout its entire life but has texturally remained coarse and rough. This texture appears to be consistent among full-sized individuals but should not be treated as diagnostic as young specimens often do not develop this texture until well after chamber orientation has become irregular. Furthermore, this texture is not observed in specimens from the high-latitude Northern Hemisphere (Moreno et al., 2014; Lübbers & Schönfeld, 2018), potentially indicating that these belong to a separate subspecies or cryptic species. Chambers typically become larger as coiling progresses, but often cease to do so after chamber orientation becomes irregular. The planispiral section usually has 5–8 chambers per whorl.

*Recorded stratigraphic range.* Carboniferous to Recent (as a morphospecies).

*Occurrence.* Found in salt marshes, mangrove forests, and partially saline lakes worldwide. At Aramoana, the species also thrives in the marine influenced portion of coastal sand dunes. Reported from New Zealand, Tasmania (Callard et al., 2011), South Africa (Fürstenberg et al., 2006), Hawaii (Resig et al., 1974), the Caribbean (Cushman & Brönnimann, 1948; Laut et al., 2017), Chile (Jennings et al., 1995), Brazil (Semensatto, 2020), the east and west coasts of the United States of America (Dreher, 2006; Hawkes et al., 2010; Dreher & Flocks, 2011; Milker et al., 2015a, b; Avnaim-Katav et al., 2017), northern Portugal (Moreno et al., 2014), and Iceland (Lübbers & Schönfeld, 2018).

*Trochamminita salsa* Cushman & Brönnimann, 1948

Figs. 2d–e

*Labrospira salsa* Cushman & Brönnimann, 1948. (Cushman & Brönnimann, 1948, p. 16, pl. 3, figs. 5–6). Type Locality: Maracas Bay River, Trinidad.

*Trochamminita salsa* Cushman & Brönnimann, 1948. (Saunders, 1957, p. 15, pl. 1, figs. 3–8; Jennings et al., 1995, p. 119, pl. 1, figs. 2–8; Dreher, 2006, p. 99, pl. III, figs. 10a–11c; Southall et al., 2006, p. 172, pl. 1, figs. 6–7; Vance et al., 2006, p. 118, pl. 1, fig. 11; Callard et al., 2011, p. 125, pl. 1, figs. 16–19, Figueira et al., 2012, p. 209, figs. 2L–M; Laut et al., 2017, p. 136, pl. 6k; Semensatto, 2020, pl. 3, Fig. 42)

#### DIAGNOSIS

As with all prior descriptions, *T. salsa* is described as a planispiral to slightly irregular-growing species, typically using silt-sized grains with occasional argillaceous material to form the walls for its inflated chambers. Final apertures vary in number (typically between one and four) and shape considerably, though there is a clear preference towards two (also observed by Callard et al., 2011), margined by a small lip which projects outwards into the younger chamber (see Fig. 2d), and bound internally by small tooth-like projections, which have not been observed in *T. irregularis* specimens. Apertures vary in shape considerably but are typically kidney-shaped or circular. *Trochamminita salsa* chamber walls are typically smooth to polished in texture, and each whorl may have 5–8 chambers. Occasionally, terminal chambers curve forwards so much that the apertural face pushes against the earlier whorl, making it unobservable, as observed on the specimen displayed in Figure 2e. All chambers are subspherical, inflated, and increase in size with coiling.

*Recorded stratigraphic range.* Recent.

*Occurrence.* Known from salt marshes and mangrove swamps across the Southern Hemisphere, including New Zealand, Australia, (Apthorpe, 1980; Callard et al., 2011); the Falkland Islands (Newton et al., 2021); Chile (Jennings et al., 1995); and Brazil (Passos et al., 2017; Semensatto et al., 2020). Also sporadically reported from North American marshes, such as those in New Orleans (Dreher, 2006), and North Carolina (Vance et al., 2006) as well as the Caribbean (Cushman & Brönnimann, 1948; Saunders, 1957; Laut et al., 2017).

## CONCLUSIONS

Morphological and geographic evidence supports the separation of *T. salsa* from *T. irregularis*, though it is recommended that future genetic work be performed to conclusively test this. Furthermore, a morphological separation has been discovered (texture, aperture shape and number, chamber shape) and differences in preferred elevation between morphological forms (as well as a likely difference in geographic distribution) and between specimens generally referred to as *Trochamminita irregularis*, which are revealed to represent two species: *T. irregularis* (*sensu stricto*), as re-described in Saunders (1957), and *Pseudotrochamminita malcolmi* (n. gen., n. sp.). *Pseudotrochamminita malcolmi* is identified as distinct for the first time and found to be present in two geographically distant sites across New Zealand. The difference in vertical habitat ranges between these two species means that distinguishing them during surveys for sea-level research will enable more precise and accurate estimates of past sea level.

