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Invasive Japanese foraminifera in a south-west Australian estuary

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Abstract. An invasive foraminiferan is recorded for the first time in an Australian estuary. *Trochammina hadai*, originally described as endemic from Japan and subsequently found to be alien in coastal waters of California and Brazil, has been identified in estuarine sediment in the vicinity of Bunbury Port in Western Australia. Species determination is based on morphological, molecular and ecological similarities to the Japanese type. The species has not been recorded in other estuaries in Australia. Bunbury Port is a major exporter of woodchip to Japan and the introduction of *T. hadai* may have come from ballast water out of shallow-draught woodchip vessels. Small sediment samples of estuarine mud obtained at water depths of ~5 m contain abundant *T. hadai* (on average ~0.4 mm in adult diameter) that are easily recognised in microscopic view of the sediment surface by their bright reddish-brown colour. The collection of sediment samples from the estuarine floor and ballast water, and the examination of these for foraminifers, may provide a useful indicator in estuaries for the possible presence of other exotic species, particularly in the vicinity of ports.

Keywords: agglutinated foraminifera, Bunbury Port, Collie River, invasive distribution, Leschenault Inlet, *Trochammina hadai*, Western Australia.

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Introduction

The introduction of alien species to a marine ecosystem threatens indigenous biodiversity and ecology (Bax *et al.* 2003). Various invasive species in shallow marine environments have been documented in 'plague' proportions due to rapid increases in populations in their new environments (e.g. sea anemones, gastropods, crustaceans, fish, seagrasses and algae; Ceccherelli *et al.* 2000; Smith *et al.* 2002; Hunt and Behrens Yamada 2003; Lanfranconi *et al.* 2009; Edelist *et al.* 2013; Patris *et al.* 2019). In Western Australian estuaries and shallow lagoons, invasive species from diverse taxonomic groups have been recorded (e.g. fish, comb jellyfish, hydroids, dinoflagellates, polychaetes, bryozoans and diatoms; Dürr and Semeniuk 2000; Bolton and Graham 2004; Wells *et al.* 2009; Russell *et al.* 2012; Smale and Childs 2012; Dias *et al.* 2015; Simpson *et al.* 2016).

Foraminifera are shelled protozoans commonly found in marine sediment. They form distinctive estuarine benthic faunas (Murray 1991; Scott *et al.* 2001). The tests (shells) of foraminifera are either calcareous, carbonate-cemented agglutinated, or organic-cemented agglutinated, and are usually chambered in many different arrangements that have taxonomic importance (Loeblich and Tappan 1987). Foraminifera have been recorded as prolific in estuarine sand, mud and marshes in previous studies on Western Australian estuaries (McKenzie 1962; Quilty 1977; Revets 2000; Quilty and Hosie 2006; Parker 2009; Ostrognay and Haig 2012; Haig 2020). Although some species are cosmopolitan, none has been recognised as invasive.

In our ongoing survey of estuarine foraminifera from south-west Australia, a species morphologically similar to *Trochammina hadai* Uchio, 1962 has been found in Leschenault Inlet and the connected Collie River adjacent to Bunbury Port (Fig. 1). *T. hadai* was first described from Japan in shallow water off the mouth of the Shinano River (Uchio 1962) and later reported in large populations from Lake Hamana, a brackish lagoon, south-east Japan (Matsushita and Kitazato 1990). *T. hadai* has subsequently been described as an invasive species in estuaries along the west coast of North America and the east coast of South America (McGann *et al.* 2000, 2012; Eichler *et al.* 2018).

In order to better understand whether the Western Australian *Trochammina* morphotype is an invasive species, this paper: (1) compares its morphology with the type material of *T. hadai* from Japan; (2) makes molecular comparisons between live specimens retrieved from Western Australia and the material analysed by Pawlowski *et al.* (1997) and Pawlowski and Holzmann

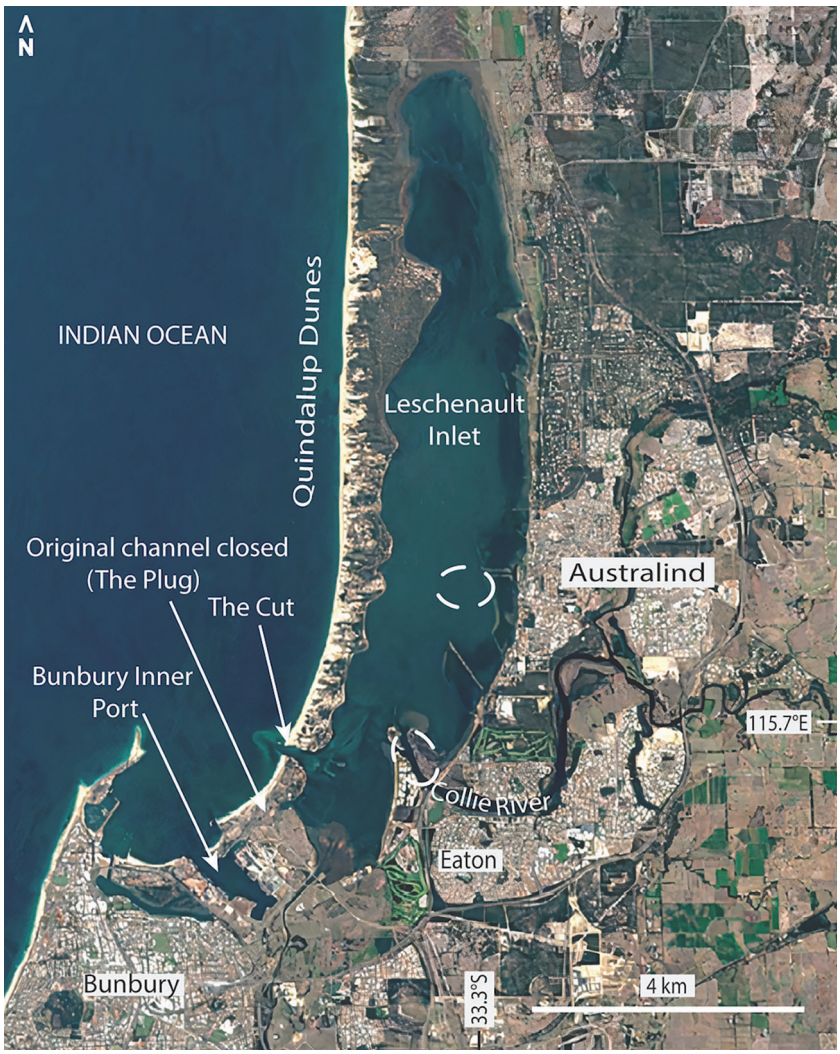

Fig. 1. Google Earth image of Leschenault Inlet and Collie River, Western Australia, showing sample collection areas (circled with white dashed line; for sample coordinates, see Table S1) and the recent anthropogenic modifications, including 'The Cut', 'The Plug' and Bunbury inner port. The location of Leschenault Inlet in Australia is shown in Fig. 10.

(2014) from Lake Hamana, Japan and San Francisco Bay, US; (3) determines the distribution of these morphotypes elsewhere in Australia and on other continents; (4) documents the occurrence of *Trochammina* in Leschenault Inlet and Collie River and determines the associated foraminiferal species in the present-day assemblages; and (5) interprets the factors associated with the occurrence of the species in Leschenault Inlet and Collie River (e.g. potential vectors of introduction, such as established shipping and trade and the origination of that trade) in order to determine whether the distribution may be invasive due to anthropogenic activities.

Setting: Leschenault Inlet and Collie River estuary

Specimens of the potential invasive foraminiferal species identified here come from Leschenault Inlet and the connected Collie River estuary adjacent to Bunbury Port. Leschenault Inlet (Fig. 1) is a long, narrow, shallow estuarine lagoon with a maximum water depth of 5 m. On the western (seaward) side, it is bordered by a ridge referred to as the Quindalup Dunes (Fig. 2) formed during the Holocene *c.* 7000 years ago (Brearley 2005). On its eastern side, the Mandurah–Eaton Ridge (Wurm and Semeniuk 2000) borders the estuary and includes the town of Australind. The development of the estuary is the sum of the early Holocene marine transgression that reached as far as the Pleistocene Mandurah–Eaton ridge, and the mid- to late Holocene development of the Quindalup Dunes, composed of wind-blown quartz–carbonate sand, on its seaward side (McArthur and Bettenay 1974; Semeniuk and Meagher 1981; Semeniuk *et al.* 1989). The Collie River flows into Leschenault Inlet towards its southern end.

