

***Ammobaculites* (Foraminifera): living fossils in southern Western Australian estuaries**

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Abstract

Ammobaculites assemblages are recorded from five localities selected during reconnaissance sampling of shallow-water mud in the hyposaline reaches of Wellstead Estuary, Kalgan River, Frankland River, Walpole Inlet and Hardy Inlet. The aim of the study was to: (1) find potential living populations that in future could be the subject of biological, including molecular, investigations, and (2) describe the morphological variation in the recovered assemblages. In the geological record, *Ammobaculites* is one of the longest ranging multichambered genera within the Phylum Foraminifera, and is common in shallow-marine mudstone facies of Gondwanan/Australian interior basins of the Late Paleozoic and Mesozoic. The southern Western Australian estuarine *Ammobaculites* are compared to five main morphotypes recognized in this genus among the global estuarine fauna. The most common form here is referred to *Ammobaculites* sp. ex. gr. *A. exiguus*; and another species, although related to one of the morphotype groups, does not appear to have close counterparts elsewhere. Species confirmation and comparisons to morphologically close forms in eastern Australian and on other continents must await future rDNA sequence study. The modern *Ammobaculites* are also compared to Australian continental fossil assemblages from the Permian, Triassic and Cretaceous, in which there are close morphological analogues. The modern types are living fossils whose future study could contribute to resolution of questions concerning the geological longevity of the genus, the morphological and potential genetic conservatism within the genus, and how such similar morphotypes that thrive in isolated ephemeral mud in marginal-marine environments can disperse across regions and continents in both space and time.

KEYWORDS: Organic-cemented agglutinated foraminifers, Wellstead Estuary, Kalgan River, Frankland River, Walpole Inlet, Hardy Inlet, Permian, Triassic, Cretaceous

Manuscript received 4 May 2020; accepted 16 June 2020

INTRODUCTION

Foraminifera are present in almost all marine environments (Murray 1991) and also have a long evolutionary history (Pawlowski *et al.* 2003) that is represented in fossil assemblages throughout the Phanerozoic (see review by Haig *et al.* 2018, on the Western Australian record). The oldest preserved foraminifers belong to organic-cemented agglutinated groups that build their tests mainly from silicate grains. These conservative groups display minor changes in morphology over long periods of time (Haig & McCartain, 2010). Some genera that are present in modern Western Australian estuaries have close morphological counterparts that lived in Permian to Cretaceous restricted estuarine-like interior seas across Australia (Haig *et al.* 2018), and elsewhere extending back 350 million years to the Early Carboniferous (Mississippian). The genera include *Ammobaculites* Cushman selected by Haig (1979, 2004) to characterize foraminiferal assemblages of the ancient estuarine-like interior seas as the *Ammobaculites* Association.

To understand better the palaeoecology of fossil *Ammobaculites* and the implications this has for interpreting marine conditions within ancient interior

continental basins as far back as the Late Paleozoic, it is important to gain a greater knowledge of modern *Ammobaculites* in estuarine situations. This includes identifying the degree of morphological variation within a species; using molecular techniques to assist in species recognition and relationships among close morphotypes; and gaining better insights into the biology of the species (especially microhabitat preference, food sources, reproduction cycles, test construction, selectivity of agglutinated material, and means of dispersal). Such studies require considerable time and inputs from more than one laboratory. A prerequisite for these studies is locating suitable assemblages in modern estuaries that are easily accessible and are likely to contain numerous living representatives.

In a reconnaissance of estuaries along the southern coast of Western Australia during September 2019 and February 2020, abundant to common *Ammobaculites* were found at five sites (Fig. 1; Appendix 1). The aim of this paper is to document the assemblages found at these localities. As the first step to a better understanding of *Ammobaculites* in this region, the morphological variation among tests is recorded and illustrated, and possible specific relationships are discussed that could be tested by molecular techniques. Morphotypes are compared with those found among fossil assemblages and the reasons for any conservatism in morphology

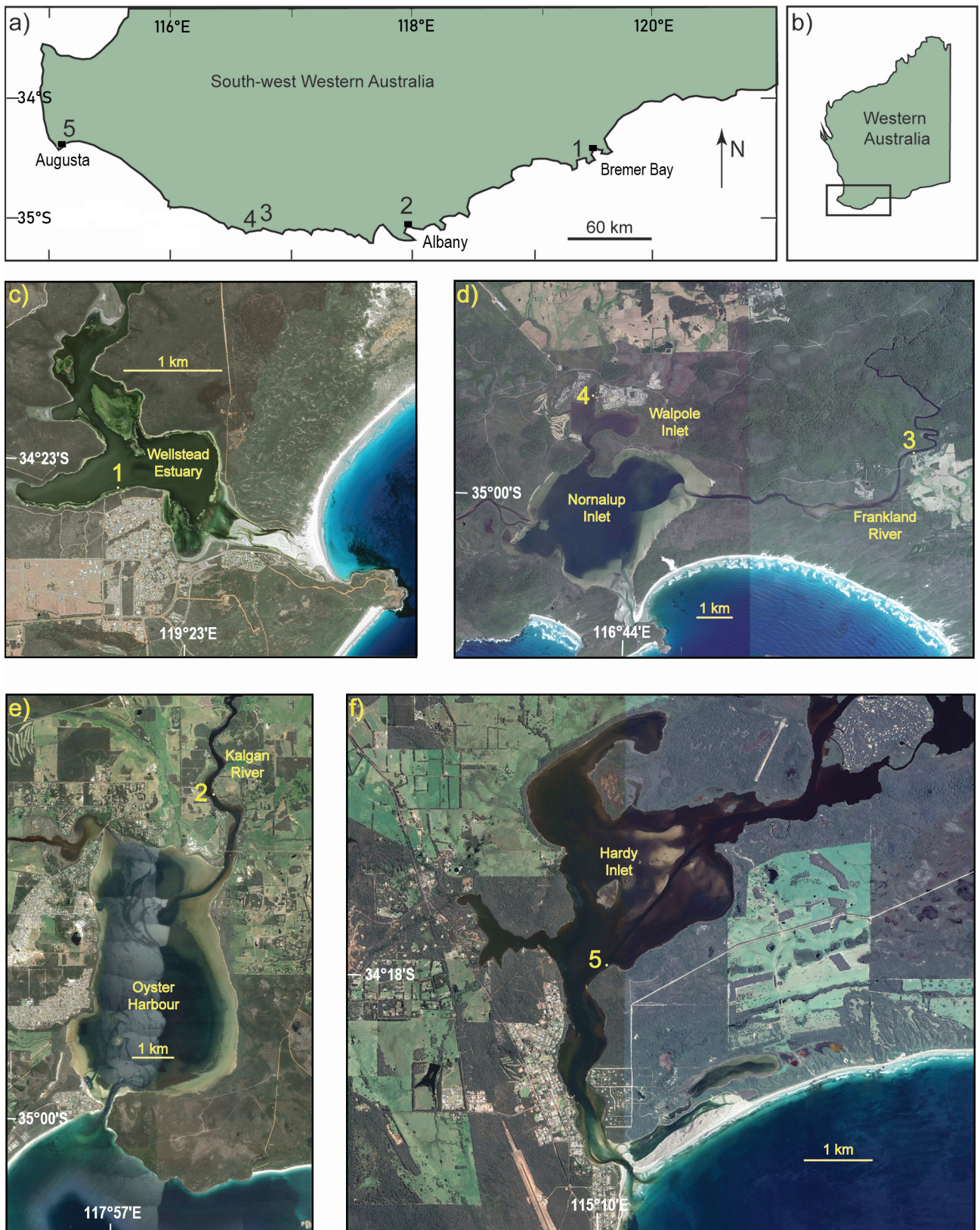


Figure 1. Google Earth images of sampled localities in (c) Wellstead Estuary, Bremer Bay, locality 1; (d) Frankland River, locality 3, and Walpole Inlet, locality 4; (e) Kalgan River, locality 2; and (f) Hardy Inlet, locality 5.

are canvassed. Future biological research, especially into microhabitat preference and means of dispersal, could support or negate such contentions.

SIGNIFICANCE OF AMMOBACULITES

Cushman (1910) established the genus *Ammobaculites* based on the agglutinated foraminifer *Spirolina agglutinans* d'Orbigny (1846) from the Middle Miocene, Badenian, of the Vienna Basin. D'Orbigny (1846, p. 137, 138, pl. 7, figs 10–12) did not designate a type specimen for *S. agglutinans*, but illustrated line drawings of a test in lateral, peripheral and terminal (apertural) views. These show a specimen, about 1 mm long, including a broad involute coil with 4.5 chambers exposed, and a straight uniserial final stage, composed of three almost cylindrical chambers, that is positioned eccentrically on the initial coil. The aperture is illustrated and described as an oblong opening. As indicated by Kaminski & Gradstein (2020), the lectotype chosen by Papp & Schmid (1985, p. 54, pl. 45, figs 7, 9) is valid rather than that selected by Loeblich & Tappan (1964, p. C241, fig. 151, nos 6a, b). The lectotype has features close to d'Orbigny's (1846) illustrated specimen apart from an additional uniserial chamber and a partly obscured aperture. With the provision of a lectotype for the type species, the name "*Ammobaculites*" is firmly established, but the concept of this genus and its other species is less than settled. According to Papp & Schmid (1985), *Ammobaculites agglutinans* comes from a deep-water calcareous clay facies where it is extremely rare.

In many descriptions of *Ammobaculites*, little information is given on wall structure, and in particular the type of cement that agglutinates the grains forming the test although this may be a critical character in suprageneric classification. Agglutinated foraminifera fall into two main groups based on cement (Loeblich & Tappan 1989) as outlined below.

(1) Organic (glycosaminoglycan)-cemented types (Hedley 1963; Towe 1967; Mendelson 1982; Langer 1992; Allen *et al.* 2000) usually agglutinate silicate grains (mainly quartz, but sometimes also an abundance of other silicate minerals as shown, for example, by Armynot du Châtelet *et al.* 2013). Occasionally carbonate fragments are included in the test where these are present in the substrate, as in the type specimens of *Ammobaculites agglutinans* (see Kaminski & Gradstein 2020).

(2) Carbonate-cemented species contain either calcite or aragonite as the cement (Murray 1973, Bender & Hemleben 1988, Robert & Murray 1995).

Among the phylogenetic relationships charted by Pawlowski *et al.* (2003, fig. 1) the few species analysed that belong to multichambered organic-cemented agglutinated taxa (*viz.* species of *Arenoparella*, *Haplophragmoides*, *Reophax*, *Spiroplectammina* and *Trochammina*) cluster together. These are distant from the carbonate-cemented agglutinated cluster of *Siphoniferoides*, *Textularia* and *Bigenerina*. The carbonate-cemented types probably had their origin among calcareous microgranular forms with single-layered walls that belonged to primitive Fusulinata in the Upper

Devonian and Lower Carboniferous, as suggested by the works of Piller (1990) and Rigaud *et al.* (2015).

