

Competition for space drives morphological abnormalities in the epiphytic foraminifer *Vertebralina striata* in Mangles Bay, Western Australia

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Abstract

Aberrant morphologies are common in a foraminiferal assemblage living on the ribbon-like seagrass *Posidonia* in the shallow waters (<3 m) of Mangles Bay, Cockburn Sound, Western Australia. *Vertebralina striata* is one of the most conspicuous and abundant foraminifers living in the seagrass meadows. Although abnormal tests occur throughout the year, a sample collected in the Australian Summer contained an unusually high abundance of *Vertebralina* with deformed tests living amongst the dense tufted brown alga *Sphacelaria*, epiphytic on mature parts of *Posidonia* leaves. Many mature specimens of *V. striata* have deformed final uniserial chambers with earlier trochospiral chambers unaffected. Abnormalities include bifurcation and trifurcation of chambers, as well as cavities and depressions in the walls. These are associated with *Sphacelaria* thalli which obstruct chamber addition in adult tests by restricting living space. Seasonal growth patterns in both *Posidonia* and its epiphytic *Sphacelaria* may result in natural increases in the abundance of abnormal *Vertebralina* tests in summer.

Keywords: Miliolida, abnormal growth, *Sphacelaria*, algal–foraminiferal interaction, *Posidonia* epiphytes

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INTRODUCTION

Seagrass meadows are common on sand banks in the inner neritic zone of southwest Australian coastal waters (McMahon *et al.* 1997; Graham 2000; Carruthers *et al.* 2007). The ribbon grass *Posidonia* (including *Posidonia australis* and *Posidonia sinuosa*) is one of the major constituents among the phytocenosis described in these meadows (Gobert *et al.* 2006; Carruthers *et al.* 2007). *Posidonia* is a photosynthetic organism that undergoes vigorous growth over summer and a low growth rate in winter when there is lower light intensity and the water is colder (Cambridge 1975; Walker & McComb 1988). During late spring to autumn, their leaves start shedding from the root, forming extensive areas of floating wrack (McComb *et al.* 1981; Silberstein 1985). *Posidonia* leaves are host to a diverse epiphytic biota including algae, minute diatoms with siliceous frustules, benthic foraminifers, sponges, hydrozoans, bryozoans, micro-bivalves, micro-gastropods, ostracods and other minute crustacea, and *Spirorbis* tubeworms (Gordon & Parker 1991; Trautman & Borowitzka 1999; Semeniuk, 2001; Brown, 2005; Prado *et al.* 2008). Common algae include the tufted brown alga *Sphacelaria*, and scale-like encrustations of calcareous coralline algae.

In summer, at water depths <3 m, *Posidonia* in Mangles Bay (Fig. 1a, b) commonly has a dense cover of *Sphacelaria*, at least on the upper portions of many leaves (Fig. 1c). *Sphacelaria* consists of very short, branching upright, elongate and moderately angled

thalli (filaments) that vary from dark to light brown (Tsuda 1972; Huisman & Walker 1990; Ateweberhan & Prud'homme van Reine 2005). Associated with the short tuft-like *Sphacelaria* are many living foraminifers—eukaryotic unicellular microorganisms with tests revealing different chamber structures and shapes. Among the most common foraminifers living in spaces between thalli, are the porcelaneous *Vertebralina striata* d'Orbigny and *Peneroplis planatus* Fichtel & Moll. These species can be seen without magnification. Examination of *Posidonia* leaves during January 2022 yielded an unusually high abundance of *V. striata* with morphological deformities and less-common deformed *P. planatus*.

In Shoalwater Bay, just south of Mangles Bay, Trautman & Borowitzka (1999) documented a great increase in abundance of *Sphacelaria* and some other algae on *Posidonia* leaves from low levels during winter, after shedding of leaves during autumn (April–May), to dense growths in late summer (March). Our observation of abundant deformed *V. striata* was made at the height of the Australian summer, when the epiphytic algal growths were dense on the upper portions of *Posidonia* leaves (Fig. 1b, c).