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## FIGURE CAPTIONS

FIGURE 1. Relative positions of sites and the positions of surveyed transects for which the data and specimens presented in this study were collected. Aerial images obtained via ©Google Earth.

FIGURE 2. Typical specimens of *Trochamminita salsa* and *Trochamminita irregularis* with zoomed panels displaying their apertures.

FIGURE 3. Typical specimens of *Pseudotrochamminita malcolmi* (new genus, new species).

Holotype specimen: Fig. 3a. All specimens from both Figures 2–3 are taken from Transect 1 of the salt marsh at Pauatahanui Inlet and are available to access from the National Palaeontological Collection, GNS Science Ltd. The holotype specimen of *Ps. malcolmi* is specimen TF 1678, while the two paratypes are TF 1679 (3b) and TF 1680 (3c). Further data, including elevational data for each species, will be fully published in forthcoming works.

FIGURE 4. Vertical distributions of *T. irregularis*, *T. salsa*, *Pseudotrochamminita malcolmi* (new genus, new species), and *Polysaccamina ipohalina* given as a percentage of the total foraminiferal assemblage at Pauatahanui and Aramoana salt marshes. Note the different scales on the x-axis. The highest occurrence of foraminifera is approximately coincident (within ~10 cm) with the highest annual tide (Wright et al., 2011).

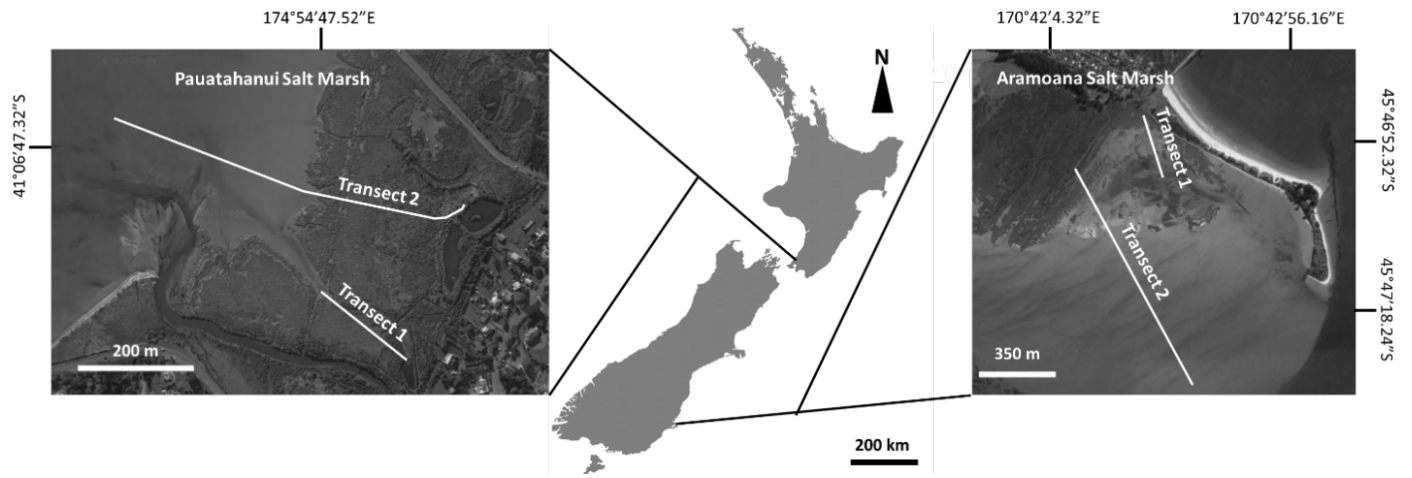
FIGURE 5. Two specimens of *Polysaccamina ipohalina* from Aramoana salt marsh. Aperture oriented up (a), and left (b). Both scale bars 200  $\mu\text{m}$ .