The organic-cemented agglutinated types had a far longer evolutionary history than the carbonate-agglutinated foraminifera, and are known at least from the Early Cambrian (e.g. undisputed unilocular types described from West Africa by Culver 1991, 1994). Undisputed multilocular agglutinated foraminifera with organic cement (*viz.* *Reophax*) are known from at least the Middle Ordovician (Gutschick 1986). Although "*Ammobaculites*-like" morphotypes were described by Scott *et al.* (2003) from the Cambrian of Nova Scotia, their chamber arrangements are unclear and the identifications are unconvincing. Illustrated specimens identified as *Ammobaculites* from the Silurian by Kaminski & Perdana (2017) have ambiguous chambers and from the Devonian by Holcová & Slavik (2013) have uncertain wall composition, and require further evaluation. *Ammobaculites* was well established in shallow interior-sea faunas by the Mississippian (Early Carboniferous; Haig & McCartain 2010, appendix 3).

Ammobaculites is not included in Pawlowski & Holzmann's (2020) molecular database of foraminifera. As discussed by Haig & McCartain (2010, p. 375) it belongs within the Family Haplophragmoididae. The basic morphotype of initial coil followed by uniserial erect stage is also represented in unrelated groups of foraminifera: for example, *Endotabanella* and *Endotriadella* (see Vachard *et al.* 1994) among the Fusulinata; *Coscinospira*, *Monalysidium* and *Spirolina* (see Loeblich & Tappan 1987) among the Miliolata; and *Marginulinopsis* (see Loeblich & Tappan 1987) among the Nodosariata.

On continental platforms, carbonate-cemented agglutinated foraminifera are restricted to normal marine and hypersaline shelf seas (Murray 1973). Although organic-cemented agglutinated species are present here, their frequencies are usually much lower than calcareous foraminifera. The organic-cemented types become abundant in the hyposaline reaches of shallow estuaries and interior seas. In present-day environments, *Ammobaculites* assemblages are most common in estuarine organic-rich mud facies (Ellison 1972, Murray 1991), although species are also present on continental shelves and in the deep sea, albeit at much lower frequencies (Murray 1991, Holbourn *et al.* 2013, Kaminski & Gradstein 2020). Among the estuarine *Ammobaculites* reported globally, five broad morphotypes are recognized (Table 1). The type species, *A. agglutinans*, typifies morphotype A. From Australian estuaries (Tables 2, 3), six global species names have been used in identifications together with two new species based on local faunas, including one from Western Australia. Most of the published records of *Ammobaculites* in Australian estuaries contain few illustrations of the morphotypes present and variability is often poorly described.

Shallow interior seas that flooded over the Eastern Gondwanan–Australian continent from about 300 to 80 Ma contain abundant *Ammobaculites* faunas in organic-rich mudstone facies. The oldest *Ammobaculites* assemblages here are Permian (Crespin & Parr 1941; Parr 1942; Crespin 1945, 1947, 1958; Belford 1962, 1968, Ludbrook 1967; Scheibnerová 1982; Foster *et al.* 1985,

Table 1

List of *Ammobaculites* species names used in identification of global estuarine faunas (forms later transferred to *Ammotium* are not included). The species are assigned to broad morphotypes (A–E) to facilitate comparisons with the Western Australia *Ammobaculites*.

A. Species with an initial broad involute planispiral coil and a later cylindrical uniserial stage of lesser diameter positioned excentrically above coil.

Type species of *Ammobaculites*:

Spirolina agglutinans d'Orbigny, 1846, p. 137, pl. 7, figs. 10–12. [Lectotype: Papp & Schmid, 1985, p. 54, pl. 45, figs. 7, 9; plus one other specimen from type assemblage pl. 45, fig. 8]: Middle Miocene, Vienna Basin, Austria.

Other species:

Ammobaculites? *barwonensis* Collins 1974, p. 9, pl. 1, figs 3a, b (holotype): Barwon estuary (only at type locality 56-C9, “muddy sand, right bank of Barwon River on N. boundary of Area 56” ~ 38.2647°S, 144.5083°E).

Ammobaculites exiguus Cushman & Bronnimann 1948, p. 38, pl. 7, figs 7a, b (holotype), 8 (paratype): Shoreline (0–3 m), Gulf of Paria, Trinidad.

Ammobaculites formosensis Nakamura 1937, p. 14, p. 133, pl. 10, figs 1a, b: Neogene (? Pliocene), Taiwan. [Fide Ellis & Messina 1945 et seq.]

Ammobaculites neusensis Grossman 1967, p. 49, pl. 1, figs 1, 6: Neuse, Pamlico and Punga rivers and Pamlico Sound, North Carolina.

Ammobaculites pamlicoensis Grossman 1967, p. 48, pl. 1, figs 12, 16, 17: Neuse, Pamlico and Punga rivers and Pamlico Sound, North Carolina.

B. Species with cylindrical uniserial portion positioned centrally above initial involute planispiral coil

Ammobaculites balkwilli Haynes 1973, p. 25–27, pl. 2, figs 2, 3; pl. 29, figs 5, 6; text-fig. 4, nos 1 (holotype), 2–5 (paratypes): Dovey Marshes, Cardigan Bay, Wales.

Ammobaculites josephi Acosta 1940, p. 271, pl. 49, figs 2 (paratype), 7 and 10 (holotype): Gulf of Santa Maria, Cuba [Fide Ellis & Messina 1945 et seq.]

Ammobaculites villosus Saidova 1975, p. 93, pl. 25, fig. 12 (holotype): 156 m water depth off west coast of South Island, New Zealand [fide Ellis & Messina 1945 et seq.]

C. Species with broad initial involute coil and excentric variably compressed and slightly to distinctly flabelliform uniserial stage, with elongate terminal aperture.

Ammobaculites amarus Hada 1957, p. 30, 31, text-figs. 10a–d: Hijirippu and Mochirippu brackish-water lakes, southeast Pacofoc coast of Hokkaido.

Ammobaculites dilatatus Cushman & Bronnimann 1948, p. 39, pl. 7, figs. 10a, b (holotype, 11 (paratype): Shoreline (0–3 m), Gulf of Paria, Trinidad.

Ammobaculites directus Cushman & Bronnimann 1948, p. 38, pl. 7, figs 3a, b (holotype), 4 (paratype): Shoreline (0–3 m), Gulf of Paria, Trinidad.

Ammobaculites diversus Cushman & Bronnimann 1948, p. 38, pl. 7, figs 5a, b (holotype), 6 (paratype): Shoreline (0–3 m), Gulf of Paria, Trinidad.

Ammobaculites exilis Cushman & Bronnimann 1948, p. 39, pl. 7, figs 9a, b (holotype): Shoreline (0–3 m), Gulf of Paria, Trinidad.

Lituola (*Haplophragmium*) *foliaceum* Brady 1881, p. 50. [Brady 1881 p. 45 inferred that figures of this species were to be included in a larger monograph. This was published as *Haplophragmium foliaceum*; Brady 1884, p. 304, 305, pl. 33, figs. 20–25; deep sea, Atlantic, Pacific, Southern oceans. [Placed in *Ammomarginulina* by Barker 1960, p. 68; and to *Eratidus* by Jones 1994, p. 40; this is the type species of *Eratidus* Saidova 1975]

Ammobaculites morenoi Acosta 1940, p. 272, pl. 49, figs 1 (paratype), 3 and 8 (holotype): Port of Santa Maria, Cuba [Fide Ellis & Messina 1945 et seq.]

D. Species with partially evolute initial coil and cylindrical to slightly compressed uniserial stage excentric on coil

Ammobaculites crassus Warren 1957, p. 32, pl. 3, figs 5 (holotype), 6–7 (paratype): [with slightly oblique sutures; ? transitional to *Ammotium fragile* Warren 1957, pl. 1, figs 14 (paratype), 15 (holotype)]: interconnected lakes in Louisiana coastal marshlands.

Ammobaculites subcatenulatus Warren 1957, p. 32, pl. 3, figs 11 (holotype), 12–13 (paratype): interconnected lakes in Louisiana coastal marshlands.

E. Species with broad planispiral coil, and only slight development of a compressed excentric uniserial stage

Ammobaculites howelli Acosta 1940, p. 273, pl. 49, fig. 11 (holotype): Port of Santa Maria, Cuba [Fide Ellis & Messina 1945 et seq.]

Conkin & Conkin 1993; Palmieri 1993, 1994; Haig 2003, 2004, 2018; Dixon & Haig 2004; Haig *et al.* 2017, appendices 11, 13, 15, 17, 19; Haig & Mory 2016). Triassic *Ammobaculites* species have been described (Heath & Apthorpe 1986; Apthorpe 2003; Haig & McCartain 2010) from mudstone facies in axial basins of the East Gondwana interior rift basins discussed by Haig *et al.* (2018) and the Papuan Basin (Kristan-Tollmann 1988, 1990). No *Ammobaculites* have been described from the Jurassic of Australia because few foraminiferal studies have been published on the marine Jurassic that is

confined mainly to the New Guinea margin, and the East Gondwana Interior Rift and successor basins. A broad representation of the genus is present in mid-Cretaceous marine mudstone facies that flooded vast areas of the Australian continent (Crespin 1944, 1953, 1963; Taylor 1964; Ludbrook 1966; Scheibnerova 1976; Haig & Barnbaum 1978; Haig 1980, 1981, 2004, 2005; Jones & Wonders 1992; Haig & Lynch 1993; McLoughlin *et al.* 1995; Holbourn & Kaminski 1997; Campbell & Haig 1999; Howe *et al.* 2000; Taylor & Haig 2001; Dixon *et al.* 2003; Haig *et al.* 2004; Stilwell *et al.* 2012).

Table 2*Ammobaculites* previously illustrated from Western Australian estuaries and inlets.

