

The serpulid polychaete *Rotulispira* from the Late Cretaceous of Western Australia

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ABSTRACT – Four species of the serpulid polychaete *Rotulispira* are described from Late Cretaceous strata in the Perth and Southern Carnarvon basins in Western Australia. New species described are *Rotulispira glauerti* sp. nov. and *Rotulispira apiaria* sp. nov., from late Santonian to early Campanian chinks, and *Rotulispira protea* sp. nov. from a late Maastrichtian marl. *Rotulispira glauerti* and *R. apiaria* sometimes formed a commensal relationship with the hydroid *Protulophila gestroi* Rovereto, 1901. This is the first record of hydroids from the Cretaceous of Australia. Distribution of the hydroids on the serpulid tubes, combined with the location of gastropod predatory incisions on *R. protea*, allow an assessment to be made of the likely life orientation of these species. *Rotulispira protea* is remarkable for the extremely high levels of phenotypic plasticity that it displays. Severe environmental stress is known to induce increased levels of phenotypic plasticity in living organisms. This phenomenon in *Rotulispira* suggests that severe environmental stress might have been a contributory factor in the end-Cretaceous mass extinction event.

KEYWORDS: Polychaeta, Serpulidae, mass extinction, phenotypic plasticity, environmental stress, Cretaceous, Australia

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INTRODUCTION

A number of species of serpulid polychaete worms long assigned to *Rotularia* (s.l.) are known from the Late Jurassic to the Late Eocene (Savazzi 1995; Vinn 2008; Astibia et al. 2016; Hasan Vand et al. 2018; Elorza and Astibia 2018, 2020), and are relatively common components of many Cretaceous marine faunas. These polychaetes all inhabited a spiral calcareous tube and had a worldwide distribution. They lived primarily in shallow marine sediments, and are most commonly found in relatively fine-grained sediments, such as chinks, greensands and clays. Unlike many other serpulids, shell growth in these ‘rotulariids’ followed a developmentally more controlled growth programme, resulting in the characteristic tightly-coiled spiral tube, with a straightened terminal shaft. The coils can be planispiral, trochospiral, or both.

There has been ongoing debate in the literature about how this suite of spiral-tubed serpulids, as typified by *Rotularia* and *Rotulispira*, with their apparent free, unattached habit, were orientated on or within the sediment. Savazzi (1995) favoured a lifestyle with

the coiled tubes lying on the sediment surface. This orientation, along with the extended terminal tubes, he argued, provided a ‘snowshoe’ function, diminishing the risk of the animal sinking into the sediment. It thus functioned as a reclining suspension feeder. Seilacher et al. (2008), on the other hand, favoured an orientation with the final tube acting like a chimney, and pointing vertically out of the sediment, into which the rest of the tube was partially buried.

Prior to this study, no species of *Rotulispira* had been described from Australia. One of the four species of this genus described in this paper has, for over a century, been compared with a form from the Aptian Toolebuc Limestone in Queensland which was described on the basis of a single slab covered by numerous specimens. Etheridge (1907) described this species as *Spirulaea gregaria*. Subsequently it became regarded as a species of *Rotularia* (Regenhardt 1961) or, more recently, *Rotulispira* (Jäger 2004, p. 210). Etheridge (1913) considered a form from the Late Cretaceous Gingin Chalk in the Perth Basin in Western Australia as conspecific with the Queensland species. Since that time no further studies of the polychaete fauna of the Late Cretaceous of

Western Australian have been undertaken and subsequent references to this form have followed Etheridge's species assignment (e.g. McNamara et al. 1993).

Extensive collecting from Late Cretaceous deposits in Western Australia, mainly in the last three decades of the twentieth century, has revealed a much greater range of forms than previously recognised. Two species, including the form Etheridge (1913) considered to be *Spirulaea gregaria*, have been recognised in the Gingin Chalk in the Perth Basin and are herein assigned to *Rotulispira*. In the Southern Carnarvon Basin the same pair of species is found in the contemporaneous Toolonga Calcilutite, although the frequency of occurrence of the different species varies greatly between the two lithostratigraphic units. Two further species of *Rotulispira* are described from the younger Miria Formation.

Rotulispira was originally described as *Praerotularia*, a subgenus of *Rotularia*, proposed by Lommerzheim (1979). Jäger (1993) subsequently demonstrated that *R. (Praerotularia)* was synonymous with *Rotulispira* Chiplonkar and Tapaswi, 1973. The rationale for this decision, which is followed herein, is discussed in more detail below. I follow the recent practice of regarding *Rotulispira* as being of generic status (Ippolitov et al. 2014). Interestingly, species assigned by Lommerzheim (1979) to *Praerotularia* (now *Rotulispira*) became very rare in the northern hemisphere from the Turonian through to the Maastrichtian (Jäger 1993), a period when they are particularly common in Western Australia. Despite the presence of extensive Paleocene and Eocene carbonates in the Southern Carnarvon Basin, neither *Rotulispira*, nor *Rotularia* have, to date, been found in these younger deposits.

A characteristic feature of the species of *Rotulispira* described herein is the large difference in extent of phenotypic plasticity exhibited by the four species, with little being shown by the two older species, but extremely high levels in the two species occurring in the late Maastrichtian Miria Formation. This is despite *Rotularia* and *Rotulispira* possessing the most rigid developmental programmes of any serpulids (Seilacher et al. 2008). The extent to which this is a phenotypic manifestation of environmental conditions pertaining at the end of the Cretaceous is examined, as it potentially has a bearing on the causative agents of the end-Cretaceous mass extinction. The rationale behind this approach derives from research on a range of living organisms that has shown that there is a strong causal link between severe environmental stress and elevated levels of phenotypic plasticity (Bretsky and Lorenz 1969; Parsons 1987, 1989, 1993; Holloway et al. 1990; Hoffman and Parsons 1991; Hoffman and Hercus 2000; Stanton et al. 2000; Badyaev 2005). Furthermore, as stress levels increase, so does the likelihood of extinction.

Some of the species of *Rotulispira* from the Western Australian Late Cretaceous deposits show evidence of bioclaustration, in which the hydrozoan *Protulophila gestroi* Rovereto, 1901 lived commensally with the serpulids. This is the first time that this phenomenon has been described from the fossil record in Australia. The distribution of the hydroids on the serpulid tubes is examined, in conjunction with an assessment of the distribution of predatory incisions in one of the species of *Rotulispira*, and their relevance to the mode of life of *Rotulispira* is investigated.

GEOLOGICAL SETTING

GINGIN CHALK

Late Cretaceous deposits in Western Australia are confined to the Perth and Southern Carnarvon basins (Figure 1). In the Perth Basin they are characterised by a mixture of greensands and glauconitic chalks, in lithostratigraphic order from the lowest unit, the Molecap Greensand, which is conformably overlain by the Gingin Chalk, followed by the Poison Hill Greensand (Figure 2). Specimens of *Rotulispira* in the Perth Basin are confined to the Gingin Chalk. This is a unit of chalk and chalky marls, which are often glauconitic, especially in the upper part. The formation outcrops intermittently over a distance of about 90 km between Gingin in the south and Dandaragan in the north. The type section, at McIntyre Gully in Gingin, 80 km north of Perth, is about 22 m thick (Feldtmann 1963). It contains numerous burrowed omission surfaces, and the lower part is a sandy glauconitic marl, with some phosphatic intraclasts (Gale et al. 1995). The basal part is known to be of Santonian age on the basis of the presence of *Uintacrinus socialis* in the lower 4 m, followed by 2–2.5 m with *Marsupites testudinarius* (Feldtmann 1963). A Campanian age for the upper part is shown by the incoming of *Broinsonia parca* 1 m below the top (Shafik 1990; Haig 2002). Evidence from ostracods (Ballent and Whatley 2007) suggests that the Gingin Chalk was a relatively warm water deposit (with a minimum at 10°C) laid down on a shallow shelf at a depth of about 100 m.

The fauna is dominated by bivalves (Feldtmann 1951, 1963), in particular *Inoceramus*, and brachiopods (Craig 1999) and to a lesser extent cirripedes, crinoids, ammonites, sponges (Buckeridge 1983), sharks (McNamara et al. 1993) and corals (Jell et al. 2011), along with rare echinoids (McNamara 1986). *Rotulispira* occurs throughout this unit, as does another serpulid, *Orthoconorca pyramidale* (Etheridge, 1913). The dominant *Rotulispira* species is *R. glauerti* sp. nov., with much rarer occurrences of *R. apiaria* sp. nov.

TOOLONGA CALCILUTITE

Carbonates are far more extensively developed, both geographically and temporally, in the Southern Carnarvon Basin, which lies to the north of the Perth Basin (Figure 1). The lateral equivalent of the Gingin Chalk in the Southern Carnarvon Basin to the north is the Toolonga Calcilutite which, like the Gingin Chalk, forms the first carbonate unit in the Cretaceous sequence of this area (Lynch 1991). This unit is far more extensive in areal extent than the Gingin Chalk, outcropping sporadically from near Kalbarri in the south to the Giralia Range, some 600 km to the north, and ranging in age from mid-Coniacian to early Campanian (see Haig 2002). As Gale et al. (1995) have pointed out, the Toolonga Calcilutite is a true chalk, being composed mainly of calcareous nannofossils and foraminifers. The type section on the north side of the Murchison River is 26 m thick (Johnstone et al. 1958). Both *Uintacrinus socialis* and *Marsupites testudinarius* are present in the lower part of the unit, indicating an Upper Santonian age for the lower part of the section in the Kalbarri region. Young (2016) documented *Uintacrinus socialis* over a thickness of almost 4 m, overlain by a sequence 2 m thick with *Marsupites testudinarius*. *Rotulispira*, especially *R. apiaria*, is particularly common in the *Marsupites testudinarius* zone. The associated fauna is dominated by broken plates of large species of *Inoceramus* and the ostreid *Pycnodonte vesiculare* (Darragh and Kendrick 1991), with minor brachiopods (Craig 1999) and echinoids.

The upper part of the section, from immediately above the *Marsupites testudinarius* zone, shows a marked lithological change, involving the appearance of chert nodules, which increase in concentration up the section, and the development of a more marly chalk. With this lithological change there is also a faunal change, with the abundant *Inoceramus* disappearing and the ostreids becoming rarer. Cirripedes, which are rare in the lower part of the section, increase in abundance. *Rotulispira* is still present, but species abundances change markedly, with *R. glauerti* being almost as common as *R. apiaria*. Specimens of *Rotulispira* with the commensal hydroid *Protulophila gestroi* Rovereto, 1901 appear at slightly higher levels within this part of the section, about 5 m above the top of the *Marsupites* zone. This 5 m of strata is also characterised by the presence of the ammonite aptychus *Spinptychus*, a form hitherto not recognised in the Cretaceous of Australia. The disappearance of *Marsupites testudinarius* below this level, and the occurrence of *Broinsonia parca* in the upper part of the Toolonga Calcilutite indicates an early Campanian age for this part of the section (Lynch 1991; Gale et al. 1995). Howe et al. (2000) have suggested that the Toolonga Calcilutite was deposited in water depths in excess of 100m during the Santonian and early Campanian.

