

# EVOLUTION OF TROCHAMMINOIDS (TROCHOSPIRAL ORGANIC-CEMENTED AGGLUTINATED FORAMINIFERA): EXAMPLES FROM THE LOWER PERMIAN OF WESTERN AUSTRALIA

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## ABSTRACT

Trochamminids are the oldest trochospiral group of foraminifera. An exceptionally well-preserved assemblage, found in the Lower Permian (Sakmarian, ~294–290 Ma) of Western Australia, includes *Trochammina geoffplayfordi* n. sp., *Trochammina gloveri* n. sp., *Trochamminopsis teichertii* n. sp., and *Tritaxis crespinae* n. sp. *Verispira holmesorum* n. sp. seems related to broader Trochamminoidea. These represent the oldest known well-preserved representatives of the superfamily. By the Sakmarian, trochamminids, remarkably like modern species, had developed in a shallow-water interior sea with muddy substrate; some may have lived in the flocculent surface layer of the mud, and some were epibionts. No potential trochospiral ancestor is known among calcareous foraminifera of the Late Paleozoic. Triassic *Duostomina* seems to be the oldest calcareous taxa with simple trochospiral coiling (also having an inner organic lining). Molecular analyses of modern species suggest that morphotypes like the Permian *Trochammina* lie at some genetic distance from *Trochammina inflata* (type species of the genus).

## INTRODUCTION

*Trochammina* is the oldest recognised multichambered trochospiral foraminifera in the stratigraphic record. Family Trochamminidae based on the genus *Trochammina* Parker & Jones, 1859, with type species *Trochammina inflata* (Montagu, 1808) is the earliest group of trochamminoids, with the oldest representative known from the Late Paleozoic, probably the Early Carboniferous (Loeblich & Tappan, 1987). Grain aggregates described from the Cambrian by Scott et al. (2003) do not show distinct chambers (or cement-infilled cavities) nor foramina connecting chambers. Among the Carboniferous trochamminids, placement into genera is uncertain because of poor preservation (including obscured apertures and deflated deformed chambers). *Reophax* Montfort, 1808 (revised by Brönnimann & Whittaker, 1980), is considered the first rectilinear, uniserial multichambered foraminifera with organic-cemented, coarse siliceous agglutination (viz., *Reophax backriveranus* Gutschick, 1986, from the Ordovician). The evolution of multichambered foraminifera from the Ordovician to the first appearance of trochamminids in the Mississippian is poorly known (Kaminski et al., 2009).

Exceptionally well-preserved specimens of trochamminids with distinct morphological features (e.g., aperture, lip, inflated chambers) are found by acid digestion of carbonate nodules from earliest Permian mudstone (Sakmarian, ~294–290 Ma; Cohen et al., 2013, updated May 2023) in the Irwin Basin in Western Australia. The studied horizon in the

Holmwood Shale is above a level with abundant Sakmarian ammonoids (viz., *Juresanites* and *Uraloceras*; at about 80 m above base of the formation; Leonova, 1998, 2011, 2018; Haig et al., 2022). It is below the Fossil Cliff Member that forms the upper part of the Holmwood Shale (Haig et al., 2014) and includes the ammonoid *Metalegoceras kayi*, which Leonova (2011) regarded as Sakmarian. The studied level and the *Juresanites* beds and Fossil Cliff Member belong to the *Pseudoreticulatispora pseudoreticulata* Spore-Pollen Zone (Foster et al., 1985; Haig et al., 2022; Daniel Peyrot, personal communication, May 2023). The present study shows that the species described here represent the oldest well-preserved trochamminids that can be assigned, based on aperture-lip position and original chamber shape, to *Trochammina*, *Trochamminopsis* Brönnimann, 1976, and *Tritaxis* Schubert, 1921. A related form referred to *Verispira* Palmieri, 1988, is placed amongst the broader Trochamminoidea. *Trochammina*, *Trochamminopsis*, and *Tritaxis* are based on type species found in modern environments.

In order to understand the early evolution of trochamminids, we (1) record the diversity of the Irwin Basin Sakmarian assemblages; (2) establish the palaeoenvironment in which these trochamminids lived; (3) compare with Carboniferous and other Permian types and contrast assumed life habitats; (4) examine the stratigraphic record to identify periods of diversification among trochamminids and to determine possible ancestral forms; (5) outline the broad morphological evolution based on the stratigraphic record; and (6) consider why trochamminid evolution seems so conservative.

## NEW IRWIN BASIN TROCHAMMINOIDS

### GEOLOGICAL SETTING

The Irwin Basin (Clarke et al., 1951) is part of the complex East Gondwanan Interior rift system (Fig. 1). It formed the most restricted part of a marginal rift, including the Merlingleigh, Byro, Coolkalaya, and Irwin basins (Fig. 1) that splayed from the main axis of the rift system (Haig et al., 2014, 2017). Marine conditions in the Irwin Basin were shallow and seasonally estuarine-like (Haig, 2003). The Lower Permian succession consists of Asselian glaciogenic deposits (Nangetty Formation), Sakmarian marine shale deposits (Holmwood Shale), early Artinskian nearshore sand deposits (High Cliff Sandstone), mid-Artinskian fluvial-deltaic deposits (Irwin River Coal Measures); late Artinskian–Kungurian marine shale and sand (Carynginia Formation) and probable late Kungurian–Roadian shore face and fluvial sands (Wagina Sandstone; Haig et al., 2022). The studied beds are from 50–60 m below the top of the Holmwood Shale (Figs. 1, 2). At the studied site (28.94785°S; 115.54700°E), the Holmwood

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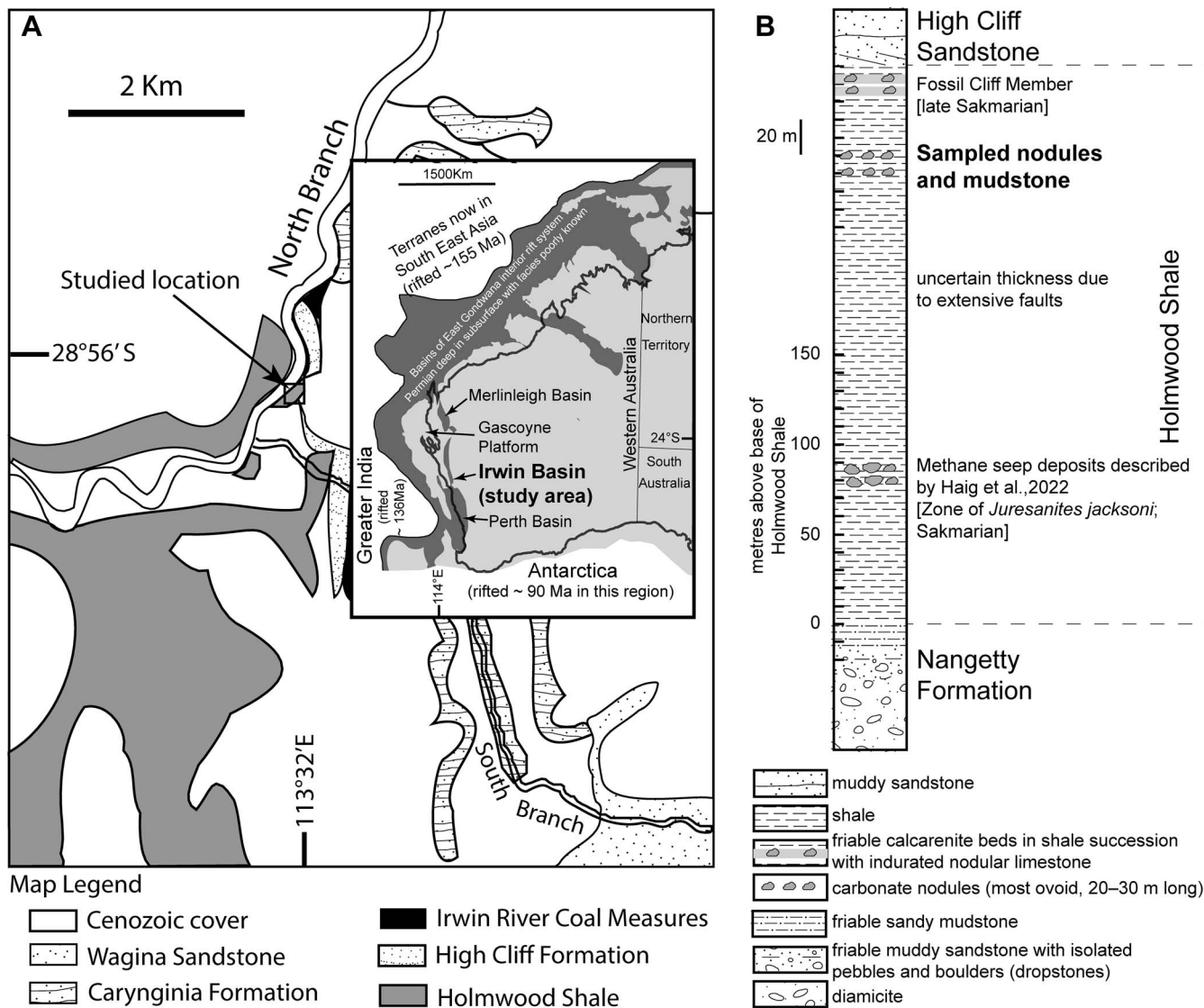


FIGURE 1. A) Map of the northern branch of the Irwin River (based on McLoughlin, 1992, fig. 4D) showing the sampled locality (28.94785°S; 115.54700°E). Insert map shows the relationship of the studied Irwin Basin to the Merlinleigh Basin in the same series of marginal rift basins that splay from the axial part of the East Gondwana Interior rift system that occupies the now western margin of Australia. B) Stratigraphic log of the Holmwood Shale in the Irwin Basin (modified from Haig et al., 2022). The sampled carbonate nodules are present 50–60 m below the contact with the High Cliff Sandstone.

Shale is composed of massive friable blue-grey shale with scattered, generally ovoid-shaped, carbonate nodules up to 50 cm in diameter (Fig. 2C).

The nodules are blue-grey mud cemented with carbonate. Fossils within the nodules, including the organic-cemented agglutinated foraminifers that in life had flexible tests, are not deflated or deformed. This suggests these are early diagenetic nodules formed in seafloor mud (Pirrie & Marshall, 1991; Marshall & Pirrie, 2013). The biogenic components found in the nodules include spores and pollen, marine phytoplankton, macroalgae (cf. *Litostroma*, see Haig et al., 2022), sponge spicules, bryozoan fragments, brachiopods, crinoid columnal plates, ostracods, rare gastropods, and wood fragments, as well as foraminifera. The foraminifera include organic-cemented siliceous agglutinated types (*Thuraminoides*, *Teichertina*, *Sacculinella*, *Placentamina*, *Lagenamina*, *Hyperamina*, *Kechenotiske*, *Sansabaina*,

*Tolypamma*, *Ammodiscus*, *Glomospirella*, *Kunklerina*, *Reophax*, *Caronia*, *Aaptotoichus*, *Spiroplectamina*), calcareous types such as miliolids (*Calcitornella*, *Hemigordius*) and Nodosarians (*Protonodosaria*, *Vervilleina*). The trochamminoids among the organic-cemented agglutinated assemblage are the subject of this paper.