<i>Ammobaculites agglutinans</i> (d'Orbigny)	McKenzie 1962, p. 119, pl. 1, fig. 4; Oyster Harbour and lower King River. Quilty 1977, p. 89, fig. 10; Hardy Inlet, lower Blackwood River. Quilty & Hosie 2006, pl. 1, fig. 1; Swan River. Melville Water.
<i>Ammobaculites exiguus</i> (Cushman & Bronnimann)	Ostrognoy & Haig 2012, fig. 5, nos. 13, 20; Collie, Murray, Serpentine rivers.
<i>Ammobaculites villosus</i> Saidova	Reverts 2000, pl. 1, figs. 2–3; Leschenault Inlet.
<i>Ammobaculites yardiensis</i> Parker	Parker 2009, p. 13, figs. 10a–h, 11a–d; near-shore lagoon, Mangrove Bay, Ningaloo Reef.
<i>Ammobaculites</i> sp. of Quilty 1977	Quilty 1977, p. 89, fig. 11; Hardy Inlet, lower Blackwood River.
<i>Ammobaculites</i> sp. of Reverts 2000	Reverts 2000, pl. 1, fig. 1; Leschenault Inlet.

Table 3Illustrated records of *Ammobaculites* and some related morphotypes published from elsewhere in Australia with species nomenclature as originally used.

<i>Ammobaculites exiguus</i> (Cushman & Bronnimann)	Bell 1978, p. 134–135, fig. 4; Limeburners Bay, Victoria. Bell 1996, pl. 1, fig. b; River Tamar, Tasmania. Bell & Drury 1992, fig. 4.10; Mallacoota Inlet, Victoria. Strotz 2003, p. 169, pl. 1, fig. 5; Tuross Estuary and Coila Lake, New South Wales. Strotz 2012, fig. 4(nos. 5–6b), Appendix B, p. 4, 5; St Georges Basin, New South Wales. Strotz 2015, fig. 3E; Smiths Lake, New South Wales.
<i>Ammobaculites barwonensis</i> Collins locality.	Collins 1974, p. 9, pl. 1, figs. 3a, b (sp. nov. as <i>Ammobaculites</i> ?); Barwon River estuary, one Apthorpe 1980, p. 225, pl. 28, figs 4, 5, 10–13; Gippsland Lakes, Victoria. Bell & Drury 1992, figs. 4.7–4.9; Mallacoota Inlet, Victoria. Bell, 1995, p. 229, fig. 2.2; Lower Barwon River and Lake Connemare, Victoria. Bell 1996, pl. 1, fig. k; River Tamar, Tasmania. Cann et al. 2000, pl. 1, figs. f, g; northern Spencer Gulf, South Australia. Strotz 2003, p. 169, pl. 1, figs. 6, 7; Tuross Estuary and Coila Lake, New South Wales.
<i>Simobaculites barwonensis</i> (Collins)	Strotz 2012, fig. 4, nos. 7a, b, Appendix B, p. 5, 6; St Georges Basin, New South Wales. Strotz 2015, fig. 3F; Smiths Lake, New South Wales.
<i>Ammobaculites reophaciformis</i> Cushman	Cann et al. 1988, figs. 9a, b; Gulf St. Vincent, South Australia (possibly the agglutinated miliolid <i>Nubeculina advena</i> Cushman 1924, p. 53, pl. 19, figs. 1–4). Cann et al. 2000, pl. 1, figs. c–e; hypersaline estuary, Far Northern Spencer Gulf, South Australia.
<i>Ammobaculites agglutinans</i> (d'Orbigny)	Apthorpe 1980, pl. 28, fig. 9; Gippsland Lakes, Victoria. Yassini & Jones 1989, p. 255, Fig. 10, no. 5; Lake Illawarra, New South Wales. Yassini & Jones 1995, p. 70, 71, figs. 46–48, 50; "coastal lagoons and muddy facies of the inner shelf", south-eastern Australia; specific localities not given.
<i>Ammobaculites subcatenulatus</i> Warren	Albani 1978, p. 364, 365, fig. 6E; Broken Bay estuary, New South Wales. Yassini & Jones 1995, p. 71, figs. 44, 45; "strictly coastal lagoons", south-eastern Australia; specific localities not given.
<i>Ammobaculites foliaceus</i> (Brady)	Albani 1978, p. 364, described but not figured; Broken Bay estuary, New South Wales. Yassini & Jones 1989, p. 255, fig. 10, no. 4; Lake Illawarra, New South Wales. Yassini & Jones 1995, p. 71, figs. 51–53; "coastal lagoons and muddy facies of the inner shelf", south-eastern Australia; specific localities not given.
<i>Ammobaculites</i> sp. of Yassini & Jones, 1989	Yassini & Jones 1989, p. 255, fig. 10, no. 6; Lake Illawarra, New South Wales.

Fossil *Ammobaculites* are most common in mud facies of the large interior seas of the Cretaceous (Aptian–Albian) and the shallow marginal-rift seas of the East Gondwana interior rift system in the Western Australia Permian (Haig *et al.* 2017, 2018) and coeval shallow-water basins in eastern Australia (Crespin 1958; Palmieri 1994). As indicated by Haig (1979, 2003, 2004) the interior seas had estuarine-like water conditions with periods of hyposalinity

and water-column stratification. The foraminiferal assemblages in these facies were characterized as the *Ammobaculites* Association by Haig (1979, 2004) who recognized equivalents in the vast interior basins of North America (particularly Mississippian and Cretaceous) and Western Siberia (Cretaceous). In contrast to the fossil assemblages from the estuarine-like Australian interior-seas, *Ammobaculites* species are a rare component of foraminiferal assemblages in the more open-marine

mud facies of the Permian and Triassic axial basins in the East Gondwana Interior Rift, and in the open-marine parts of the continental margin basins of the Cretaceous. These areas are characterized by carbonate-cemented agglutinated foraminifers and greater diversity in the overall foraminiferal fauna. The broad pattern of the fossil distributions parallels that noted by Murray (1973) for modern assemblages, except there are fewer large shallow interior seas in humid climatic belts at present than during some intervals in the past when global sea-level was higher and continents were in different tectonic configurations.

LOCALITY DETAILS OF STUDIED ASSEMBLAGES

Studied assemblages of *Ammobaculites* were selected from one site each in five different estuaries/inlets (Fig. 1, Appendix 1). Samples of dark mud or sandy mud were collected using a small pipe dredge designed to scrape a veneer of sediment from the estuarine floor. The dredge was deployed from the shoreline or from a kayak or dinghy. Samples of the mud were washed over a 125- μ m mesh sieve and the residue dried for inspection under a stereomicroscope. Images of representative specimens were taken in reflected light using focus stacking and rendering techniques.

All samples were from estuaries or connected rivers well away from the estuarine mouths. No evidence was observed of reworked foraminifers from mid-Holocene highstand deposits (up to ~ 2 m above present sea-level; Baker *et al.* 2001) that are common in the lower reaches of Western Australian estuaries, or from tests derived from the present-day to Pleistocene wind-blown coastal sand dunes in the region. The samples were not immersed in rose-bengal to detect living specimens because staining of protoplasm within the opaque thick agglutinated tests of genera such as *Ammobaculites* is difficult to observe. Living specimens will be found most easily by observing collected mud in aquaria. The colour and preservation of the tests recovered during this study, all with brown organic material incorporated in their walls, suggests that these were either alive or recently dead.

Of the five estuaries/inlets sampled (Appendix 1), the only previous record of foraminifers, including *Ammobaculites*, is from Hardy Inlet (Quilty 1977). McKenzie (1962) recorded the distribution of foraminifers, including rare *Ammobaculites*, in Oyster Harbour into which the Kalgan River flows (Fig. 1e). Comprehensive sampling has not been done at the other sites.

1. Wellstead Estuary

Wellstead Estuary at the mouth of the Bremer River (Fig. 1c) is often closed by an extensive sand bar for many years (as shown in the 2018 Google Earth image, Fig. 1c), and at other times it is open to incursions of normal-salinity sea water. The salinity is highly variable depending on closure of the estuary and seasonal rainfall conditions in the small catchment (Brearley 2005). At the time of collection of the studied assemblage in February 2020, the estuary mouth was closed and water levels within the estuarine basin were very low, much less

than the normal 1m water depth. The studied sample (Appendix 1) was taken from the edge of a modern serpulid reef that parallels the shore about 30 m from the shoreline. The water depth at the site was about 10 cm and the substrate consisted of black organic-rich mud. Besides the foraminifers, other components of the washed sand residue from the mud were abundant ostracods, fragments of serpulid tubes, rare bulbous gastropods, rare charophytes, very rare thin-walled bryozoans, and abundant faecal pellets. Salinity was not measured. This site is about 2.5 km from the river mouth, when it is open. In early summer after a winter influx of freshwater and opening of the river mouth it would have salinities approaching normal-marine conditions in contrast to hypersaline conditions (up to 70 psu) when the estuary mouth is closed and water levels are low due to dry conditions (Brearley 2005).

2. Kalgan River

The Kalgan River flows into Oyster Harbour (Fig. 1e) and is microtidal in the reach of the river that includes the studied assemblage (Brearley 2005). At the collecting site (2 on Fig. 1e; Appendix 1) the salinity was 33 psu during an interval of very low rainfall for the region. Under normal weather conditions the salinity would be lower just after winter rains but with marked seasonal changes through the year (Brearley 2005). The sand fraction of the studied mud sample is mainly quartz. Rare gastropod and bivalves together with some indeterminate mollusc debris are also present.

3. Frankland River

The Frankland River drains some of the highest rainfall parts of southern Western Australia (McFarlane *et al.* 2020) and discharges a high volume of fresh water, especially in winter (Brearley 2005). It drains into the large Nornalup Inlet, which has a narrow permanent opening to the sea (Fig. 1d). The studied *Ammobaculites* assemblage comes from muddy sand facies at site 3 about 6.3 km upstream from the mouth of the river into Nornalup Inlet (Table 1). Salinity at the time of collection was 5 psu. The sand fraction of the sediment is mainly quartz but also includes bivalves and gastropods.

4. Walpole Inlet

The small, shallow Walpole Inlet situated at the north-west edge of Nornalup Inlet (Fig. 1d) has only a small local-river input and a salinity (15 psu) higher than the Frankland River (Table 1). The studied assemblage comes from near the shore in the restricted northern part of the inlet. The sand fraction of the mud contains mainly quartz, but also includes large centric diatom frustules and fragments of bivalves and gastropods.

5. Hardy Inlet

Hardy Inlet (Fig. 1f) is the estuary for the Blackwood River and receives the largest volume of freshwater compared to the input into any of the other south coast estuaries because of a high-rainfall hinterland (Brearley 2005; McFarlane *et al.* 2020). Salinity changes seasonally with the greatest influx of freshwater during winter, and with a saltwater bottom wedge advancing up the lower estuary in summer. The studied assemblage was

collected in September 2019 (Appendix 1). No salinity measurement was made at the time of collection. Salinity profiles for April (early Autumn), May (late Autumn), June (Winter) and October (Spring) 1974 presented by Brearley (2005) suggest that at this shallow-water site salinity is probably variably hyposaline throughout the year. The sand fraction of the studied sediment sample consists mainly of quartz. Bivalve fragments are rare.