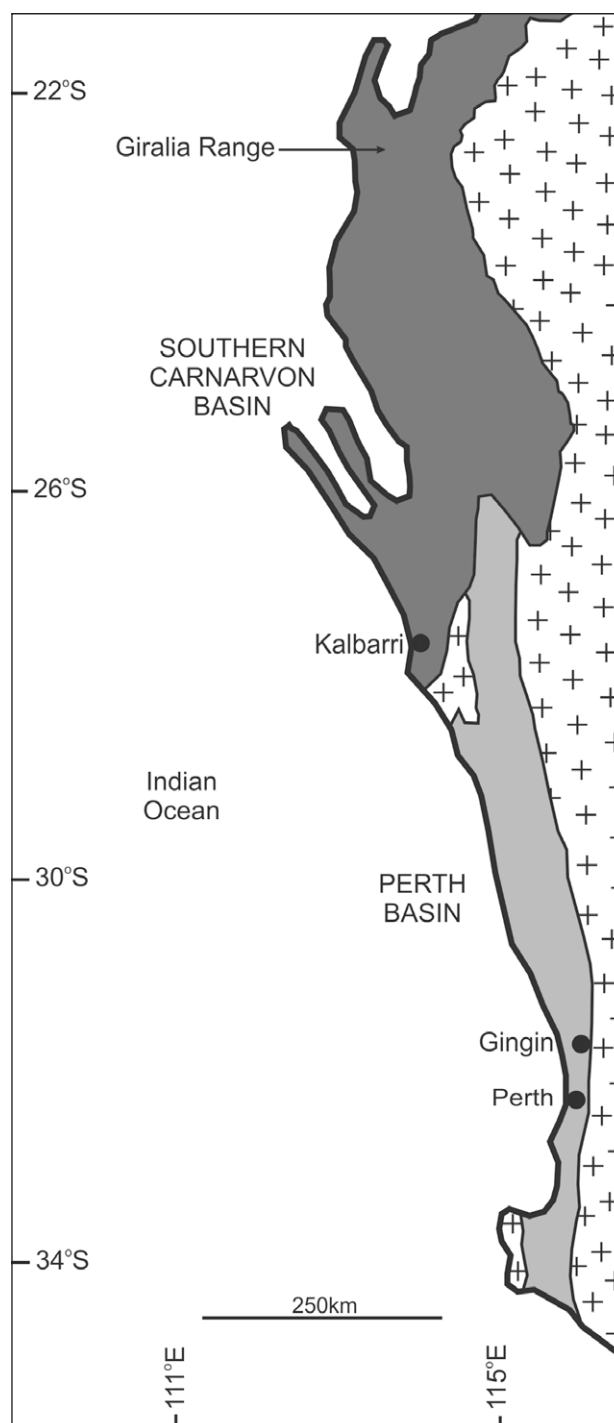


FIGURE 1 Map of the south-western Western Australian coastline showing the three principal collecting localities: Gingin in the Perth Basin and Kalbarri and the Giralia Range in the Southern Carnarvon Basin.

MIRIA FORMATION

The youngest unit in which species of *Rotulispira* have been found in the Southern Carnarvon Basin is the Miria Formation. This is a thin unit that outcrops in the Giralia Range immediately south of Exmouth Gulf. It consists of a cream calcarenite 0.6–2.0 m thick and is

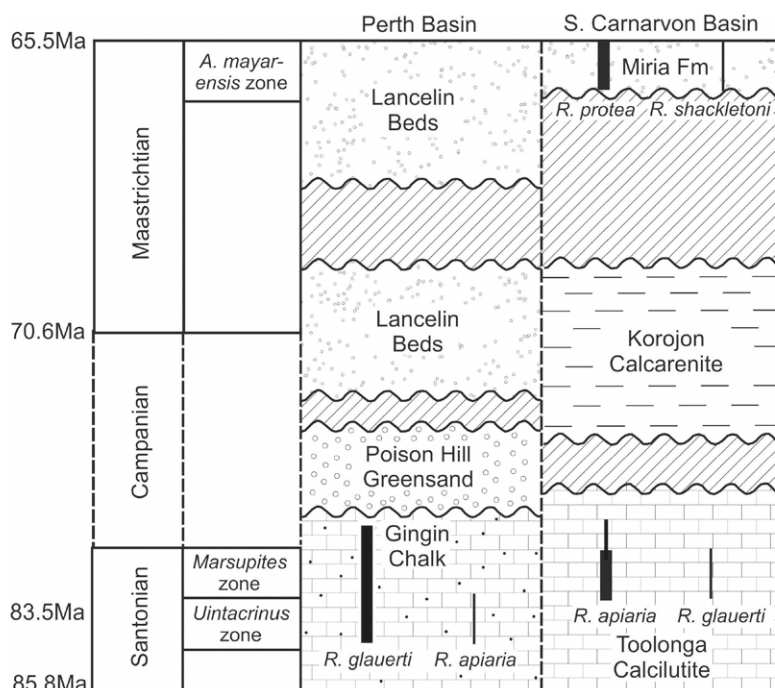


FIGURE 2 Chart showing the stratigraphic distribution of species of *Rotulispira* in the Late Cretaceous of the Perth and Southern Carnarvon basins. Thickness of species' range lines indicative of relative abundance of the taxa.

underlain by the Korojon Calcarenite, which overlies the Toolonga Calclutite (Figure 2). The Korojon Calcarenite is composed mainly of broken, large *Inoceramus* fragments. The junction between this unit and the Miria Formation is marked by a massive phosphatic horizon. Phosphatic grains and nodules are locally abundant within the Miria Formation, and much of the rich fossil assemblage consists of phosphatic steinkerns (Henderson and McNamara 1985a). The dominant polychaete is *Rotulispira protea* sp. nov. The beds also contain one of the richest late Maastrichtian marine invertebrate faunas in the world with nearly 100 species of molluscs having been described – 30 species of ammonites (Henderson and McNamara 1985b; Henderson et al. 1992), 30 species of bivalves (Darragh and Kendrick 1991), 35 species of gastropods (Darragh and Kendrick 1994) and one species of scaphopod (Darragh and Kendrick 1994) — along with 14 species of corals (Jell et al. 2011) and four species of brachiopods (Craig 1999). The unit is considered to be of late Maastrichtian age, occurring in the *Abathomphalus mayaroensis* zone (Shafik 1990). The Miria Formation is disconformably overlain by the Paleocene Boongerooda Greensand.

MATERIAL EXAMINED

Specimens used in this study are housed in the collections of the Western Australian Museum, Perth (WAM); Australian Museum, Sydney (AM) and the Sedgwick Museum, University of Cambridge (CAMSM).

SYSTEMATIC PALAEOLOGY

Class Polychaeta Grube, 1850

Family Serpulidae Rafinesque, 1815

Genus *Rotulispira* Chiplonkar and Tapaswi, 1973

Rotularia (*Praerotularia*) Lommerzheim, 1979: 174.

TYPE SPECIES

Rotulispira stoliczkai Chiplonkar and Tapaswi, 1973 by original designation.

REVISED DIAGNOSIS

Planispiral to trochospiral coiling, with ornament of fine to coarse transverse lirae or rugosities. Tube with circular cross section, lacking keels.

REMARKS

The polychaete *Rotulispira* is characterised by its possession of a calcareous tube that forms a regular, tight coil and which carries an ornamentation of transverse lirae or rugosities. The early whorls are often not preserved, but when they are, as in some of the late Maastrichtian material described herein, they can be seen to be either uncoiled, or loosely coiled. Subsequently the tubes form either an evolute or an involute coil. They may be planispiral or trochospiral or both. The final portion of the tube is directed tangentially away from the shell, as in related forms previously all placed in *Rotularia* (s.l.), and may be

straight or gently curved (see Savazzi 1995, Fig. 31). The surface sculpture is variable between, and sometimes within, species, varying from fine, transverse lirae, to coarse irregular callosities. While in most species the nature of the coiling and the sculpture show relatively little intraspecific variation, and are useful in species characterisation, in other species these features show much wider ranges of variation.

Rotularia (s.l.) has been subdivided into four subgenera: *R. (Rotularia)*, *R. (Praerotularia)*, *R. (Australorotularia)* and *R. (Tectorotularia)*. These subgenera have since been raised to generic status (Jäger 2004; Ippolitov et al. 2014). *Rotularia* (s.s.) comprises species that range in age from the Danian to the Late Eocene and are characterised by a general lack of transverse ornament, and presence or absence of keels. *Australorotularia* Macellari, 1984 ranges from the Kimmeridgian to Maastrichtian, has a tricarinate keel in all growth stages, and often the development of external callosity. The forms assigned to *Praerotularia* Lommerzheim, 1979 probably comprise only Cretaceous species (Jäger 1993) that are characterised by the possession of large tubes with transversely wrinkled surfaces, either with or without longitudinal ornament. *Tectorotularia* Regenhardt, 1961 is a Hauterivian to Maastrichtian group of species with a planar spiral and quadrangular to hexangular cross section.

Prior to Lommerzheim's (1979) study, Chiplonkar and Tapaswi (1973) described a new *Rotularia*-like genus of serpulid from the ?Maastrichtian of India that they called *Rotulispira*. They distinguished this form from *Rotularia* on the basis of the final, straightened part of the tube, arguing that the walls of the tube did not thicken, as in species of *Rotularia*, and that neither was the tube cemented to the preceding whorls. As Jäger (1993) has pointed out, these are very dubious characters on which to separate this form from *Rotularia* (s.l.). This is particularly so given that Vinn (2008) has shown that in the type species of *Rotularia*, *R. spirulea*, the tube is actually relatively thinner at the tube opening. Even so, because of the presence of transverse wrinkles and a tube with a circular cross section, the form described by Chiplonkar and Tapaswi (1973) can readily be accommodated within the group defined as *R. (Praerotularia)* by Lommerzheim (1979). However, the name *Rotulispira*, proposed by Chiplokar and Tapaswi (1973) takes precedence over *Praerotularia*.

Interestingly, despite species of *Australorotularia* being largely restricted to the Southern Hemisphere (Macellari 1984), none of the four species described herein from the Late Cretaceous of Western Australia belongs in this subgenus. All species possess tubes with a circular cross section and ornament consisting of transverse lirae or rugosities. As such, they can all be accommodated within *Rotulispira*. As Jäger (1993) has observed, forms assigned to this genus compose the 'main line' of Cretaceous forms formerly referred to *Rotularia*, *Rotulispira* being the most speciose of these genera.

***Rotulispira glauerti* McNamara, sp. nov.**

Figure 3

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Serpula bogneriensis Sowerby; Etheridge 1907: 38.

Serpula sp. cf. *S. (V.) concava* Sowerby; Glauert 1910: 123.

Spirulaea gregaria Etheridge; Etheridge 1913: 13, pl. 1, figs 1–7; Feldtmann 1963: 102.

Serpula ampullacea Sowerby; Glauert 1925: 9, 11.

Rotularia (Rotularia) gregaria (Etheridge); Regenhardt 1961: 99, pl. 8, fig. 9; Macellari 1984: 1104.

Spirulaea (Tubulostium?) gregaria Etheridge; Feldtmann 1963: 105.

Rotularia gregaria (Etheridge); Playford et al. 1976: 188; Lommerzheim 1979: 175; McNamara et al. 1993: 10, figs 36–37; Jäger 2004: 142.