Water quality in the estuarine environment varies seasonally, resulting from minor rainfall and river outflow in summer and by much increased river flow following intensive rainfall in winter (Hubertz and Cahoon 1999; Dürr and Semeniuk 2000).

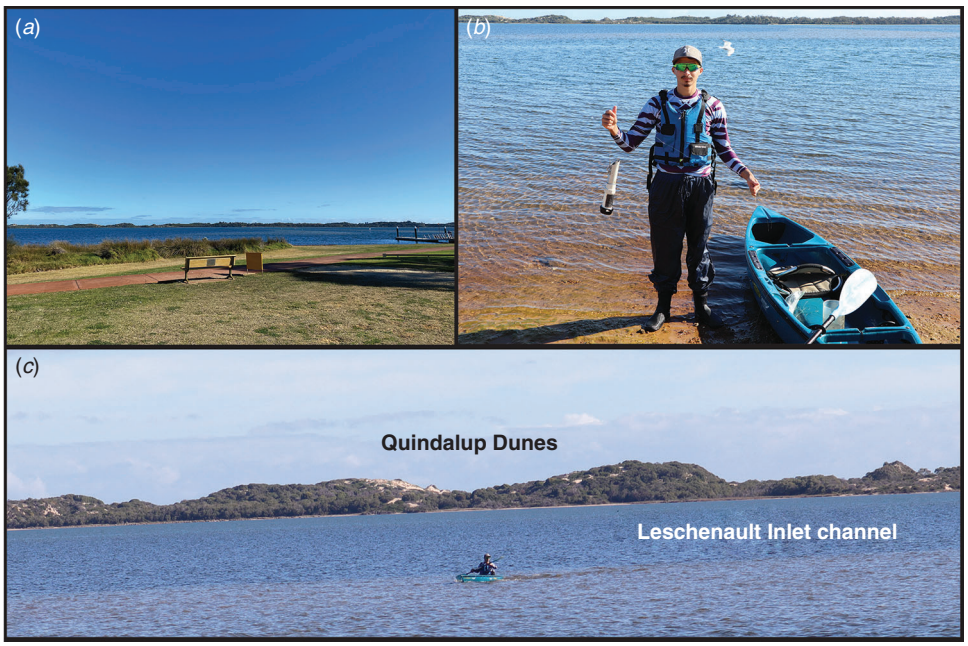

Fig. 2. (*a*) View of the study site from Leschenault Inlet car park and the boat jetty at Australind. (*b*) Pipe dredge and kayak used to sample mud in the middle of the channel. (*c*) View showing the Holocene Quindalup Dunes on the seaward side of Leschenault Inlet. The kayak is in the middle channel on its eastern landward side.

Water quality is also affected by peripheral anthropogenic activities (Pen *et al.* 2000). Prior to 1951, Leschenault Inlet was dominantly brackish (<30 psu) over wintertime. After 'The Cut' was first opened (Fig. 1), the salinity concentration has varied between hypersaline in summer to brackish in winter, the latter being due to the heavy inflow of fresh water from rain and Collie River discharge (Dürr and Semeniuk 2000). This results in salinity stratification due to the difference in density between a top freshwater layer and variably saline water below a depth of 2 m. Waves generated by wind, and storms in mid-July to mid-August, are mainly responsible for the mixing of the water column and the disturbance of bottom sediments (Charteris and Deeley 2000; Li *et al.* 2007). Water temperatures are subject to seasonal and daily fluctuations. In summer, the maximum water temperature can reach 25°C; in winter, it can fall to 14°C (Brearley 2005). A previous study conducted in Leschenault Inlet between October 1986 and March 1987 (austral summer) showed that water salinity varied from 33.5 to 45.0‰ and that oxygen concentrations fluctuated between 5.7 and 10.8 mg L^{-1}, although the water depths at which the measurements were taken were not mentioned (Wurm and Semeniuk 2000, tables 2, 3). The salinity of the Collie River recorded in August 2005 (austral winter) at a sample site with the presently identified *T. hadai*-like morphotype varied from 0.4‰ at a water depth of 0.3 m to 32.1‰ at a depth of 2 m, showing distinct stratification (Site C3 in Ostrognay and Haig 2012). At this site, in April 2006, the oxygen concentration varied between 90.5% saturation at a water depth of 0.3 m and 100.2% at a water depth of 2.2 m (Ostrognay and Haig 2012). No data are available to demonstrate similar winter stratification in Leschenault Inlet.

The estuarine sediment is mainly marine mud, calcareous and quartz sand and organic detritus. The distribution of mud was mapped by Wurm and Semeniuk (2000, fig. 4) based on limited sample points. An area of >50% mud occurs along the central axis of the Inlet (Fig. 1, 3) at a depth of ~4–5 m. On the western side, erosion of the Quindalup Dunes provides sand that progrades into the estuary. The quartz–carbonate sand is heterogeneously distributed along the shoreline (Semeniuk and Meagher 1981).

Materials and methods

Sample localities

Kitazato and Matsushita (1996) indicated that *T. hadai* is more prolific between autumn and winter. Therefore, the Leschenault Inlet and Collie River were sampled on three different dates at the beginning of the 2020 austral winter: 22 May 2020 (sunny, clear weather), 4 June 2020 (sunny, clear weather) and 18 June 2021 (high tide, before rainfall). The Leschenault Inlet was sampled using a kayak at 12 localities (see Table S1 of the Supplementary material) along the eastern side of the middle channel, ~700 m from the shoreline (Fig. 1, 2*a*, *c*). The samples were collected via a small pipe dredge (Fig. 2*b*). At each sample location, global positioning system (GPS) coordinates were taken (Table S1). The tethered pipe dredge was thrown from the kayak and retrieved, providing a shallow scoop of the surface mud. The collected mud was transferred into a labelled flat, shallow, plastic container and covered with estuarine water.

Sample processing and analysis

In the laboratory, the samples were left to settle and then examined under a stereomicroscope to observe the living *Trochammina*. These were picked and mounted on a cardboard slide. To obtain additional specimens, the mud fraction was

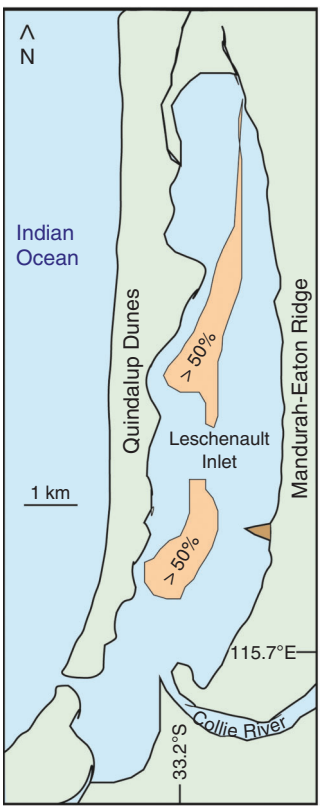

Fig. 3. Map of Leschenault Inlet. The area shaded in light brown illustrates where the mud content is >50% (based on Wurm and Semeniuk 2000, fig. 4).

decanted and the resultant sand residue examined. To illustrate the species, successive images were taken under reflected light using a biological microscope at a magnification of 10×, moving the specimen through the plane of focus. The resulting images were stacked and rendered using Helicon focus software (Helicon Soft). Scanning electron micrographs were taken of the umbilical sides and apertures of selected specimens. The specimens were dried at room temperature, mounted in required orientations using carbon tape on standard metal stubs, and coated with 10 nm of platinum before imaging. Samples and isolated specimens are curated in the Earth Science Museum at the University of Western Australia (Table S1).