AMMOBACULITES ASSEMBLAGES

Illustrations of the five assemblages discussed here (Figs 2–6) show considerable variability within each assemblage and among assemblages and highlight difficulties in making taxonomic discrimination based solely on test morphology. Some the variation can be attributed to different growth stages of individuals. Other aspects of difference are due to the types and grain sizes of particles used in construction of the test. There also may be different generations, reflected in morphology, in the complex reproductive cycles of species present. Measurements based on the illustrated specimens also show the variability present (Table 4). Broad morphotypes (A–E) recognized among global estuarine *Ammobaculites* (Table 1) are used here in initial designation of the specimens found in the south-coast estuaries.

1. Wellstead Estuary

Almost all of the specimens of *Ammobaculites* found at site 1 (Fig. 2) belong to global morphotype A (Table 1) that is characterised by an erect uniserial stage positioned excentrically above a broad involute planispiral initial stage. The degree of excentricity varies between extremes as illustrated by the specimen shown in Figure 2o (extreme morphotype A) and tests shown in Figures 2f, l and r (which approach morphotype B). Specimens with very limited development of a uniserial stage (Fig. 2a–c) are regarded as juveniles based on the diameter of the planispiral coil being within the range of other specimens (Table 4).

Chambers in the initial coil are obscure with sutures mainly flush or slightly depressed. The last whorl has 6–7 chambers; earlier whorls are hidden. The coil has a consistent narrow and moderately deep umbilicus. In some tests, the axis of the planispiral coil varies slightly during growth and the initial stage in these forms is asymmetric (e.g. Fig. 2o, p). This feature is indicative of slight instability in the planispiral mode of coiling and is not suitable for taxonomic discrimination.

Up to six chambers form the uniserial stage. The final chambers in the series are cylindrical with variable inflation of the sides and terminal face. The initial one or two chambers of the series are compressed similar to those in the planispiral coil. The uniserial stage shows little difference in width along its length. The sutures between the final chambers are usually depressed. There is a gradual increase in chamber size during growth, to a maximum test length of 0.66 mm (at stage with six uniserial chambers), but adult chambers are usually broader than high.

The aperture is terminal in the uniserial stage. In final cylindrical chambers it is circular (Fig. 2e), but in the first

chamber of the uniserial stage it may be oblong (Fig. 2d). The apertural outline is variably irregular due to protruding agglutinated grains.

The wall is pale grey when dry, but under water is pale brown with a darker brown outline between chambers in the initial coil. The agglutinated grains are poorly sorted with a maximum dimension of up to 0.11 mm. Because no other agglutinated types are present, the relative grain size and any indication of selectivity in grain size cannot be assessed. Although most grains are quartz, mafic minerals are conspicuous. Rarely, the siliceous skeletons of ribbon-shaped diatom colonies are incorporated in the wall. However, no carbonate skeletal material is present despite an abundance of carbonate skeletal fragments in the sand fraction of the sediment, nor is there any carbonate cement (the tests do not react when immersed in 5% hydrochloric acid). When immersed in sodium hypochlorite, the brown matrix within the test is bleached and the walls disaggregate thereby indicating an organic cement.

2. Kalgan River

All specimens in the Kalgan River assemblage (Fig. 3) belong to global morphotype A; however, they have a less regular outline than those from the Wellstead Estuary because the average grain size of the agglutinated material in the test is coarser. The maximum size of grains observed in the test is 0.17 mm compared to 0.11 mm in the Wellstead Estuary assemblage (Table 4). As in the former, the test contains no carbonate component, and the cement is organic. In comparison to the other agglutinated species present in the sample, the test is much more coarsely agglutinated and the surface is rougher than in the fine-grained, slightly rough *Scherochorella* and *Caronia* and the very fine-grained and smooth *Trochammina* and *Haplophragmoides*. The *Ammobaculites* may be agglutinating the coarsest quartz and mafic grains available to them in the sediment. Confirmation of this requires a sediment grain-size analysis. No biogenic carbonate fragments are included in the test.

The diameter of the planispiral coil has a larger range than for the equivalent initial stage in specimens from Wellstead Estuary, but a similar number of chambers in the final whorl is present (viz. 6–7). Because of the coarse agglutination, in many specimens the umbilicus is not a well-defined hollow and sutures between chambers are obscure. Irregularities in initial coiling are present similar to those observed in some of the Wellstead Estuary specimens. The uniserial chambers are defined by depressed sutures, at least between the final chambers. The maximum number of uniserial chambers found is four (Table 4; Fig. 3) and the uniserial chambers increase gradually in size with little change in width through the series. Adult uniserial chambers are cylindrical (Fig. 3d, f), whereas the early uniserial chambers tend to be slightly compressed (Fig. 3e). In most specimens the shape of the terminal aperture is variable due to the coarse-grained test, but is more elongate in early uniserial chambers (Fig. 3d, e).

Some tests with the largest diameters of the planispiral coil (0.33 – 0.36 mm; Fig. 3a, f, h), limited uniserial development, and maximum test lengths of 0.43 – 0.47 mm are either extreme variants within the morphotype

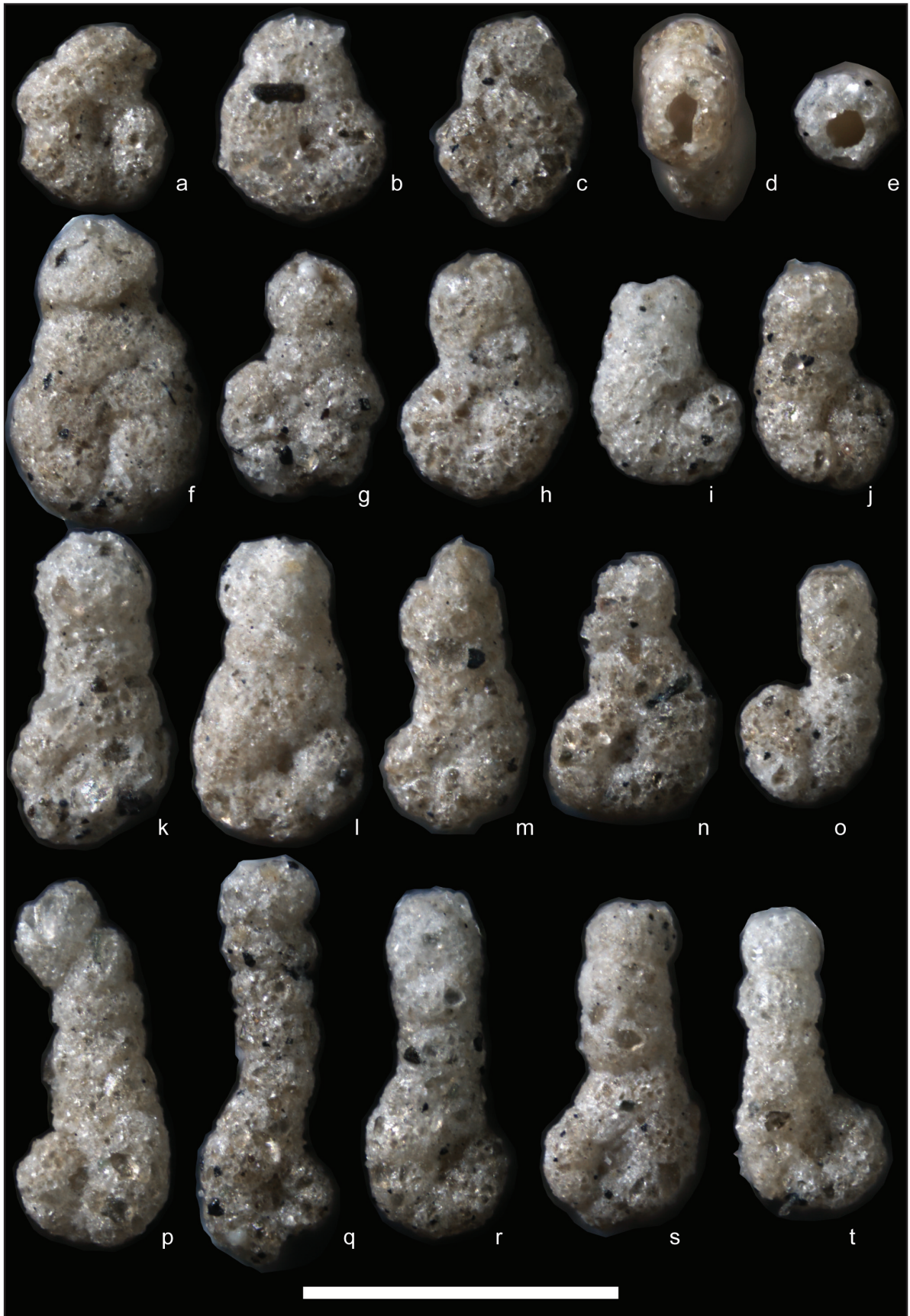


Figure 2. *Ammobaculites* assemblage from Wellstead Estuary, locality 1. All specimens belong to global estuarine morphotype A, and are assigned to *Ammobaculites* sp. ex. gr. *A. exiguus* (Cushman & Bronnimann); d and e are apertural views. Bar scale is 0.5 mm.