MATERIAL EXAMINED

Holotype

Australia: Western Australia: WAM 07.255 from the Gingin Chalk, Gingin (Figure 3A–C). This specimen was figured as *Spirulaea gregaria* Etheridge, 1907 by Etheridge (1913, pl. 1, fig. 2).

Paratypes

Australia: Western Australia: WAM 74.1286a–d,k,p from the Gingin Chalk, quarry on One Tree Hill, Gingin (*Uintacrinus socialis* zone, late Santonian).

Other material

Australia: Western Australia: Gingin Chalk: WAM 2423, 3997 (3 specimens), 4719–4725, 5324–5328, 5402, 68.582, 68.655 (11), 71.494 (10), 74.1286 (95) (excepting those listed above as paratypes), 75.1202 (20) from same locality and horizon as the paratypes; WAM 92.670 (5), quarry on Molecap Hill, Gingin (*Marsupites testudinarius*) zone, late Santonian; 6190, 68.585, 68.669 (2), 74.1257 (7), 87.333 (2), lower part of McIntyre Gully, Gingin (late Santonian); WAM 74.1308, 76.2248 (3), Spring Gully, Gingin; WAM 76.2255 (9), near Ginginup Spring, Gingin; WAM 62.201 (4), quarry behind cemetery, Gingin; 10091 (14) 63.113 (3), 'Gingin'; WAM 78.4449 (2), 79.2305, gully NNW of 'Wandilla' Homestead, Dandaragan; WAM 80.1304, gully 1km NE of Kayanaba Homestead, Dandaragan.

Toolonga Calcilutite: Meanarra Hill, Kalbarri, WAM 91.866, 98.247, 2023.16; WAM 6680, Murchison House Station; WAM 7290–1, Thiridine Bluff, 6.4–8.0 km NNE of Murchison House Station.

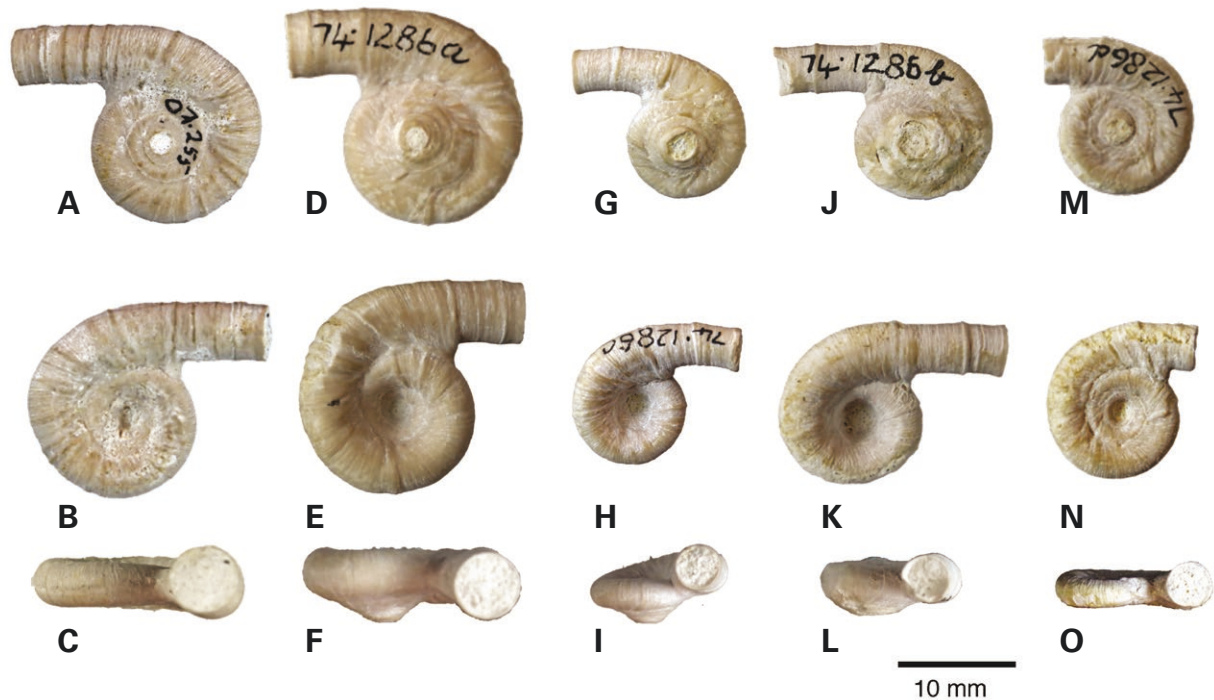


FIGURE 3 *Rotulispira glauerti* sp. nov. A–C, holotype WAM 07255 from Gingin, Western Australia, Gingin Chalk: A) ventral; B) dorsal; C) lateral views. D–F, paratype WAM 74.1286a from One Tree Hill, Gingin, Western Australia, Gingin Chalk: D) ventral; E) dorsal; F) lateral views. G–I, paratype WAM 74.1286c from One Tree Hill, Gingin, Western Australia, Gingin Chalk: G) ventral; H) dorsal; I) lateral views. J–L, paratype WAM 74.1286b from One Tree Hill, Gingin, Western Australia, Gingin Chalk: J) ventral; K) dorsal; L) lateral views. M–O, paratype WAM 74.1286d from One Tree Hill, Gingin, Western Australia, Gingin Chalk: M) ventral; N) dorsal; O) lateral views.

STRATIGRAPHIC RANGE

Late Santonian (*Uintacrinus socialis* and *Marsupites testudinarius* zones) to Early Campanian.

DIAGNOSIS

Planispiral to weakly trochospiral. Last whorl generally planispiral, on same plane as final straight part. Umbilicus relatively wide. Cicatrix of early attachment small. Tube usually thin, with fine, closely spaced transverse lirae, and occasional thick lirae; evolute to weakly involute.

DESCRIPTION

Maximum known diameter of spiral is 21.3 mm. Spiral varies between planispiral and trochospiral, with height of spiral being about 30% of maximum width in planispiral specimens, increasing to 50% in most trochospiral specimens, with a few up to 55%; the mean for all specimens is 40% (Figure 4). Spiral has just over three whorls, before forming an uncoiled, straight final part (Figure 3A,D,G,J). Last whorl invariably planispiral, even though first two may be trochospiral. Final part generally lies on same plane as last whorl. Almost all sinistrally coiled, with just 1% dextral. Umbilicus relatively wide, 35–50% of maximum spiral width (Figure 4). Whorls of spiral are moderately cemented together; evolute to weakly involute, overlapping earlier whorls by up to about one-third

their width. Cicatrix representing attachment site of earliest whorls small, varying between 2.3 and 3.3 mm in width (mean of 2.7 mm; $n = 7$).

Tube diameter gradually increases, but becoming relatively wider in last half whorl. Straight part of whorl of even width or slightly decreases toward the aperture. Final tube width occupies 25–45% of maximum spiral diameter, average being 35%. Tube ornamented by very closely spaced, well-defined, transverse lirae (Figure 3A,E,K). Periodically much thicker lirae are present, at irregular intervals, particularly on the mature part of the spiral (Figure 3A,G). Cross section of tube is circular, the tube wall being very thin in 80% of specimens. In other 20% walls thicker, up to nearly one third of tube diameter.

REMARKS

For nearly 90 years the common spiral serpulid found in the Gingin Chalk and occasionally in the Toolonga Calcilitite has been referred to generally either as *Spirulaea gregaria* (e.g. Etheridge 1907) or *Rotularia gregaria* (e.g. McNamara et al. 1993). Examination of the type material (AM F10345) of Etheridge's species (consisting of a single slab covered by in excess of 200 specimens from the Early Cretaceous of Queensland — see Etheridge 1907, plate 57) reveals that the two forms are not conspecific. While both the Western Australian and Queensland forms possess a tube with a circular

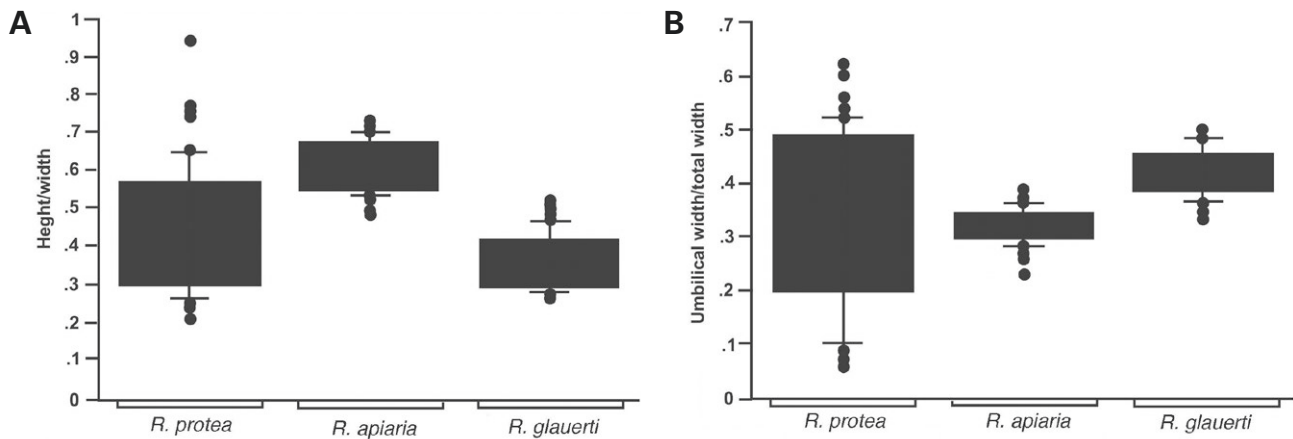


FIGURE 4 Box plots of: A) height/width ratio in *Rotulispira protea* (n = 51, mean = 0.448, S.D. = 0.167), *Rotulispira apiaria* (n = 51, mean = 0.613, S.D. = 0.066) and *Rotulispira glauerti* (n = 51, mean = 0.363 S.D. = 0.072); B) umbilical width/total width ratio in *Rotulispira protea* (n = 50, mean = 0.349, S.D. = 0.169), *Rotulispira apiaria* (n = 50, mean = 0.325, S.D. = 0.032) and *Rotulispira glauerti* (n = 50, mean = 0.430 S.D. = 0.045). Central box extends from 25th to 75th percentiles, line extends to 10th and 90th percentiles.

cross section and transverse lirae, the Queensland specimen has developed distinct longitudinal grooves on either side of the keel, suggesting that it belongs in *Tectorotularia* (Jäger 1993, p. 87). Moreover, it has a more slender whorl, this being particularly evident in the straight, final shaft, which has a diameter only about one quarter of the spiral width and is usually gently curved; it is always a low trochospiral shape, never planispiral; it has weaker transverse lirae; and has a slightly narrower umbilicus than *R. glauerti*.

The type species of *Rotulispira*, *R. stoliczkai* Chiplonkar and Tapaswi, 1973, is, unfortunately, known only from a poorly illustrated single specimen from a 'sandy limestone' from the Campanian to Maastrichtian Ariyalur Group in southern India (Chiplonkar and Tapaswi 1973, pl. 11, figs 2, 12). It would appear to be more tightly coiled and trochospiral than *R. glauerti*.