Morphological abnormalities and inhibited shell growth in benthic foraminifers have mostly been attributed to pollution and heavy metal contamination (Alve 1995 and references within; Yanko *et al.* 1998; Le Cadre & Debenay, 2006; Eliahu *et al.* 2020). Boehnert *et al.* (2020), however, found that test deformations did not correspond to historic heavy metal contamination and suggested that other environmental stressors were

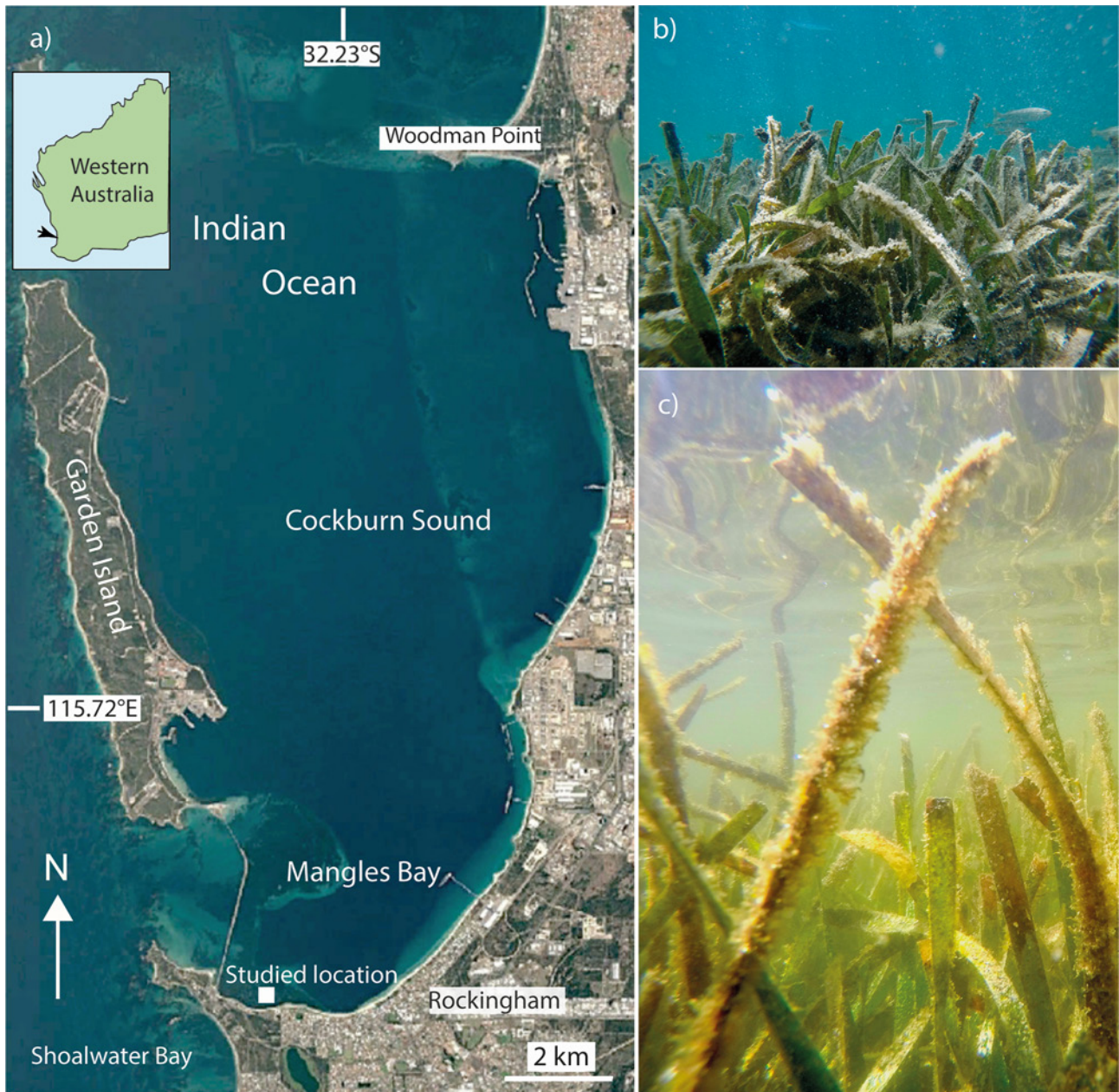


Figure 1. a) Google Earth image of Mangles Bay in the Cockburn Sound region, showing the locality investigated in January 2022 (represented by the white square 32.2744°S; 115°7054°E); b) Underwater photo of the *Posidonia australis* seagrass meadow; and c) closeup view of *Posidonia australis* leaves covered by epiphytic algae and other micro-benthic biota.