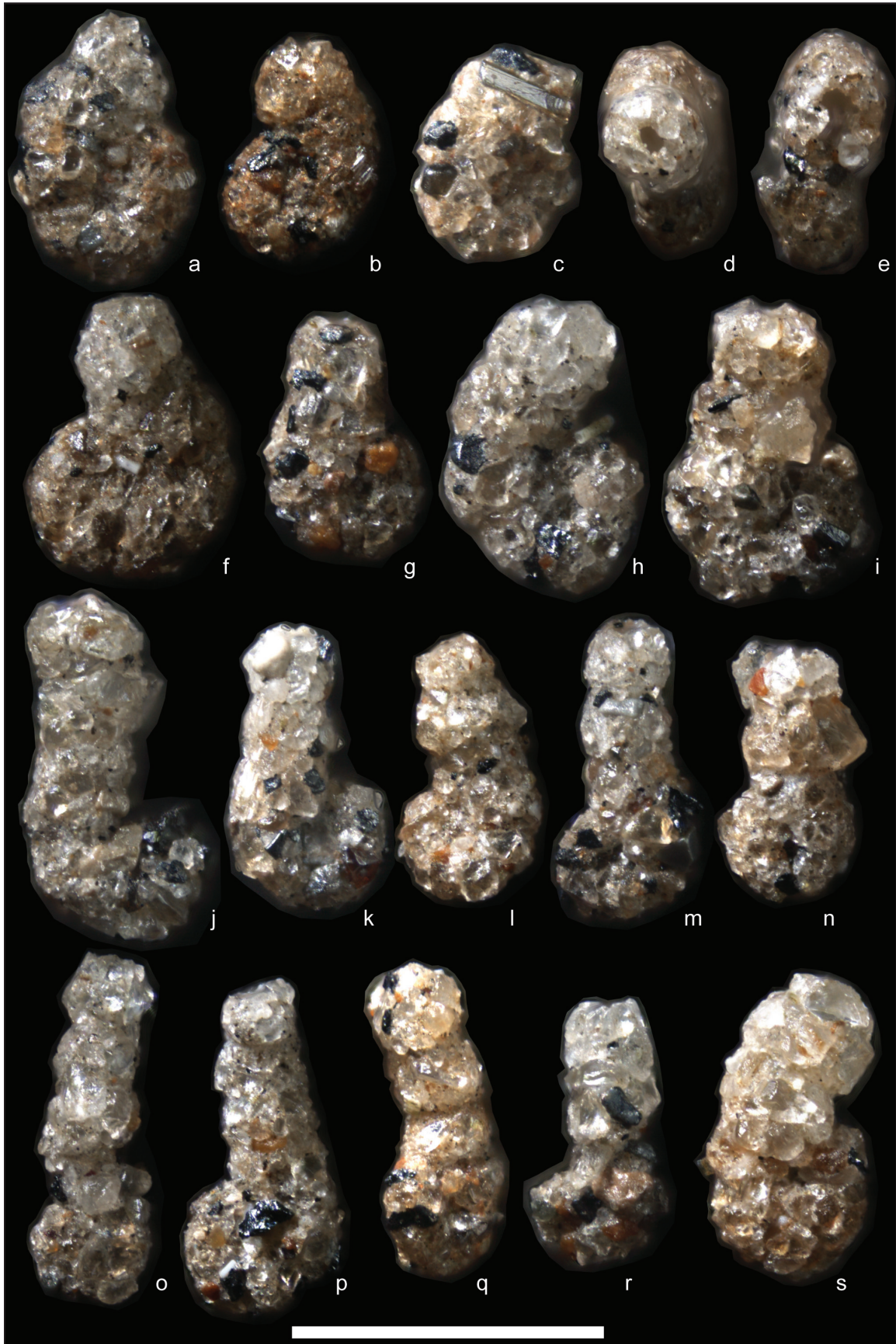


Figure 3. *Ammobaculites* assemblage from Kalgan River, locality 2. All specimens belong to global estuarine morphotype A, and are assigned to *Ammobaculites* sp. ex. gr. *A. exiguus* (Cushman & Bronnimann); d and e are apertural views. Bar scale is 0.5 mm.

A complex or belong within morphotype E (Table 1; see later discussion). They could also be dimorphs in the reproductive cycle. A much larger sample size and molecular analyses of living specimens is required in order to resolve this question.

3. Frankland River

The limited assemblage of *Ammobaculites* found here is included in this discussion because the only tests that have comparable planispiral stages to those at sites 1 and 2, lack well developed uniserial stages (Fig. 4a–i). The maximum diameter of the planispiral coil, the number of chambers in the last whorl, and the non-carbonate composition and coarsely agglutinated rough surface of the wall are similar to those found at the previous sites. Among the other agglutinated foraminifers at this locality, *Miliammina* has a slightly rough, fine-grained wall; and *Trochammina* and *Haplophragmoides* have very fine-grained smooth walls.

At this locality tests have only developed to an early uniserial stage. Possibly suitable environmental conditions for their development are short because the large seasonal influx of freshwater through the river keeps salinity very low for long periods (see Appendix 1). This can be tested through examining the development of living specimens from this site in laboratory cultures at optimum conditions.

Rare specimens of a robust morphotype (Fig. 4j) that appears to be a different *Ammobaculites* are present at this site. The coarsely agglutinated wall obscures the chamber

arrangement, but an initial tight coil (perhaps with an irregular coiling axis) is followed by a uniserial stage of three broad cylindrical chambers. The aperture is terminal and rounded. Further material is required before the generic identification can be confirmed. Similar forms are present in the Walpole Inlet and Hardy Inlet assemblages.

4. Walpole Inlet

The assemblage in Walpole Inlet includes two distinct morphotype groups: A (Fig. 5a–i, k, ?) and B (Fig. 5m–u). Morphotype A consists mainly of tests that include only the planispiral stage and rarely the addition of a single uniserial chamber. These are slightly smaller in diameter than equivalent growth stages at sites 1–3 and 5 (Table 4). They are morphologically similar to the common types found in the Frankland River at site 3 and have similar wall characteristics. Rare specimens (e.g. Fig. 5g, h) have a more developed uniserial stage of up to four chambers. The adult uniserial stage is cylindrical and the aperture is terminal (Fig. 5f, h).

The other group (B) represented here belongs with the robust specimen (Fig. 4j) from the Frankland River. These tests are more coarsely agglutinated than morphotype-A specimens and reach a longer test length at a growth stage with four uniserial chambers. The uniserial stage is erect above the initial coil. Because of the coarse agglutination, the chamber arrangement is variably obscure, especially in the initial coil, which has about four bulbous chambers exposed. Initial coiling in many of the specimens seems slightly irregular, but not

Table 4

Measurements made on the illustrated assemblages of *Ammobaculites* in the south coast estuaries. Diameters of the initial coil and the width and length of uniserial stage and test are given as an average with the range of values in parenthesis. All dimension measurements are in millimetres.

Character	1. Wellstead Estuary	2. Kagan River	3. Frankland River	4. Walpole Inlet	5. Hardy Inlet
Max. diameter initial coil	0.25 (0.21–0.30)	0.27 (0.19–0.36)	0.26 (0.19–0.30)	A. 0.23 (0.18–0.27) B. 0.19 (0.16–0.22)	A. 0.26 (0.22–0.30) B. 0.23 (0.20–0.29)
No. chambers in final whorl of coil	5–7	~ 6	~ 6	A. ~ 6 B. ~ 4	A. ~ 6 B. ~ 4
No. uniserial chambers	1–6	1–4	0–1	A. 0–4 B. 1–4	0–4
Max. width 1st uniserial chamber	0.16 (0.12–0.22)	0.16 (0.13–0.24)	0.15 (0.11–0.18)	A. 0.12 (0.09–0.16) B. 0.14 (0.12–0.16)	A. 0.15 (0.12–0.17) B. 0.19 (0.15–0.22)
Max. width last uniserial chamber	0.15 (0.12–0.19)	0.16 (0.11–0.19)		A. 0.14 (0.12–0.14) B. 0.17 (0.14–0.20)	A. 0.14 (0.12–0.16) B. 0.20 (0.12–0.27)
Max. width uniserial stage	0.16 (0.12–0.22)	0.17 (0.15–0.24)		A. 0.14 (0.11–0.14) B. 0.17 (0.14–0.20)	A. 0.15 (0.12–0.16) B. 0.21 (0.15–0.27)
Max. length uniserial stage	0.25 (0.11–0.44)	0.25 (0.11–0.39)	0.10 (0.08–0.13)	A. 0.16 (0.07–0.25) B. 0.21 (0.09–0.38)	A. 0.18 (0.12–0.26) B. 0.35 (0.25–0.56)
Max. length test	0.45 (0.28–0.66)	0.47 (0.36–0.56)	0.31 (0.24–0.38)	A. 0.34 (0.26–0.50) B. 0.36 (0.25–0.52)	A. 0.37 (0.28–0.44) B. 0.53 (0.39–0.77)
Max. grain size in wall	0.11	0.17	0.11	A. 0.10 B. 0.13	A. 0.14 B. 0.12
No. specimens measured	18	16	9 (5 with uniserial stage)	A. 9 (7 with uniserial stage) B. 7	A. 10 (9 with uniserial stage) B. 5

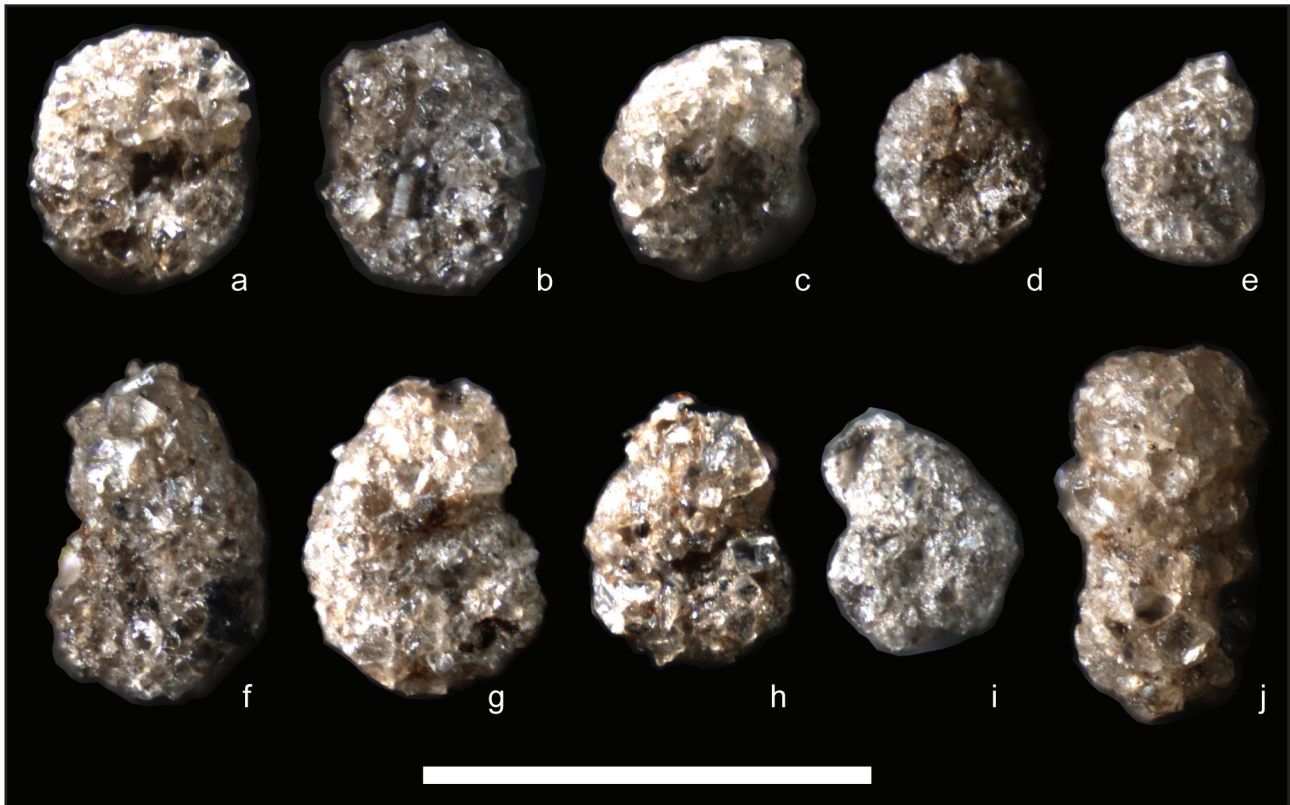


Figure 4. *Ammobaculites* assemblage from Frankland River, locality 3. Specimens a–i are considered to be juveniles of global estuarine morphotype A and are assigned to *Ammobaculites* sp. ex. gr. *A. exiguus* (Cushman & Bronnimann). Specimen j is a representative of global estuarine morphotype B and is left in open nomenclature as *Ammobaculites* sp. Bar scale is 0.5 mm.

streptospiral as in *Bulbobaculites* Maync. The aperture is a similar terminal opening (Fig. 5u) but is often blocked by agglutinated or extraneous material (Fig. 5p). Many live foraminifers when disturbed agglutinate grains over apertures and any other large pores (e.g. Haig *et al.* 2020, fig. 14G).

