Tremblin, C. M., & Walker, J. K. (2025). How did it get here? First record of *Trochamminita irregularis*, a cosmopolitan estuarine organic-cemented agglutinated foraminifer, in south-west Western Australia. *Journal of The Royal Society of Western Australia*, *108*, 1. https://doi.org/10.70880/001c.129191

Journal of The Royal Society of Western Australia
Vol. 108, 2025

How Did It Get Here? First Record of *Trochamminita irregularis*, a Cosmopolitan Estuarine Organic-Cemented Agglutinated Foraminifer, in South-West Western Australia

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Keywords: Estuarine-marsh foraminifera, biogeography, microhabitat, migratory birds, southwest Australia
https://doi.org/10.70880/001c.129191

Abstract

The cosmopolitan organic-cemented agglutinated foraminifer *Trochamminita irregularis* previously identified in Australian salt marshes of the Gippsland Lakes in Victoria and Little Swanport Estuary in Tasmania, has been recognised for the first time in Western Australia in the Hay River connected to Wilson Inlet, in the south-west of the State. The irregular test and chamber shapes may be related to the species mode of living restricted to the upper-marsh or river-margin environments in organic-rich sediment associated with filamentous rhizomes/stolons of marsh vegetation. Morphological variation may also be due to highly variable seasonal to daily environmental changes ranging from tidal variation, salinity changes (within a hyposaline range) and variable river flow. *Trochamminita*'s fragmented global distribution could likely be attributed to attachment to migratory waterbirds dispersing it along major flyways such as the East Australasian Flyway where Australia acts as one of the main foraging and breeding ground for these birds. The discovery of the species in the Hay River allows some preliminary investigations of the micro-living habitat of *Trochamminita* and its potential means of dispersion. Molecular and more in-depth ecological studies on living *T. irregularis* are required to more fully understand this global and ecologically significant marsh indicator species.

INTRODUCTION

Salt marshes and surrounding coastal estuarine vegetation act as dynamic intertidal ecosystems located at the interface between terrestrial and marine environments (Brearley, 2005; Reed et al., 2009). Present along most estuaries worldwide, these muddy, anaerobic and organic-rich microhabitats are characterized by halophytic vegetation – withstanding fluctuations between brackish and freshwater conditions caused by daily and seasonal change. These habitats not only are recognised for their extensive ecosystem services, serving as natural buffers against coastal erosion and flooding, but are also home to a diversity of micro- to macro-organisms, encompassing amphipods, foraminifers, bivalves and gastropods (Murray, 2014; Pennings & Bertness, 2001; Ross et al., 2009). The complex zone of rhizomes and stolons at the edge of the marsh comprises an intricate matrix, that accounts for a highly interconnected web of biological and physical processes promoting nutrient cycling and oxygen regulation (Vernberg, 1993).

Trochamminita irregularis (Cushman and Brönnimann) is one of two species known within its genus, belonging among the organic-cemented agglutinated foraminifera that do not secrete a calcium-carbonate component in their test. These differ from carbonate-cemented agglutinated foraminifera and other groups that produce calcium carbonate through biomineralization. The species is characterised by highly variable whorl arrangements, often reaching up to four in adult specimens. Its chambers initially coil in a planispire, with the test axis shifting and twisting during later development. *Trochamminita irregularis* differs from the other species within its genus, *Trochamminita salsa* (Cushman and Brönnimann), by its asymmetrical chamber arrangement, and its wider adaptability to salinity change, compared to a more saline condition for *T. salsa*. *Trochamminita irregularis* has a broad and cosmopolitan distribution, spanning diverse geographic and ecological regions (Fig. 1, Table 1). In North America, it is found along the Atlantic and Pacific coasts, including upper marshes of Oregon (e.g., Salmon River and South Slough), Texas (Trinity River), North Carolina (Outer Banks), and Florida (Everglades). It also occurs in estuarine systems like the Pascagoula River in Mississippi and Bayou Lafourche in Louisiana. Further south, in South America, it inhabits mangrove and marsh systems in Brazil (Caeté River) and French Guiana (Kaw estuary). Its presence in Europe is notable in inland saline springs of Germany and upper marshes in Iceland and Portugal (e.g., Caminha Marsh). In the Southern Hemisphere, *T. irregularis* is distributed across various wetlands and marshes in Australia (e.g., Little Swanport in Tasmania) and New Zealand (e.g., Mokomoko Inlet and Pauatahanui Inlet). It has also been recorded in the saline environments of Lake Verlorenvlei, South Africa, in the estuarine lagoon of Seitu in Malaysia and in the tropical mangroves of Saint Vincent Bay, New Caledonia.

This preliminary study aims to **(i)** document the first discovery of *Trochamminita irregularis* in a southwestern Australian estuary, **(ii)** describe its micro-living habitat in Hay River, Wilson Inlet; and **(iii)** consider the pathways of its global distribution.