DNA extraction, PCR amplification and sequencing

Single-cell DNA extractions were carried out for six specimens of the *Trochammina* from Leschenault Inlet (Fig. S1 of the Supplementary material). Living specimens mounted on cardboard slides and dried at room temperature were sent by express mail (over 5 days) to the University of Geneva, Switzerland at ambient temperatures and extracted upon arrival using guanidine lysis (buffer following the protocol detailed in Pawlowski 2000). The 3′ fragment of the small subunit ribosomal RNA *SSU* rDNA gene was amplified by semi-nested polymerase chain reaction (PCR) using primer pairs s14F3 (ACGCAMG-TGTGAAACTTG)–s20r (GACGGGCGGTGTGTACAA) for the first amplification and s14F1 (AAGGGCACCACAA-GAACGC)–s20r for the second amplification. This fragment represents the standard barcoding fragment in foraminifera (Pawlowski and Holzmann 2014). In total, 35 and 25 cycles were performed for the initial and the semi-nested PCR respectively, with an annealing temperature of 50°C for the first and 52°C for the second. The amplified PCR products were purified using a High Pure PCR Cleanup Micro Kit (Sigma–Aldrich). Sequencing reactions were performed using a BigDye Terminator cycle sequencing kit (ver. 3.1, Applied Biosystems). The newly acquired sequences were deposited in the EMBL/GenBank database (isolate and accession numbers are given in Table S2).

The obtained sequences were added to an existing database using the Muscle automatic alignment option as implemented in Seaview (ver. 4.3.3, see http://doua.prabi.fr/software/seaview; Gouy *et al.* 2010). The alignment of partial *SSU* rDNA sequences consists of 51 sequences, of which 6 were obtained for the present study. The alignment contains 1237 sites, with A, C, G and T nucleotide frequencies of 0.25, 0.19, 0.22 and 0.34 respectively.

A phylogenetic tree was constructed using maximum likelihood phylogeny (PhyML, ver. 3.0, see http://www.atgc-montpellier.fr/phyml/) as implemented in ATGC: PhyML (Guindon *et al.* 2010). An automatic model selection by smart model selection in PhyMl (SMS; Lefort *et al.* 2017) based on the Akaike information criterion (AIC) was used, resulting in a general time reversible + gamma distributed rate variation among sites + proportion of invariable sites (GTR+G+I) nucleotide substitution model being selected for the analysis. The initial tree is based on improved neighbour-joining (BIONJ; Gascuel 1997). Bootstrap values (BV) are based on 100 replicates.

Results

Morphological comparison to T. hadai

The Western Australian *Trochammina* specimens are morphologically similar to *T. hadai*. The holotype of *T. hadai* came from a water depth of 65 m off the Shinano River, Niigata Prefecture, Japan (Uchio 1962, pp. 387, 388, pl. 18, fig. 9a–c). The specimens in the present study (Fig. 4, 5) have a spiral side that is slightly convex, usually with a flat initial coil. They are strongly inflated on the umbilical side with a depressed umbilicus. Three whorls are present with four to six chambers, usually five, in the last whorl. The maximum test diameter is 0.17–0.55 mm in Leschenault Inlet and 0.37–0.48 mm in Collie River. The holotype of *T. hadai* has a similar test profile and has three whorls with five chambers in the last whorl; its maximum diameter is 0.52 mm. The wall of the Western Australian specimens is non-calcareous, agglutinated with clear angular quartz between 0.02 and 0.07 mm in size and rare black grains in a matrix of much finer quartz (Fig. 4–7). On the wall surface, quartz grains are positioned with flat surfaces tangential to the wall surface. The large grains do not overlap at the surface and the intervening spaces are filled by a matrix of smaller grains (Fig. 7*a*). In cross-section, the wall is a layer of closely packed grains that is several grains thick (15–20 μm), and in some sections large flatter quartz grains are positioned at the test surface (Fig. 7*b*). A similar wall structure is evident in the Japanese specimens of *T. hadai* (see Matsushita and Kitazato 1990, pl. 2; Nomura and Seto 1992, fig. 14, numbers 3a–c;

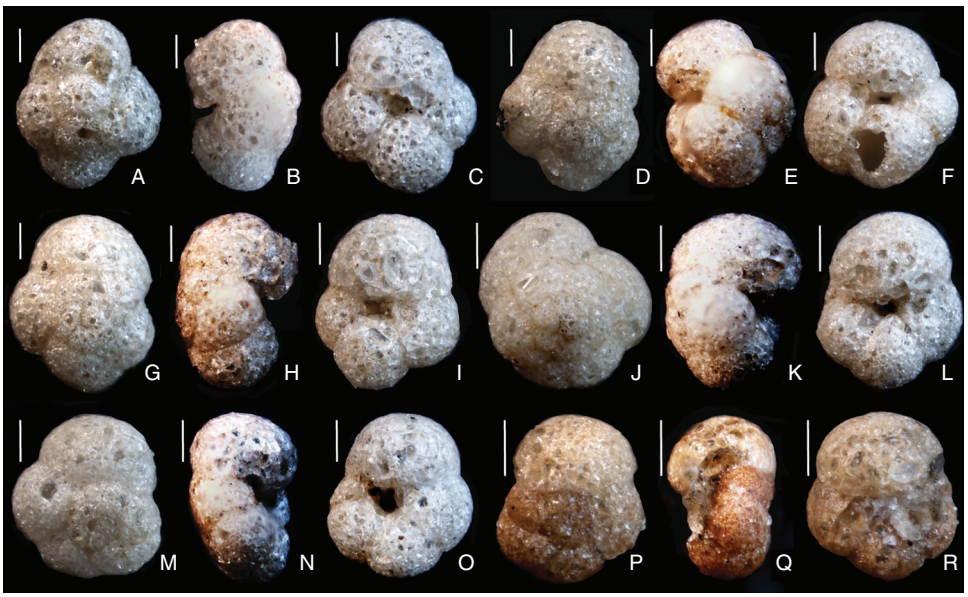

Fig. 4. Representative specimens of *Trochammina hadai* Uchio, 1962 from the Collie River. Scale bars: 100 µm. (*a–c*) UWA181330; (*a*) spiral side, (*b*) peripheral (apertural view), (*c*) umbilical side. (*d–f*) UWA181331; (*d*) spiral side, (*e*) peripheral (apertural view), (*f*) umbilical side. (*g–i*) UWA181332; (*g*) spiral side, (*h*) peripheral (apertural view), (*i*) umbilical side. (*j–l*) UWA181333; (*j*) spiral side, (*k*) peripheral (apertural view), (*l*) umbilical side. (*m–o*) UWA181334; (*m*) spiral side, (*n*) peripheral (apertural view), (*o*) umbilical side. (*p–r*) UWA181335; (*p*) spiral side, (*q*) peripheral (apertural view), (*r*) umbilical side.

Tsujimoto *et al.* 2006, fig. 6, numbers 7a–c). The test does not react with 2% HCl but disaggregates in bleach, indicating an organic cement. The colour of live specimens varies between light reddish-grey and reddish-brown (following the Munsell Soil Color Charts, see https://munsell.com/, accessed 4 November 2021). The holotype of *T. hadai* was described as reddish-brown to yellowish-brown (Uchio 1962, p. 387) but the mineralogical composition of the test and cement were not described. In the Western Australian assemblages, the aperture is a low arch. Its position varies from umbilical (e.g. Fig. 6*b*) to umbilical–extraumbilical, but only reaching to between half and three-quarters of the way to the periphery (e.g. Fig. 6*h*) to extraumbilical with a similar range to the periphery (e.g. Fig. 6*d*, *e*, *o*). In most specimens, a thin apertural lip borders the upper margin of the aperture. It is usually a very narrow ledge (e.g. Fig. 6*p*). Uchio (1962, p.388, pl.18, fig. a, b) described the aperture of the holotype of *T. hadai* as 'an arched slit at the base of the apertural face of the last chamber' and illustrated a very narrow lip in the hand-drawn figures.

In addition to Uchio's (1962) description of the type assemblage, morphological variation in Japanese *T. hadai* has been described and illustrated in Lake Hamana, Lake Nakaumi, Osaka Bay, Lake Saroma and Lake Kugushi (Matsushita and Kitazato 1990, p. 714, pl. 1, l a–c; Nomura and Seto 1992, p. 235, fig. 14, 3a, b, ?4a–c; Takata *et al.* 2006, p. 58, pl. 1, fig. l a–c; Tsujimoto *et al.* 2006, p 150, fig. 6, 7a–c, not 8a–c; Nomura and Kawano 2011, p. 50, fig. 9, 10). Matsushita and Kitazato (1990) bred *T. hadai* from Lake Hamana under controlled laboratory conditions. They found four different morphotypes based on the height of coiling and noted that test morphology varied with the seasons. In the Japanese specimens, there are usually four to five chambers in the final whorl (sometimes as many as seven) and an aperture that varies from an umbilical to extraumbilical position.