Both morphotypes have non-carbonate, organic-cemented walls. They have incorporated grains of a larger size in their tests compared to the accompanying more finely agglutinated genera with rough walls (*Caronia* and *Miliammina*).

5. Hardy Inlet

The two morphotype groups (A and B) found in Walpole Inlet and the Frankland River are also present at site 5 in the Hardy Inlet. The majority of specimens in morphotype A (Fig. 6a–j, q, r) show a greater development of the uniserial stage and are more coarsely agglutinated than those from Walpole Inlet (Table 4). They resemble more closely the Kalgan River specimens.

Morphotype B is represented by few specimens (Fig. 6k–p), but these are more robust and have the four bulbous chambers exposed in the initial coil followed by up to four uniserial chambers as at Walpole Inlet.

The morphotypes here are much more coarsely agglutinated than the accompanying agglutinated foraminifers. The coarsely agglutinated rough wall contrasts with the finely agglutinated rough wall of

accompanying *Miliammina* and *Scherochorella*, and the very fine smooth wall of *Trochammina*.

Summary of morphotypes

Two morphotype groups, following those outlined in Table 1, are represented in the studied estuarine samples. Morphotype A is present at each site and is characterized by an initial involute coil with 6–7 chambers in the final whorl followed by a uniserial stage, excentric above the coil, of up to four chambers, rarely as many as six in a maximum test length of 0.66 mm. The adult uniserial stage is cylindrical with little variation in width but is narrower than the initial coil. The wall is coarsely agglutinated and roughly finished. Juvenile tests with only the planispiral stage are present at each locality and at one site (Frankland River) they are the only forms found. In the Kalgan River assemblage, individuals with a broader than usual initial coil and a reduced uniserial stage may represent morphotype E or be at the extreme edge of the variability range of group A.

Less common representatives of morphotype B are present in the three western estuaries: Frankland River, Walpole Inlet and Hardy Inlet. These are more robust than the group A types, more coarsely agglutinated and reach a larger test length (0.77 mm at the fourth chamber of the uniserial stage). Although the initial coil seems to have a consistent four bulbous chambers exposed, the coil in some specimens is irregular. The cylindrical uniserial stage is positioned centrally above the coil.

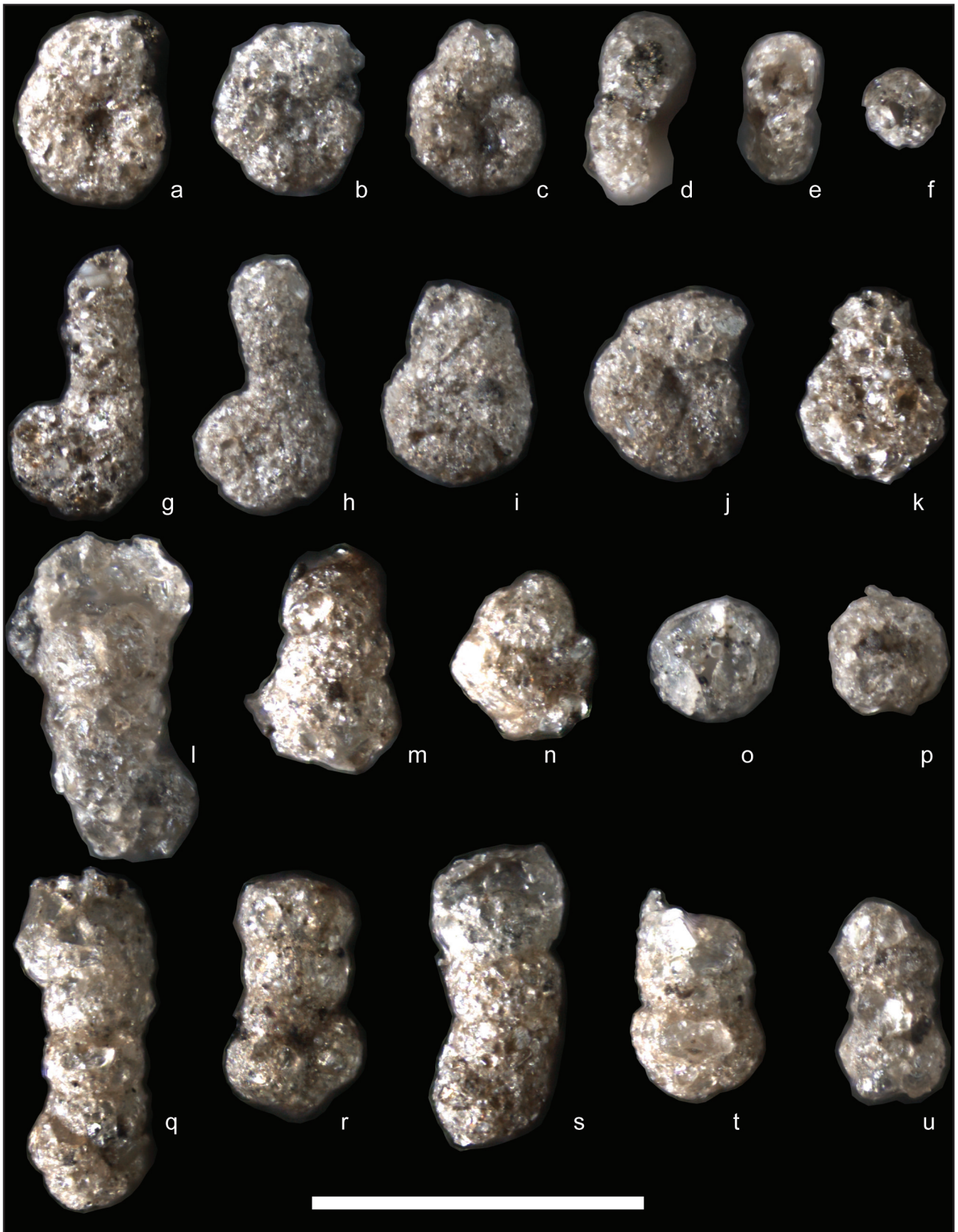


Figure 5. *Ammobaculites* assemblage from Walpole Inlet, locality 4. Specimens a–k belong to global estuarine morphotype A and are assigned to *Ammobaculites* sp. ex. gr. *A. exiguus* (Cushman & Bronnimann). Specimens l–u belong to global estuarine morphotype B and are left in open nomenclature as *Ammobaculites* sp. Bar scale is 0.5 mm.

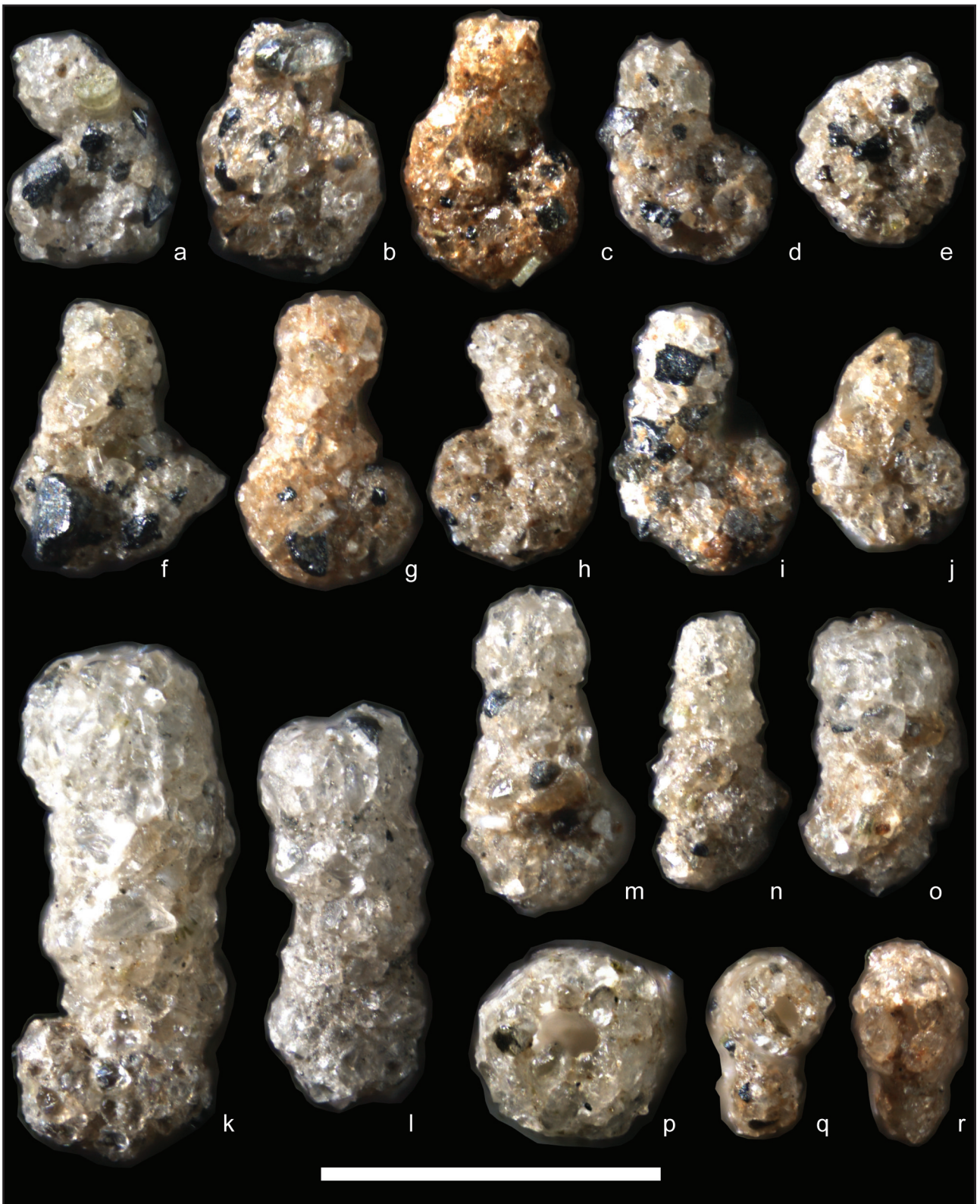


Figure 6. *Ammobaculites* assemblage from Hardy Inlet, locality 5. Specimens a–j, q, and r belong to global estuarine morphotype A and are assigned to *Ammobaculites* sp. ex. gr. *A. exiguus* (Cushman & Bronnimann); q and r are apertural views. Specimens k–o, and p belong to global estuarine morphotype B and are left in open nomenclature as *Ammobaculites* sp.; p is an apertural view. Bar scale is 0.5 mm.