NEW LOCALITY OF *TROCHAMMINITA IRREGULARIS*

Wilson Inlet is a seasonally open, broad tidal inlet located on the southern coast of Western Australia (Ranasinghe & Pattiaratchi, 1999; Brearly 2005). It is a shallow estuarine basin with an area of 48 km^2 and a mean depth of 1.8 m, exhibiting freshwater conditions in the winter months and brackish conditions in the summer (Lukatelich et al., 1987; Twomey & Thompson, 2001). The Hay River (Fig. 2a) is one of three main tributaries (with salinity varying from freshwater 8-10 ppt in winter to brackish 27-28 ppt in the summer months) flowing into the inlet, and it accounts for 65% of the annual streamflow into the estuary (Ranasinghe & Pattiaratchi, 1999). The Hay River catchment features two distinct landform types: with (1) a western re-

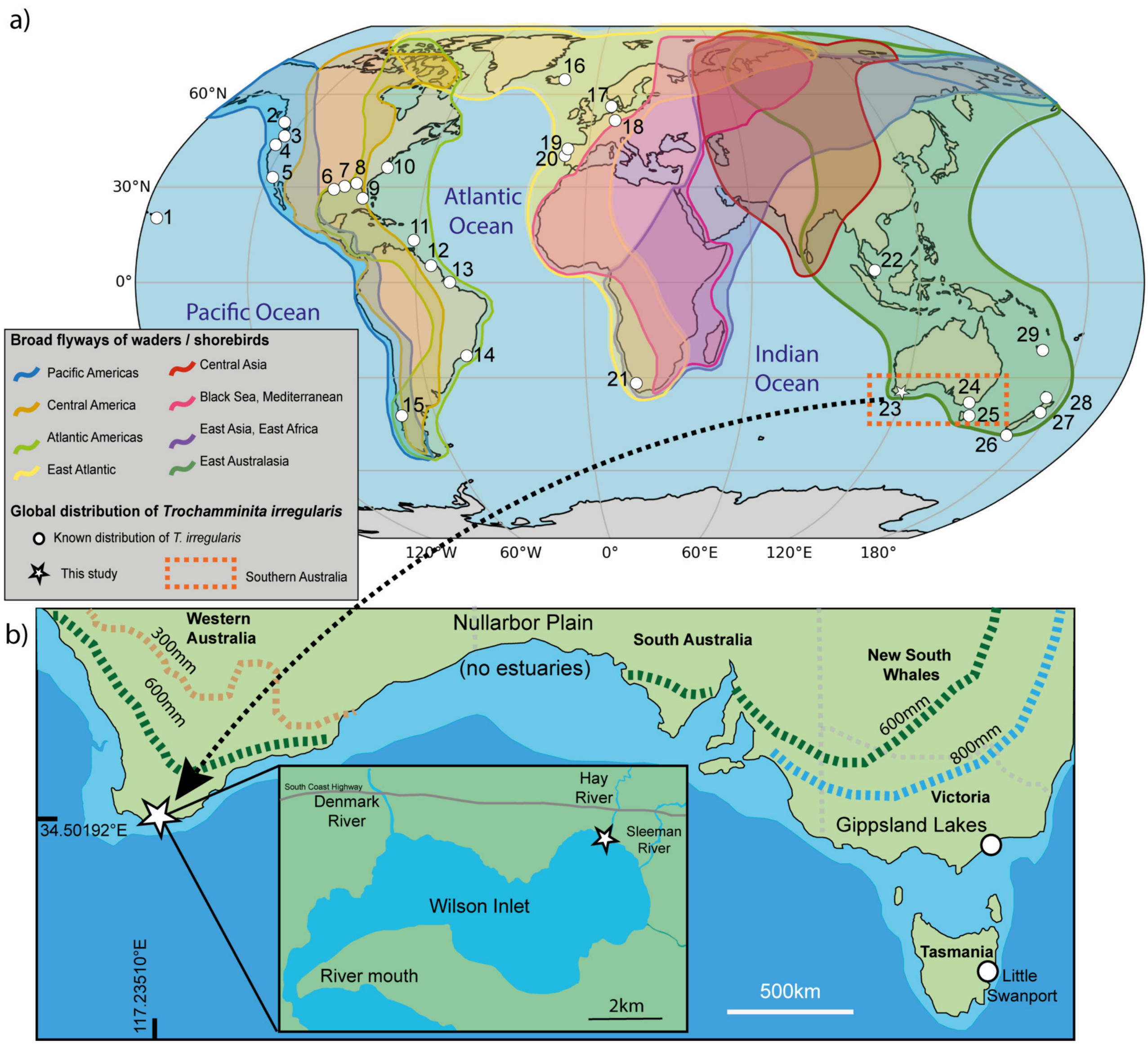

Figure 1. Distribution of *Trochamminita irregularis*. a) Global distribution (white circles, number referenced in Table 1) in relation to the eight broad major avian flyways including Pacific Americas, Central America, Atlantic Americas, East Atlantic, Central Asia, Black Sea-Mediterranean, East Asia-East Africa, and East Australasia (adapted from Bamford et al., 2008); b) enlarged view with average annual isohyets (Bureau of Meteorology, 2024) of the southern Australian coastline showing Locality 23 (starred, studied area) near mouth of Hay River flowing into Wilson Inlet, and Gippsland Lakes and Little Swanport Estuary, the only other localities where *T. irregularis* has been recorded in Australia.