Rotulispira glauerti can be distinguished from *Rotulispira spirulaeoides* (Glaessner, 1958), from the Cenomanian of Papua New Guinea in having whorls that are broadly rounded throughout, lacking the shallow, longitudinal grooves on either side of the keel; having a wider umbilicus and a thinner tube wall. The Western Australian species differs from *Rotulispira chathamensis* (Boreham, 1959) from the early to mid-Cretaceous of Chatham Islands in having a much wider umbilicus, narrower tubes, less callosity on the later whorls, as well as the lack of longitudinal grooves. *Rotulispira concava* (J. Sowerby, 1813) from the Albian Upper Greensand of southern England has thicker shell walls, more callosity and coarser lirae.

Rotulispira phillipsi (Roemer, 1841) from the Speeton Clay (C beds) of Early Cretaceous Hauterivian age in Yorkshire, England, has more strongly developed rugosity with a thicker tube than *R. glauerti*. Moreover, it has a more variable spiralling pattern, being generally far more trochospiral. Its coiling is much weaker, resulting

in a wider umbilicus. Also, whereas *R. glauerti* has a consistent direction of coiling, with all but 1% showing dextral coiling, in *R. phillipsi* 57% show dextral coiling and 43% sinistral (n = 21) (based on specimens CAMSM B11742–50, 53323–53330, 53332, 53334–53336).

ETYMOLOGY

Named after Ludwig Glauert, former Keeper of Geology and Ethnology, Curator and then Director of the Western Australian Museum, in recognition of his contribution to Western Australian palaeontology, and for collecting many of the specimens used in the description of this species.

Rotulispira apiaria McNamara, sp. nov.

Figure 5

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Serpula gregaria Etheridge; Clarke and Teichert 1948: 39.

Serpula fluctuata Sowerby; Lynch 1991: 105.

MATERIAL EXAMINED

Holotype

Australia: Western Australia: WAM 78.933a from the late Santonian (*Marsupites testudinarius* Zone) Toolonga Calcilutite, Meanarra Hill, Kalbarri (Figure 5A–C).

Paratypes

Australia: Western Australia: WAM 75.186a, 91.865a–c from the same horizon and locality as the holotype.

Other material

Australia: Western Australia: Toolonga Calcilutite: WAM 67.296 (3 specimens), 74.1179 (47), 75.18 (16), 78.933 (8), 79.2908 (26), 79.2909, 80.1016 (18), 84.1750 (7), 88.247 (2), 88.317 (4), 91.865 (27), 91.870, 97.710 (3), 98.246 (4), Meanarra Hill, Kalbarri; WAM 88.199 (2), 88.205 (2), 88.222, 88.283 (3), Murchison House Station, 1 km N of Yalthoo Bore; WAM 6680-3, 82.2569 (2), 88.874 (2), 94.304 (2), Murchison House Station; WAM 87.619 (8) Yaringa Station, Shark Bay.

Gingin Chalk: WAM 87.331, McIntyre Gully, Gingin, WAM 76.2234, gully south of Ginginup Spring, Gingin.

STRATIGRAPHIC RANGE

Late Santonian (*Uintacrinus socialis* and *Marsupites testudinarius* zones) to Early Campanian.

DIAGNOSIS

Initially planispiral, becoming strongly trochospiral, average mean height slightly more than half spiral width. Umbilicus relatively narrow. Cicatrix of early attachment relatively large. Tube robust, moderately involute, usually thick, with fine, closely spaced, gently curved transverse lirae and occasional thick rugosities.

DESCRIPTION

Maximum diameter of spiral 25.0 mm. Initially planispiral for at least the first one-and-a-half whorls up to a diameter of about 6 mm; then becomes strongly trochospiral (Figure 5), with height of spiral varying about 50–75% of maximum width, with an average of 60% (Figure 4A); apical angle in later whorls 60–70°. Spiral has up to three-and-three-quarter whorls, before forming uncoiled, straight final part. Last whorl continues trochospiral pattern of the previous whorls by still curving slightly upward. Therefore, straight final part, although growing away from final whorl in a horizontal direction instead of continuing slight upward-directed trend of the trochospiral, lies on a somewhat higher level than most of last whorl. All sinistrally coiled. Umbilicus relatively narrow, 22–40% of maximum spiral width (Figure 4B). Whorls of spiral moderately involute with later whorls tightly coiled and strongly overlapping earlier whorls, sometime completely enveloping them. Cicatrix representing attachment site of earliest whorls relatively large, varying between 3.5 and 8.7 mm in width (mean of 5.6 mm; n = 16).

Tube robust; diameter gradually increases but becomes particularly wider in last half whorl. Straight part of whorl of even width or slightly decreases toward aperture. Final tube width occupies 35–55%

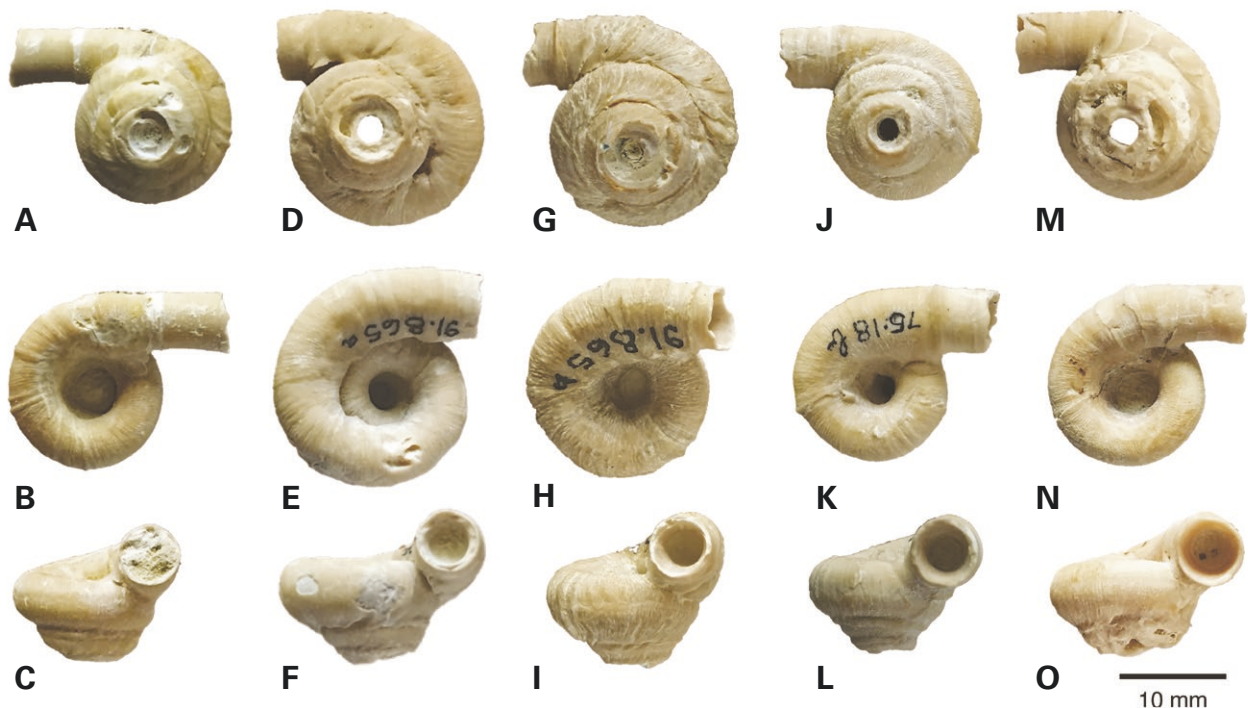


FIGURE 5 *Rotulispira apiaria* sp. nov. A–C, holotype WAM 78.933a from Meanarra Hill, Kalbarri, Western Australia, Toolonga Calcilutite: A) ventral; B) dorsal; C) lateral views. D–F, paratype WAM 91.865a from Meanarra Hill, Kalbarri, Western Australia: D) ventral; E) dorsal; F) lateral views. G–I, paratype WAM 91.865b from Meanarra Hill, Kalbarri, Western Australia: G) ventral; H) dorsal; I) lateral views. J–L, paratype WAM 75.186a: J) ventral; K) dorsal; L) lateral views. M–O, paratype WAM 91.865c from Meanarra Hill, Kalbarri, Western Australia: M) ventral; N) dorsal; O) lateral views.

of maximum spiral diameter, with an average of 42%. Tube ornamented by very closely spaced, well-defined, gently curved transverse lirae. Occasionally much thicker lirae are present, at irregular intervals (Figure 5). The tube is circular, the tube wall being very thick, up to nearly one-third of tube diameter.

DISCUSSION

Rotulispira apiaria can be distinguished from the contemporaneous *R. glauerti* in a number of ways. It has relatively larger and more robust whorls that form a tighter, more involute whorl than in *R. glauerti*. Its predominantly trochospiral form, with initial planispiral coiling, is in contrast to *R. glauerti* which either has planispiral coiling throughout or has initial trochospiral coiling before becoming planispiral. Coiling is tighter in *R. apiaria*, resulting in a smaller umbilicus. This is further enhanced by the greater width of the tube in later whorls. Furthermore, the final, straight portion of the tube is at a lower plane than the preceding last coiled part of the tube. The tube walls are invariably thick in *R. apiaria*, whereas they are usually thin in *R. glauerti*.

Of other predominantly trochospiral species of *Rotulispira*, *R. apiaria* differs from *Rotulispira phillipsi* (Roemer, 1841) from the Speeton Clay Formation (C beds) of Early Cretaceous Hauterivian age in Yorkshire, England, in its weaker rugosity; more consistent trochospiral coiling, unlike *R. phillipsi* which varies from strongly trochospiral to almost planispiral; tighter coiling, so narrower umbilicus; and more consistent direction of spiralling. As noted above, 57% of specimens of *R. phillipsi* show dextral coiling, the rest sinistral, whereas in *R. apiaria* all known specimens are sinistrally coiled.

Rotulispira apiaria differs from the type species *R. stoliczkai* Chiplonkar and Tapaswi, 1973 from the Campanian to Maastrichtian Ariyalur Group in southern India in being more tightly coiled and having a less rugose tube.

ETYMOLOGY

After *apiarium*, the Latin for ‘beehive’, alluding to the conical shape of the species, reminiscent of a medieval beehive.

Rotulispira protea McNamara, sp. nov.

Figure 6

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MATERIAL EXAMINED

Holotype

Australia: Western Australia: WAM 07.256d from the Miria Formation, Giralia Range, gully 0.3 km SW of grid on Bullara-Giralia road, 12 km W of Giralia Homestead.

Paratypes

Australia: Western Australia: All from the Miria Formation, Giralia Range: WAM 71.250b, Cardabia Station, CY Creek, southern tributary; WAM 71.279, Cardabia Station, CY Creek, west bank of southern tributary; WAM 88.54, Giralia Station, big gully near camp, WNW of West Tank; WAM 90.218b, Giralia Station, large eastward draining gully, c. 1 km NW of West Tank; WAM 07.256c, from same locality as the holotype.