In a previous study of foraminifers from Leschenault Inlet (Revets 2000), *T. hadai*-like morphotypes were identified as *Paratrochammina challengeri* Brönnimann & Whittaker (1988, p. 43, 44, fig. 16 H–K) and *Paratrochammina simplissima* (Cushman & McCulloch, 1948; a new name for *Trochammina pacifica* var. *simplex* Cushman & McCulloch, 1939, p. 104, pl. 11, fig. 4 a–c). However, *P. challengeri* differs from *T. hadai* by its very large globigeriniform test (up to 2 mm diameter), and as such does not conform to the Leschenault specimens. *P. simplissima* also differs from *T. hadai* by its less inflated periphery and its more rapid increase in chamber size in the last whorl. The specimens recorded by Revets (2000) fall within the range of variability observed here for *T. hadai*. Ostrognay and Haig (2012, p. 143, fig. 6, 8–10) recorded the species in the Collie River as *Paratrochammina* sp. The present study found umbilical–extraumbilical variation in the apertural position and some variation in the apertural lip (Fig. 6). Because of this, the species is referred to *Trochammina* Parker & Jones, 1859 with type species, *Trochammina inflata* (Montagu, 1808; neotype designated by Brönnimann and Whittaker 1984). There seems to be no substantial difference between apertural shape, position and lip in Western Australian populations of *T. hadai* and *T. inflata* that would warrant a different generic assignment, although molecular comparisons outlined in the phylogenetic analysis presented below indicate that *Trochammina* is polyphyletic.

McGann *et al.* (2012, fig. 2, 2A–3C) illustrated the species from California and then, in Brazil, Eichler *et al.* (2018, pl. l A–K) described and illustrated *T. hadai*. In the North American

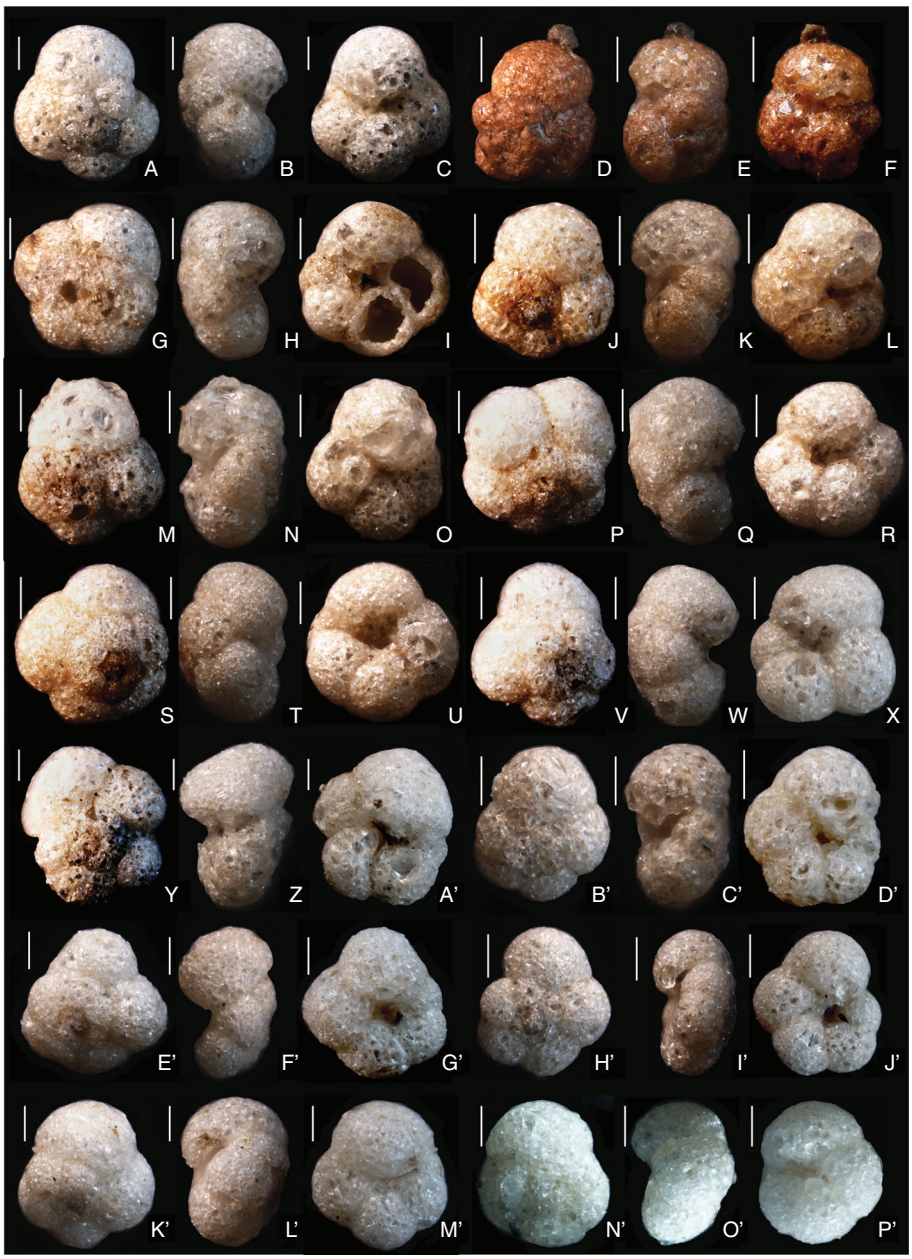

Fig. 5. Representative specimens of *Trochammina hadai* Uchio, 1962 from Leschenault Inlet. Scale bars: 100 µm. (*a–c*) UWA181315; (*a*) spiral side, (*b*) peripheral (apertural view), (*c*) umbilical side. (*d–f*) UWA181316; (*d*) spiral side, (*e*) peripheral (apertural view), (*f*) umbilical side. (*g–i*) UWA181317; (*g*) spiral side, (*h*) peripheral (apertural view), (*i*) umbilical side. (*j–l*) UWA181318; (*j*) spiral side, (*k*) peripheral (apertural view), (*l*) umbilical side. (*m–o*) UWA181319; (*m*) spiral side, (*n*) peripheral (apertural view), (*o*) umbilical side. (*p–r*) UWA181320; (*p*) spiral side, (*q*) peripheral (apertural view), (*r*) umbilical side. (*s–u*) UWA181321; (*s*) spiral side, (*t*) peripheral (apertural view), (*u*) umbilical side. (*v–x*) UWA181322; (*v*) spiral side, (*w*) peripheral (apertural view), (*x*) umbilical side. (*y–a′*) UWA181323; (*y*) spiral side, (*z*) peripheral (apertural view); (*a′*) umbilical side. (*b′–d′*); UWA181324; (*b′*) spiral side; (*c′*) peripheral (apertural view), (*d′*) umbilical side. (*e′–g′*) UWA181325; (*e′*) spiral side, (*f′*) peripheral (apertural view), (*g′*) umbilical side. (*h′–j′*) UWA18132; (*h′*) spiral side, (*i′*) peripheral (apertural view), (*j′*) umbilical side. (*k′–m′*) UWA181327; (*k′*) spiral side, (*l′*) peripheral (apertural view), (*m′*) umbilical side. (*n′–p′*) UWA181329; (*n′*) spiral side, (*o′*) peripheral (apertural view), (*p′*) umbilical side.