#### SAMPLE PROCESSING AND ANALYSIS

Sampled carbonate nodules extracted from the friable Holmwood Shale were acid-digested in a dilute solution of 5% HCl. This allowed dissolution of the carbonate cement and disaggregation of the organic-rich muddy sediment forming the nodules. Non-calcareous biogenic material was preserved as well as moulds of calcareous skeletal debris. After digestion, the sediment residues were dried and examined under a



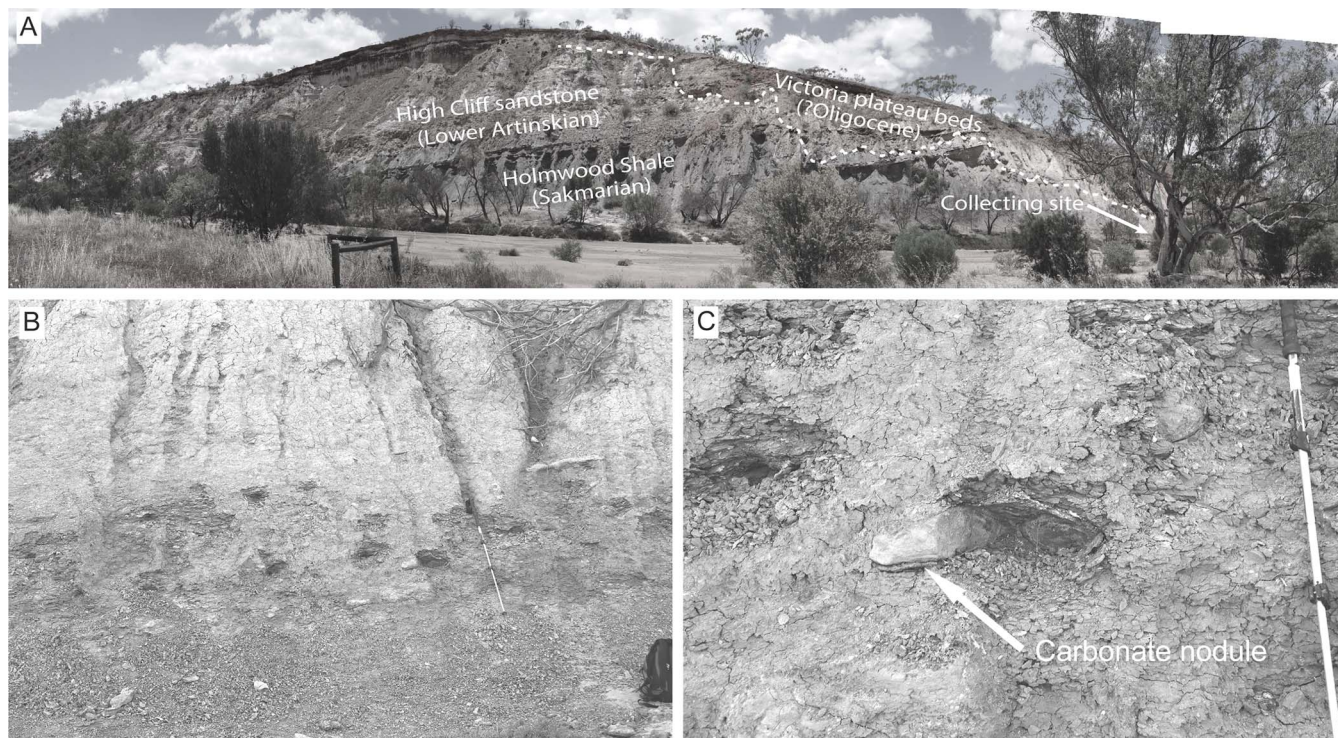


FIGURE 2. A) View of High Cliff on the southern bank of the North Branch of the Irwin River showing the position of the studied site. B) Outcrop of friable shale with scattered carbonate nodules at the studied site. C) View of carbonate nodule in friable mudstone.

stereomicroscope in the laboratory. The trochamminoids were carefully picked from the residue with a silver sable-hair brush 3/0 to avoid damaging or crushing the specimens and mounted on micropaleontological cardboard slides. To illustrate the trochamminoid assemblage, successive reflected light micrographs at different focus planes were taken under a biological compound microscope. The resulting images were stacked and rendered using Helicon Focus software (Helicon Soft). More detailed examination of the wall structure of uncoated specimens was performed using an environmental scanning electron microscope (SEM) under low vacuum. The specimens were dried at room temperature, mounted in required orientations using carbon tape on standard metal stubs before imaging. Measurements of the quartz grains forming the wall agglutination were performed using the measuring tool in Adobe Photoshop. All figured specimens, residues, and nodules are curated in the collection of the Earth Science Museum at the University of Western Australia.

#### SYSTEMATIC DESCRIPTIONS

All five new species belong among the organic-cemented agglutinated foraminifera that do not secrete a calcium-carbonate component for their test. They are taxonomically separate from the carbonate-cemented agglutinated foraminifera and other groups that produce calcium carbonate through biomineralization. Apart from the organic-cemented types, agglutinated species belong to: (1) carbonate-cemented textulariids; (2) Fusulinata (see descriptions and illustrations for Mississippian *Plectinopsis*, *Rectopravina*, *Praekoktjubina* by Vachard et al., 2014); and (3) Miliolida (see modern *Ammomassilina alveoliniformis*, *Nubeculina advena*, *Quinqueloculina agglutinans*, *Quinqueloculina arenata*, *Quinqueloculina* cf. *crassatina*, *Quinqueloculina*

*parkeri*, *Quinqueloculina* cf. *pittensis*, *Quinqueloculina* cf. *subrugosa*, *Quinqueloculina wiesneri*, and *Schlumbergerina alveoliniformis* illustrated by Haig, 1988).

Organic (glycosaminoglycan)-cemented types (Hedley, 1963; Towe, 1967; Mendelson, 1982; Langer, 1992; Allen et al., 2000) usually agglutinate silicate grains (mainly quartz). Occasionally carbonate fragments are included in the test where these are present in the substrate (e.g., type specimens of *Ammobaculites agglutinans* described by Kaminski & Gradstein, 2020). The organic-cemented agglutinated foraminifera have a separate evolutionary history to the other agglutinated groups (see Discussion). The studied species are illustrated by rendered light micrographs (Figs. 3–8) and scanning electron micrographs of uncoated specimens (Fig. 9).

Superfamily TROCHAMMINOIDEA Schwager, 1877

Family TROCHAMMINIDAE Schwager, 1877

Genus *Trochammina* Parker & Jones, 1859

Type species: *Trochammina inflata* Montagu, 1808

(neotype, Brönnimann & Whittaker, 1984, pl. 1, fig. 1)

*Remarks.* *Trochammina* differs from *Trochamminopsis* Brönnimann, 1976 (see below), by its lower trochospiral test with looser coiling and aperture in an extraumbilical-umbilical rather than umbilical position.

*Trochammina geoffplayfordi* n. sp.

Figs. 3.1a–3.6c, 8.2, 9.2

*Type material.* Holotype UWA182163 (Figs. 3.1a–c); paratype UWA182164 (Figs. 3.2a–c); paratype UWA182165

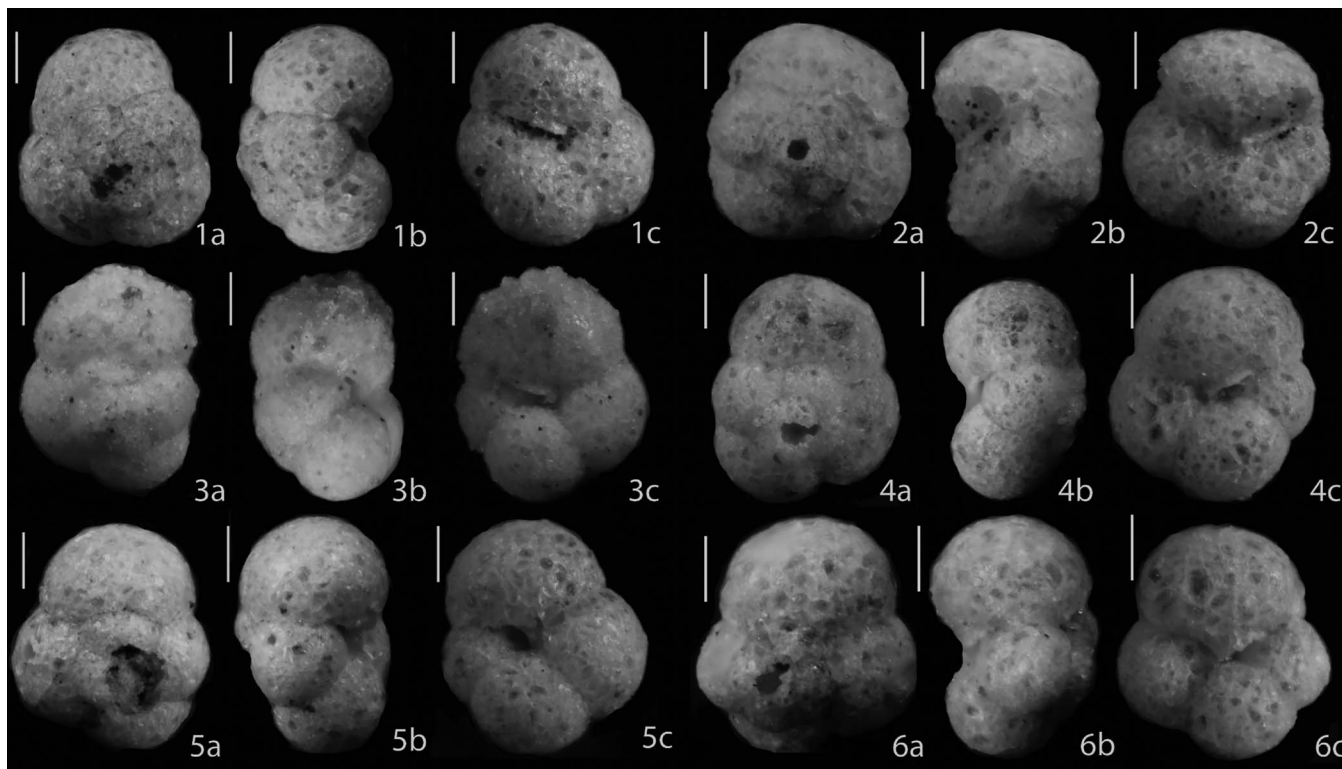


FIGURE 3. *Trochammina geoffplayfordi* n. sp. (scale bars = 100  $\mu$ m; rendered reflected-light micrographs). **1a–c** holotype UWA182163, **1a** spiral side, **1b** peripheral (apertural view), **1c** umbilical side. **2a–c** paratype UWA182164, **2a** spiral side, **2b** peripheral (apertural view), **2c** umbilical side. **3a–c** paratype UWA182165, **3a** spiral side, **3b** peripheral (apertural view), **3c** umbilical side. **4a–c** paratype UWA182166, **4a** spiral side, **4b** peripheral (apertural view), **4c** umbilical side. **5a–c** paratype UWA182167, **5a** spiral side, **5b** peripheral (apertural view), **5c** umbilical side. **6a–c** paratype UWA182168, **6a** spiral side, **6b** peripheral (apertural view), **6c** umbilical side.

(Figs. 3.3a–c); paratype UWA182166 (Figs. 3.4a–c); paratype UWA182167 (Figs. 3.5a–c); paratype UWA182168 (Figs. 3.6a–c); paratype UWA182248 (Fig. 8.2); paratype UWA182190 (Fig. 9.2).