gion characterized by a rolling, dissected lateritic terrain that transitions into lateritic uplands (Lukatelich et al., 1984). In contrast, (2) the eastern portion of the catchment, which also includes the Sleeman River catchment, consists of lateritic sandplain swamps and plains interspersed with gravelly ridges (Lukatelich et al., 1984). The low relief in this area results in swampy flats surrounding the stream channels (Fig. 2b). The soils are primarily leached sands and yellow-mottled soils, which support jarrah scrub, and sandplain heaths (Lukatelich et al., 1984).

Trochamminita irregularis is found in low abundance in shoreline environments near the confluence of Hay River and Wilson Inlet at coordinates 34.970089°S, 117.4692702°E (Fig. 2c). It forms <20% of the marsh foraminiferal fauna in a systematic pick of dead and live individuals, alongside *Ammonia haigi* Haywood and Holzmann, *Trochammina inflata* (Montagu), and *Elphidium* sp., and lives among riparian vegetation including *Sarcocornia quinqueflora* Bunge ex Ung.-Sternb. (Fig. 2d), *Baumea* sp. and *Juncus* sp. (Fig. 2e). The substrate is composed of fine silty mud with very rare shelly material.

Morphological variability (Fig. 3a–l) of the test of *T. irregularis* could likely be shaped by the intertwining pattern of above-ground stolons at the base of the vegetation. The multiple apertures and their varying position either at the base of the ultimate chamber or areal in the apertural face of this chamber (Figs. 3j, k, l) may be a potential morphological adaptation to maximise food uptake and to facilitate the protrusion of the pseudopodia in 3-dimensions, while attached to the filamentous stolons/rhizomes. In the slightly deeper part of the Hay River (>0.5 m water depth), the seagrass *Ruppia megacarpa* Manson is found in occasional patches growing in a mix of sandy and silty mud. *Trochamminita irregularis* was not found in this habitat.

Table 1. Selected worldwide sites with *Trochamminita irregularis*, including habitat zones and records of associated foraminifers.