responsible. Similarly, Sagar *et al.* (2021a, b) cultured the porcelaneous foraminifer *Amphisorus hemprichii* under different levels of heavy metal contamination and did not find any significant test abnormalities. Several studies have shown relationships between natural salinity, oxygen, temperature, and/or pH variability and increased incidence of test aberrations in foraminifers (e.g. Boltovskoy *et al.* 1991; Geslin *et al.* 2002; Meriç *et al.* 2009; Li *et al.* 2020). Geslin *et al.* (2002) further showed that abnormalities could form during the reconstruction of tests damaged by hydrodynamic processes. Consorti *et al.* (2020) considered abnormalities in the tests of *P. planatus* to be a response to incrustation of filamentous

cyanobacteria covering the tests and impeding the protoplasmic stream during the addition of new chambers. The interaction between algal epiphytes and foraminifera on seagrasses and competition for space, however, have not been considered as forming morphological irregularities in any foraminifer.

To better understand the morphological deformities in the porcelaneous foraminifer *Vertebralina*, this paper (1) describes its occurrence on *Posidonia* leaves in Mangles Bay; and (2) examines the relationship between *Vertebralina* and the epiphyte *Sphacelaria* on the leaves. It also compares the deformities with those described for the species elsewhere.

LOCATION, MATERIAL AND METHODS

Cockburn Sound is home to a diverse marine biota with shared habitats (including seagrass meadows) for many fish and invertebrates (Dybdahl 1979; Johnston *et al.* 2008). Mean monthly water temperature ranges from about 24 °C in summer (December–February) to below 16 °C in winter (June–August). Normal-marine salinity prevails throughout the year (Coulson *et al.* 2016). Mangles Bay is a protected bay in the southern part of Cockburn Sound (Fig. 1a), 47 km south of Perth. The bay has a low-energy shoreline and is microtidal (diurnal, with a mean tidal range <0.5 m; Hegge *et al.* 1996; Masselink & Pattiaratchi 2001; Travers 2007). Rockingham, which borders the southern shoreline of the bay, is a popular recreational area for marine activities including fishing, snorkelling, and boating in summer. The high maritime boat activity has led to the contamination of the area with Tributyltin C₁₂H₂₇Sn (TBT), a product that was applied on boats to avoid incrustations of living organisms (D A Lord & Associates Pty Ltd 2001; Department of Fisheries 2016). Its release into the aquatic environment was responsible for numerous anomalies especially in shellfish, notably oysters, and other marine invertebrates (Alzieu *et al.* 1986; Alzieu 2000; Higuera-Ruiz & Elorza 2011). In Western Australia, use of Tributyltin in protected parts of Cockburn Sound was banned in 2003.

During an ongoing study of benthic foraminifers from the seagrass meadow in southern Cockburn Sound, small lengths of fresh *Posidonia* leaf and sediment from depths down to 6 m have been examined and foraminifera counted (Tables 1, 2). Live *Vertebralina striata* and *Peneroplis planatus* are particularly abundant, especially in shallower parts of the meadow, and are clearly detected without magnification by their large flat tests that are white and purple, respectively. These species are also common constituents of the sediment sampled within the meadow. During a recent excursion in Mangles Bay (January 2022) specimens of living foraminifers from seagrass leaves intensely covered by algae were carefully picked, counted and stored in a small plastic container filled with local sea water. The foraminifers were photographed using reflected light microscopy and images rendered with Helicon focus software. Photographs were used for measuring test and chamber dimensions. An environmental scanning electron microscope under low vacuum was used to image selected uncoated specimens. Figured specimens are curated in the collection of the Earth Science Museum at The University of Western Australia.

POSIDONIA HABITAT

Posidonia australis and *P. sinuosa* form a dense meadow at the study site (Fig. 1b). In January–February 2022, the seagrass leaves were about 30 to 50 cm long and many had been cropped at the top (Fig. 1b, c). The seagrass grows on a medium to coarse sandy bottom and forms a relatively dense meadow punctuated by sandy patches caused mainly by boat moorings. At the time of study, mature leaves were covered by a dense growth of predominantly epiphytic algae (Fig. 1b, c).

On the small leaf segments examined for this study, scale-like calcareous coralline algae cover about 50% of the surface. Tufts of *Sphacelaria* occur at frequencies from <2 per cm² on long young (clean) leaves to 11–12 per cm² on mature densely covered leaves (Table 1). Much very fine detritus (mud and organic particles, including transparent gelatinous material) accumulates around the thalli. Also present are very thin, flexible, agglutinated worm tubes which run through the *Sphacelaria* growths and calcareous serpulid worm tubes. Rare bryozoans, sponges and hydrozoans also encrust on the leaf segments.