**Diagnosis.** A Permian species of *Trochammina* with four globose chambers in the last whorl (average diameter of figured specimens is 420  $\mu$ m); final chamber broader than high in both equatorial and axial view; spiral side moderately convex; umbilicus closed; wall agglutinated with angular quartz (mean grain size ca. 17.5  $\mu$ m) set in a matrix of finer siliceous grains; larger quartz grains orientated with flat surface tangential to the outer wall surface (Fig. 9.2); aperture a low basal arch extending from the umbilicus to at least one-half way to periphery but not reaching periphery, with well-developed narrow lip of uniform width bordering the upper edge of aperture.

**Description.** Test medium size (average diameter of figured specimens is 420  $\mu$ m); trochospiral with inflated globose chambers and a lobate outline. Coiling is either sinistral or dextral with no preferred direction. Umbilical side is concave with closed umbilicus; spiral side is gently convex. Coiled with 2.5 to 3 whorls and usually 4 chambers in the last whorl. Chambers in the last whorl increase gradually in size, final chamber broader than high in both equatorial and axial view. Periphery is broadly rounded. The sutures are depressed between chambers of final whorl and slightly depressed or flush between early chambers on spiral side. Initial chambers have a dark-brown inner organic lining (Fig. 8.2). The wall is composed of angular quartz grains (up to 40  $\mu$ m maximum

dimension, mean 17.5  $\mu$ m; Fig. 10) embedded in a matrix of finer quartz and with rare iron-oxide grains also present. Many of the larger quartz grains have flat surfaces tangentially aligned on the wall's outer surface giving a moderately smooth finish. The aperture is a low arch that extends from the umbilicus to half to three-quarters of the way to the periphery at the base of the last chamber. A distinct narrow lip borders the aperture on its upper side.

**Type level.** Upper Holmwood Shale, upper Sakmarian, Lower Permian (Cisuralian). Type material extracted from a carbonate-mudstone nodule 50–60 m below the contact of the Holmwood Shale and the overlying High Cliff Sandstone (Fig. 1B).

**Type locality.** High Cliff, situated on the eastern side of the North Branch of the Irwin River (28.94785°S; 115.54700°E; Fig. 1A).

**Remarks.** The species differs from modern *Trochammina inflata*, the type for the genus, by fewer and more inflated chambers in the final whorl, a shallower more-closed umbilicus and a coarser wall texture. The earliest known species attributed to *Trochammina* is *T. melhi* Conkin & Conkin (1964, p. 42, 43, holotype pl. 2, fig. 10; paratypes pl. 2, figs. 6–9, 11) from the Lower Mississippian, southwest Missouri. The type material of *T. melhi* was refigured by the Smithsonian National Museum of Natural History, Department of Paleobiology Collections, (<https://collections.nmnh.si.edu/search/paleo/>). Although it is poorly preserved, based on photographic re-illustrations of the holotype, *T. melhi* has a similar lobate outline to our new species and may have a similar four-chambered final whorl, although up to 7



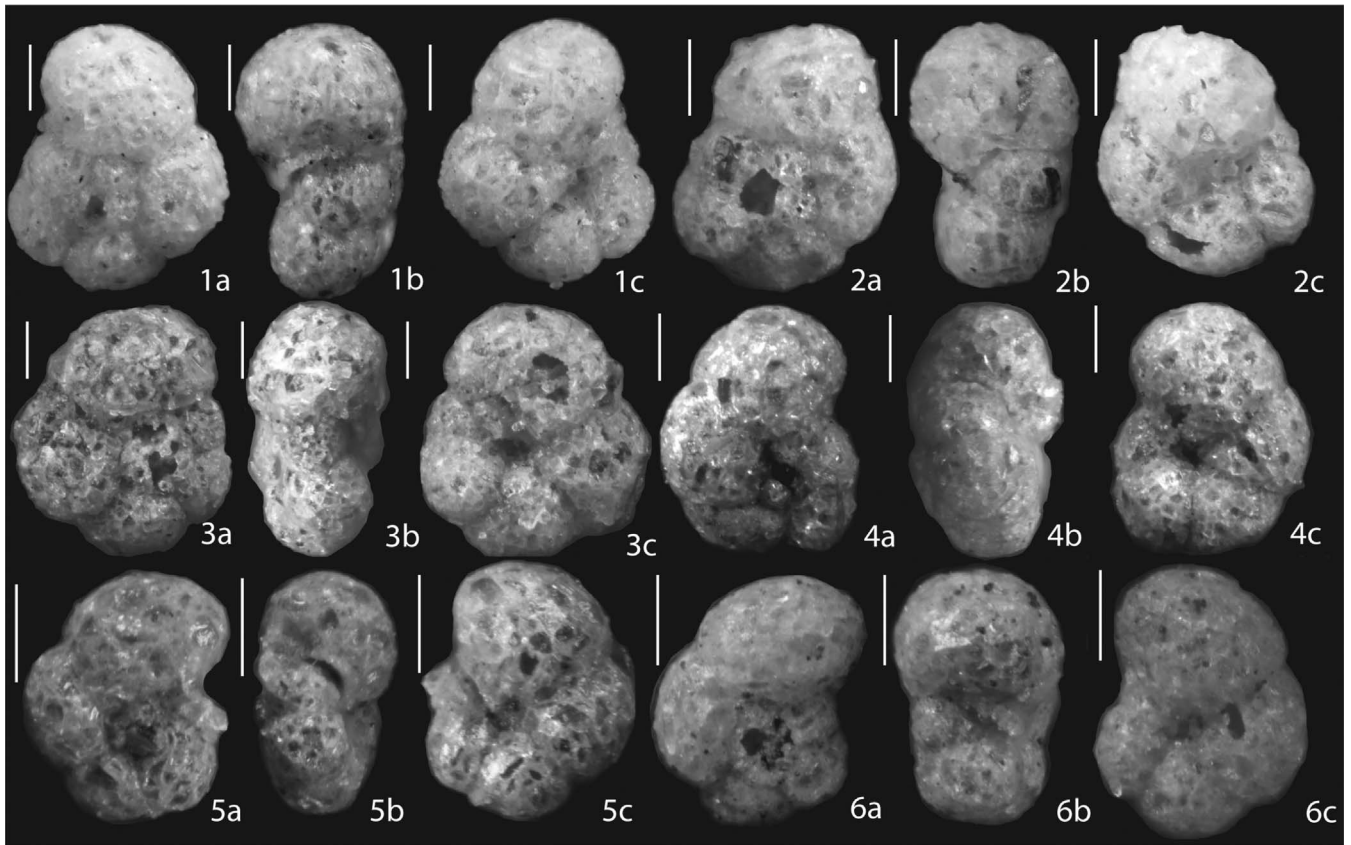


FIGURE 4. *Trochammina gloveri* n. sp. (scale bars = 100  $\mu$ m; rendered reflected-light micrographs). **1a–c** holotype UWA182169, **1a** spiral side, **1b** peripheral (apertural view), **1c** umbilical side. **2a–c** paratype UWA182170, **2a** spiral side, **2b** peripheral (apertural view), **2c** umbilical side. **3a–c** paratype UWA182171, **3a** spiral side, **3b** peripheral (apertural view), **3c** umbilical side. **4a–c** paratype UWA182172, **4a** spiral side, **4b** peripheral (apertural view), **4c** umbilical side. **5a–c** paratype UWA182173, **5a** spiral side, **5b** peripheral (apertural view), **5c** umbilical side. **6a–c** paratype UWA182174, **6a** spiral side, **6b** peripheral (apertural view), **6c** umbilical side.

chambers were described by Conkin & Conkin (1964). However, features on the umbilical side, including the aperture, are obscure on the American type. The Pennsylvanian *T. arenosa* Cushman & Waters, 1927 (pl. 27, figs. 4a–c; USNM CC 7025) and *T. grahamensis* Cushman & Waters, 1930 (pl. 6, figs. 8a–c; USNM CC 7163) are probably *Trochamminopsis* rather than *Trochammina* (see description of *Trochamminopsis teichertii* n. sp. given below).

Among the Permian species mainly known from Gondwanan interior basins in Australia, *T. geoffplayfordi* differs from *Trochammina laevis* Crespin, 1958 (pl. 21, figs. 1–4) by coiling in 2.5 whorls, rather than in 3 complete whorls; having 4 globose chambers, rather than 6 in the last whorl; and wall coarsely agglutinated rather than finely agglutinated.

*Trochammina geoffplayfordi* is a morphological analogue of *T. hadai* Uchio, 1962, a modern species occurring in the Shinano River, Japan. In shallow water of the enclosed Leschenault Inlet, Western Australia, *T. hadai* occupies the top first few centimetres of a flocculent layer of mud-facies (Tremblin et al., 2021). The species has been described as invasive in San Francisco Bay, California, USA; Flamengo Inlet, São Paulo State, Brazil; and Leschenault Inlet, Western Australia (see records cited by Tremblin et al., 2021). Features of modern *T. hadai* and Permian *T. geoffplayfordi* that may have supraspecific taxonomic significance in a future reclassification are the tangential orientation of the surfaces of large quartz grains on the outer test wall and a distinct narrow lip over the aperture.

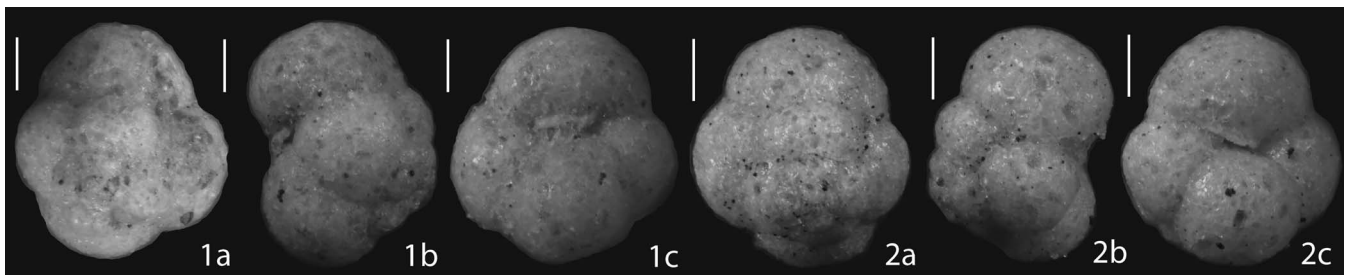


FIGURE 5. *Trochamminopsis teichertii* n. sp. (scale bars = 100  $\mu$ m). **1a–c** paratype UWA182175, **1a** spiral side, **1b** peripheral (apertural view), **1c** umbilical side. **2a–c** holotype UWA182176, **2a** spiral side, **2b** peripheral (apertural view), **2c** umbilical side.