No	*Localities*	*Countries*	*Habitat zone*	*Other foraminifers*	*References*
1	Salt Lake, Honolulu Hawaii	USA	Upper marsh	*Ammonia tepida, Haplophragmoides manilaensis, Milliamina fusca*	Resig, 1974
2	Port Alberni, British Columbia	USA	Upper marsh	*Entzia macrescens, Trochammina inflata, Haplophragmoides wilberti, M. fusca*	Clague et al., 1994; Ozarko et al., 1997
3	Salmon River, Oregon	USA	Upper marsh	*Balticammina pseudomacrescens, Haplophragmoides wilberti, Trochammina inflata, Entzia macrescens and M. fusca*	Hawkes et al., 2010; Milker et al., 2015
4	South Slough, Oregon	USA	Upper marsh	*B. pseudomacrescens, H. wilberti, T. inflata, E. macrescens, M. fusca*	Hawkes et al., 2010; Milker et al., 2015
5	Tijuana River, California	USA	Upper marsh	*E. macrescens, T. inflata, B. pseudomacrescens, H. wilberti*	Avnaim-Katav et al., 2017, 2023
6	Trinity River, Texas	USA	Upper marsh	*E. macrescens, M. fusca, T. inflata, H. wilberti.*	Brann, 1969
7	Pascagoula River and Grand Bay, Mississippi Sound	USA	Upper marsh	*A. tepida, Cribroelphidium poeyanum, C. excavatum, and Paratrochammina simplissima, Ammotium salsum, Ammobaculites exiguus, M. fusca, Arenoparrella mexicana, E. macrescens, Pseudothurammina limnetis.*	Haller et al., 2019
8	Bayou Lafourche, Louisiana	USA	Upper marsh	*T. inflata, Ammotium crassus, Ammonia parkinsoniana, Polysaccammina ipohalina, M. fusca*	Dreher, 2006
9	Florida Everglade	USA	Upper marsh	*E. macrescens, M. fusca, H. wilberti, A. mexicana, Ammonia* spp., *Elphidium* spp., *A. tepida, Helenina anderseni, T. inflata*	Z. R. Verlaak & Collins, 2021; Z. R. F. Verlaak, 2019
10	Pamlico Sound and Currituck Sound coasts of North Carolina's Outer Banks	USA	Upper marsh	*A. mexicana, H. wilberti, E. macrescens, T. inflata, M. fusca, Tiphotrocha comprimata*	Culver & Horton, 2005; Robinson & McBride, 2006
11	Maracas Bay River, north coast	Trinidad	Shallow tributary drain of the Maracas Bay River.	*H. manilaensis, H. wilberti, Trochamminita salsa, Trochammina laevigata, T. comprimata, Siphotrochammina lobata, A. mexicana*	Cushman & Brönnimann, 1948; L. Laut et al., 2017; Saunders, 1957
12	Kaw estuary and Lagoon of Montjoly	French Guinea	Mangrove swamps	*A. tepida, A. parkinsoniana, Cribroelphidium* spp., *M.* fusca	Debenay et al., 2002
13	Caete River	Brazil	Upper marsh and mangroves	*T. paranaguaensis, D. urceolata, D. oblonga*	L. L. M. Laut et al., 2016
14	Rio Itapanhaú	Brazil	Upper marsh	Not described	Moreno, 2004
15	Valdivia-Tornagaleones estuary	Chile	Upper marsh	*M. fusca, T. salsa, Haplophragmoides* spp., *Trochammina squamata*	Jennings et al., 1995
16	Melabakkarin vicinity of Reyjavik	Iceland	Upper marsh	*Haynesina orbicularis, E. macrescens*	Lübbers & Schönfeld, 2018
17	Bay of Tümlau, Schleswig-Holstein	Denmark	Upper marsh	*B.pseudomacrescens, T. inflata, E. macrescens*, and monothalamous *Ovammina opaca*	Bunzel et al., 2013
18	Saxony-Anhalt and Thuringia	Central Germany	Saline springs	*T. salsa, E. macrescens, M. fusca, S. lobata, H. manilaensis, H. wilberti*	Lehmann, 2000; Milker et al., 2023
19	Caminha marsh, Minho River	Portugal	Upper marsh	*H. manilaensis*	Fatela et al., 2014; Semensatto, 2020
20	Aveiro	Portugal	Upper marsh	*Rotaliammina concava, Lepidodeuterammina ochracea, Quinqueloculina seminula, Gavelinopsis praegeri, Paratrochammina haynesi, Remaneica helgolandica, Remaneicella gonzalezi*	Martins et al., 2019
21	Lake Verlorenvlei	South Africa	Enclosed lake, upper marsh	*Haplophragmoides* sp., *Trochammina inflata, Milliamina earlandi, Ammonia parkinsoniana, Ammonia tepida*	Fürstenberg et al., 2017
22	Setiu estuary–lagoon system, Terengganu	Malaysia	Upper marsh/ wetland	*Ammobaculites exiguus, Bruneica clypea, Caronia exilis, Haplophragmoides wilberti, Siphotrochammina lobata,* and *Trochammina inflata*	Culver et al., 2015
23	Wilson Inlet	Australia	Upper marsh, restricted Hay River	*Ammonia haigi, T. inflata, Elphidium* spp.	**This study**
24	Gippsland Lakes	Australia	At margin	*M. fusca*, *A. salsum*, *Reophax barwonensis*, "*Martinotiella* cf.	Apthorpe, 1980

	(Lake Wellington)		of lake	*communis*" (= ?*Scherochorella*), *T. inflata*	
25	Little Swanport, Tasmania	Australia	Upper marsh	*T. inflata, E. macrescens, T. salsa, M. fusca, Elphidium* sp., *H. wilberti, Quinqueloculina* sp.	Callard et al., 2011; Gehrels et al., 2012; Williams et al., 2021
26	Port Pegasus "Pikihatiti"	New Zealand	Upper marsh	*T. salsa, T. inflata, H. wilberti, M. fusca, Ammonia* spp., *E. macrescens*	Hayward et al., 1994
27	Mokomoko Inlet	New Zealand	Upper marsh	*Trochamminita* spp., *H. wilberti, M. fusca*	Garrett et al., 2022
28	Pauatahanui Inlet, southern North Island	New Zealand	Upper marsh	*T. salsa, Pseudotrochamminita malcomi, Polysaccammina ipohalina*	King, 2021
29	Saint Vincent Bay	New Caledonia	Mangroves	*M. fusca, A. mexicana, H. wilberti, T. inflata, Trochammina patensis*	Debenay et al., 2015