The most conspicuous foraminiferal species living among *Sphacelaria* on the *Posidonia* leaves are *V. striata* and *P. planatus*. These porcelaneous foraminifers are characterised by an imperforate wall composed of high-magnesium calcite crystallites (Parker 2017). They are easily distinguishable, without magnification, in the field by colour. The test of *V. striata* is white with the faint dull grey protoplasm evident, particularly in inner chambers, through the translucent wall. It also has a brown organic lining to the inner whorl of chambers (Fig. 2). In contrast, the purple–violet protoplasm, due to rhodophyte symbionts (Lee 1990; Walter *et al.* 1992), of *P. planatus* is highly visible through the very thin parts of its wall between septa.

Other living foraminifers found amongst the *Sphacelaria* include common smaller miliolids (such as *Quinqueloculina*, *Triloculina*, and *Miliolinella*), and the smaller rotaliids *Elphidium* and *Planorbulina*. Other less common foraminifers include the attached *Cornuspiramia*, *Lamellodiscorbis* and *Nubeculina*. The thalli also host a diverse range of very rare other smaller rotaliids as well as buliminids. The observed forms are well-known from other Western Australian coastal sites (Parker 2009, and personal observations of the authors).



Figure 2. Live *Vertebralina striata* among epiphytes including the tufted brown alga *Sphacelaria* on *Posidonia* leaves; note the strongly grooved ornament of this specimen, grey colour of the protoplasm and brown internal organic lining in the initial whorl. A tuft of *Sphacelaria* is present near the *V. striata*. A large *Peneroplis planatus* is in the background.

Table 1. Frequencies of live *Vertebralina* on leaf segments of *Posidonia* examined in January–February 2022 and May 2020 from Mangles Bay. The area was calculated from the length and width of the segment. Minor deformities include small incisions and cavities in the wall (e.g. Fig. 3a, h–j). Major deformities include several incised subdivisions of final chambers (e.g. Fig. 3b, c, f, g, k–m).

A. Leaf segments examined January–February 2022							
Leaf area: 23 cm², with heavy epiphyte cover				Leaf area: 46 cm², with light epiphyte cover			
Live specimen count	Total	per cm²		Live specimen count	Total	per cm²	
<i>Vertebralina</i>	116	5		<i>Vertebralina</i>	40	87	
" <i>Sphacelaria</i> " tufts	278	12		" <i>Sphacelaria</i> " tufts	76	2	
<i>Vertebralina</i> test growth stage	Total	%		<i>Vertebralina</i> test growth stage	Total	%	
Trochospiral only	50	43		Trochospiral only	25	63	
Adult - with uniserial stage	66	57		Adult — with uniserial stage	17	37	
<i>Vertebralina</i> test deformities	Normal	Minor	Major	<i>Vertebralina</i> test deformities	Normal	Minor	Major
Trochospiral (only) tests - total count	45	5		Adult tests — total count	6	9	2
% Trochospiral (only)	90	10		Adult tests — % adults	0	30	38
Adult tests — total count	11	38	17				
Adult tests — % adults	17	57	26				
B. Leaf segments scanned May 2020							
Clean leaf segments with few epiphytes							
leaf area: 61.5 cm²							
Live specimen count	Total	per cm²		Live specimen count	Total	per cm²	
<i>Vertebralina</i>	75	2		<i>Vertebralina</i>	32	0.5	
" <i>Sphacelaria</i> " tufts	491	10.9		" <i>Sphacelaria</i> " tufts	76	2	
<i>Vertebralina</i> test growth stage	Total	%		<i>Vertebralina</i> test growth stage	Total	%	
Trochospiral only	15	20		Trochospiral only	28	88	
Adult - with uniserial stage	60	80		Adult — with uniserial stage	4	12	
<i>Vertebralina</i> test deformities	Normal	Minor	Major	<i>Vertebralina</i> test deformities	Normal	Minor	Major
Adult tests — total count	19	18	23	Trochospiral (only) tests — total count	28	1	3
Adult tests — % adults	32	30	38	% Trochospiral (only)	88	3	9
Leaf segments with heavy epiphytes cover (including <i>Sphacelaria</i>)							
leaf area: 34 cm²							
Live specimen count*	Total	per cm²		Live specimen count*	Total	per cm²	
<i>Vertebralina</i>	215	6		<i>Vertebralina</i>	215	6	
Leaf area: 48 cm², with moderate epiphyte cover							
Live specimen count	Total	per cm²		Live specimen count	Total	per cm²	
<i>Vertebralina</i>	108	2		<i>Vertebralina</i>	108	2	
" <i>Sphacelaria</i> " tufts	229	4.8		" <i>Sphacelaria</i> " tufts	229	4.8	
<i>Vertebralina</i> test growth stage	Total	%		<i>Vertebralina</i> test growth stage	Total	%	
Trochospiral only	66	61		Trochospiral only	66	61	
Adult - with uniserial stage	42	39		Adult - with uniserial stage	42	39	
<i>Vertebralina</i> test deformities	Normal	Minor	Major	<i>Vertebralina</i> test deformities	Normal	Minor	Major
Adult tests — total count	26	13	3	Adult tests — total count	26	13	3
Adult tests — % adults	62	31	7	Adult tests — % adults	62	31	7