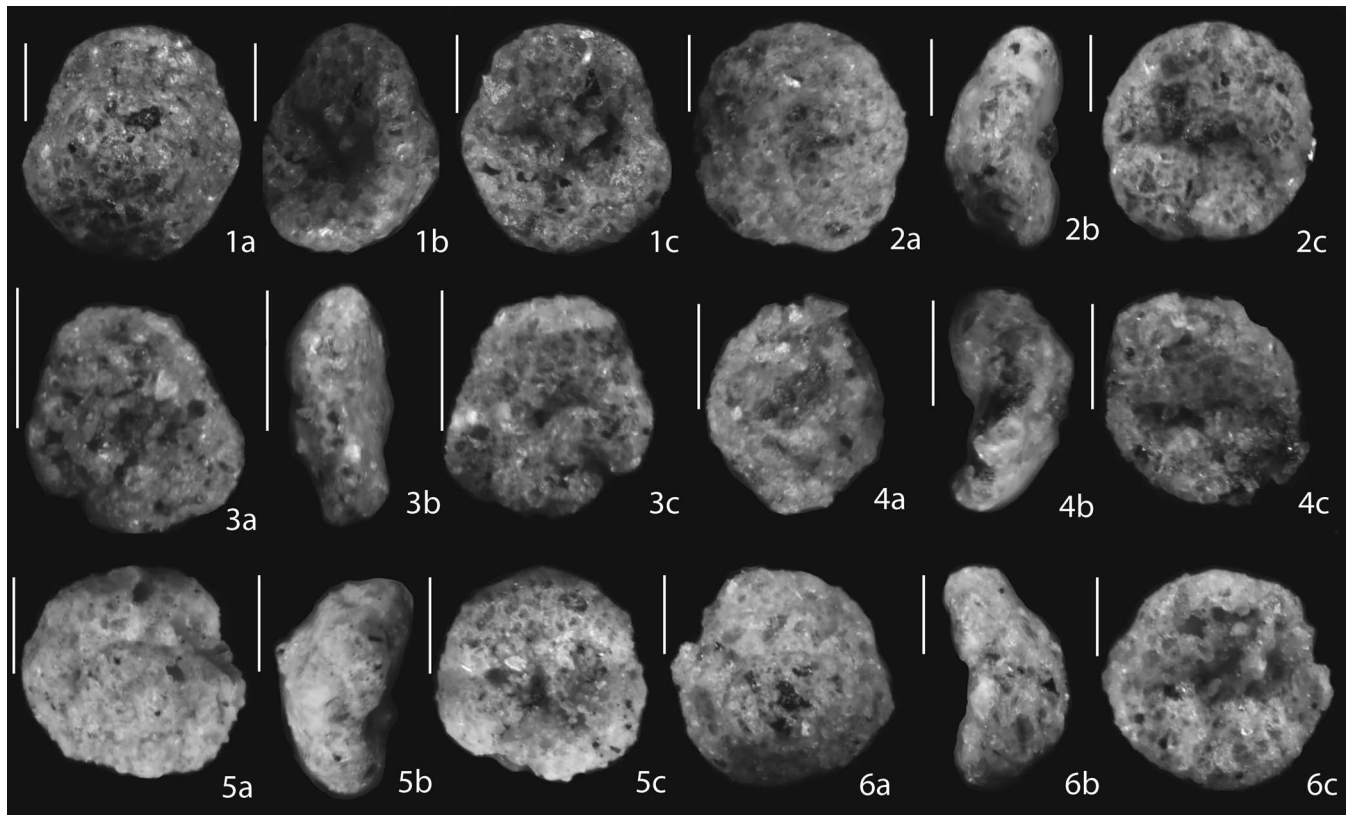


FIGURE 6. *Tritaxis crespinae* n. sp. (scale bars = 100  $\mu$ m; rendered reflected-light micrographs). **1a–c** holotype UWA182177, **1a** spiral side, **1b** peripheral (apertural view), **1c** umbilical side. **2a–c** paratype UWA182178, **2a** spiral side, **2b** peripheral (apertural view), **2c** umbilical side. **3a–c** paratype UWA182179, **3a** spiral side, **3b** peripheral (apertural view), **3c** umbilical side. **4a–c** paratype UWA182180, **4a** spiral side, **4b** peripheral (apertural view), **4c** umbilical side. **5a–c** paratype UWA182181, **5a** spiral side, **5b** peripheral (apertural view), **5c** umbilical side; **6a–c** paratype UWA182182, **6a** spiral side, **6b** peripheral (apertural view), **6c** umbilical side.

The orientation of grains in the test wall is a feature shared by some other species of *Trochammina* including coeval *T. gloveri* and modern *T. hadai*. Other *Trochammina* species (e.g., modern *Trochammina subglobigeriniformis* Mikhalevich, figured by Brönnimann & Whittaker, 1988) have rough walls with no preferred orientation of included grains. The orientation of agglutinated grains forms part of the diagnosis as it may in future provide one criterion with which to taxonomically subdivide *Trochammina*.

**Etymology.** After Professor Geoffrey Playford of the University of Queensland, for his pioneering stratigraphic work on the Holmwood Shale in the Irwin Basin.

*Trochammina gloveri* n. sp.  
Figs. 4.1a–4.6c, 8.1, 9.3–9.4

**Type material.** Holotype UWA182169 (Figs. 4.1a–c); paratype UWA182170 (Figs. 4.2a–c); paratype UWA182171 (Figs. 4.3a–c); paratype UWA182172 (Figs. 4.4a–c); paratype UWA182173 (Figs. 4.5a–c); paratype UWA182174 (Figs. 4.6a–c); paratype UWA182247 (Fig. 8.1); paratype UWA182191 (Fig. 9.3); paratype UWA182192 (Fig. 9.4).

**Diagnosis.** A species of *Trochammina* with spiral side flat or slightly convex, composed of five moderately inflated chambers in the last whorl (average diameter is 380  $\mu$ m); wall with larger quartz (mean grain size ca. 15.2  $\mu$ m) set in a matrix of smaller siliceous grains; some of large quartz grains have a

flat surface orientated tangential to the outer wall surface, others have grains that protrude giving a non-even surface; aperture extends from the umbilicus to an extraumbilical position but not over the periphery; a well-developed lip of uniform width borders the upper edge of aperture.

**Description.** Test trochospiral with moderately inflated chambers (average diameter of figured specimens is 380  $\mu$ m) and a lobate outline. Umbilical side is concave with shallow and narrow umbilicus; spiral side is slightly convex in the earliest chambers but mostly flat in the later chambers. Coiled with 1.5 to 3 whorls with 5 chambers visible in the last whorl. In the last whorl, chambers increase moderately in size as added; in the final chamber the width is greater than the height in both equatorial and axial view. The periphery is rounded with sutures depressed between chambers of final whorl and flush between early chambers on spiral side. Initial chambers have a dark-brown inner organic lining (Fig. 8.1). The wall is composed of large angular quartz grains (mean grain size ca. 15.2  $\mu$ m, Fig. 10) embedded in a matrix of finer siliceous grains. The larger quartz grains have flat and angular surfaces aligned on the wall's outer surface giving a rough finish to the test (Figs. 9.3, 9.4). The aperture is a low arch that extends from umbilicus toward the periphery at the base of the last chamber, but not over the periphery. A distinct lip of uniform width borders the aperture on its upper side.

**Type level.** Upper Holmwood Shale, upper Sakmarian, Lower Permian. Type material extracted from a carbonate-

mudstone nodule 50–60 m below the contact of the Holmwood Shale and the overlying High Cliff Sandstone (Fig. 1B).

*Type locality.* High Cliff, situated on the eastern side of the North Branch of the Irwin River (28.94785°S; 115.54700°E; Fig. 1A).

*Remarks.* *Trochammina gloveri* differs from *T. geoffplayfordi* by 5 globose chambers rather than 4 globose chambers in the last whorl with chambers increasing at a higher rate; the coil is highly variable with 1.5 to 3 whorls rather than about 2.5 whorls. The aperture extends from the umbilicus to half to three-quarters of the way to the periphery as in *T. geoffplayfordi*. No species with equivalent morphological features have been described from Carboniferous of North America or the Permian of Australia.

*Etymology.* The species is named after the late Dr. Joseph John Edmund Glover of the University of Western Australia, a sedimentologist who led many student excursions to the Irwin River region.

#### Genus *Trochamminopsis* Brönnimann, 1976

Type species: *Trochammina pusilla* Höglund, 1947 (pl. 17, fig. 4) = *Trochammina quadriloba* nom. nov. Höglund, 1948

*Remarks.* *Trochamminopsis* differs from *Globotrochamminopsis* Brönnimann and Whittaker, 1988 (type species *Globotrochamminopsis globulosa* (Cushman) = *Trochammina globulosa* Cushman, 1920), by a higher rounded spire with more globose chambers; a more broadly rounded periphery with more depressed sutures; and a single low-arched aperture that extends across the umbilicus rather than resting on the first to the penultimate chamber of the final whorl.

*Trochamminopsis teichertii* n. sp.  
Figs. 5.1a–5.2c, 8.3–8.4, 9.1

*Type material.* Paratype UWA182175 (Figs. 5.1a–c); holotype UWA182176 (Figs. 5.2a–c); paratype UWA182249 (Fig. 8.3); paratype UWA182250 (Fig. 8.4); paratype UWA182189 (Fig. 9.1).

*Diagnosis.* A Permian *Trochamminopsis* with a high, rounded spire (average test diameter is 478 µm); four large globose chambers in final whorl, increasing gradually in size; initial whorls form a highly elevated spire; umbilicus closed; aperture a low asymmetric arch positioned over the umbilicus, bordered above by a thick very narrow lip; wall agglutinated with large clear quartz grains (mean grain size ca. 18.5 µm) set in much finer matrix, giving a smooth almost polished surface.

*Description.* Test trochospiral with large globose chambers tightly coiled (average figured specimen diameter is 478 µm). Coiling is either sinistral or dextral with no preferred direction observed. The spiral side is high with lobate chambers, umbilical side is concave with closed umbilicus. The periphery is broadly rounded with very depressed sutures between chambers of final whorl and slightly depressed between early chambers on spiral side. Coiled with 2 to 3 whorls, with 4 inflated chambers in the last whorl. In the last whorl, chambers gradually increase in size; the final chamber width is wider than high in both equatorial and axial view. Initial chambers have a dark-brown inner organic lining (Fig. 8.3). The agglutinated wall includes both spherical and angular quartz grains (mean grain size ca. 18.5 µm; Fig. 10) embedded in a matrix of finer quartz grains and rare minute dark grains. Many of the quartz

grains have flat surfaces that are tangential to the wall, giving an even finish to the test surface (Fig. 9.1). Aperture is at the base of the last chamber extending as a very low arch across the umbilicus and in some specimens to a slightly extraumbilical position. A thick narrow lip borders the upper side of the aperture.

*Type level.* Upper Holmwood Shale, upper Sakmarian, Lower Permian. Type material extracted from a carbonate-mudstone nodule 50–60 m below the contact of the Holmwood Shale and the overlying High Cliff Sandstone (Fig. 1B).

*Type locality.* High Cliff, situated on the eastern side of the North Branch of the Irwin River (28.94785°S; 115.54700°E; Fig. 1A).

*Remarks.* *Trochamminopsis subobtusa* (Parr, 1942) is a closely related species first described from the Kungurian of the Merlinleigh Basin in Western Australia. Its holotype was re-illustrated by SEM image by Palmieri (1993; Skwarko, 1993, pl. 4, fig. 9) and by rendered light images by Haig 2018 (fig. 8, K–M). Parr's species differs from *T. teichertii* by a lower, less conical spiral side with less inflated chambers. The aperture on the type material of *T. subobtusa* is obscure as it is on specimens described by Crespin (1958, pl. 21, figs. 5, 6) and Haig & Mory (2016, fig. 6y–zc).

The Pennsylvanian species *Trochammina arenosa* (Cushman & Waters, 1927, pl. 27, figs. 4a–c; Cushman & Waters, 1930, pl. 6, figs. 6a–7) and *Trochammina grahamensis* (Cushman & Waters, 1930, pl. 6, figs. 8a–8c) may belong to *Trochamminopsis* but are distorted with obscured apertures (specimens are re-photographed on the Smithsonian National Museum of Natural History website, Department of Paleobiology Collections (<https://collections.nmnh.si.edu/search/paleo/>)).

*Etymology.* The late Professor Curt Teichert, internationally known stratigrapher and palaeontologist, who spent a period, including the Second World War, at the University of Western Australia.