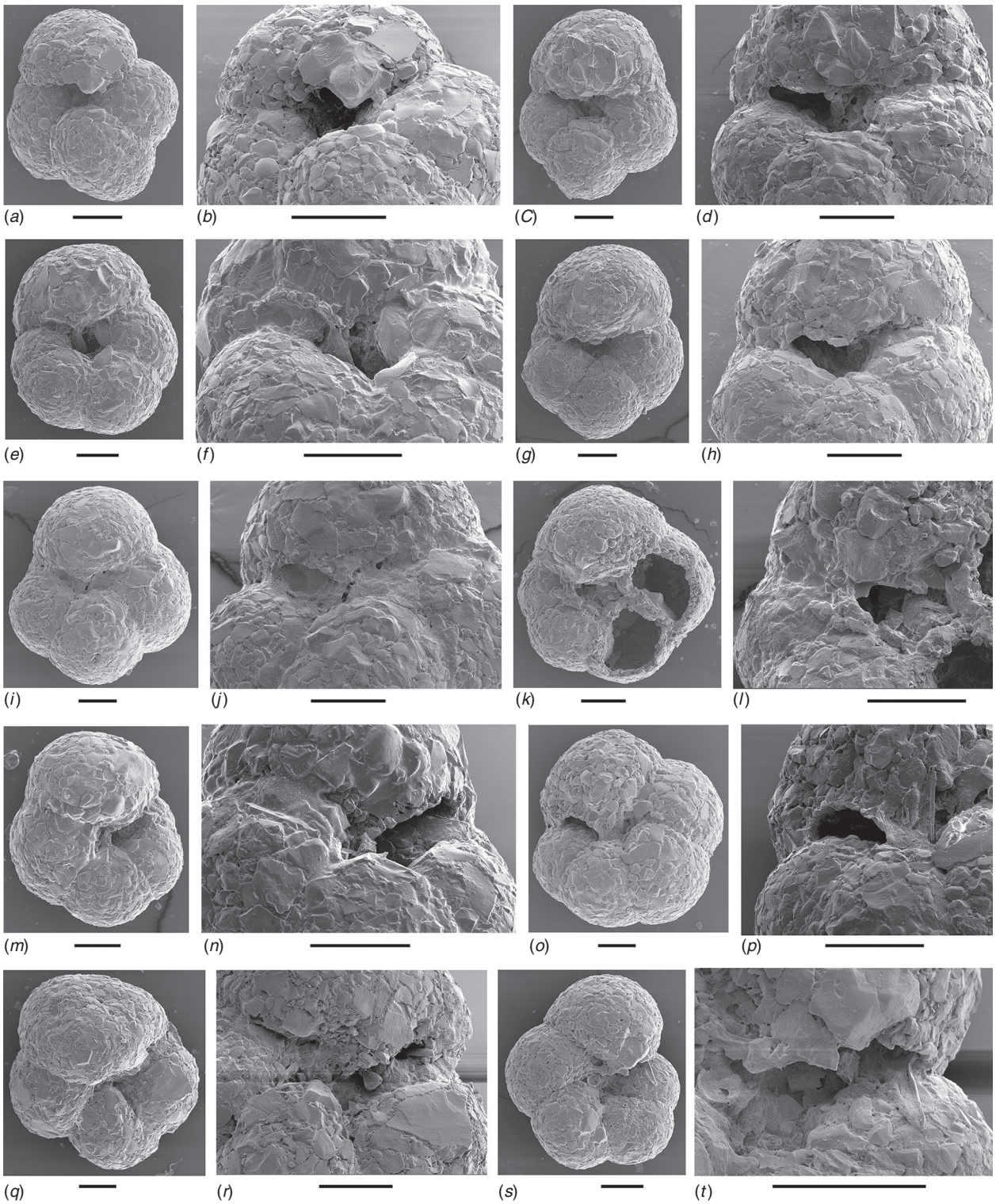

Fig. 6. Umbilical and enlarged apertural views (scanning electron micrographs) of selected specimens of *Trochammina hadai* Uchio, 1962 from Leschenault Inlet and the Collie River. The apertural views are tilted images. Scale bars: 100 µm. (*a*–*h*) Specimens from the Collie River: (*a*, *b*), UWA181330 (specimen in Fig. 4*c*); (*c*, *d*) UWA181332 (Fig. 4*i*); (*e*, *f*) UWA181334 (Fig. 4*o*); (*g*, *h*) UWA181333 (Fig. 4*l*). (*i*–*t*) Specimens from Leschenault Inlet: (*i*, *j*) UWA181315 (specimen in Fig. 5*c*); (*k*, *l*), UWA181317 (Fig. 5*i*); (*m*, *n*) UWA181318 (Fig. 5*l*); (*o*, *p*) UWA181320 (Fig. 5*r*); (*q*, *r*) UWA181323 (Fig. 5*a′*); (*s*, *t*) UWA181326 (Fig. 5*j′*).

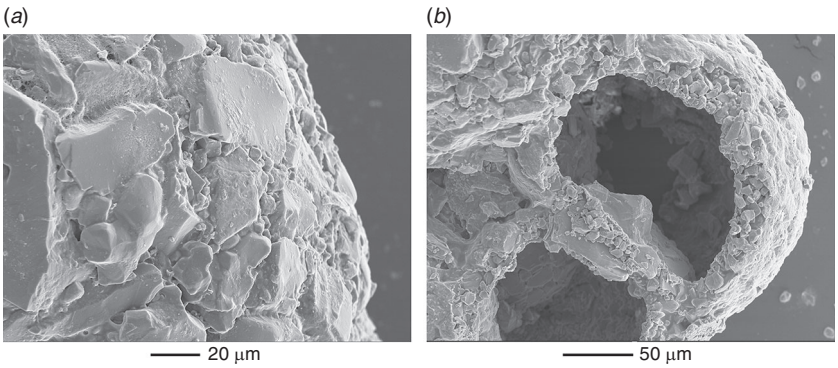

Fig. 7. Scanning electron micrographs showing the wall structure of *Trochammina hadai*. (*a*) Part of the wall surface of specimen UWA181332 showing smooth surfaces of quartz grains positioned in a pavement tangential to the wall surface. Smaller grains fill the interstices between larger grains. (*b*) View of a section through the broken wall in UWA181317.

assemblages, *T. hadai* has two to three whorls with usually five chambers in the last whorl that increase gradually in size, and an aperture that varies between umbilicate to extraumbilicate. In the Brazilian assemblages from São Paulo, *T. hadai* is mostly flat on its spiral side and has four strongly inflated chambers in the last whorl that increase proportionally in size as added. A specimen illustrated by Eichler *et al.* (2018, pl. 1, fig. a–c) has a narrow-arched aperture that is centred in the umbilicus and extends to an extraumbilical position. The aperture is bordered by a narrow lip. The initial whorls of the illustrated specimens in Eichler *et al.* (2018) have a flat initial coil on the spiral side. In one specimen (Eichler *et al.* 2018, pl. 1, fig. h), the last whorl is deflected slightly to the umbilical side, giving the appearance of a high trochospiral test. Faria *et al.* (2021) identified *Ammoglobigerina globigeriniformis* (Parker & Jones, 1865) as an invasive species in an estuary in southern Brazil south of São Paulo and indicated that it was the same as *T. hadai* identified previously in Brazil and California (see records discussed above). The specimen illustrated by Faria *et al.* (2021, fig. 2) seems morphologically closer to the type specimen of *T. hadai* (see above) than to the original specimens of *A. globigeriniformis* illustrated by Parker and Jones (1865, pl. 15, fig. 46, 47, pl. 17, fig. 96–98) and to the lectotype of this species illustrated by Loeblich and Tappan (1964, fig. 173, numbers 2a–c). We believe that *T. hadai* and *A. globigeriniformis* are separate species based on comparison of the type material.

Phylogenetic analysis

The phylogenetic tree is presented in Fig. 8. It contains 47 sequences of agglutinated foraminifera and is rooted in Reophacidae (*R. scorpiurus*, *R. spiculifer*, *R. curtus*, *R. piluliferarenulacea*). The obtained sequences cluster with *T. hadai*, supported by a BV of 100%. *T. hadai* is part of a well-supported clade (BV 86%) that contains *Srinivasania sundarbanensis*, *Eggerelloides scaber* and *T. pacifica*. Three other clades are present in the tree. One consists of *Bigenerina* sp., *Textularia gramen*, *Siphoniferoides* sp. and *Textularia agglutinans*, strongly supported by a BV of 96%. A second clade contains *Arenoparrella mexicana*, *Entzia macrescens*, *Haplophragmoides wilberti* and *Balticammina macrescens*, but is not supported by BV. A third clade, also without BV support, contains *Ammobaculites* sp., *Ammotium pseudocassis* and *Cribrostomoides* spp. Several species are branching separately: *Cyrea* spp., *Liebusella goesi*, *Spiroplectammina* sp., *Trochammina* sp. and *T. inflata*. Species represented by more than one sequence are all supported by a BV of 100%.