* Test were identified in photographic scans of leaves and were partly hidden under epiphytes. Therefore, counts of deformities could not be made.

Table 2. Frequencies of *Vertebralina striata* in sediment samples from under *Posidonia* seagrass meadows at Mangles Bay. n = number of specimens. Sediment samples were washed in freshwater, the water decanted, and the sediment dried. The volume of dry sediment was measured in a calibrated cylinder.

Sample	Water Depth (m)	Volume (cm ³)	n <i>V. striata</i>	n/cm ³	n Adults (>4 chambers)	n Bifurcated	n indented
24112018-01	0.8	1.1	65	59	41	2	32
24112018-02	2.3	1.2	44	37	23	2	23
24112018-03	2.5	1.6	23	14	14	0	13
10112018	4	1.8	8	4	6	0	5
10112018-04	4	1.7	7	4	5	0	2
10112018-05	5	1.6	33	21	8	0	3
10112018-06	6	1.5	15	10	5	0	2
11022022-01	1	0.8	37	46	5	1	20

MORPHOLOGICAL VARIATION IN *VERTEBRALINA STRIATA*

Vertebralina striata has a low trochospiral test with flattened broadly elongate chambers and a broad apertural slit that lies on the flat umbilical side along the terminal face of the last chamber (Fig. 3). The aperture is bordered by a thickened lip. An abnormal Y-shaped aperture is present in one large, deformed test (Fig. 3m). Most descriptions of the species show specimens with

final chambers still part of a trochospiral coil (Loeblich & Tappan 1987; Haig 1988; Hottinger *et al.* 1993; Parker 2009). However, some of the specimens from Mangles Bay have up to five uncoiled adult chambers (Fig. 3). A similar uncoiled morphotype from Oyster Harbour next to Albany in southern Western Australia, was attributed to *Vertebralina* sp. by McKenzie (1962, pl. 1 fig. 21). In our studied assemblage, tests vary from a juvenile trochospiral morphotype of 288 µm maximum diameter to a gerontic test with five uniserial chambers and a



Figure 3. *Vertebralina striata* extracted from around *Sphacelaria* on *Posidonia* leaves at studied locality; views of the dorsal/spiral (a–c, f, g, i, j) and ventral/umbilical (d, e, h) sides showing morphological modifications of final chambers in response to development among thalli (brown fibre-like growths) of *Sphacelaria* brown algae. Rendered reflected-light micrographs. Scale bars = 200 µm. a) UWA181398; b) UWA181399; c) UWA181400; d) UWA181401; e) UWA181402; f) UWA181403; g) UWA181404; h) UWA181405; i) UWA181406; j) UWA181407; k) UWA181408; l) UWA181409; m) UWA181410.

maximum length of 1192 μm (Fig. 4a). Considerable variation exists in the lengths of adult (uniserial) tests, e.g. at the three uniserial chamber stage, tests vary from 577–962 μm (Fig. 4a). In undeformed tests with uniserial stages, the growth pattern of chamber addition is, however, markedly irregular (Fig. 4b).