#### Genus *Tritaxis* Schubert, 1921

Type species: *Tritaxis fusca* (Williamson, 1858) revised and neotype selected by Brönnimann & Whittaker (1984, figs. 7–10)

*Tritaxis crespinae* n. sp.  
Figs. 6.1a–6.6c, 8.5–8.7, 9.5

*Type material.* Holotype UWA182177 (Figs. 6.1a–c); paratype UWA182178 (Figs. 6.2a–c); paratype UWA182179 (Figs. 6.3a–c); paratype UWA182180 (Figs. 6.4a–c); paratype UWA182181 (Figs. 6.5a–c); paratype UWA182182 (Figs. 6.6a–c); paratype UWA182251 (Fig. 8.5); paratype UWA182252 (Fig. 8.6); paratype UWA182253 (Fig. 8.7); paratype UWA182193 (Fig. 9.5).

*Diagnosis.* A Permian *Tritaxis* with a low-domed spiral side with early whorls tightly coiled and slightly elevated above the convex spiral profile (average specimen size is 246 µm, mean grain size ca. 17.3 µm); 3 to 4 chambers in final whorl; spiral sutures flush, umbilical depressed; wall with roughened surface; aperture a narrow extraumbilical arch close to the umbilicus and bordered by a wide projecting canopy-like lip.

*Description.* Test concavo-convex with flattened chambers (average specimen diameter is 246 µm). Low trochospiral coiling is either sinistral or dextral with usually 3 to 4 chambers in the last whorl, crescent-shaped in spiral and umbilical view. Umbilical side is concave with closed umbilicus; initial



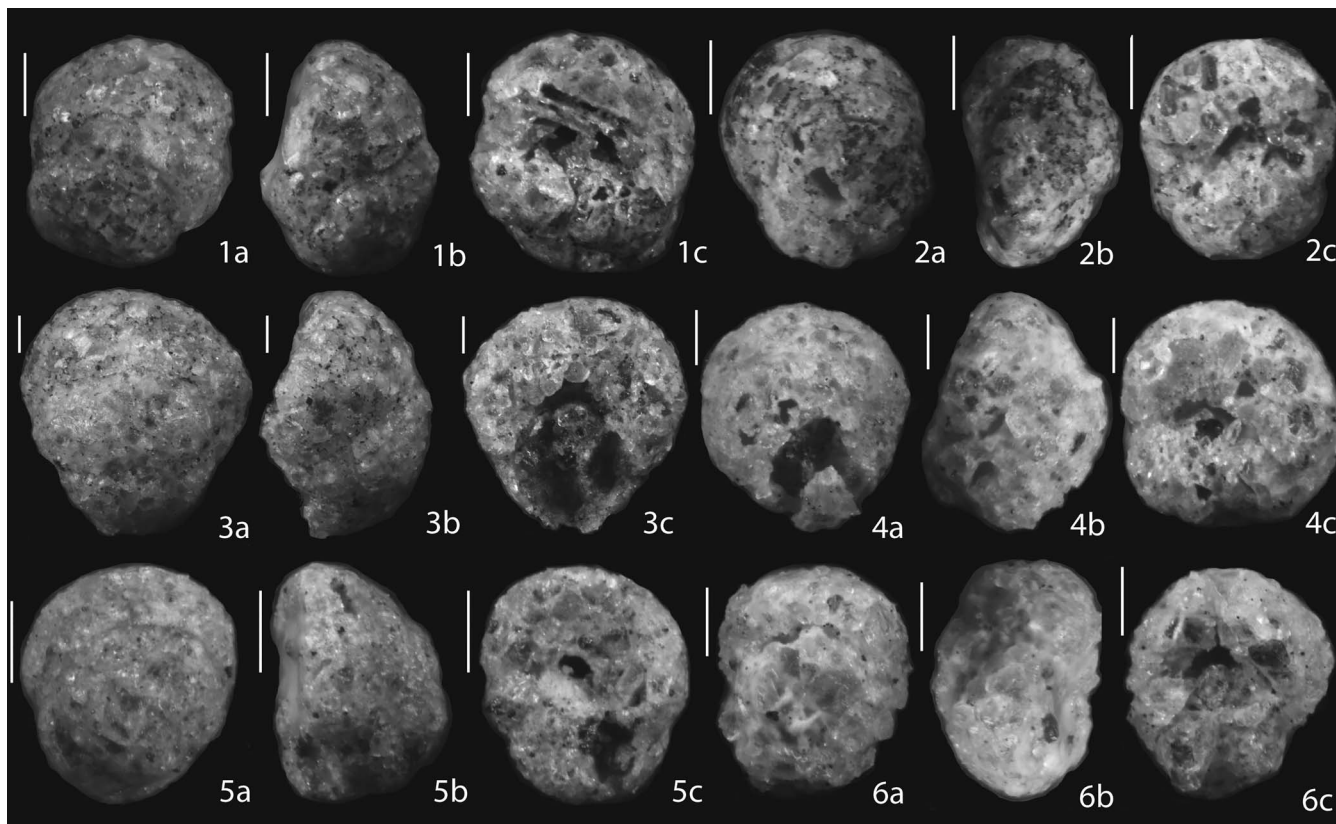


FIGURE 7. *Verispira holmesorum* n. sp. (scale bars = 100  $\mu$ m; rendered reflected-light micrographs). **1a–c** holotype UWA182183, **1a** spiral side, **1b** peripheral (apertural view), **1c** umbilical side. **2a–c** paratype UWA182184, **2a** spiral side, **2b** peripheral (apertural view), **2c** umbilical side. **3a–c** paratype UWA182185, **3a** spiral side, **3b** peripheral (apertural view), **3c** umbilical side. **4a–c** paratype UWA182186, **4a** spiral side, **4b** peripheral (apertural view), **4c** umbilical side. **5a–c** paratype UWA182187, **5a** spiral side, **5b** peripheral (apertural view), **5c** umbilical side. **6a–c** paratype UWA182188, **6a** spiral side, **6b** peripheral (apertural view), **6c** umbilical side.

whorls on spiral side are tightly coiled and slightly more convex than the average convex spiral profile. The periphery is narrowly rounded. Sutures are almost flush on the spiral side but are depressed between chambers of final whorl on the umbilical side. Initial chambers have a dark-brown inner organic lining (Figs. 8.5–8.7). The imperforate organic-cemented wall is mainly composed of small sub-angular quartz grains with scattered dark grains embedded in a finer-matrix (Fig. 9.5). The larger quartz grains (mean size ca. 17.3  $\mu$ m, Fig. 10) have rough and angular surfaces aligned tangentially to the wall outer surface giving a roughened finish to the test surface. The aperture is a single narrow arch at the base of final chamber in an extraumbilical position close to the umbilicus; bordered where preserved, by a wide projecting canopy-like lip (Figs. 6.1c, 6.2c).

**Type level.** Upper Holmwood Shale, upper Sakmarian, Lower Permian. Type material extracted from a carbonate-mudstone nodule 50–60 m below the contact of the Holmwood Shale and the overlying High Cliff Sandstone (Fig. 1B).

**Type locality.** High Cliff, situated on the eastern side of the North Branch of the Irwin River (Fig. 1A) at 28.94785°S, 115.54700°E.

**Remarks.** The aperture of the Permian *T. crespinae* has a similar shape and position to the modern neotype of *T. fusca* as illustrated by Brönnimann & Whittaker (1984, fig. 7). The living environment of *T. fusca* is not known. The

neotype was collected from deep water off the Isle of Skye, Scotland.

**Etymology.** Species named after Irene Crespin from the Australian Bureau of Mineral Resources who compiled the first monograph of Permian foraminifera from Australian basins including the Irwin Basin.

Superfamily: TROCHAMMINOIDEA? Schwager, 1877

**Remarks.** The new species (described below) from the Holmwood Shale belongs with the organic-cemented agglutinated foraminifera that do not secrete a carbonate component of the test wall. The superfamily and lower levels of suprageneric classification are uncertain because the coiling is not uniform trochospiral.

Genus *Verispira* Palmieri 1988

Type species: *Verispira jelli* Palmieri 1988 (holotype figured Palmieri, 1988, figs. 8C–E, 9C–E 11F–I)

**Remarks.** Palmieri (1988, p. 39) described the wall of *V. jelli* as “microgranular silicified” and diagnosed the genus as having a “wall composed of an inner lining and an external thicker microgranular layer.” Examination of Palmieri’s type material by us showed that the specimens were organic-cemented agglutinated types. This genus was placed by Palmieri (1988) among the calcareous globivalvulinids rather than the organic-cemented agglutinated foraminifera.



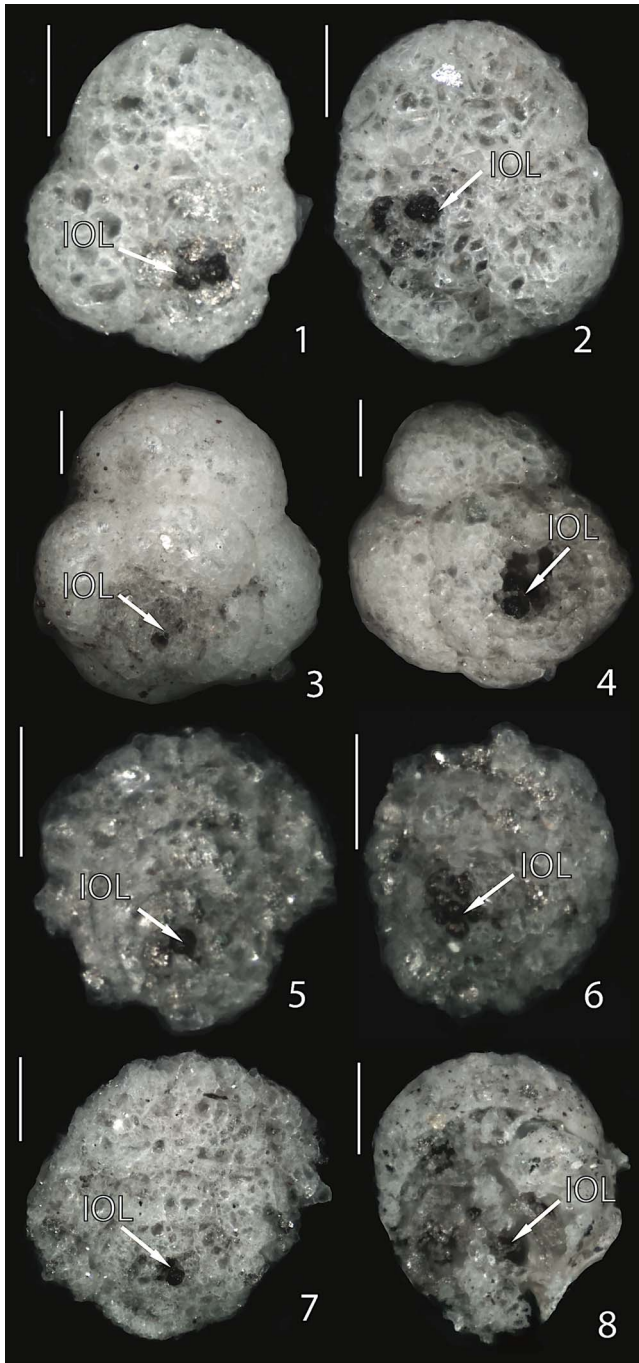


FIGURE 8. Organic cemented agglutinated trochamminoid tests and their preserved inner organic linings (arrowed). 1 *Trochammina gloveri* UWA182247. 2 *Trochammina geoffplayfordi* UWA182248. 3–4 *Trochamminopsis teichertii* UWA182249, UWA1882250. 5–7 *Tritaxis crespinae* UWA182251, UWA182252, UWA182253. 8 *Verispira holmesorum* UWA182254.