Other material

Australia: Western Australia: All from the Miria Formation, Giralia Range: WAM 71.182, 71.183, Cardabia Station, CY Creek, 3.5 km east of No. 37 Bore; WAM 71.250a,c-r, 71.251, Cardabia Station, CY Creek, southern tributary; WAM 71.278, 71.279, Cardabia Station, CY Creek, west bank of southern tributary; WAM 74.591, Cardabia Station, east side of hill 5 km north of Remarkable Hill; WAM 80.672, Cardabia Station, CY Creek, junction of main creek and southern tributary; WAM 80.696, Cardabia Station, first unnamed creek south of CY Creek; WAM 80.886, Cardabia Station, 3.5 km NNW of Section Hill, at junction of two gullies; WAM 83.2937, Giralia Station, gully 4 km south of Bullara-Giralia road; WAM 83.3012, Giralia Station, gully draining east, 1.8 km south of Bullara-Giralia road; WAM 83.3077a-b, Giralia Station, gully draining east, 2.9 km south of Bullara-Giralia road, eastward draining gully; WAM 84.948a-b, Giralia Station, 2.5 km NW of West Tank; WAM 88.54, Giralia Station, large gully immediately WNW of West Tank; WAM 90.218a,c-f, Giralia Station, large eastward draining gully, c. 1 km NW of West Tank; WAM 90.228, Giralia Station, eastward draining gully 1.7 km south of Bullara-Giralia Road; WAM 96.846, Giralia Station, large gully draining to east on north side of West Tank; WAM 07.256a-b,d, from same locality as holotype; WAM 07.257a-p, Giralia Station, large gully immediately WNW of West Tank.

STRATIGRAPHIC RANGE

Late Maastrichtian, *Abathomphalus mayaroensis* zone (Shafik 1990).

DIAGNOSIS

Extremely variable, relatively small species; spiralling either sinistral or dextral; planispiral or trochospiral or both. Coiling height low to very high; involute to strongly involute; ornamentation with either lirae or rugose throughout, or with lirae only in initial whorls, and rugose in later whorls. Final shaft often much wider than earlier whorls; curved or straight.

DESCRIPTION

Form of tube highly variable, especially in mode of coiling, tightness of coiling and degree of development of ornamentation. Unlike other species of *Rotulispira*, the early part of the tube is sometimes present. It is

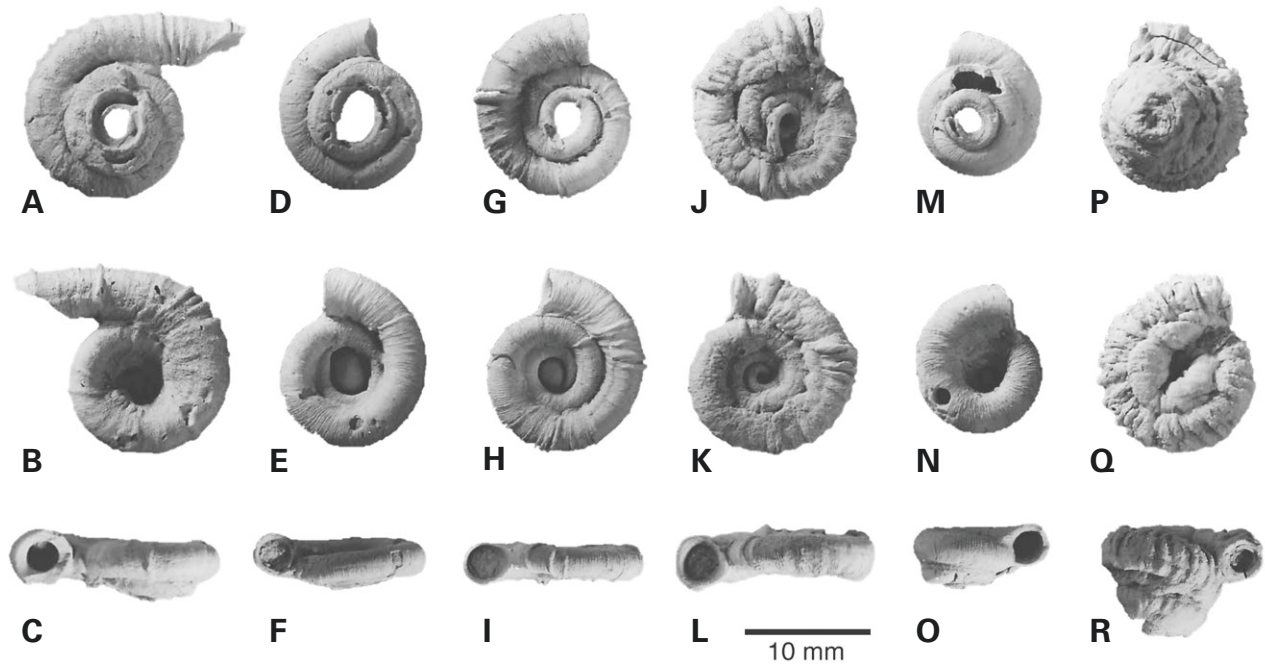


FIGURE 6 *Rotulispira protea* sp. nov. A–C, paratype WAM 71.279 from Giralia Range, Western Australia, Cardabia Station, CY Creek, west bank of southern tributary, Miria Formation: A) ventral; B) dorsal; C) lateral views. D–F, paratype WAM 07.256c from Giralia Range, Western Australia, gully 0.3 km SW of grid on Bullara-Giralia road, 12 km W of Giralia Homestead, Miria Formation: D) ventral; E) dorsal; F) lateral views. G–I, paratype 71.250b from Giralia Range, Western Australia, Cardabia Station, CY Creek, southern tributary, Miria Formation: G) ventral; H) dorsal; I) lateral views. J–L, holotype WAM 07.256d from Giralia Range, Western Australia, gully 0.3 km SW of grid on Bullara-Giralia road, 12 km W of Giralia Homestead, Miria Formation: J) ventral; K) dorsal; L) lateral views. M–O, paratype WAM 88.54, Giralia Range, Western Australia, Giralia Station, big gully near camp, WNW of West Tank, Miria Formation: M) ventral; N) dorsal; O) lateral views. P–R, paratype WAM 90.218b, Giralia Range, Western Australia, Giralia Station, large eastward draining gully, c. 1 km NW of West Tank, Miria Formation: P) ventral; Q) dorsal; R) lateral views.

almost straight to gently curved initially, before tightly coiling and looping back to run underneath initial part of tube. Maximum known diameter of spiral is 17.4 mm; may be planispiral or trochospiral. Some specimens planispiral throughout (30.2%), whereas others display various grades of trochospirality (Figure 6), varying between weakly to strongly trochospiral (35.8%). Some individuals change their mode of coiling ontogenetically, being initially trochospiral, then later in ontogeny planispiral (15.1%). Others show reverse coiling trend, initially being planispiral then becoming trochospiral later in development (18.9%). Some may even be weakly trochospiral, then planispiral, then finally showing reverse spiralling (6%), or planispiral, then trochospiral then reversed trochospiral (12%), or trochospiral to reverse trochospiral (3%).

Coiling height to width ratio of spiral very variable, ranging from 21–84% (Figure 4A), depending on degree of trochospirality; mean is 44%. Of known examined specimens, 27 coil sinistrally and 25 dextrally. Spiral has up to three and two-thirds whorls, before forming an uncoiled, straight final part, although some form straight final part of tube after only two and a half

whorls. Generally, no tube expansion in final shaft, but in one (WAM 07.257k) large expansion, with an almost doubling of tube diameter (see Figure 10C).

Umbilicus very variable in extent from wide to non-existent, 58% to 0% (Figure 5B). Planispiral shells may be evolute, whereas those with trochospiral coiling vary between weak to strongly involute due to variability in tightness of coiling. In general, the more trochospiral the tube, the tighter the coiling. Tube diameter gradually increases during growth. Straight part of whorl of even width or slightly increases toward the aperture. Final tube width occupies 25–42% of maximum spiral diameter, with a mean of 32%. Ornamentation extremely variable (Figure 6); all specimens with closely spaced, prominent transverse lirae. In about half of specimens coarse ribs are present arising from swelling of bundles of lirae. Specimens may carry these ribs throughout (35.2%) or lack them entirely (64.8%) or, more generally, develop rugosity on last whorl or part of it. Both planispiral and trochospiral forms may be rugose (Figure 6J–L,P–R), but ribs are more common in trochospiral forms. Rugosity, where present, more pronounced on umbilical side. Thickness of tube wall

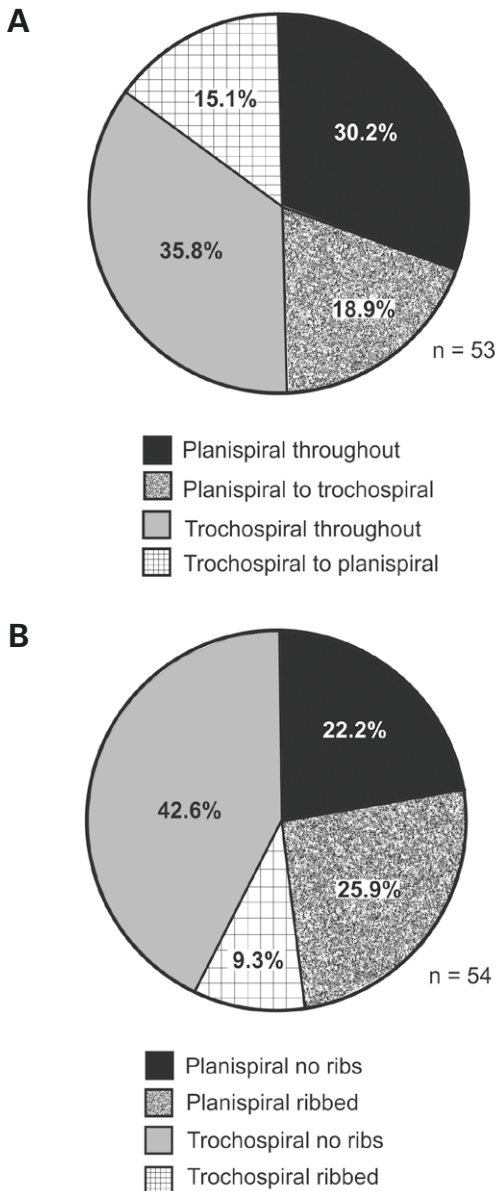


FIGURE 7 A) variation in spiralling pattern; B) variation in presence of ribs in planispiral and trochospiral forms in the annelid *Rotulispira protea* from the Miria Formation.

highly variable, in planispiral to weakly trochospiral forms thin throughout. However, in more tightly coiled forms, secondary thickening more evident, particularly lining the umbilicus (Figure 6Q). This deposit may be so extensive that umbilicus is completely closed.

REMARKS

Rotulispira protea differs from *R. glauerti* in having many individuals that are not planispiral; many, unlike *R. glauerti*, with coarsely developed rugae and some with greatly expanded terminal tube. There are a few individuals within the species that, like *R. glauerti*, are planispiral and possess only fine lirae, but they can be distinguished by their lack of an attachment cicatrix. *R. protea* can be distinguished from *R. apiaria* in

that many specimens are not trochospiral. Moreover, many, unlike *R. protea*, do not have coarse rugosity or infilled umbilicus. There are some individuals of *R. protea* that mimic *R. apiaria* in being trochospiral and having a similar ornamentation, but these generally are more rugose and lack the large attachment cicatrix characteristic of *R. apiaria*.