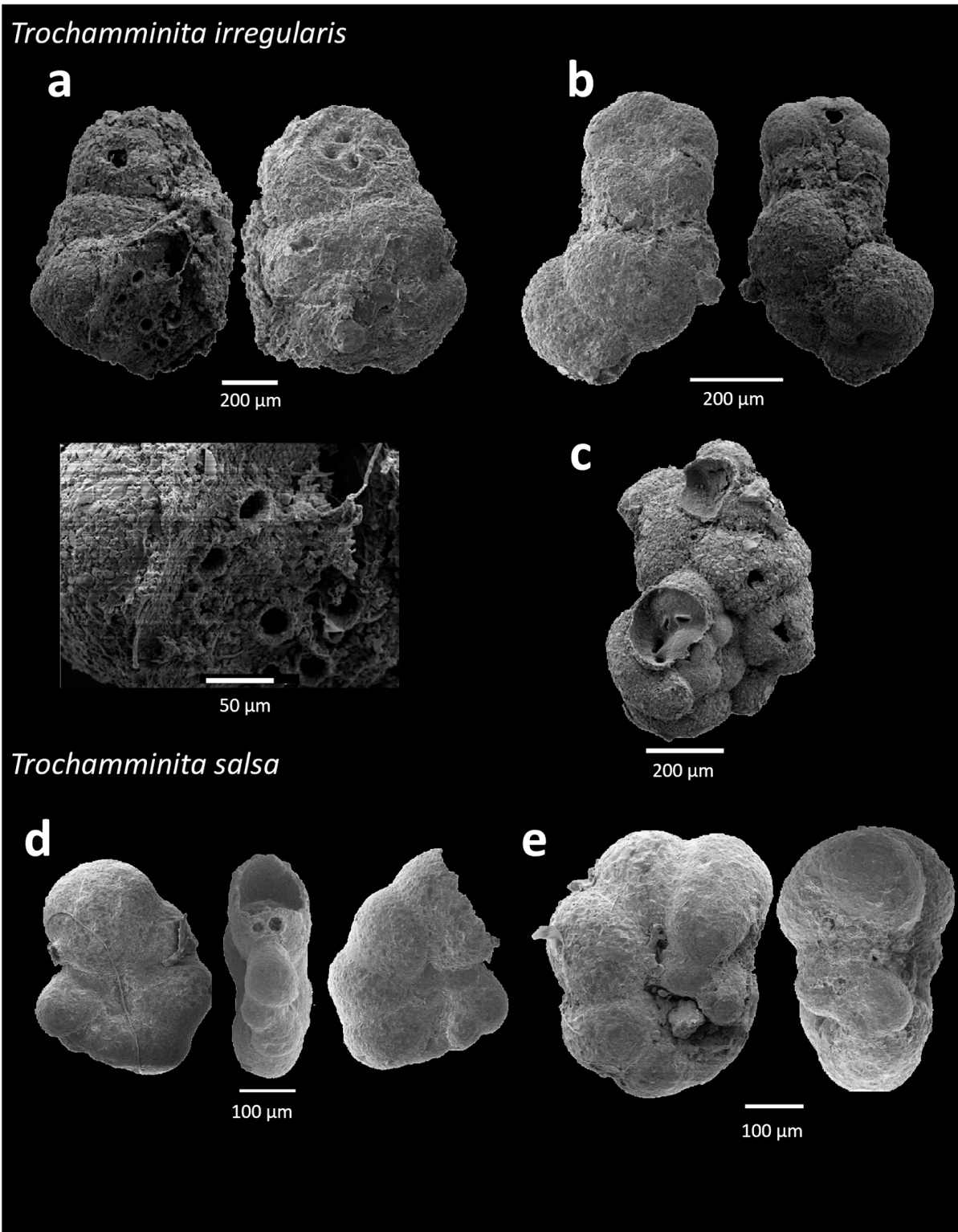
FIGURE 6. Colour variation of the chitin layer of two *Ps. malcolmi* specimens from Aramoana, as visible when light is shone through a specimen. Specimen a oriented aperture up, scale bar 250  $\mu\text{m}$ , specimen b oriented aperture left, scale bar 350  $\mu\text{m}$

FIGURE 7. Specimens of *Trochamminita irregularis* (a) and *Pseudotrochamminita malcolmi* (b) from Lutregala Marsh, Tasmania. Image Credit (both photomicrographs): Sophie Williams. Both specimens oriented aperture-top, scale bars 250  $\mu\text{m}$  (a) and 20  $\mu\text{m}$  (b).



2566 KING, FIGURE 1.





*Pseudotrochamminita malcolmi*