*Verispira holmesorum* n. sp.  
Figs. 7.1a–7.6c, 8.8, 9.6

*Type material.* Paratype UWA182183 (Figs. 7.1a–c); paratype UWA182184 (Figs. 7.2a–c); paratype UWA182185 (Figs. 7.3a–c); paratype UWA182186 (Figs. 7.4a–c); holotype UWA182187 (Figs. 7.5a–c); paratype UWA182188 (Figs.

7.6a–c); paratype UWA182254 (Fig. 8.8); paratype UWA182194 (Fig. 9.6).

*Diagnosis.* An organic-cemented siliceous agglutinated species with a low *Ataxophragmium*-like spire and an apertural face that is flat to partially concave (average test diameter is 373  $\mu\text{m}$ ); spiral side a high slightly asymmetric dome; periphery angled with rounded margin; sutures flush or very slightly depressed; wall of mainly large angular and subrounded quartz grains (mean grain size ca. 30.8  $\mu\text{m}$ ) in a finer siliceous matrix; aperture a low curved arch that extends from the umbilicus to one fourth of the way to the periphery at the base of the last chamber, bordered by a narrow lip.

*Description.* Test in a low *Ataxophragmium*-like spire with a broadly flattened umbilical side, where the apertural face is flat to partially concave, and a high slightly asymmetric dome on the spiral side (average diameter of figured specimens is 373  $\mu\text{m}$ ). The periphery is angled with a rounded margin. The coil changes axis during growth and is either sinistral or dextral, consisting of 2 to 4 whorls. The irregular-shaped chambers expand in size as added and strongly overlap the prior chambers. Sutures are very slightly depressed or flush. Initial chambers have a dark-brown inner organic lining (Fig. 8.8). On the spiral side, the final chamber has a low crescentic outline; on the umbilical side, the final chamber is broad and occupies almost half of the test. On the umbilical side, 3–4 chambers are visible; the umbilicus is closed. Wall is composed of mainly large angular quartz (mean size 30.8  $\mu\text{m}$ , Fig. 10) and subrounded quartz grains embedded with a finer siliceous matrix. The position of the quartz grains is well-aligned to the wall outer surface giving a partly smooth finish to the test surface (Fig. 9.6). Aperture is a low curved arch that extends from the umbilicus to one fourth of the way to the periphery at the base of the last chamber. A distinct narrow lip borders the aperture on its upper side.

*Type level.* Upper Holmwood Shale, upper Sakmarian, Lower Permian. Type material extracted from a carbonate-mudstone nodule 50–60 m below the contact of the Holmwood Shale and the overlying High Cliff Sandstone (Fig. 1B).

*Type locality.* High Cliff, situated on the eastern side of the North Branch of the Irwin River (28.94785°S; 115.54700°E; Fig. 1A).

*Remarks.* The Artinskian species described by Palmieri (1994) from the Bowen Basin in Queensland are smaller than *V. holmesorum* from the Sakmarian Holmwood Shale and have a greater number of chambers in the test. *Trochammina careyi* Conkin & Conkin (1993) from the Permian of Tasmania may belong to the same genus as *V. holmesorum* but has a much larger test (diameters range to 990  $\mu\text{m}$ ).

*Etymology.* Species named after the Holmes family of Holmwood Station, who for almost 100 years have allowed students and staff from the University of Western Australia to visit important geological sites on their property.

## DISCUSSION

### THE HOLMWOOD SHALE, ANCIENT ANALOGUE OF MODERN ESTUARINE MUD FACIES

The Holmwood Shale was deposited on a low-gradient sea-floor in a partly enclosed shallow-water interior sea (Haig et al., 2014, 2017, 2022). An estuarine-like environment was

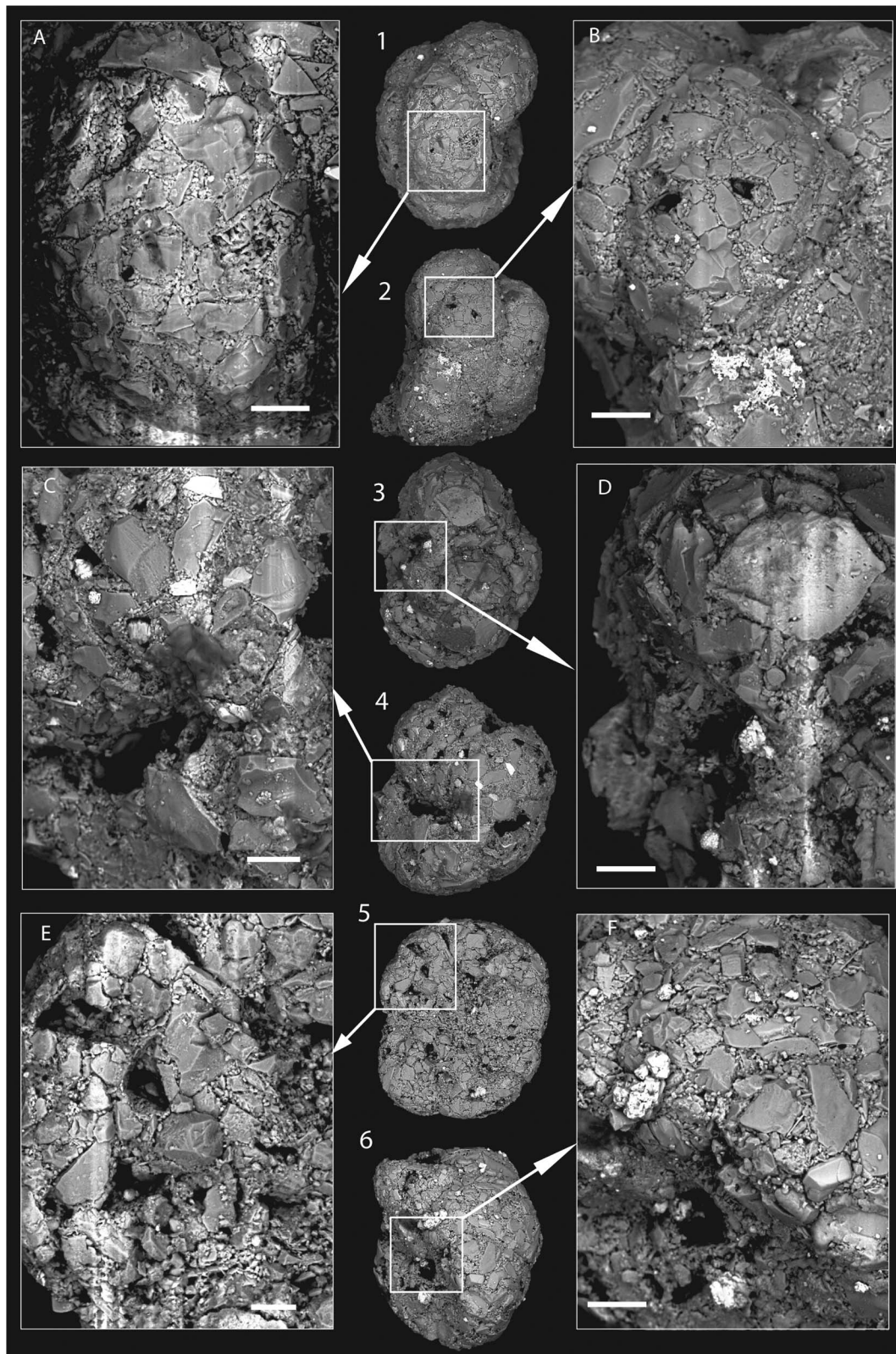


FIGURE 9. Scanning electron micrographs of selected specimen showing the variation in the wall agglutinated of **1** *Trochamminopsis teichertii* UWA182189. **2** *Trochammina geoffplayfordi* UWA182190. **3-4** *Trochammina gloveri* UWA182191, UWA182192. **5** *Tritaxis crespinae* UWA182193. **6** *Verispira holmesorum* UWA182194. The enlarged view (A-F) gives details of the orientation of quartz grains positioned in a pavement tangential to the wall surface giving a smooth surface.



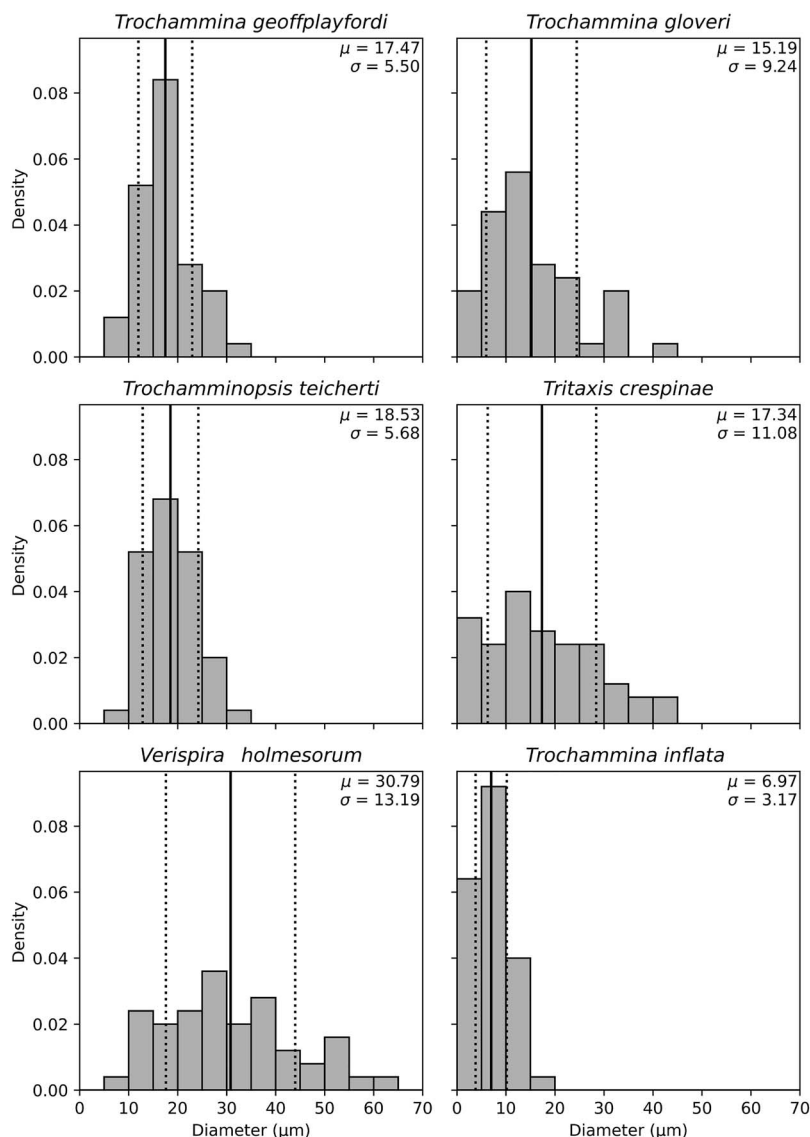


FIGURE 10. Quartz grain measurements on trochamminoid tests, contrasted to the modern *Trochammina inflata* (type species of the genus). Note the variability of grain aggregation on the wall surface.

present, probably with variable hyposaline to normal-marine salinity, during deposition of the formation (Haig et al., 2018, 2022). The fauna recorded in the methane seep deposits low in the Holmwood Shale indicate normal marine salinity (Haig et al., 2022). Porcelaneous foraminifera as well as crinoids, brachiopods, and bryozoans found in the carbonate nodules suggest that normal-marine conditions were also present at the studied site 50–60 m below top of the Holmwood Shale. These and rare algal macrophyte fragments (*Litostroma*) and sponge spicules indicate very shallow-water conditions. *Litostroma*, first described from a Pennsylvanian shale in Oklahoma, was a single-celled thick thallus, composed of irregular-shaped cells with minute perforations. Modern monostromatic algae *Smithora* and *Porphyra*, living on hard surfaces in the upper photic zone, may be similar to *Litostroma* (Harlin, 1973; Neefus et al., 2008). In the Holmwood sea, *Litostroma* may have anchored to skeletal fragments (e.g., brachiopod shells and crinoid stems) in the seafloor mud or to surfaces of partly emergent nodules.