Serpulids are renowned for generally exhibiting a fairly high degree of phenotypic plasticity (Jäger 1993; Savazzi 1995), but as Seilacher et al. (2008) have pointed out, species of *Rotularia* (s.l.) followed stricter developmental growth programmes, and therefore exhibited far less variability in form of their calcareous tubes than in other serpulids. The only previously recorded exception to this is *Rotulispira shackletoni* (Wilckens, 1910) as discussed below. The late Maastrichtian *Rotulispira protea* displays an even more extreme degree of variability, far greater than in any other species of the genus, including *R. shackletoni*, especially when compared with the earlier Late Cretaceous species present in the Southern Carnarvon and Perth basins, the late Santonian to early Campanian *R. glauerti* and *R. apiaria*.

Of the 60 known individuals of *Rotulispira protea*, hardly any two are alike. Extreme variability occurs in mode of coiling, in particular whether dextrally or sinistrally coiled, whether planispiral or trochospiral, and tightness of coiling; and extent and development of ornamentation, in particular whether ribs are present or absent. Direction of coiling can be either sinistral (52%) or dextral (48%). This is in contrast to *R. glauerti* in which all but 1% coil sinistrally and in *R. apiaria* in which 100% coil sinistrally. While the variability in coiling demonstrated by *R. protea* is not unique for species of *Rotulispira*, the extent of the variation in spiralling is. Almost a third (31%) are entirely planispiral, other individuals displaying various grades of trochospirality, varying between weakly to strongly trochospiral (Figure 7). Other individuals changed their mode of coiling ontogenetically, some being initially trochospiral, then later in ontogeny becoming planispiral. Other individuals showing the reverse coiling trend, starting with planispiral coils, then become trochospiral later in development. In *R. glauerti* and *R. apiaria* the style of coiling remains constant within each species.

In *R. protea* the height to width ratio is more than twice as variable as in *R. glauerti* and *R. apiaria* (Figure 4A). In part due to this variation in styles of coiling in *R. protea*, combined with variation in the tightness of coiling, the width of the resultant umbilicus varies much more than in the earlier species. Planispiral shells may be evolute, whereas those with trochospiral coiling are weak to strongly involute, showing varying degrees of tightness of coiling. In general, the more trochospiral the shell, the tighter the coiling. As a consequence, the ratio of umbilical width to maximum width in *R. protea* is about four times more variable than in either *R. glauerti* or *R. apiaria* (Figure 4B). Whereas the other species of

Rotulispira have relatively consistent ornamentation, *R. protea* shows an enormous variation (Figure 6). All whorls may be ribbed or they may lack them entirely, with every variation in between. Ribs may be present or absent in both planispiral and trochospiral forms.

Tube thickness is also very variable in *Rotulispira protea*. In planispiral to weakly trochospiral forms it is thin throughout. However, more tightly coiled tubes have secondary thickening, particularly lining the umbilicus. This may be developed to such an extent that the umbilicus becomes completely closed (Figure 6Q). There is extreme variation in the size of the final, straightened part of the tube in *R. protea*, where in some individuals the uncoiled tube may be up to four times wider than in the coiled part (Figure 10C). In others there is little variation in width ontogenetically, as is invariably the case in *R. glauerti* and *R. apiaria*.

ETYMOLOGY

After the Greek God *Proteus*, who had the ability to change his shape at will, alluding to the extremely variable nature of the species.

Rotulispira shackletoni (Wilckens, 1910)

Figure 8

Serpula (*Burtinella*?) *shackletoni* Wilckens 1910: 6–7, pl. 1, figs 1–2.

Rotularia shackletoni (Wilckens); Ball 1960: 23–25, pl. 4, fig. 1a–b, pl. 7, figs 6–12; Savazzi 1995: 75.

Rotularia (*Rotularia*) *shackletoni* (Wilckens); Macellari 1984: 1114, fig. 11J–K.

Rotulispira shackletoni (Wilckens); Jäger 1993: 87.

MATERIAL EXAMINED

Australia: Western Australia: WAM 07.258 from the late Maastrichtian Miria Formation, northern Giralia Range.

REMARKS

Rotulispira shackletoni (Wilckens, 1910) has been described from James Ross Island, Snow Hill Island and Seymour Island, off the northern Antarctic Peninsula, where it occurs in the late Maastrichtian lower López de Bertodano Formation (Montes et al. 2019). The species is characterised by its large, robust, tumid tube, with pronounced callosity at the whorl sutures (Ball 1960). These features are all apparent in the single specimen attributable to this species from the Miria Formation. This specimen is 29.3 mm in maximum whorl diameter. Material described by Ball (1960) averaged 22–26 mm,

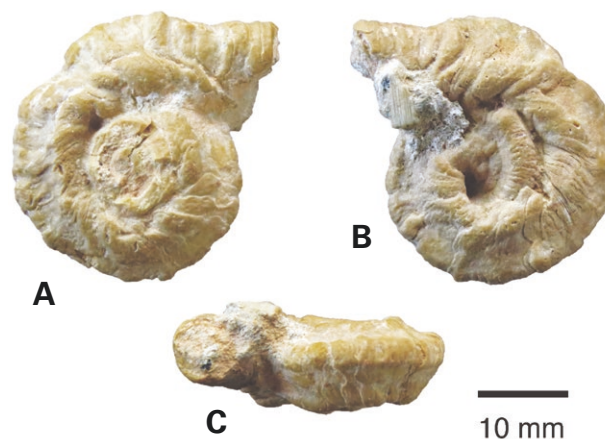


FIGURE 8 *Rotulispira shackletoni* WAM 07.258, northern Giralia Range Western Australia, Miria Formation: A) ventral; B) dorsal; C) lateral views.

with a maximum of 34 mm. The Miria Formation specimen is coiled dextrally and has extensively developed sutural callosities developed even in the early whorls. This trait is characteristic of *R. shackletoni* and differentiates this specimen from the common Miria Formation form, *R. protea*.

What the two late Maastrichtian species both have in common, though, are very high levels of phenotypic variation. Like *R. protea*, material of *R. shackletoni* from James Ross Island analysed by Ball (1960) has a spiral that varies from planispiral to strongly trochospiral; roughly equal numbers of sinistral and dextral coiling; a whorl profile that varies from rounded to sub-angular; growth lines that are variable in orientation and extent of development; and spiral profiles that are widely variable, as are the planes of coiling and position of the aperture (Ball 1960).

PALAEOECOLOGY

HYDROID–SERPULID BIOCLAUSTRATION

A number of specimens of both *Rotulispira glauerti* (Figure 9A) and *R. apiaria* (Figure 9B) have tubes in which the surface carries a number of small, regularly spaced perforated pustules. They occur as associated sets of circular to oval, slit-like openings about 0.2 mm in diameter or maximum length. They are located on swollen, elongate protuberances that vary in maximum length between 0.3 and 0.7 mm. These elongate protuberances are aligned parallel to the axis of the tube, often in an *en echelon* pattern, and are perforated at the end closest to the serpulid's aperture. The perforation is encircled by a swollen ridge. When such 'infestations' occur, they are present around the entirety of the tube, and may be on both dorsal and ventral surfaces.

Such structures have previously been described in a range of serpulids (e.g. Scrutton 1975, Radwańska 1996, Niebuhr and Wilmsen 2005, Wilmsen et al. 2007, Zágóršek et al. 2009, Kamali Sarvestani et al. 2016, Słowiński et al. 2020). They were originally described as *Protulophila gestroi* by Rovereto (1901) who considered them to be a ctenostomatous bryozoan. Scrutton (1975), however, argued convincingly that they represent the activity of a hydroid living in a mutualistic association with the serpulids that they infested. The chambers within the serpulid tube occupied by the hydroids were not formed by boring activity, but by their being incorporated into the tube by calcification as the serpulid grew (Scrutton 1975, p. 264), an example of bioclaustration (Palmer and Wilson 1988). This is shown by deflection of growth lines around the location of the hydroid symbiont. In life a ring of hydroids were present close to the opening of the serpulid tube, the hydroid tentacles facing away from the opening of the serpulid tube (Scrutton 1975, text-fig. 5b). If, as Seilacher et al. (2008) have argued, the straightened part of the tube of *Rotularia* represents a chimney extruding from an otherwise buried spiral serpulid tube, then the hydroid might have been taking advantage of eddying currents created by the movement of the tentacular crown of the serpulid. However, as discussed below, such a life orientation is not likely in *Rotulispira*.

In the Late Cretaceous of Western Australia, the frequency of occurrence of *Protulophila gestroi* varies between the species, with 2.4% (n = 123) of *R. glauerti* and 11.7% (n = 137) of *R. apiaria* being infested. These are far lower levels than the c. 40% recorded by Wilmsen et al. (2007) for the Cenomanian material they examined. Interestingly, the late Maastrichtian *R. protea* shows no evidence of having been infected by *P. gestroi* at all. In addition to the Western Australian examples, Late Cretaceous examples of *P. gestroi* have been described from the Cenomanian of Germany (Niebuhr and Wilmsen 2005; Wilmsen et al. 2007), the Campanian and Maastrichtian of Poland (Radwańska 1996) and the Turonian of the Czech Republic (Zágóršek et al. 2009). The presence of *Protulophila gestroi* in the two late Santonian species of *Rotulispira* in Western Australia, *R. glauerti* and *R. apiaria*, represents the first record of this hydroid and hydroid–serpulid symbiosis in the Mesozoic of Australia.

GASTROPOD PREDATION ON *ROTULISPIRA* SPECIES

Unlike *Rotulispira glauerti* and *R. apiaria*, which show no obvious evidence of having suffered predation, *R. protea* underwent a significant degree of predation, as shown by the presence of circular to oval incisions through the serpulid tube. Such incisions occur in 16.6% of specimens (n = 60). Two of the predated serpulids have oval incisions, a single one occurring on the ventral

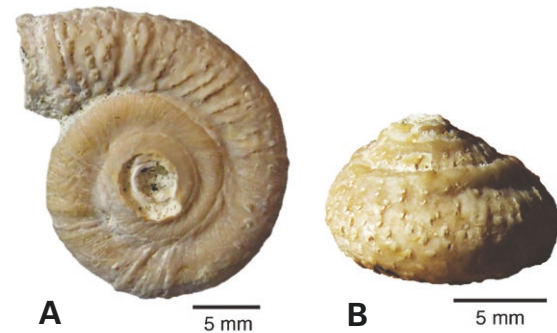


FIGURE 9 A) *Rotulispira glauerti* sp. nov., WAM 2423, from One Tree Hill, Gingin, Western Australia, Gingin Chalk, ventral view showing bioclaustration with the hydroid *Protulophila gestroi* Rovereto, 1901; B) *Rotulispira apiaria* sp. nov., WAM 91.870, from Meanarra Hill, Kalbarri, Western Australia, Toolonga Calcilutite, oblique lateral view showing bioclaustration with the hydroid *Protulophila gestroi* Rovereto, 1901.