DISCUSSION

Associated foraminifers with *Trochamminita irregularis*

Worldwide species associations

Trochamminita irregularis commonly coexists with a variety of foraminiferal species that inhabit similar marsh, estuarine, and mangrove ecosystems. In temperate and subtropical marshes, it is often found alongside species such as *Entzia macrescens* (Brady), often referred to *Jadammina,* and *Miliammina fusca* (Brady), which are well-known indicators of high-marsh environments (Table 1). The association with *Trochammina inflata*, another marsh specialist, is consistent in regions like Oregon, New Zealand, and South America. In saline springs, it is found with *E. macrescens* and *Siphotrochammina lobata* Saunders, highlighting its adaptability to high salinity and fluctuating environmental conditions. In tropical and subtropical ecosystems, *T. irregularis* cohabits with *Arenoparrella mexicana* (Kornfeld), *Haplophragmoides wilberti* Anderson, and species of *Ammonia* (Table 1). Other notable cohabitants include *Balticammina pseudomacrescens* Brönnimann, Lutze & Whittaker in northern marshes (e.g., Oregon) and *Trochamminita salsa*, a species found in South America, Germany, and New Zealand. In Portugal, Australia, and Malaysia, *T. irregularis* is also associated with species often referred to as *Quinqueloculina "seminula"* (Linnaeus), *Paratrochammina haynesi* (Atkinson), and *Polysaccammina ipohalina* Scott, which are indicative of brackish to marine transitions. By understanding these co-occurrences, it does underline the ecological versatility and habitat diversity in which *T. irregularis* evolved but also raises significant questions about dispersal of the species.

Hay River species association

Based on previous and continuing studies on Western Australian estuaries, the Hay River site described here is the only locality where *Trochamminita irregularis* has been found in the State (Table 2). The dominant foraminiferal species at the Hay River study site are the calcareous trochospiral *Ammonia haigi* and the organic-cemented agglutinated trochospiral *Trochammina inflata*. Apart from the Hay River site, *T. inflata* is known from 12 of the other 28 world-wide *T. irregularis* sites listed on Table 1, and species of *Ammonia* were recorded from six of the sites. These species are known from many of the other estuaries in south-west Western Australia. Questions exist, that require much further work and cannot be answered in this short note, about why different species are associated with *Trochamminita* in the marsh associations at different localities (Table 1), and why *T. irregularis* has not been found at other sites in Western Australia containing associated marsh foraminifers (based on extensive unpublished work on most estuaries from Esperance in the east to Carnarvon in the north-west).

Biogeographical fragmentation: potential means of distribution

The global distribution of *T. irregularis* is highlighted by a fragmented pattern ranging from tropical to temperature regions, and by differences in associated species almost all of which are confined to marshes and river-margin situations under mainly brackish water conditions. Most estuaries are disconnected spatially and in geological time. This is very apparent between the two known occurrences of *Trochamminita irregularis* on the southern coastline of Australia, Gippsland Lakes in the east and Hay River in the west, with about 1500 km of the >2500 km shoreline between these sites lacking river inflow and estuaries.

Dispersal of estuarine foraminifera has been suggested to occur by different means including anthropogenic interventions (ballast water, e.g., Tremblin et al., 2021), or from natural mechanisms (drifting of foraminiferal propagules in the current, e.g. Alve, 1999, and rafting e.g., Finger, 2018). Bird-mediated dispersal of riverine invertebrates including foraminifera has been suggested in the literature through ectozoochory and endozoochory, where the biota get into feathers, feet or directly in the birds digestive systems (Coughlan et al., 2017; Riedel et al., 2011). Dispersal events by birds may be rare but because of the large migratory waterbird populations and the countless days of migration from their departure point to their destination, the cumulative rate of rare dispersals make these significant.

In the Australian context, dispersal of estuary-bound foraminifers must have been across large terrestrial spaces (either north-south or east-west) or over large tracts of ocean surrounding the continent. Australia is located at the edge of one of eight major flyways for migratory land and waterbirds (Fig. 1). This flyway accounts for about 700 species of birds flying from as far away as Siberia in the north and to New Zealand in the South. In their foraging, waterbirds may unintentionally transport *T. irregularis* through their feathers, feet, or digestive systems as they migrate across vast distances. Five species of waterbirds including the Eurasian Coot (*Fulica atra*), Red-necked Stint (*Calidris ruficollis*), Silver Gull (*Chroicocephalus novaehollandiae*), Fairy Tern (*Sternula nereis*) and Caspian Tern (*Hydroprogne caspia*), share the three localities where *Trochamminita irregularis* has been recorded in Australia (Birdlife Western Australia, 2024; Bryant, 2002; Hansen et al., 2024). Under extreme conditions foraminiferal protoplasm can remain viable for long periods of time, up to two years, as described by Alve and Goldstein (2010). It has also been shown from fish-gut contents that more than 20% of foraminiferal protoplasm is still viable even after days of being digested (Guy-Haim et al., 2017). In the case of *T. irregularis*, their asexual reproduction, as well as their flexible, imperforate, and highly variable tests built on an organic template, and their ability to construct their tests using surrounding fine siliceous sand grains, probably make them likely to quickly regener-