Living conditions of trochamminoids from the Holmwood Shale based on their morphology and lithofacies association can be interpreted from the life habitats of modern taxa belonging to this superfamily. In Western Australia, the life modes of two modern *Trochammina* have been well documented. The apertural position and the width of the umbilicus (allowing previous apertures to remain open) are indicators of living habitats. *Trochammina inflata* (type species of *Trochammina*) is known globally, living as an epiphyte on exposed stems and roots of marsh vegetation. In the neotype of *Trochammina inflata*, described by Brönnimann & Whittaker (1984, their figs. 4, 5), the umbilicus is broad and open, and the upper border of the low-arched aperture, with a narrow well-defined lip, terminates in the umbilical cavity. Similar observations are made by the present authors on *T. inflata* living in marshes in southwest Australia. *Trochammina hadai* Uchio, 1962, has been recorded living in the upper 1 cm of mud on the floor of Lake Hamana at water depth of <10 m

(Matsushita & Kitazato, 1990). The species was recorded living aperture down in a flocculent mud layer on an estuary floor at about 5 m water depth in Western Australia (Tremblin et al., 2021, their fig. 9). The umbilical and apertural details of *T. hadai* are more variable than *T. inflata* (Tremblin et al., 2021, their figs. 4–6). Compared to *T. inflata*, morphotypes of *T. hadai* have a more restricted umbilicus, although some have a similar aperture and lip arrangement (e.g., Tremblin et al., 2021, their figs. 6d, f, j, n, p, r); in others the aperture spans the umbilicus (Tremblin et al., 2021, their figs. 6h, l, t).

Apertural positions and chamber shapes of *Trochammina geoffplayfordi*, *T. gloveri*, and *Trochamminopsis teichertii* suggest similar living conditions to *T. hadai*, which lives aperture facing down in a flocculent mud layer (Fig. 11B). The concavo-convex and plano-convex tests in *Tritaxis crespinae* and *Verispira holmesorum* are probably indicative of an epibiontic lifestyle, for example (1) on *Litostroma* thalli with the aperture facing downward on the blade, (2) on invertebrate skeletal debris, or (3) on exposed surfaces of previously formed carbonate nodules (Fig. 11A). Modern epiphytic foraminifera (e.g., *Planorbulina*, *Acervulina*, *Cyclocibides*) on seagrass blades and seaweed thalli, secrete an adhesive substance (glycosaminoglycan-like) that maintains strong attachment to the host surface (DeLaca & Lipps, 1972; Langer, 1993). Glycosaminoglycan is an unbranched polysaccharide commonly found in organic cement, organic linings, and matrix deposits both in benthic and planktonic foraminifera, and it also plays an important role in the biomineralization process of types with calcareous tests (Lowenstam & Weiner, 1989; Langer, 1992). The organic cement and inner organic linings of the Permian trochamminoids were probably a glycosaminoglycan-like material.

#### TROCHAMMINOID EVOLUTIONARY HISTORY

Trochamminoids have a known evolutionary history dating from the Mississippian. The Mississippian *Trochammina melhi* is the oldest known trochospiral foraminifera, but its placement into a genus is tentative because of poor preservation (including an obscured aperture). It is possible that the Carboniferous species belong to two genera *Trochammina* and *Trochamminopsis* (Fig. 12), but details of apertures are lacking because the tests of figured specimens are distorted and variably deflated.

As represented in the studied assemblage by the Sakmarian (294–290 Ma; Fig. 12), three genera of trochamminids and one related trochamminoid had evolved. These are the oldest known representatives of the superfamily that are preserved with inflated chambers and undistorted apertures, and they are among the oldest known trochospiral foraminifera. In the Holmwood Shale, spiral organic linings of foraminifera have been recorded (Playford, 2021, their fig. 9L, M), probably derived from the trochamminids. They all have in common (1) an inner organic lining in the earliest chambers of the test; (2) agglutination of larger angular quartz grains in a matrix of finer quartz grains; and (3) apertures with distinct lips, but with differentiation in type of lip and apertural position. Species of *Trochammina*, *Trochamminopsis*, and *Tritaxis* have well-developed lips over their apertures with patterns of chamber addition and wall agglutination specific to each species. An apparently related species with a low-*Ataxophragmium*-

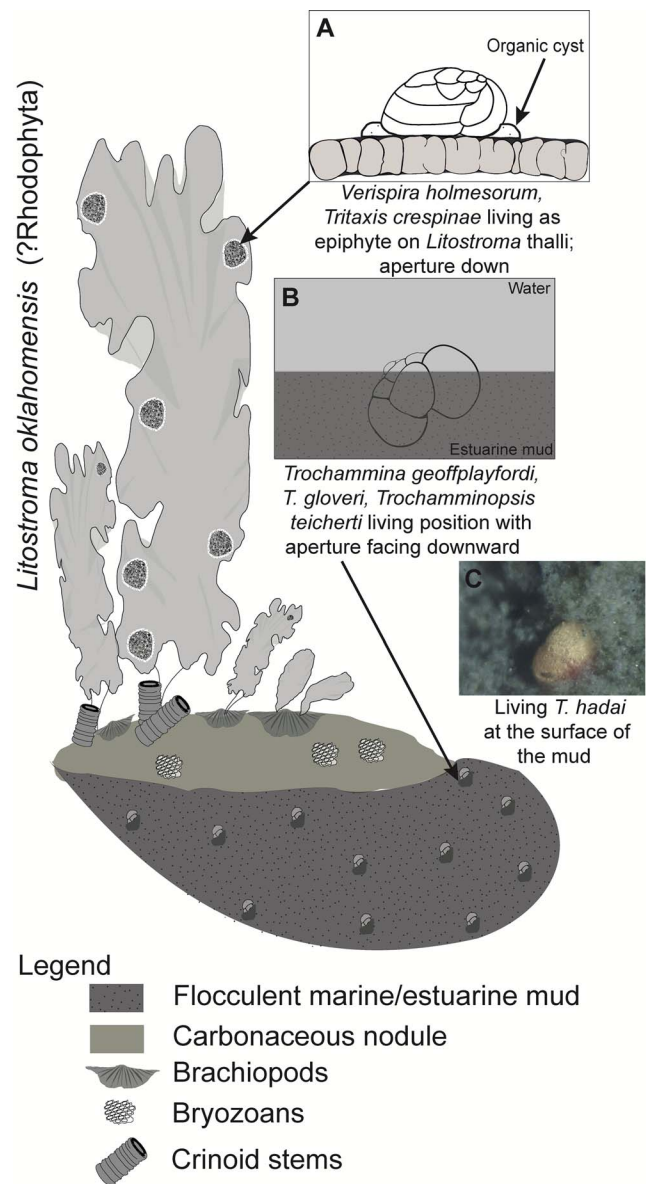


FIGURE 11. Palaeoecological reconstruction of the possible living habitats of studied trochamminoids associated with estuarine mud and the red algal macrophyte *Litostroma*. **A**, Trochamminoid *Verispira holmesorum* living as epiphyte on *Litostroma* sheet-like thalli with the aperture facing down on the blade; note the protective fence-like organic cyst that surrounds the specimen. **B**, Trochamminids showing only the last two chambers of the final whorl with also the aperture downward in the flocculent mud layer. **C**, living position of *Trochammina hadai* photographed from Leschenault Inlet.

like spire and an apertural face that is flat to partially concave had also appeared by 290 Ma. Early diversification of genera (which may have started during the Pennsylvanian with the evolution of *Trochamminopsis* from *Trochammina*; Fig. 12) was followed during the Late Jurassic–Early Cretaceous (149–100 Ma; Fig. 12) by diversification of genera (viz. *Calyptamina*, *Portatrochammina*, *Insculptarenula*, and *Lepidoparatrochammina*) based on chamber shape, and then in the Cenozoic by diversification related to development of areal and multiple apertures.