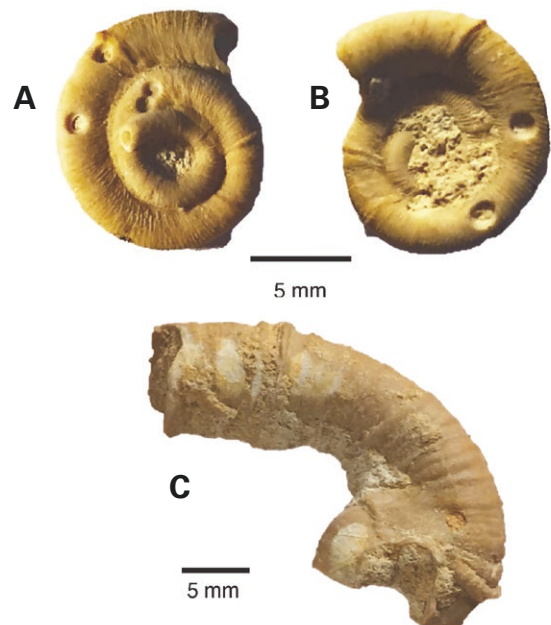


FIGURE 10 *Rotulispira protea* sp. nov., A–B, WAM 71.250i from Giralia Range, Western Australia, Cardabia Station, CY Creek, southern tributary, Miria Formation: A) ventral; B) dorsal views, showing circular gastropod predation incisions on both ventral and dorsal surfaces. C) WAM 07.257k from Giralia Range, Western Australia, Giralia Station, large gully immediately WNW of West Tank, Miria Formation, showing circular gastropod incision on ventral surface. Note the extremely large, curved final shaft.

surface in WAM 83.3012, while on WAM 71.250k three of the four incisions are also on the ventral surface and one on the dorsal. The instigator of this type of incision is not known.

The remaining predated *R. protea* specimens bear bevelled, circular incisions, the outer diameter being about twice that of the internal incision. The diameter of the outer incision ranges from 0.7 mm to 1.4 mm, with a mean of 0.95 mm ($n = 13$). Most of the specimens have single incisions (e.g. Figures 6E,N, 10C), but WAM 71.250i has four circular, bevelled incisions on the ventral surface and two on the dorsal (Figure 10A–B). The bevelled shape of the incisions suggests that the serpulids were preyed upon by naticid gastropods. A single naticid species, *Gyrodont aff. supraplicatus* (Conrad, 1858) has been recorded from the Miria Formation (Darragh and Kendrick 1994). This species has been implicated in predation on bivalves within the Miria Formation (Darragh and Kendrick 1991) and is a likely candidate as the predator of *R. protea*.

The gastropods appear to have preferentially targeted those individuals of *R. protea* that were largely bereft of any significant degree of ribbing or rugosity (Figures 6E,N, 10), with 60% of predated specimens being largely smooth forms, which also have a noticeably thinner tube. Moreover, targeted serpulids were either planispirally coiled or just weakly trochospiral. These patterns could suggest that the development within the population of forms with very coarse rugosity acted as a deterrent to predation by naticids.

The occurrence of predatory incisions on both the dorsal and ventral surfaces, with 40% having incisions on their dorsal surface, 30% on their ventral surface and 30% with multiple incisions on both dorsal and ventral surfaces, suggests that the spiral serpulid tube was, in life, raised above the level of the substrate. This interpretation is supported by the presence in those specimens of *R. glauerti* and *R. apiaria* that have bioclaustrations of hydroids within the serpulid tube (Figure 9). These extend on to the ventral surface close to the attachment cicatrix. This implies that during life *Rotulispira* was not free-living, but, like other serpulids, was attached to a substrate, though most of the tube was raised above it. Separation would have been post-mortem, leaving a distinctive cicatrix. Whether the serpulid attached to a hard substrate, such as the ubiquitous *Inoceramus* fragments, or, like many modern serpulids, to large-fronded seaweed (Teagle et al. 2018; Rossbach et al. 2021), cannot be confirmed.

PHENOTYPIC PLASTICITY

There is ample evidence from a wide range of living organisms that levels of phenotypic variation, as well as underlying genotypic variation, are elevated during periods of severe environmental stress (Bretsky and Lorenz 1969; Parsons 1987, 1989, 1993; Holloway et al. 1990; Hoffman and Parsons 1991; Hoffmann and Hercus

2000; Stanton et al. 2000; Badyaev 2005; Chevin and Hoffmann 2017; Mallard et al. 2020). Consequently, it has been argued (Parsons 1989) that during stressful periods in evolutionary history variability in the broadest sense may be increased, with the result that genomic reorganizations could be induced in response to rapid environmental change. Increasing environmental stress even further, to extreme levels, can ultimately result in extinction. It is likely that the margin between high levels of variation arising from stress, and species extinction may be very small (Hoffman and Parsons 1991).

Experiments on living populations have shown that many different factors can induce stress leading to increased levels of phenotypic plasticity. These include desiccation, anoxia, chemical stress and temperature (Parsons 1989). Investigation of the incidence of high levels of phenotypic plasticity in the fossil record therefore has the potential to provide insights into periods of severe environmental stress in the geological past. As such, if extreme phenotypic plasticity occurred in some taxa immediately prior to a major mass extinction, particularly as illustrated here by *Rotulispira protea*, this may indicate the extent to which environmental stress played a role in such extinction events.

PHENOTYPIC PLASTICITY IN THE MIRIA FORMATION FAUNA

The late Maastrichtian Miria Formation contains a rich fauna dominated by ammonites (Henderson and McNamara 1985a; Henderson et al. 1992), bivalves (Darragh and Kendrick 1991), gastropods (Darragh and Kendrick 1994), and brachiopods (Craig 1999). One of the characteristic features of this fauna is the high level of phenotypic plasticity displayed not only in *Rotulispira* but also in some of these other groups, particularly in some species of heteromorph ammonites, bivalves and brachiopods. This is in contrast to the late Santonian–early Campanian Gingen Chalk and Toolonga Calcilutite faunas that show no evidence of enhanced phenotypic plasticity whatsoever.

The morphological features that are most affected by phenotypic variability differ between the various groups. In the case of *Rotulispira*, it is particularly noticeable in the coiling pattern and variability of ornamentation (see above). In bivalves it is also principally in variations in surface ornamentation, specifically rib density, as it is in ammonites. For instance, individuals of the bivalve *Chlamys cracenticostata* Darragh and Kendrick, 1991 have between three and 156 ribs (Figure 11). Phenotypic plasticity is very high in heteromorph ammonites compared with non-heteromorph ammonites, as typified by *Diplomoceras cylindraceum* (Defrance, 1816) and *Glyptoceras rugatum* (Forbes, 1846), this species originally having been described as ten different species in two genera (Brunnschweiler 1966), but now regarded as a single highly variable species (Henderson et al. 1992). In brachiopods shell convexity and concentration

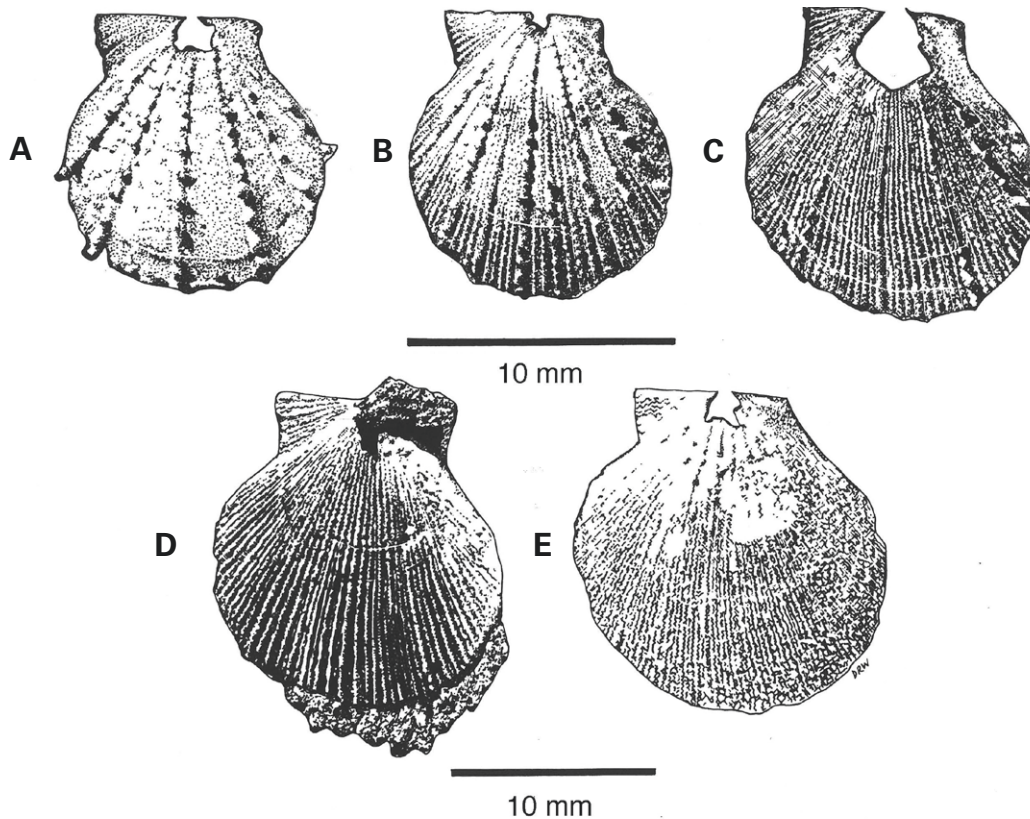


FIGURE 11 Variation in the bivalve *Chlamys cracenticostata* Darragh and Kendrick, 1991 from the Miria Formation, Giralia Range, Western Australia: A) WAM 87.376; B) WAM 87.377; C) WAM 71.309; D) WAM 87.372; E) WAM 83.2871.

of ribbing, as well as periodicity of growth disruption lines, are the most variable traits. In the brachiopod *Zenobiathyris mutabilis* Craig, 1999, rib variation is very much greater than in the slightly younger Paleocene *Tegulorhynchia boongeroodaensis* McNamara, 1983 and the slightly older Santonian–Campanian *Inopinatarcula acanthodes* (Etheridge, 1913) (Figure 12C).

Of those elements of the Miria Formation fauna that experienced elevated levels of phenotypic plasticity, the annelids, brachiopods and bivalves were all plankton feeders. What ammonites fed upon is open to debate (Westermann 1996). The fundamental distinction between heteromorph and non-heteromorph ammonites is that the Miria Formation non-heteromorphs show little evidence of high levels of phenotypic plasticity. This may be due to fundamental differences in life history strategies, especially in modes of feeding. It has been proposed that many heteromorphs were more sluggish than non-heteromorph ammonites (Klinger 1981), with forms like *Nostoceras* having been interpreted as microphagous feeders. Non-heteromorph ammonites, that show much more restricted levels of morphological variation, are generally thought to have been carnivorous, feeding from higher up the food chain (Westermann 1996).

The absence of high levels of phenotypic plasticity in any of the extensive Miria Formation gastropods, none of which were filter feeders, lends support to the argument that filter feeders were more affected by the severe environmental stress that may have preceded the terminal Cretaceous/Paleogene extinction event (Sheehan and Hansen 1986). However, the distinction between deposit and filter feeders can quite often be blurred, as many deposit feeders have the ability to switch between deposit and suspension feeding (Levinton 1996).