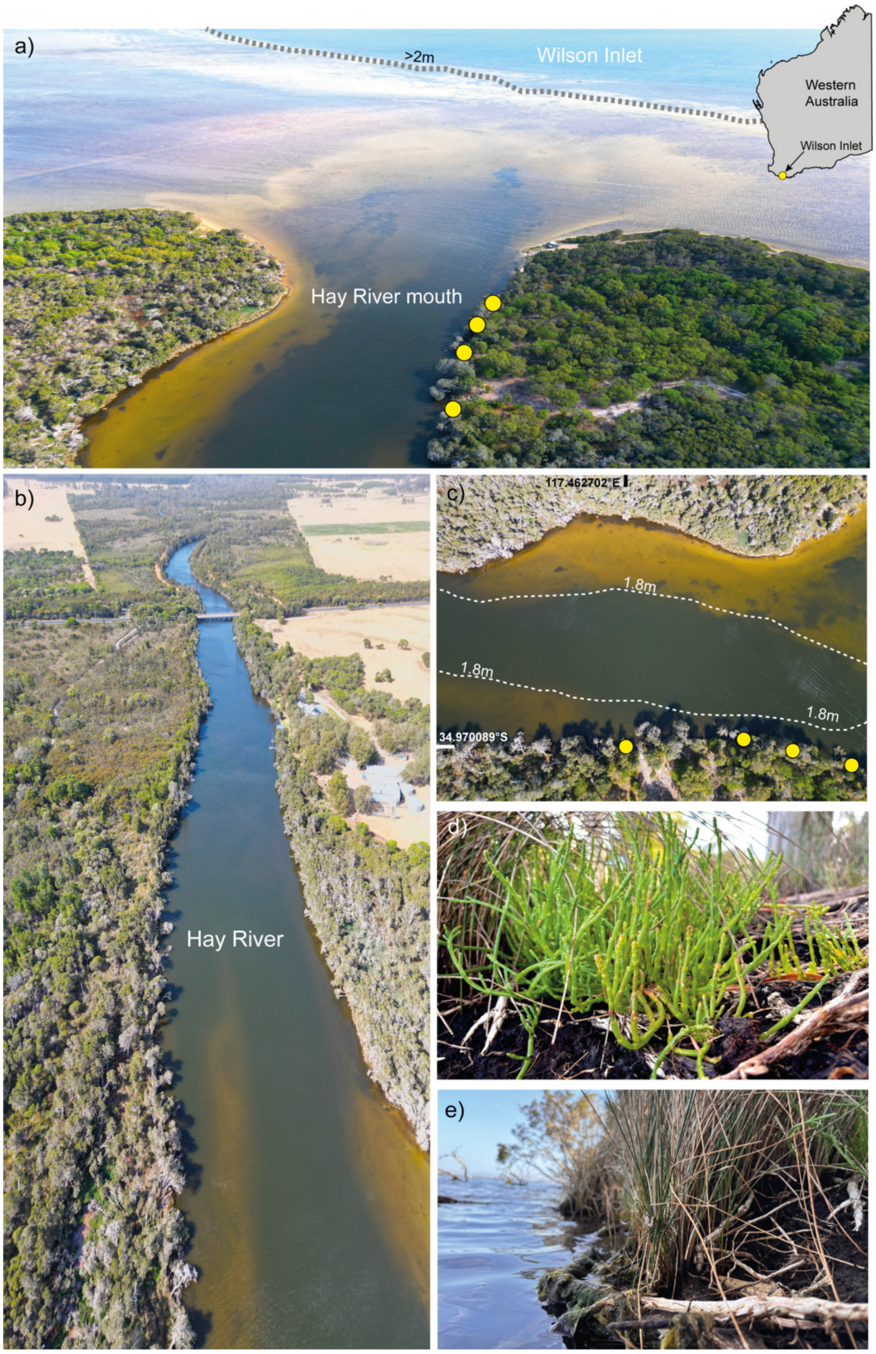

Figure 2. Drone images of the Hay River connected to Wilson Inlet. a) view of Hay River mouth flowing into Wilson Inlet (yellow dots – localities of sampled *Trochamminita irregularis*); b) view of Hay River upstream from sampled sites; c) close-up view of river channel adjacent to the sampled sites; d, e) common salt-marsh vegetation including (d) *Sarcocornia quinqueflora* Bunge ex Ung.-Sternb. and (e) *Baumea* sp. and *Juncus* sp., where *T. irregularis* lives.

ate a population when an environmentally suitable habitat is encountered. The other taxa associated with *T. irregularis* could have been transported via the same mechanisms. The occurrence of *T. irregularis* in Hay River adds to the presently known record of the species distribution and emphasizes the ecological importance of studying salt-marsh environments in Western Australia and elsewhere and using foraminifers as markers for not only possible recent introductions, but also as environmental proxies.