Comparison to modern Trochammina *known from other Western Australian estuaries*

In south-west Australian estuaries and inlets, trochamminid species referred to as *T. inflata*, *Trochammina ochracea*, *P. challengeri* and *P. simplissima* have been recognised (Table 1). *T. inflata* is the type species of *Trochammina* and is distinguished from *T. hadai* by its smooth, finely agglutinated wall and five to six chambers in the last whorl that are ovoid rather than globular in peripheral view. *T. inflata* is commonly found in abundance in marshes surrounding estuaries in Western Australia; by contrast, *T. hadai* seems confined to water deeper than 3 m and lives in estuarine mud. The species referred to by Revets (2000) as *T. ochracea* is a distinctive species with a compressed trochospire and multiple chambers in the last whorl (10 chambers in his figured specimen) and is better placed in *Lepidodeuterammina*. The *Paratrochammina* species identified by Revets (2000) in Leschenault Inlet are discussed above and are here considered to fall within the range of variability of *T. hadai*.

Comparison to modern estuarine Trochammina *known from elsewhere in Australia*

Studies in other parts of Australia have shown that *T. inflata* is widespread in Australian estuaries (Table 2). Other trochamminids illustrated include morphotypes attributed to *Trochammina sorosa* Parr (also referred to as *Portatrochammina*), *Paratrochammina stonei* and *Paratrochammina bartrami* Hedley, Hurdle & Burdett, 1967 (Table 2). *T. hadai* has not been recorded. *T. sorosa* was originally described from Maria Island, Tasmania, in 122–155 m deep water. Unlike *T. hadai*, it has a distinctly elevated spiral side, including the first whorl (Parr 1950, pl. 5, fig. 15–17). The inflated globular chambers resemble those of *T. hadai*. The aperture was not illustrated, but

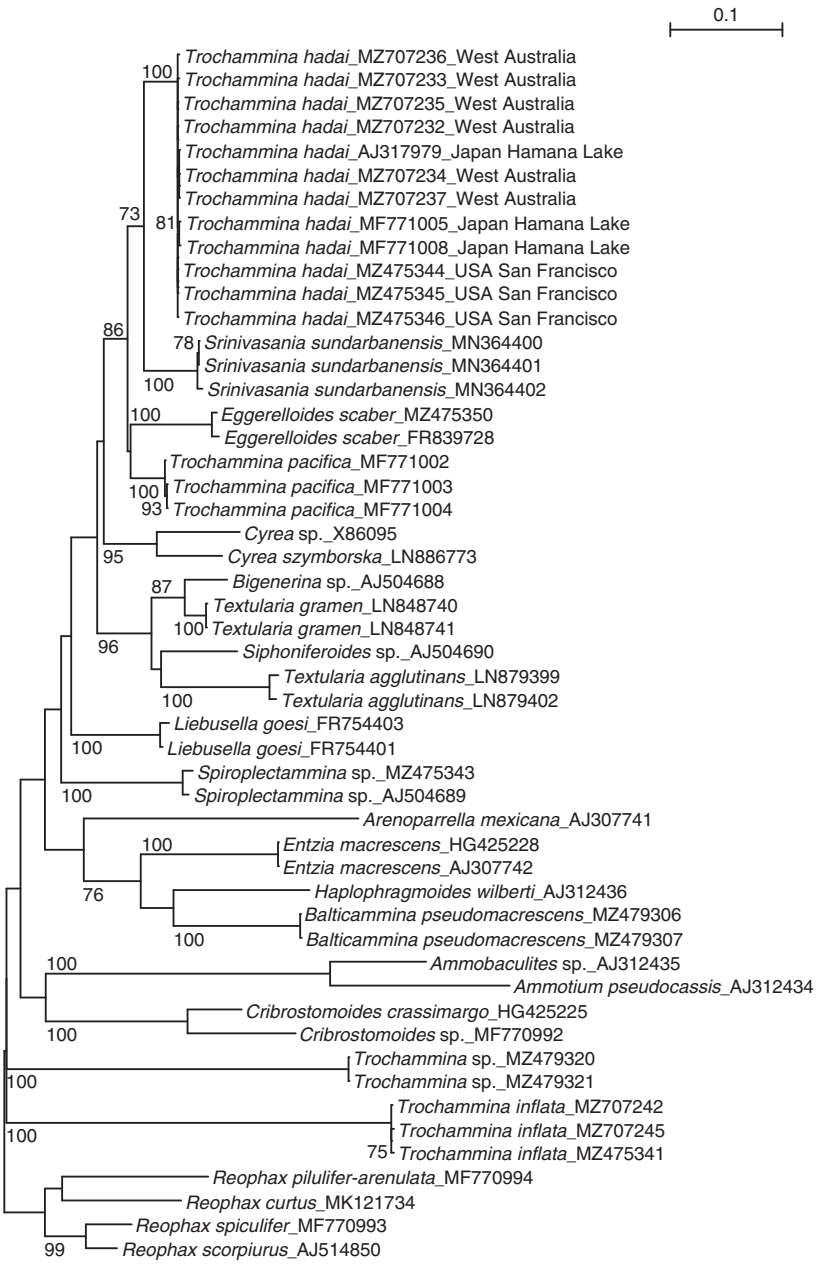

Fig. 8. PhyML phylogenetic tree based on the 3′ end fragment of the *SSU* rRNA gene, showing the evolutionary relationships of 51 agglutinated foraminiferal taxa. The tree is rooted in Reophacidae (*R. scorpiurus*, *R. spiculifer*, *R. curtus*, *R. pilulifer-arenulacea*). Sequenced specimens are identified by their accession numbers. Numbers at nodes indicate bootstrap values (BV). Only BV >70% are shown.

was described as a 'narrow opening at the base of the last chamber' (Parr 1950). The specimens illustrated by Bell and Drury (1992) and Bell (1996) also show a conical spiral side with inflated chambers, but the aperture was not illustrated. The New South Wales species referred to as *Portatrochammina sorosa* lacks the inflated chambers of Parr's (1950) species and does not belong within *Trochammina*. Specimens referred to *P. stonei* and *P. bartrami* have compressed chambers, in contrast with the inflated chambers of *T. hadai*.

Although not illustrated, the record of '*Trochammina globigeriformis*' by Narayan and Pandolfi (2010, table 1) from Moreton Bay in the Brisbane region of Queensland is intriguing. *T. globigeriniformis* (= type species of *Ammoglobigerina*; see Loeblich and Tappan 1987, p. 120) usually has just over three chambers in the last whorl and is mainly found in deep water. Its record in shallow Moreton Bay needs re-evaluation. The species recorded by Narayan and Pandolfi (2010) in the vicinity of the Port of Brisbane may represent *T. sorosa* or *T. hadai*.

Table 1. Trochamminid species previously illustrated from Western Australian estuaries and inlets

Species	Localities	Authors
Trochammina inflata (Montagu, 1808)	Oyster Harbour	McKenzie (1962, p. 126, pl. 1, fig. 8)
	Hardy Inlet	Quilty (1977, pl. 86, fig. 12)
	Murray River	Ostrognay and Haig (2012, p. 148, fig. 6)
Trochammina ochracea (Williamson, 1858)	Leschenault Inlet	Revets (2000, pl. 1, fig. 29–30) (Here regarded as belonging to *Lepidodeuterammina* Brönnimann & Whittaker, 1983)
Paratrochammina challengeri (Brönnimann & Whittaker, 1988)	Leschenault Inlet	Revets (2000, pl. 1, fig. 15–16) (Here regarded as *T. hadai*; see text)
Paratrochammina simplissima (Cushman & McCulloch, 1948)	Leschenault Inlet	Revets (2000, pl. 1, fig. 17–18) (Here regarded as *T. hadai*; see text)

Table 2. Trochamminid species illustrated from present-day estuarine or marginal marine environments elsewhere in Australia
NSW, New South Wales