Agglutinated quartz is the main component of the wall in both morphotypes, but conspicuous mafic grains are also present. Grain-size selectivity is obvious compared to the accompanying agglutinated foraminifers of other genera. The tests do not contain carbonate material, although an abundance of carbonate skeletal debris is present within the mud at some of the sites. An organic cement binds the grains.

Based on morphological criteria, each group probably represents just one species. Molecular (rDNA) gene sequence analyses are required in order to determine the genetic diversity here. Several factors make such a study of particular interest: (1) the studied river systems are separated by large distances and are not interconnected at present nor in the past; (2) the estuaries are closed to the open ocean for long intervals or have tenuous connections to the ocean; (3) the mud habitats of the *Ammobaculites* assemblages are confined to parts of the estuaries and are not contiguous through the estuaries and onto the high-energy inner continental shelf which has a well-sorted sand substrate. These *Ammobaculites* populations may have remained isolated for a considerable time with the only connection between them coming from chance migration, for example in mud on birds' feet.

COMPARISON TO KNOWN AUSTRALIAN AMMOBACULITES

Most previous records of *Ammobaculites* in modern Western Australian estuaries belong to morphotype A but have been attributed to three different species named from outside the Australian region with a further two left in open nomenclature (Table 3). An additional species, tentatively assigned to *Ammobaculites* (*viz.* *A. yardiensis* Parker 2009), is certainly distinct but requires further study, particularly of the initial chamber arrangement.

Previous reports of morphotype A in Western Australia include the illustrated specimens of McKenzie (1962), Quilty (1977) and Quilty & Hosie (2006) referred to *A. agglutinans*, *A. exiguus* of Ostrogay & Haig (2012), and *A. villosus* and perhaps *A. sp.* and *Haplophragmoides sp.* (as juvenile morphotypes) as recognized by Revets (2000). All of these forms seem to lie within the morphological range exhibited by morphotype A in the estuaries studied here and possibly belong to the one species.

In eastern Australia (Table 3), of specimens assigned to *A. exiguus* and *A. agglutinans*, only those illustrated by Strotz (2012, 2015) from central New South Wales estuaries closely resemble the Western Australian morphotype A. These have about six chambers in the initial broad coil and a rough coarsely agglutinated wall. The specimen from South Australia illustrated by Cann *et al.* (2000) and attributed to *A. barwonensis* may be equivalent (see discussion below), as well as the morphotype identified by Yassini & Jones (1995) as *A. subcatenulatus* (it lacks the evolute initial coil and the elongate uniserial chambers of the holotype of *A. subcatenulatus*, here referred to morphotype D, Table 1).

Ammobaculites sp. of Quilty (1977, fig. 11) from Hardy Inlet belongs to morphotype B that is also reported in the present study from this inlet and from the Frankland

River and Walpole Inlet. The elongate specimen identified as *Psammospaera sp.* by Quilty (1977, p. 87, fig. 7), with an especially atypical test shape for this genus, may also belong here. This morphotype has not been illustrated from eastern Australian assemblages.

The eastern Australian form referred to *Ammobaculites barwonensis* by Apthorpe (1980), Bell & Drury (1992), Bell (1995, 1996) and Strotz (2003), and transferred to *Simobaculites* by Strotz (2012, 2015) is distinct from Western Australian *Ammobaculites* and belongs within global morphotype C (Table 1). It seems close to *Ammobaculites amarus* Hada (1957). Whether the type specimen of *Ammobaculites? barwonensis* as figured by Collins (1974, pl. 1, figs 3a, b) belongs within the highly variable range of morphotype C at the other localities has not been documented at the type locality where one specimen has been described. Collin's type specimen may equally fit within morphotype A because it has a cylindrical uniserial stage positioned excentrically above a broad initial coil of comparable dimensions to the morphotype-A individuals reported from Western Australia and appears to have, as drawn, a similar rough coarsely agglutinated wall. Morphotype A differs from the eastern Australian morphotype C by having a rougher, usually more coarsely agglutinated wall, consistent cylindrical adult uniserial chambers with circular cross-sections, as well as an absence of flaring of the uniserial stage in the spectrum of variability found in one assemblage.

COMPARISON TO GLOBAL ESTUARINE AMMOBACULITES

Among known estuarine species attributed to morphotype A (Table 1) the Western Australian representatives of this group are most similar in outline to *A. exiguus* but are larger relative to growth stage, both in the initial coil and the uniserial stage. This may reflect environmental influence. The holotype and paratype illustrated by Cushman and Bronnimann (1948) demonstrate extremes of variability in the uniserial stage (erect to slightly irregular) that is also illustrated by the Western Australian specimens. The holotype housed in the Smithsonian National Museum of Natural History, and refigured by a rendered reflected-light image (<http://n2t.net/ark:/65665/3ff5d8631-13b2-4433-ba2d-90d90d101632>) seems morphologically very similar in particular to some of the specimens from Wellstead Estuary (e.g. Fig. 2r, s). *Ammobaculites exiguus* has been recorded from many localities world-wide (Hayward *et al.* 2018).

It seems improbable that a Western Australian estuarine *Ammobaculites* could be conspecific with a Middle Miocene deep open-water species of the genus. The lectotype of *Ammobaculites agglutinans*, as illustrated by SEM image (Papp & Schmid 1985, pl. 45, fig. 7), is much larger than any specimen recovered in Western Australian assemblages. This specimen has fewer chambers in the final whorl of the planispiral coil and has adult uniserial chambers becoming slightly longer than wide at the fourth uniserial-chamber stage (in contrast to the relatively broad, lower chambers of most of the Western Australian specimens). On

morphological grounds, the Western Australian types are not conspecific with the type species of *Ammobaculites* (viz. *A. agglutinans*). None of the other morphotype A species known globally in estuaries (Table 1) closely resemble the specimens studied here.

Revetz (2000) placed a group-A individual (see Table 2) in *Ammobaculites villosus*. Saidova's (1975) species is here attributed to morphotype B with erect uniserial stage centrally placed above the initial coil (Table 1). This is a much larger upper bathyal species, with type locality at 156 m off the west coast off the South Island of New Zealand, than the estuarine Western Australian type. Specimens from the Timor Sea assigned to *A. villosus* by Loeblich and Tappan (1994, pl. 7, figs 12–15) are group-A morphotypes that more closely resemble the lectotype of *A. agglutinans* than Saidova's (1975) type illustration of *A. villosus*.

Among *Ammobaculites* of group B in the global estuarine fauna (Table 1), the holotype and paratypes of *Ammobaculites balkwilli* have about four inflated chambers exposed in the initial coil similar to the specimens of this group found in the studied Western Australian estuaries. However, the shape of adult uniserial chambers (elongate in *A. balkwilli*) differs from the Western Australian types which have lower uniserial chambers. The specimen figured as *A. balkwilli* by Allen *et al.* (1999, pl. 1, fig. 4) seems closer to *A. exiguus* (morphotype A) than to typical *A. balkwilli* (morphotype B). *Ammobaculites josephi*, another coastal group-B species (Table 1), also has more elongate adult chambers than the Western Australian form.

COMPARISON TO AUSTRALIAN FOSSIL AMMOBACULITES

Among the Australian fossil assemblages are representatives of morphotypes A, B, C and E (Fig. 7). Most of the fossils, which range from Permian to Cretaceous, were recovered from friable mudstone by physical disaggregation and washing the sample using water over a 150 µm-mesh sieve. Within these agglutinated assemblages, tests contain no carbonate material although accompanying foraminifers usually include types with calcite/aragonite walls with crystalline ultrastructure. As noted by Haig (1980, 2003, 2004, 2018) and Haig & McCartney (2010), the fossil *Ammobaculites* from the shale facies often have distorted deflated tests deformed during burial in sediment and indicative of an original flexible shell due to organic cement binding the grains as in the modern types. During early diagenesis in the sediment, siliceous cement as overgrowths on agglutinated grains bind the test into a rigid fossil. When recovered by HCl acid digestion from early diagenetic calcareous mudstone nodules which are present at some horizons within the mudstone successions, perfectly preserved tests emerge in the residue (e.g. Haig & Barnbaum 1978, fig. 2g) but these often fall apart due to lack of cement when touched by a fine brush.

Ammobaculites belonging to morphotypes A and B from very shallow-water mud facies in the Australian Permian (e.g. Fig. 7a–h) and Cretaceous (e.g. Fig. 7x–zg) have rough, coarsely agglutinated walls similar to the modern estuarine types in Western Australia, and

agglutinate some of the largest grains available in their life environment compared to some of the accompanying agglutinated species. This may be a very conservative genetic character for these morphotype groups within the genus. The Triassic types (e.g. Fig. 7i–s) come from deeper-water more open-marine calcareous mud facies where coarse grains in the sand fraction of the sediment are lacking.

As noted by Haig & McCartney (2010), significant diversification among *Ammobaculites*-related groups commenced during the Triassic, with *Kutsevelia* Dain (1978), resembling modern morphotype E, firmly established by this time (e.g. Fig. 7t–v). Elsewhere, *Kutsevelia* is well known from the Jurassic, and is common in shallow-water mud facies of the Australian mid-Cretaceous interior sea (Fig. 7zk, zl). These types correspond to morphotype E among modern assemblages (Table 1), and are morphologically similar to the large planispiral forms found in the Kalgan River (e.g. Fig. 3a, f, h).