Future work should involve (1) genetic analysis to understand the connectivity of the various estuarine *Trochamminita* populations worldwide including in areas of overlap of the migratory flyways, as well as the genetic drift along possible migratory pathways; (2) seasonal ecological monitoring of *T. irregularis* in the Hay River, to note species dynamics under varying climatic conditions; and (3) analyses of mud detritus attached to feathers and feet as well as the faecal content of migratory birds to determine if attached mud and faeces could facilitate the foraminiferal migration.

CONCLUSIONS

Trochamminita irregularis, a species recognized for its global distribution, previously recorded in Australia only in the Gippsland Lakes (Victoria) and Little Swanport Estuary in Tasmania, has now been identified in the Hay River of Wilson Inlet, located in south-western Australia. This species is distinguished by its variable chamber mor-

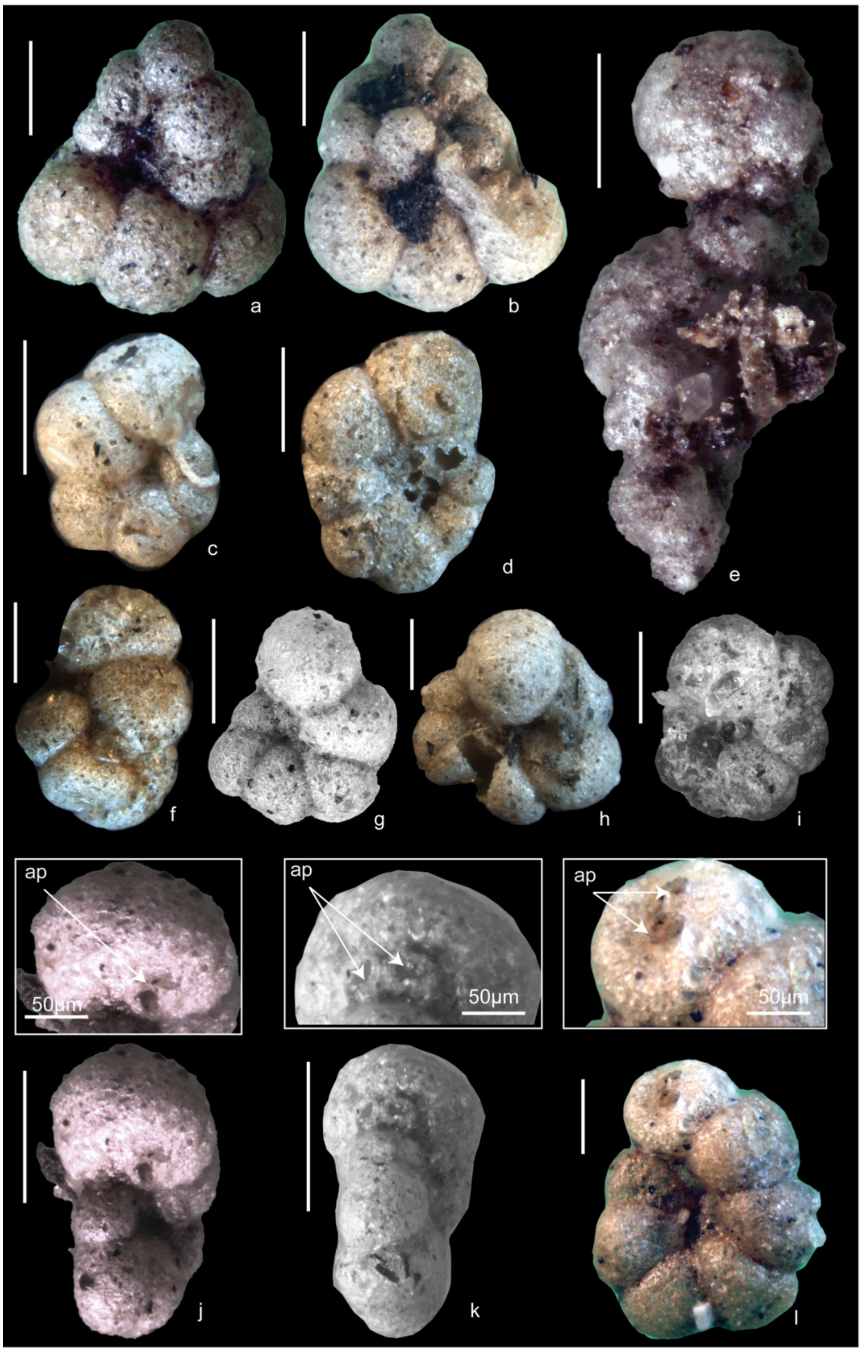

Figure 3. *Trochamminita irregularis* (Cushman and Brönnimann) from the Hay River sites shown in Fig. 2, emphasizing the morphological variation in test shape, agglutination, coiling and chamber arrangement, and position of apertures (ap). Bar scale = 200μm, unless indicated.