Species	Localities	Authors
Trochammina inflata (Montagu, 1808)	Northern Spencer Gulf, South Australia	Cann *et al.* (2000, pl. 1, fig. k–m)
	Barwon River, Victoria	Parr (1945, pl. 8, fig. 4a, b)
	Lake Connewarre, Victoria	Bell (1995, fig. 2.10)
	Mallacoota Inlet, Victoria	Bell and Drury (1992, fig. 4.13)
	Little Swanport Estuary, Tasmania	Callard *et al.* (2011, pl. 1, fig. 16–19)
	Tuross Estuary and Coila Lake, NSW	Strotz (2003, pl. 1, fig. 12, 13)
	Lake Illawarra, NSW	Yassini and Jones (1989, fig. 10, 1–3); Yassini and Jones (1995, p. 192, fig. 61–63)
	St Georges Basin, NSW	Strotz (2012, fig. 4, 12–13)
	Smith's Lake, NSW	Strotz (2015, fig. 3M)
	Mangroves; Cocoa Creek, near Townsville, Queensland	Horton *et al.* (2003, p. 231, pl. 1, fig. 5a–d); Woodroffe *et al.* (2005, pl. 1, fig. 6a, b) (same specimen as illustrated by Horton *et al.* 2003)
Trochammina sorosa (Parr, 1950)	Mallacoota Inlet, Victoria	Bell and Drury (1992, fig. 4.12)
	Tamar River and Port Dalrymple, Tasmania	Bell (1996, p. 8, pl. 1, fig. l)
Portatrochammina sorosa (Parr, 1950)	St Georges Basin, NSW	Strotz (2012, fig. 4, 10–11)
	Tuross Estuary and Coila Lake, NSW	Strotz (2003, pl. 5, fig. 15–17)
Paratrochammina bartrami (Hedley, Hurdle & Burdett, 1967)	St Georges Basin, NSW	Strotz (2012, fig. 4, 14, 15(?))
	Smith's Lake, NSW	Strotz (2015, fig. 3N, O)

Habitat in Leschenault Inlet and Collie River

T. hadai and *Ammonia haigi* Hayward & Holzmann are the dominant species in the Leschenault Inlet samples. Also present are *Ammobaculites* sp., *Ammonia* cf. *ariakensis* Akimoto, *Ammonia* cf. *quiltyi* Hayward & Holzmann, *Cornuspira planorbis* Schultze, *Elphidium* cf. *advenum* (Cushman), *Elphidium* cf. *excavatum* (Terquem), *Elphidium gunteri* Cole, *Nonion subturgidum* (Cushman), *Quinqueloculina* cf. *littoralis* (Collins) and *Spiroloculina* sp. In the Collie River sample with rare *T. hadai*, *A. haigi* is dominant and is accompanied by *Elphidium* cf. *crispum* (Linnaeus), *E.* cf. *excavat*um, *E. gunteri*, *Elphidium* cf. *simplex* Cushman and *Quinqueloculina* spp., including *Q.* cf. *littoralis*, *Q. milletti* (Wiesner) and *Q.* cf. *seminula* (Linnaeus).

At the sampled localities in Leschenault Inlet and Collie River, marine mud forms the substrate of the middle boat channel at a water depth of between 3 and 5 m. It was in this mud that live *T. hadai* were found. Observations under the microscope suggest that the sediment surface layer consists of clotted mud that is flocculent (Fig. 9). As Manning *et al.* (2011) noted, flocculation plays a major role in mud sedimentation processes within estuaries. Below the flocculent layer is a denser, muddy sand with abundant ovoid faecal pellets with a mean length of 400 μm and, in places, fine to medium quartz.

Live foraminifers at the top of the flocculent layer include scattered *T. hadai* (Fig. 9*a*, *d*) and *Spiroloculina* sp. (Fig. 9*a*, *e*, *f*). *T. hadai* are easily recognisable by their bright pinkish-red to reddish-brown colour. The specimens were found living with the periphery of the test vertical and the aperture downward in the mud. Only one or two chambers of the last whorl were visible at the surface of the flocculent layer (Fig. 9*b–d*). Furthermore, live *Spiroloculina* sp. were also vertically suspended at the top of the flocculent layer with the aperture facing down (Fig. 9*a*, *e*, *f*). *Trochammina* and *Spiroloculina* were the only live foraminifers observed at the surface of the mud. The mode of life of these imperforate species, with the aperture facing downwards in the flocculent mud layer, differs from that suggested by Lipps (1983) for many foraminifers, which apparently keep their apertures above the sediment–water interface and protrude their pseudopodia into the free water column for suspension feeding.

The faecal pellets may belong to *Palaemonetes australis* Dakin, 1915, a shrimp first described in Western Australian

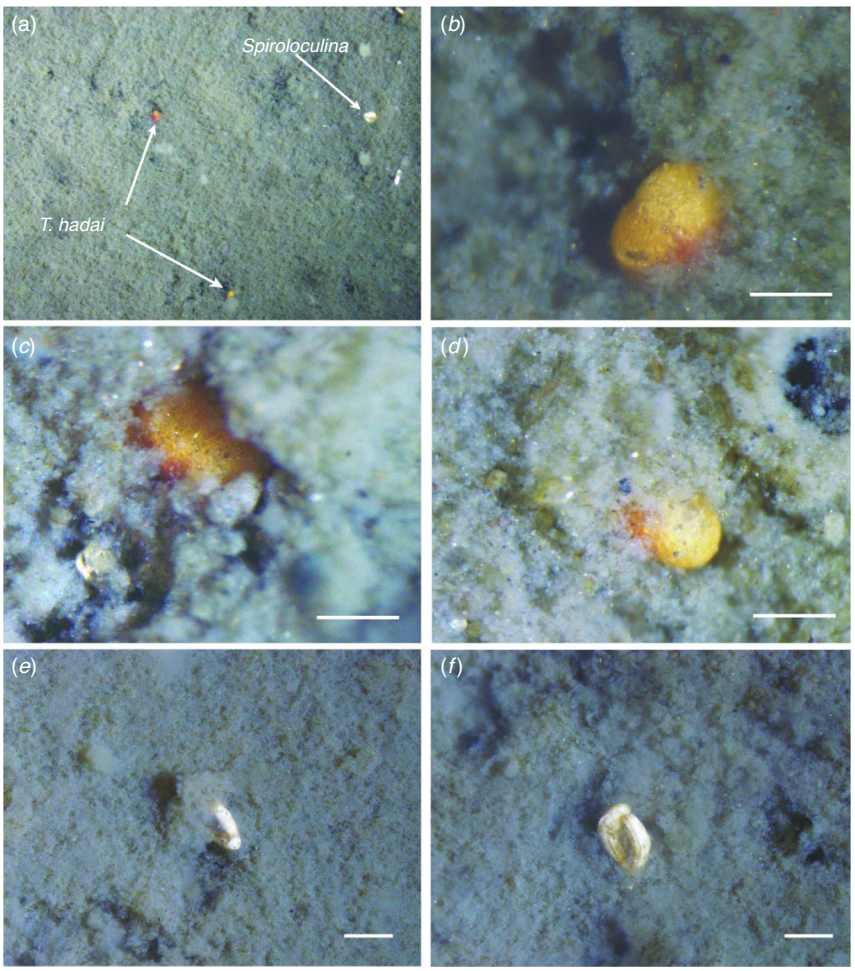

Fig. 9. (*a*) Living environment of *Trochammina hadai* and *Spiroloculina* sp. in the flocculent marine mud. (*b–d*) Life position of *T. hadai* showing one to three chambers of the last whorl exposed at the surface, with the peripheral margin vertically inclined so the aperture is downwards. (*e*, *f*) Life position of *Spiroloculina* sp. 1 showing the apertural end down in the flocculent mud. Scale bars: ~400 μm (*b–d*); ~200 μm (*e*, *f*).

estuaries, in the lower part of the Swan River. Its occurrence has been widely recorded in estuaries all along the south-west of Western Australian (Boulton and Knott 1984). *P. australis* can cope with radical salinity changes, varying from acid fresh water to full salt water, as part of seasonal variation (Bray 1976). In the flocculent layer of the mud, small shrimps were observed to reconstruct their burrows shortly after the mud was disturbed.