It has been shown that there was a close correlation between feeding strategy in echinoids and their survivorship during the late Maastrichtian, suggesting that a crucial factor in the Cretaceous/Paleogene extinctions was nutrient supply (Smith and Jeffrey 1998). Certain deposit feeding echinoids show preferential survival compared with other feeding types, suggesting that extinction in echinoids may have been nutrient-driven. This may have arisen from a reduction in phytoplankton abundance in the late Cretaceous, as a consequence of a combination of abiotic factors inducing nutrient stress (Barrera 1994). Such stress might have emanated from increasing levels of unpredictability of nutrient supply. Support for this view comes from the presence of pronounced disturbance

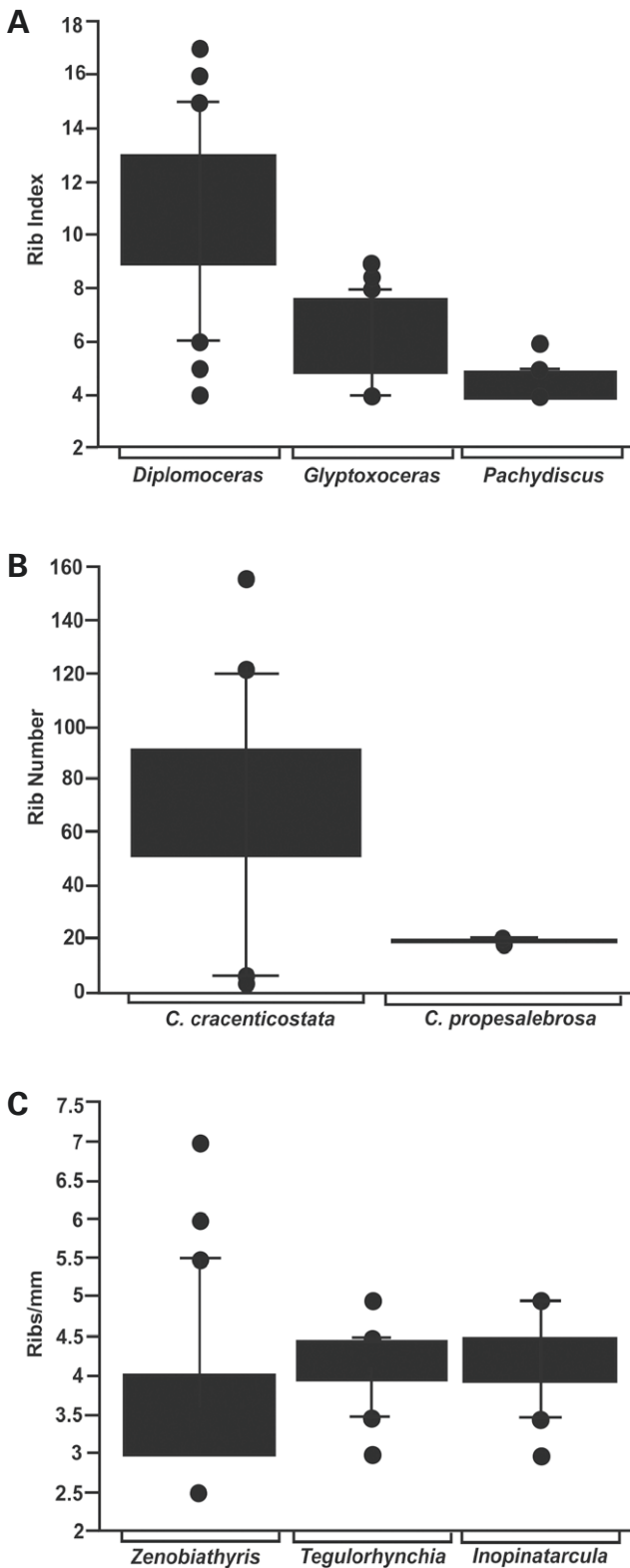


FIGURE 12 Box plots of: A) rib index in the Miria Formation heteromorph ammonites *Diplomoceras cylindraceum* (n = 50, mean = 11.220, S.D. = 3.112) and *Glyptoxoceras rugatum* (n = 85, mean = 6.429, S.D. = 1.442) and the non-heteromorph ammonite *Pachydiscus jacquoti australis* (n = 43, mean = 4.686, S.D. = 0.578); B) rib number in the Miria Formation bivalves *Chlamys cracenticostata* (n = 25, mean = 67.920, S.D. = 38.512) and *Chlamys propesalebrosa* (n = 25, mean = 20.320, S.D. = 0.945); C) number of ribs per millimetre in the brachiopods *Zenobiathyris mutabilis* from the Miria Formation (n = 56, mean = 0.3777, S.D. = 1.022), *Tegulorhynchia boongeroodaensis* from the Late Paleocene Cardabia Formation (n = 50, mean = 4.080, S.D. = 0.488) and *Inopinatarcula acanthodes* from the Santonian-Campanian Gingin Chalk (n = 49, mean = 4.235, S.D. = 0.531). Central box extends from 25th to 75th percentiles, line extends to 10th and 90th percentiles.

lines in the brachiopod *Zenobiathyris mutabilis* from the Miria Formation (Craig 1999). Not only does this species show higher phenotypic plasticity than other contemporaneous and older brachiopods, but it is the only species to possess such distinctive disturbance lines. The pronounced irregularity in the frequency of occurrence of these lines points to irregular, and prolonged, periods of environmental stress resulting in periodic cessation of shell growth.

Interestingly the stratigraphic sequence in which the Miria Formation occurs lends some support to the argument for a stressed environment. Below the Miria Formation is a relatively thick calcareous unit, the Korojon Calcarenite, which contains vast numbers of broken fragments of a very large species of the bivalve *Inoceramus*. Near the top of this unit phosphate nodules start appearing. When they do so the inoceramids are absent. They then reappear, suggesting that the cold water upwelling associated with the production of the phosphatic nodules was inimical to the inoceramids, perhaps due to an increase in flux of nutrients. The junction between the Korojon Calcarenite and the Miria Formation is marked by a massive, thick phosphate horizon, indicative of more prolonged periods of cold, nutrient-rich water upwelling adversely affecting organisms adapted to low nutrient environments. This horizon is also within the final biozone of the Cretaceous, the *Abathomphalus mayaroensis* zone (Shafik 1990). The Miria Formation itself is rich in phosphate, with the fossils being preserved as phosphatic steinkerns (Henderson and McNamara 1985b). This raises the question of whether the repeated, prolonged pulses of cold water upwelling onto the shelf were sufficient to induce the environmental stress that induced increased phenotypic plasticity. Moreover, could this have been related to a sudden increase in nutrient supply to organisms more adapted to relatively low nutrient conditions?

To establish the significance of the presence of very high levels of phenotypic plasticity in some taxa requires ascertaining whether, as observed in the Western Australian Maastrichtian deposits, it is a purely local phenomenon or whether it occurred in wider regional or cosmopolitan settings. One indication of a more global effect comes from *Rotulispira* present in late Maastrichtian deposits in islands off the Antarctic Peninsula.

As detailed above, Ball (1960) has shown that *R. shackletoni* from the late Maastrichtian of James Ross Island off the Antarctic Peninsula shows high levels of phenotypic variation in spirality, direction of coiling, whorl profile and orientation and extent of development of growth lines, like *R. protea*. There is also evidence for a more global occurrence of the elevated levels of phenotypic plasticity in microfossils from other parts of the world. Very high levels that increase steadily up to the Cretaceous/Paleogene boundary, have been documented in the planktic foraminifer *Contusotruncana fornicata-contusa* lineage from the South and North Atlantic (Kucera and Malmgren 1998). This lineage contains a proportion of Kümmerform specimens. In these specimens the last chamber is of reduced size which, according to Berger (1971), arises due to environmental stress. Other authors (e.g. Hecht and Savin (1970) have correlated the occurrence of the smaller final chamber with a reduction in water temperature (although it should be noted that Olsson (1973) was not convinced of the link between Kümmerform foraminifers and environmental stress). There is a gradual increase in percentage of these forms between 69.5 to 68 Ma, from 10% to 70%, followed by a decrease down to 20% to 66.5 Ma. Of further significance to this discussion is the fact that the last 0.5 million years prior to the Cretaceous/Paleogene boundary, 'were marked by high-amplitude fluctuations in this variable' (Kucera and Malmgren 1998, p. 53), suggesting that periods of environmental stress were not continuous, but also fluctuating widely.

Fluctuation in chamber number was also pronounced in this last 0.5-million-year period. The range of variation in chamber number also shows an increase in the last one million years. Shell conicity, which increased steadily from 69 to 65 Ma, shows a steady increase in extent of phenotypic variability, reaching a maximum in variability again during the last 0.5 million years of the Cretaceous (Kucera and Malmgren 1998, Fig. 6). The onset of these changes in both morphology and increase in variability coincide, according to Kucera and Malmgren (1998), with the onset of the global late Maastrichtian surface water cooling.

DEVELOPMENTAL FACTORS ENABLING INCREASED PHENOTYPIC PLASTICITY

A unifying factor in the phenotypic plasticity evident in the four groups of Miria marine invertebrates — annelids, heteromorph ammonites, bivalves and brachiopods — is its expression in ornamentation, in particular ribbing. In these groups the extent of ribbing tends to increase ontogenetically, indicating that high intraspecific variation was a product of a breakdown of developmental constraint, affecting either rate or duration of growth, or both. Severe environmental stress is known to affect aspects of developmental

constraint directly, such as variations in time of onset of maturation (Hoffman and Parsons 1991). Furthermore, there is increasing evidence that environmental factors, such as changing temperature and food availability, play a prominent role in inducing developmental plasticity. In a number of studies on living gastropods and bivalves (Martín-Mora et al. 1995) variation in shell morphology has been shown to have been induced directly by environmental factors, predominantly perturbations in temperature and nutrient supply.

While phenotypic plasticity has long been seen as facilitating the origin of evolutionary novelty, speciation and macroevolution (West-Eberhard 1989), increased levels of phenotypic plasticity also have their downside in the costs incurred as a result of reduced fitness (De Witt et al. 1998). These include developmental instability, genetic costs, like epistasis and pleiotropy, and reduced fecundity. The consequence can be that the species become more prone to extinction as environmental stress levels increase. In their exhibition of very high levels of phenotypic plasticity, these annelids, ammonites, brachiopods and bivalves that lived close to the end of the Cretaceous, but before the Cretaceous/Paleogene boundary itself, can be perhaps regarded as being harbingers of what was to come: a world in which terrestrially induced environmental stress became so intense that they, and many other species, became extinct.

CONCLUSION

A number of authors have argued that the Earth's biosphere was under severe stress well before the end of the Cretaceous (Archibald 1996; Abramovich and Keller 2002; Askin and Jacobsen 1996; Kauffman 1994; Elorza et al. 2001; Keller 2012, 2014; Kitch et al. 2022) and that this led to a decline in biodiversity during the Late Cretaceous (Donovan 1989; Zinsmeister 1997). It has been suggested that increased Late Cretaceous biological stress was induced by rapidly deteriorating global environments arising from palaeoceanographic, climatic and volcanic effects, such as eustatic fall in sea level, fluctuations in CO₂ levels, glaciation and cooling, perturbations in nutrient levels, giant forest fires, atmospheric pollution by NO₂ and acid rain, or a combination of some or all of these (Caldiera et al. 1990; Smith and Jeffrey 1998). In particular, it has been argued by a number of workers that prolonged volcanic activity that produced the Deccan traps may also have been a major influence (e.g. Van Valen 1984; Officer and Drakes 1985; Keller et al. 2009). Thus it could be argued that any of these factors, either in isolation or in combination, would have had the potential to induce the high levels of phenotypic plasticity displayed by some elements of the Miria Formation fauna.

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