phology, multiple apertures, and flexible test. It occupies the muddy substrate at the base of upper marsh vegetation, in a habitat where environmental factors such as tidal changes and salinity fluctuations within a general hyposaline range may shape its development. The fragmentary wide distribution of the species may be associated with migratory waterbirds, which could facilitate its spread in mud attached to feathers and feet or in faeces. Further molecular and ecological research is essential to clarify its dispersal mechanisms and ecological role, particularly as an important indicator species in coastal ecosystems.

ACKNOWLEDGEMENTS

This paper is the result of discovering *Trochamminita irregularis* in samples collected in September 2019 by David Haig, Bruce Hayward, Mark Gunson and Jenny Bevan, in the Hay River. David Haig is thanked for his assistance in the field and in discussions; Siri Kellner of the University of Western Australia Earth Science Museum is thanked for her curatorial assistance. The authors are grateful to the two anonymous reviewers for their helpful comments and suggestions that have improved the manuscript. All materials are curated in the Earth Science Museum of the University of Western Australia.

Submitted: January 19, 2025 AWST. Accepted: January 28, 2025 AWST. Published: February 14, 2025 AWST.

Table 2. Presence and Absence of *Trochamminita irregularis* from estuaries around Australia.

Localities	*Latitude and Longitude*	*States*	*Occurrence*	*References*
Cocoa Creek	19.288° S, 147.005 °E	QLD	Absent	Horton et al., 2003; Woodroffe et al., 2005
Thomatis Creek, Barron River	16.846° S, 145.719° E	QLD	Absent	Haslett, 2001
South Alligator River	12.247° S, 132.403° E	NT	Absent	Wang & Chappell, 2001
Tuross Estuary and Coila Lake	35.736° S, 150.112° E	NSW	Absent	Strotz, 2003
Lake Illawarra	34.557° S, 150.841° E	NSW	Absent	Yassini & Jones, 1989
St George Basin	35.092° S, 150.596° E	NSW	Absent	Strotz, 2012
Smith Lake	32.251° S, 152.532° E	NSW	Absent	Strotz, 2015
Broken Bay estuary	33.566° S, 151.312° E	NSW	Absent	Albani, 1978
Minnamurra River	34.634° S, 150.847° E	NSW	Absent	Lal et al., 2020
Comerong Island	34.889° S, 150.735° E	NSW	Absent	Lal et al., 2020
Carama Inlet	34.993° S, 150.783° E	NSW	Absent	Lal et al., 2020
Currambene Creek	35.020° S, 150.667° E	NSW	Absent	Lal et al., 2020
Little Swanport Estuary	35.007° S, 150.215° E	TAS	**Present**	Callard et al., 2011
Tamar River and and Port Dalrymple	41.110° S, 146.798° E	TAS	Absent	Bell, 1996
Northern Spencer Gulf	33.007° S, 137.844° E	SA	Absent	Cann et al., 2002
Port Pirie	33.177° S, 138.008° E	SA	Absent	Cann et al., 2002
Lake Connewarre	38.226° S, 144.487° E	VIC	Absent	Bell, 1995
Mallacoota Inlet	37.563° S, 149.746° E	VIC	Absent	Bell & Drury, 1992
Barwon River estuary	38.292° S, 144.391° E	VIC	Absent	Parr, 1945
Gippsland LakeS, Victoria	38.091° S, 147.760° E	VIC	**Present**	Apthorpe, 1980
Mangrove Bay, Ningaloo Reef	21.962° S, 113.946° E	WA	Absent	Parker, 2009
Oyster Harbour	35.028° S, 117.884° E	WA	Absent	McKenzie, 1962
Hardy Inlet	33.541° S, 115.545° E	WA	Absent	Quilty, 1977
Murray River	34.300° S, 140.800° E	WA	Absent	Ostrognay & Haig, 2012
Leschenault Inlet and Collie River	33.283° S, 115.699° E	WA	Absent	Ostrognay & Haig, 2012; Revets, 2000; Tremblin et al., 2021
Wellstead Estuary	33.704° S, 118.396° E	WA	Absent	*pers. obs.*
Kalgan River	34.976° S, 117.741° E	WA	Absent	*pers. obs.*
Frankland River	33.957° S, 116.027° E	WA	Absent	*pers. obs.*
Walpole Inlet	34.969° S, 116.730° E	WA	Absent	*pers. obs.*
Mandurah marsh	32.548° S, 115.716° E	WA	Absent	*pers. obs.*
Hay River	34.970°S, 117.469°E	WA	**Present**	This study

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