Discussion

Species identification and distribution in Australia

As demonstrated above, the Japanese *T. hadai* shares close morphological features with the species recorded here from Leschenault Inlet and the mouth of the Collie River. In recent years, molecular analysis has increasingly been used to confirm the identification of species from distant areas. The molecular signature of the Western Australian specimens corresponds to that of *T. hadai* from Japan and San Francisco (Fig. 8). The life mode of *T. hadai* described by Matsushita and Kitazato (1990) from specimens in Lake Hamana in Japan seems similar to that of Western Australian morphotypes. In Japan, *T. hadai* was shown to live mostly in the top centimetre of sediment on the floor of Lake Hamana in water depths <10 m. In Leschenault Inlet, *T. hadai* live partly submerged in sediment on the top of the flocculent marine mud in water that is ~5 m deep. In Shinano Bay, Japan, Uchio (1962) found the holotype of the species at a greater water depth (65 m), but the specimen may have been transported downslope out of the river during spring and summer freshwater outflow. High maritime activity by vessels navigating in and out of the river may also have contributed to its wide distribution into deeper waters adjacent to the river mouth. Because of close morphological similarity, a consistent molecular signature and ecological equivalence, the Western Australian morphotypes are identified as *T. hadai*.

T. hadai from Leschenault Inlet and the mouth of the Collie River has not been recorded elsewhere in south-west Australia, including Oyster Harbour and Kalgan River (McKenzie 1962), Hardy Inlet (Quilty 1977), Swan Estuary (Quilty and Hosie

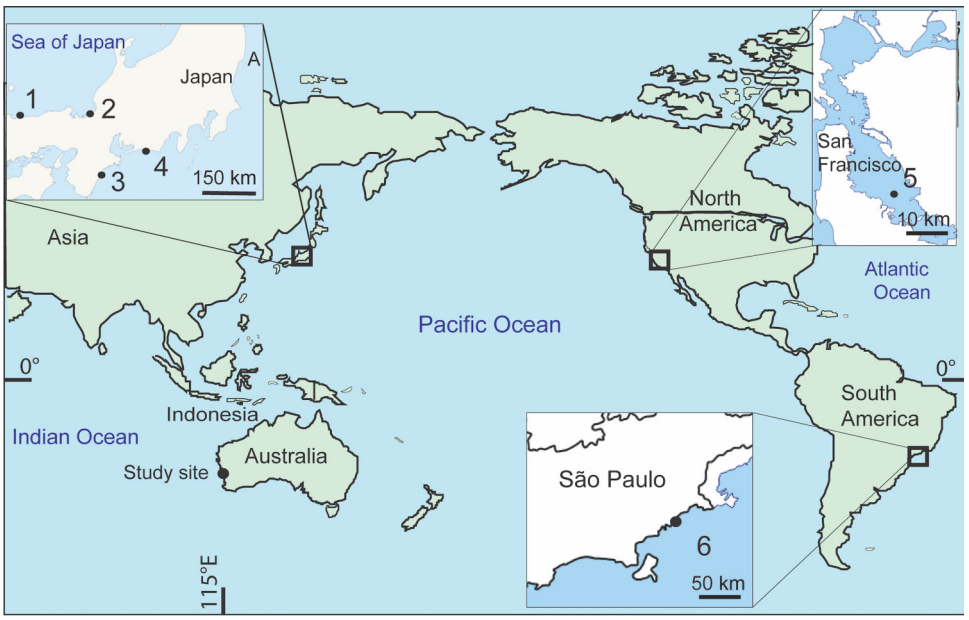

Fig. 10. Distribution of *Trochammina hadai* described as an endemic species in (1) Lake Nakaumi, western Japan; (2) Lake Kugushi, western Japan; (3) Osaka Bay, southern Japan; (4) Lake Hamana, eastern Japan; and invasive in (5) San Francisco Bay, California and (6) Flamengo Inlet, Ubatuba, Brazil.

2006) and the Murray and Serpentine rivers (Ostrognay and Haig 2012). It is absent from the Young River and Stokes Inlet, Jerdancuttup River, Phillips River, Wellstead Estuary, Hay and Denmark rivers, Franklin River, Walpole Inlet, Vasse River, Harvey and Peel inlets and the Canning, Moore, Irwin, Greenough, Chapman, Murchison and Gascoyne Rivers (D. W. Haig, J. H. Parker and C. M. Tremblin, pers. obs.; for locations, see Brearley 2005). Furthermore, the species has not been recorded in eastern Australian estuaries, although the record of a possibly similar species from Moreton Bay near Brisbane Port (Narayan and Pandolfi 2010) requires further investigation. Because it has not been recorded elsewhere in the estuaries and inlets around Australia, *T. hadai* is considered to be invasive in the Leschenault Inlet and Collie River.

Possible means of introduction

The continuous passage of marine vessels coming to Australia for commercial purposes may be a vector for the introduction of exotic species. Anthropogenic introductions are primarily due to cargo de-ballasting at the port of arrival (Firestone and Corbett 2005; Bailey 2015). Ballast water ensures the stability of the ship in transit. The vessel takes in ballast water as it unloads its cargo and discharges ballast water as it loads cargo. In Australia, 85% of ballast water discharged comes from the Asian region, of which more than 50% originates from Japanese ports (Kerr 1994). Japanese companies are the major exporters of woodchip from Australia. They use small vessels with shallow draughts for easy mobility and navigation in shallow water up to a depth of ~20 m (Hutchings 1992). Because of this, they are more likely to disturb and take in bottom sediment when loading ballast water.

T. hadai had been introduced into Leschenault Inlet and Collie River by at least May 1999 when samples were collected for the study of Revets (2000), in which he identified morphotypes that the present study considers to be *T. hadai*. No previous sampling for foraminifers in this estuarine system has been reported. The original estuarine mouth has been altered by the building of Bunbury Port. In 1837, Bunbury Harbour was one of the major stations, after Fremantle and Albany, involved in pelagic or shore-based whaling activities in south-west Australia (Gibbs 1995, 2000). The whale quest became financially lucrative when the local fisheries were supported by American and French whale ships in the late 1850s. A period of large exportation to the US of the prolific catch was reported between 1867 and 1869. However, growing conflicts between the Western Australian settlers and American whalers in Bunbury in the 1870s caused the foreign vessels to cease activity in Bunbury and to pursue whaling in King George Sound in Albany until 1888 (Gibbs 2000). Between 1945 and 1975, considerable changes were made to the Bunbury coastline for the new port. The original open mouth of the estuary was closed ('The Plug') in 1951 when the new entrance to Leschenault Inlet ('The Cut') was opened (Fig. 1; Brearley 2005, fig. 4-4). From the 1970s to the present day, Bunbury Port has become a worldwide maritime hub exporting coal, woodchip, plantation timber and agricultural engines (Agriculture Fisheries and Forestry Australia and Invest Australia 2003; Australian Bureau of Agricultural and Resource Economics and Sciences 2016). Japan is the dominant importer of woodchip from Bunbury (Agriculture Fisheries and Forestry Australia and Invest Australia 2003). The *Hoyo Maru* in 1982 was the first Japanese vessel recorded in Bunbury Harbour to transport woodchip back to Japan.

To confirm the mode of introduction of *T. hadai* into the estuarine system adjacent to Bunbury port, two aspects for further study should be pursued: (1) coring of the bottom

sediment in the estuary at sites where *T. hadai* is now abundant in order to establish the time of introduction of the species; and (2) sampling the ballast water and associated sediment from incoming ships in Bunbury Harbour to detect live foraminifers. Representatives of *T. hadai* will be readily identifiable in the sediment cores under microscopic examination and it should be possible to determine the date of introduction of the species using ^{204}Pb analysis of unaltered carbonate shells or organic plant material. Because *T. hadai* and other foraminifers are of sand size, they will be easily identified in ballast sediment.

This study demonstrates that foraminiferal species can be included among the invasive marine taxa in Australian estuaries. The presence of *T. hadai* may indicate a Japanese origin, presumably transported in ballast water sediment. *T. hadai* may also provide an indicator, identified by simple microscopic examination, for the detection of other more elusive exotic species derived from Japanese estuaries.

Data availability

Samples and isolated foraminiferal specimens are curated in the Earth Science Museum at the University of Western Australia (Table S1). The newly acquired molecular sequences were deposited in the EMBL/GenBank database (isolate and accession numbers are given in Table S2; photographs of specimens sequenced are shown in Fig. S1).

Conflicts of interest

The authors declare that they have no conflicts of interest.

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