Among *Ammobaculites*-related groups, the Australian mid-Cretaceous assemblages show further diversification although this commenced during the Jurassic elsewhere. *Bykoviella* Korchagin (1964) with slightly irregular broad initial coil and reduced uniserial stage (e.g. Fig. 7zh) and *Simobaculites* Loeblich & Tappan (1984) with broad initial coil and moderately compressed uniserial stage are present in the restricted-marine mud facies of the Australian Cretaceous. It is remarkable how similar *Simobaculites raghavapuramensis* (e.g. Fig. 7zi, zj) described by Taylor & Haig (2001) from the Barremian Muderong Shale of the Southern Carnarvon Basin is to the modern morphotype C types from eastern Australia attributed to *Simobaculites* by Strotz (2012, 2015). Not only is the architecture of the test similar but the finely agglutinated smooth wall is also equivalent. The modern and Cretaceous types co-occur with coarsely agglutinated rough-surfaced morphotype A representatives.

Another addition in the Australian Cretaceous is the appearance of rare *Ammomarginulina* Wiesner (1931) in the interior-sea mud facies (e.g. Fig. 7zm). These seem to be among the oldest *Ammomarginulina* known in the global record. Species of the genus differ from those of *Ammobaculites* in the inclined chambers (and sutures) of the uniserial stage. *Ammomarginulina* is absent from Western Australian estuarine assemblages, but is known from such faunas elsewhere (sometimes designated as *Ammobaculites* or *Ammotium* Loeblich & Tappan 1953 which typically has an *Astacolus*-like rather than *Marginulina*-like adult chamber arrangement).

DISCUSSION

This reconnaissance analysis of *Ammobaculites* from estuaries along the south coast of Western Australia, raises three major questions:

1. For organisms that live in isolated benthic mud habitats in unconnected estuaries, why do similar morphotypes appear in these environments? Are they the same species? If so, what are the means of species dispersal in what are marginal-marine, ephemeral, unconnected habitats.



Figure 7. Fossil *Ammobaculites* from mud facies of Eastern Gondwanan-Australian interior seas. Bar scales are 0.1 mm. Specimens a–h, Permian species; a, *Ammobaculites* sp. belonging to morphotype B, from Haig (2018); b–f, *Ammobaculites woolnoughi* belonging to morphotype A, but transitional to B, from Haig (2003); g, h, *Ammobaculites wandageensis* belonging to morphotype A, from Haig & Mory (2016). Specimens i–w, Triassic species; i, j, *Ammobaculites duncani* belonging to morphotype B, from Haig & McCartney (2010); k–o, *Ammobaculites rhaeticus* belonging to morphotype A, from Haig & McCartney (2010); p, t–v, *Kutsevelia beggi* belonging to morphotype E, from Haig & McCartney (2010); q–s, *Ammobaculites zlabachensis* belonging to morphotype A, from Haig & McCartney (2010); w, *Carteriella manelobasensis*, although with broad planispiral coil and uniserial adult stage, may not be closely related to *Ammobaculites* but a derivative of *Haplophragmoides*–*Labrospira*, from Haig & McCartney (2010). Specimens x–zm, Cretaceous species; x, *Ammobaculites australis* belonging to morphotype A, from Haig (1980); y, *Ammobaculites humei* belonging to morphotype B, from Campbell & Haig (1999); z–zd, *Ammobaculites humei* belonging to morphotype B, from Dixon *et al.* (2003) and Haig *et al.* (2004); ze, zf, *Ammobaculites grossus* belonging to morphotype B, from Taylor & Haig (2001); zg, *Ammobaculites hofkeri* belonging to morphotype B, from Taylor & Haig (2001); zh, *Bykoviella* sp. cf. *B. elenae* from Taylor & Haig (2001); zi, zj, *Simobaculites raghavapuramensis* belonging to morphotype C, from Taylor & Haig (2001); zk, zl, *Kutsevelia implanus* belonging to morphotype E, from Campbell & Haig (1999); zm, *Ammomarginulina* sp. A of Haig (1980).

2. Why is there such a close similarity between modern *Ammobaculites* species in the estuarine (hyposaline) mud habitats in Western Australia with those in similar situations on remote continents? Is this because of morphological adaptation to a similar life habitat or is there a close genetic link as suggested, for example, by the pattern of grain-size agglutination compared with accompanying agglutinated species belonging to other genera.

3. Does the conservatism in morphological evolution witnessed in the fossil record over hundreds of millions of years suggest conservatism in genetic makeup that may also link to the widespread discontinuous distribution patterns of modern assemblages. The distributions of morphological-based species in the fossil record back as far as the Permian, show similar widespread distribution patterns to the modern, essentially cosmopolitan, morpho-species. Intriguing, during the Permian and early Mesozoic, there were no birds' feet to transport mud and the contained living foraminifers from adjacent estuaries or interior seas.

The answers to these questions rely on future detailed biological analyses, especially of molecular rDNA sequences as is being done for another widespread estuarine group centred on the calcareous *Ammonia tepida* (see Holzmann & Pawlowski 2000). Challenges will include identification of living individuals and extraction of uncontaminated protoplasm from the test. Because of its extremely long and seemingly conservative fossil record as one of the earliest multichambered foraminifers, *Ammobaculites* will provide an intriguing subject for this type of research.

In compiling lists of species names for fossil and extant foraminifers, a pragmatic approach is often employed. The present study has shown when morphological variation of the test is investigated, questions about species placements abound. At the reconnaissance stage of this study, a broad morphotype classification is used. The morphotype A individuals from the studied estuaries seem to belong to one species, but this needs testing by molecular methods. They are designated as "*Ammobaculites* ex. gr. *A. exiguus*" because of morphological resemblance to *Ammobaculites exiguus*. The morphotype-B species has no close estuarine counterpart known elsewhere and is left in open nomenclature (viz. *Ammobaculites* sp.)

CONCLUSIONS

1. Assemblages of *Ammobaculites* from five localities in estuaries on the south coast of Western Australia are described. The assemblages come from mud facies in hyposaline parts of the estuarine systems, including Wellstead Estuary, Kalgan River, Frankland River, Walpole Inlet and Hardy Inlet.

2. Five main morphotype groups (designated A–E) recognized among the global estuarine fauna are used for comparison with the morphotypes at the studied sites. The Western Australian types belong to two widespread groups known elsewhere: (A) species with an initial broad involute planispiral coil and a later cylindrical uniserial stage of lesser diameter positioned excentrically above the coil; and more rarely (B) species

with a cylindrical uniserial portion positioned centrally above the initial involute planispiral coil. Rare large specimens from the Kalgan River approach morphotype E (viz. species with broad planispiral coil, and only slight development of a compressed excentric uniserial stage) but may be extreme variants of morphotype A at this locality. Morphotype D (like A, but with a partially evolute initial coil) has not been located. Despite being known from eastern Australian estuaries morphotype C (viz. species with broad initial involute coil and excentric variably compressed and slightly to distinctly flabelliform uniserial stage, with elongate terminal aperture) is absent from the known Western Australian assemblages.

3. The Australian fossil record of *Ammobaculites* in Permian, Triassic and Cretaceous mud facies contains very similar morphotypes to their modern counterparts, and suggest great conservatism in morphological evolution. This also may apply to grain-size selectivity in test construction.

4. The modern *Ammobaculites* are living fossils and future biological research on these organisms, including using molecular techniques, may answer intriguing questions about dispersal from isolated and ephemeral estuarine mud habitats over regional and global scales, and also about the tempo of genetic drift and evolution in this genus. Greater knowledge of habitat and life strategies may provide insights into the palaeoenvironments of ancient larger estuarine-like basins where *Ammobaculites* fossils are common.

ACKNOWLEDGEMENTS

This study was helped greatly by the assistance, foraminiferal discussions and great company provided by Bruce Hayward, Mark Gunson and Jenny Bevan in the field during September 2019, and by Angela Schoen in the Wellstead Estuary in February 2020. The Oceans Graduate School at The University of Western Australia provided an inspiring environment in which to undertake the work. Bruce Hayward and Justin Parker are thanked for their useful reviews.

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Appendix 1

Localities of studied *Ammobaculites* assemblages, and associated foraminifers.

No.	Locality	Description	Foraminiferal assemblage
1	Wellstead Estuary, Bremer River at 34.38623°S, 119.37593°E; collected 19 February 2020	~20 cm water depth (low water level due to drought and estuary closed off from sea). Black mud ~2 m out from edge of serpulid reef. No salinity measurement at time of collection. Salinity variable (hyposaline to hyposaline) according to Brearley (2005)	<i>Ammobaculites</i> assemblage: Fig. 2a–t; associated foraminiferal genera: <i>Ammonia</i> (abundant), <i>Elphidium</i> (common), <i>Quinqueloculina</i> (rare)
2	Kalgan River at 34.93757°E, 117.97474°S; collected 25 September 2019	~10 cm water depth (toward low tide). Muddy fine sand ~2 m from shoreline close to start of bioturbated zone. Salinity, 33 ppt.	<i>Ammobaculites</i> assemblage: Fig. 3a–s; associated foraminiferal genera: <i>Trochammina</i> (common), <i>Scherochorella</i> (rare), <i>Caronia</i> (rare), <i>Haplophragmoides</i> (rare), <i>Ammonia</i> (rare), <i>Elphidium</i> (rare), <i>Quinqueloculina</i> (rare)
3	Frankland River at 34.99082°S, 116.81575°E; collected 26 September 2019	~1 m water depth. Muddy sand from edge of reeds along shoreline on eastern bank. Salinity, 5 ppt.	<i>Ammobaculites</i> assemblage: Fig. 4a–j; associated foraminiferal genera: <i>Trochammina</i> (abundant), <i>Miliammina</i> (common), <i>Ammonia</i> (abundant), <i>Elphidium</i> (common), <i>Haplophragmoides</i> (rare)
4	Walpole Inlet at 34.97792°S, 116.72483°E; collected 26 September 2019	~2 m water depth. Black muddy sand. Salinity, 15 ppt.	<i>Ammobaculites</i> assemblage: Fig. 5a–u; associated foraminiferal genera: <i>Miliammina</i> (abundant), <i>Scherochorella</i> (common), <i>Caronia</i> (rare)
5	Hardy Inlet, Blackwood River at 34.29855°S, 115.16844°E; collected 29 September 2019	~1 m water depth. Muddy bioturbated sand with molluscan shell debris and filamentous "algae". No salinity measurement at time of collection.	<i>Ammobaculites</i> assemblage: Fig. 6a–r; associated foraminiferal genera: <i>Scherochorella</i> (common), <i>Miliammina</i> (common), <i>Trochammina</i> (very rare), <i>Ammonia</i> (rare), <i>Elphidium</i> (rare)