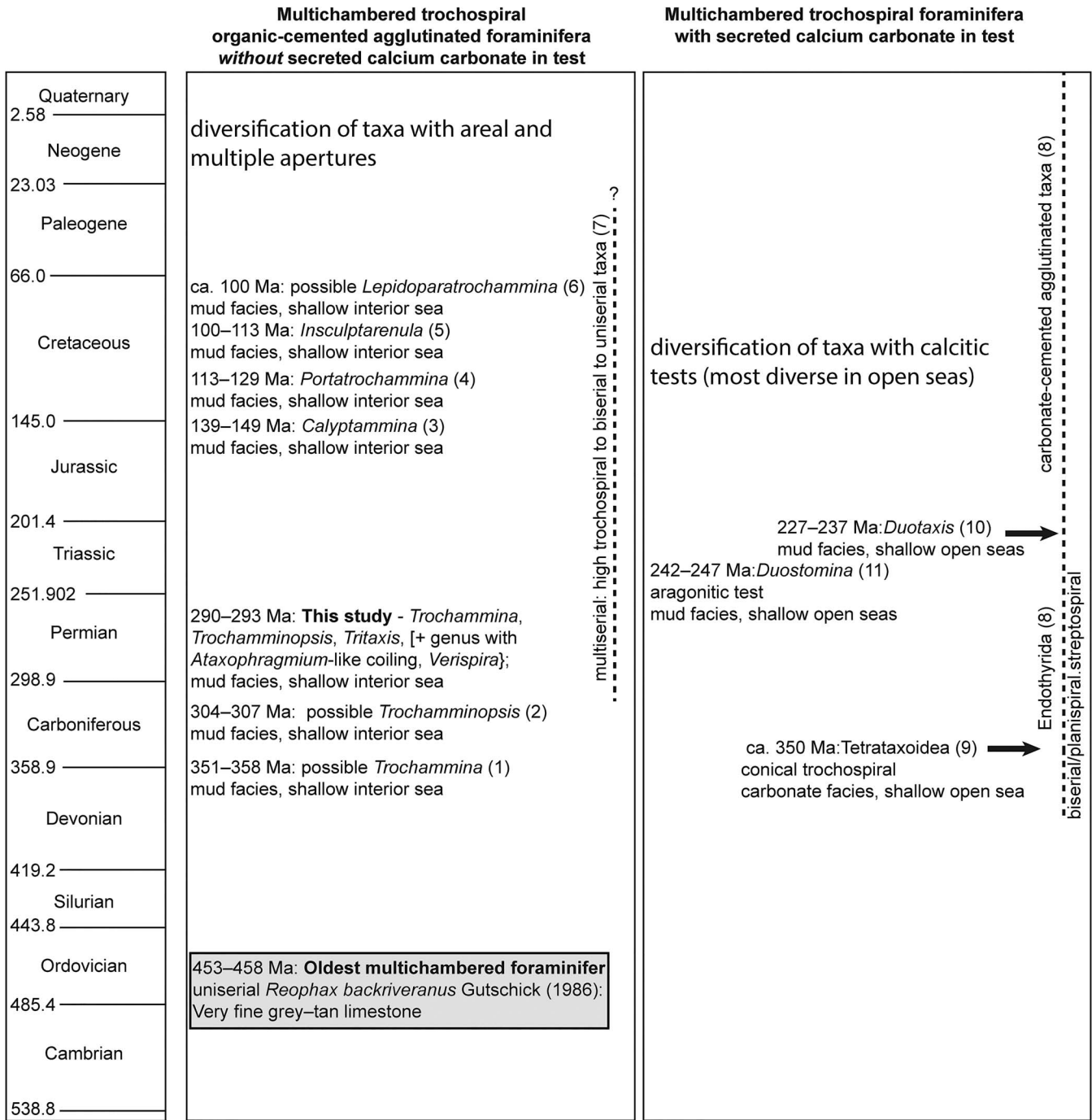


FIGURE 12. Stratigraphic position of the studied trochamminoid assemblage in relation to (1) species records that are among the stratigraphically oldest for the genera *Trochammina* Parker & Jones, 1859; *Trochamminopsis* Brönnimann, 1976; *Tritaxis* Schubert, 1921, *Verispira* Palmieri, 1988, *Calyptammina* Nagy & Basov, 1998, *Portatrochammina* Echols, 1971, *Insculptarenula* Loeblich & Tappan, 1985, *Lepidoparatrochammina* Brönnimann & Whittaker, 1986; and (2) the stratigraphic records of other important trochospiral foraminiferal groups (including the genera *Duostomina* Kristan-Tollmann, 1960; *Duotaxis* Kristan, 1957). Sources for records: **1** *Trochammina mehli* Conkin & Conkin, 1964, aperture obscure. **2** *Trochammina arenosa* Cushman & Waters, 1927, deflated test, aperture obscure. **3** *Calyptammina praegyroidiniformis* Bystrova & Kossitskaja in Bystrova, 1984. **4** *Trochammina davenportensis* Ludbrook, 1966, and *Trochammina raggatti* Crespin, 1944 (see also Crespin, 1963). **5** *Trochammina subinflata* Crespin, 1963. **6** *Trochammina calima* Loeblich & Tappan, 1950. **7** Stratigraphic range of high trochospiral to biserial to uniserial group of organic-cemented agglutinated taxa including *Gaudryinopsis*, *Gaudryinella*, *Verneuilinoides*, *Uvigerinammina*. following Haig & McCartain (2010). **8** connection between Endothyrida and later carbonate-cemented agglutinated taxa suggested by Vachard et al., (2010) with conical Tetrataxioidea (**9** see Loeblich & Tappan, 1987) the oldest known group that includes an initial trochospiral stage, and *Duotaxis* (**10** see Kristan, 1957, and Haig et al., 2007) as the oldest known carbonate-cemented agglutinated group with an initial trochospiral stage. **11** oldest age recorded by Zaninetti (1976) recorded for *Duostomina*.

In line with their morphological evolution, by 294–290 Ma, trochamminoids not only lived in seafloor mud but were epibionts (possibly including epiphytes) on objects on the seafloor. The very close morphological similarities between the Permian and modern trochamminids suggests that highly variable shallow-water estuarine-type environments, where both are common, may have promoted morphological conservatism over an immense interval of time (at least 300 Myr).

The origin of the trochamminoids is difficult to discern from the known stratigraphic record of foraminifera. It seems unlikely that they arose from among groups that built their tests, at least in part, of secreted carbonate (Fig. 12). It also suggests an organic-walled predecessor that evolved the ability to organically cement agglutinated grains to form a more rigid test.

The short-ranged calcareous late Paleozoic Tetrataxidea have a very different conical test, spiral arrangement, and layered wall structure (see Loeblich & Tappan, 1987; Vachard et al., 2010) to the early trochamminoids. The other spiral late Paleozoic Endothyrida are mainly planispiral to streptospiral and lack trochospiral representatives. The first carbonate-secreted trochospiral tests that resemble trochamminoids (although with very different apertural arrangements, but with similar organic linings in initial whorls) are among the aragonitic *Duostomina* of the Middle Triassic Robertinida. The first trochospiral carbonate-cemented agglutinated types are probably from the Middle Triassic–Early Jurassic *Duotaxis* and *Siphovalvulina* (Fig. 12; Haig et al., 2007, tables 3, 4).

This early evolution of trochospiral foraminifera has been documented only in shallow marine facies. Almost nothing is known of foraminiferal assemblages from deep oceanic sediment of the Paleozoic and early Mesozoic. Brönnimann & Whittaker (1988) recorded very diverse trochamminoid assemblages from modern deep-sea sediments. It may be that the evolution of trochospiral foraminifera took place in deep-sea rather than shallow epicontinental basins. The close similarity of *Trochammina geoffplayfordi* with modern *T. hadai* suggests very conservative morphological evolution. Seemingly, *Trochamminopsis teichertii* is like the modern type species of *Trochamminopsis* found in muddy sediment in a Norwegian fjord (Höglund, 1947). Among trochamminids characterized by an arched aperture at the base of the final chamber, the morphological evolution implied by stratigraphically oldest known occurrences cited in Figure 12 suggests that the shape of chambers and the tightness and elevation of the coil are features that may have most taxonomic importance at genus/species level. For example, *Trochamminopsis* is separated from *Trochammina* by its very tight coiling (which results in the aperture spanning the umbilicus) and its elevated spire; *Tritaxis* differs by its thin concavo-convex test and few chambers per whorl; *Calyptammina* differs by its elevated umbilical side, slowly expanding chambers with trapezoidal terminal faces; *Portatrochammina* differs by a lobe from the final chamber covering the umbilicus; *Insculptarenula* differs by its rapidly enlarging chambers being inflated around the umbilicus giving the terminal face a triangular aspect; and *Lepidoparatrochammina* differs in its compressed broad spire with a greater number of chambers in final whorl. *Paratrochammina* Brönnimann, 1976 (type species *P. madeirae* Brönnimann, 1976), was separated from *Trochammina* by having a basal

aperture that extended across the umbilicus toward the periphery. More importantly, in *P. madeirae*, the spire and chambers are more compressed than in *Trochammina*, and the peripheral profile is roundly angled rather than globose (Brönnimann, 1979). The life mode of *P. madeirae* is not known.

Among modern *Trochammina*, the infaunal *T. hadai* lies at some distance from the type species *T. inflata* in molecular analyses based on the 3' end fragment of the SSU rRNA rooted in species of *Reophax* (Tremblin et al., 2021, their fig. 8). Phylogenetic classifications based on molecular analysis of the modern fauna must also take into account the stratigraphic distribution of fossil species. Among multi-chambered organic-cemented agglutinated foraminifera from shallow seas, especially those with estuarine characteristics, Haig & McCartney (2010) showed the very conservative morphological development and similarity in faunal structure within the Hormosinidae, Haplophragmoididae, Spiroplectamminidae, and Verneulinoididae as well as the Trochamminidae from the Carboniferous to the Cretaceous. Many of these families have living representatives that closely resemble the fossil morphotypes (e.g., see Tremblin et al., 2021 for *Trochammina*; Haig, 2020 for *Ammobaculites*). Most of these forms are infaunal in mud. Although some genetic drift will have occurred over the last 294 Myr, the morphological evolution within *Trochammina* has been extremely conservative. Perhaps being adapted for life in mud in a highly variable environment is ideal for very slow evolution and escaping major mass extinctions. In comparison, shallow-water foraminifers from open-ocean settings suffered severely from mass extinctions as illustrated in their stratigraphic ranges (Loeblich & Tappan, 1987).

## CONCLUSIONS

By the Early Permian (late Sakmarian, 294–290 Ma) representatives of *Trochammina*, *Trochamminopsis*, and *Tritaxis* had developed morphologies very similar to their modern representatives. They exhibit the same variation in chamber shape and coiling, apertural position, apertural lip development, agglutination patterns, and inner organic linings as in the modern analogues. Their morphology and the host mudstone facies suggest that three species, *Trochammina geoffplayfordi*, *Trochammina gloveri*, and *Trochamminopsis teichertii* may have lived in a flocculent-mud layer on an estuarine-like seafloor. *Tritaxis crespinae* and a related *Verispira holmesorum* were possibly epiphytes on the monostromatic alga *Litostroma* or epibionts on skeletal debris on the muddy seafloor.

Poorly preserved trochamminids had appeared during the Carboniferous but known representatives have deflated tests with very deformed umbilical sides and obscured apertures. The earliest forms from the Mississippian may be a *Trochammina* but later forms in the Pennsylvanian possibly include *Trochamminopsis*. By the Early Permian, the five species studied here belonging to four genera were present in shallow water interior continental seas. The Late Paleozoic evolution of trochamminids in the deep sea is unknown.

The Carboniferous–Early Permian trochamminids are the oldest known trochospiral foraminifera. We have not recognised a possible ancestor among the contemporaneous calcareous Tetrataxidea or Endothyrida. The morphologically closest calcareous trochospiral forms belong to *Duostomina* of the Triassic (which also has an inner organic lining).



Following the initial Carboniferous–Early Permian diversification of the trochamminids, a further interval of change mainly affecting the shape of chambers took place during the Late Jurassic–Early Cretaceous. During the Cenozoic, trochospiral morphotypes with complex multiple apertures evolved. The few molecular analyses done on modern trochamminid species suggest that the *Trochammina hadai* group (including the early Permian *T. geoffplayfordi* and *T. gloveri*) are at some distance from *Trochammina inflata* (the type species of the genus). The presence of morphotypes that are almost identical in modern estuaries and late Paleozoic interior seas suggest that trochamminid evolution was very conservative, possibly due to adaptation to highly variable environments.

Future work should involve revision of Late Jurassic and Cretaceous trochamminids of the second evolutionary radiation. Carbonate nodules in mudstone facies in the Carboniferous and in the Upper Devonian should be investigated for well-preserved trochamminid assemblages to extend the record of genera back in time and to look for possible ancestral forms.

#### ACKNOWLEDGMENTS

Clément Tremblin is deeply grateful for a Loeblich and Tappan Research Student Award 2022 given by the Cushman Foundation to pursue the ongoing study on the evolution of the trochamminids. I am thankful to Dr. Liliana Stoian, Dr. Natalie Schroeder, and Dr. Caitlin Syme for their assistance, access to the Permian and Cretaceous collections and the facilities provided at the South Australia Drill Core Reference Library, Adelaide, Geoscience Australia, Canberra and Queensland Museum, Brisbane respectively. Brian Huber sent photographed images of the Carboniferous *Trochammina* from the Cushman Collection the Smithsonian National Museum of Natural History, Washington, D.C., USA. Kailah Thorn of The University of Western Australia is thanked for her curatorial assistance, and Jenny Bevan for proofreading drafts of the manuscript. Daniel Peyrot provided palynological information on the studied material and support for Clément Tremblin to access a scanning electron microscope. We thank the Oceans Graduate School at The University of Western Australia for facilitating the voluntary research internship of Clément Tremblin and the Honorary Senior Research Fellowship of David Haig. The authors acknowledge the facilities, and the scientific and technical assistance of Microscopy Australia at the Centre for Microscopy, Characterisation & Analysis, The University of Western Australia, a facility funded by the University, and State and Commonwealth Governments. The isolated specimens mounted on cardboard slides are curated in the Earth Science Museum at the University of Western Australia. The authors declare that they have no conflicts of interest.

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Received 30 January 2023  
Accepted 19 May 2023



Cushman  
Foundation for  
Foraminiferal  
Research