Wall ornamentation is highly variable between specimens and even between adjacent chambers. It can vary from unornamented and smooth (e.g. early parts of test in Figs. 3c and i), to finely striate as is typical of the species and most specimens (Figs. 3d–i). The striae extend the length of the chamber and are 2–4 μm wide (mean $\sim 3 \mu\text{m}$). In many large specimens, large grooves may

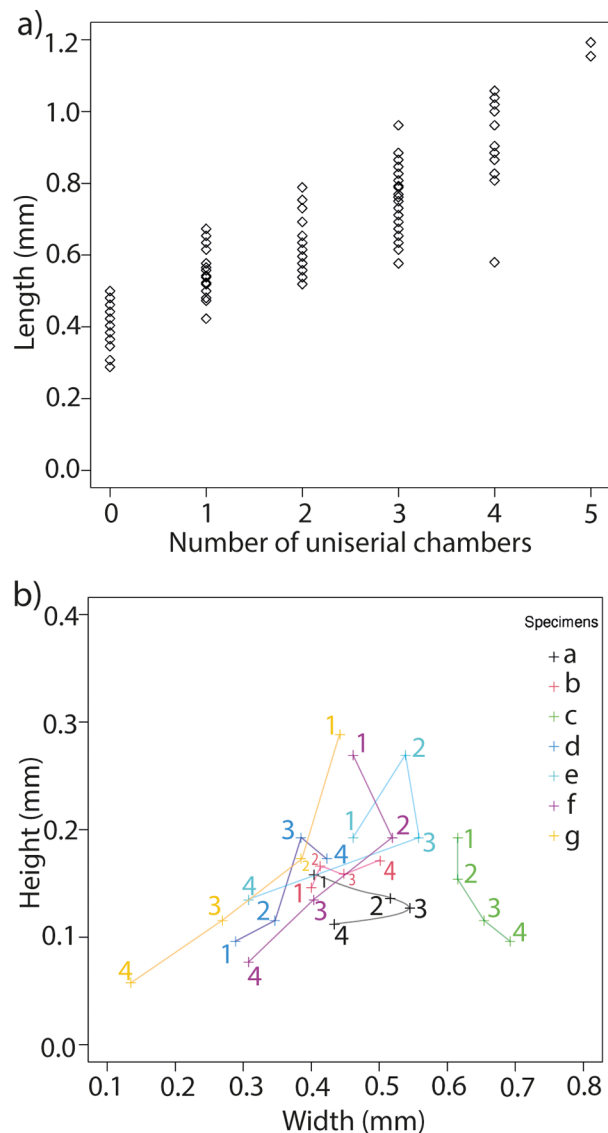


Figure 4. Measurements on tests of *V. striata* collected from small leaf segments (23 cm^2 of leaf surface): a) Length of test against number of uniserial chambers with '0' being tests with only trochospiral development; and b) Highly irregular growth patterns in the uniserial stages of seven tests that lack abnormalities; progressive changes (1–4, added uniserial chambers) are represented by a plot of maximum chamber height vs maximum chamber width.

be present that are typically parallel to the direction of growth and extend for most of the height of the chamber (Fig. 3). The grooves are much larger than the striate ornament, ranging in width from 12 to 20 μm (mean $\sim 15 \mu\text{m}$) and are superimposed by the fine striae. The shapes of the grooves vary and may be linear (Fig. 3e), irregular (Fig. 3h), sinuous (Fig. 3h), broken (Fig. 3b), or curved (Fig. 3f), which is in part due to the chamber shape and tightness of coiling at the stage of chamber development. The wall of the test is thinner at the grooves, exposing parts of the chamber lumen and the foraminifer to increased light intensity, as observed in live specimens (see Fig. 2). In some specimens, numerous long thin irregular marks that are perpendicular to the coiling direction and wall ornament were observed under SEM (e.g. Fig. 5d). The nature of these is uncertain but given that they show no distinct excavation of the test wall, are parallel to the apertural face and appear to be restricted to the last chamber, they are possibly wrinkles in an organic lining. Further study is required to confirm the nature of these marks.

The final chambers of some tests bifurcate (Fig. 3b, c, h, j, l, m) or trifurcate (Fig. 3f, g, k). Small cavities and indentations also exist in the wall of many tests (Fig. 3g). Some indentations are clearly the linear impressions of *Sphacelaria* thalli (Fig. 5b). These abnormalities, particularly branched chambers, are found mainly in large specimens with uniserial mature stages (Fig. 3j). The abnormalities are much less common in the earlier trochospiral chambers and were not observed in tests with less than four final chambers. The causes of abnormalities mainly influenced chamber growth during the final stages of test development in mature specimens.

Chamber addition has been observed in several specimens (Fig. 6). A transparent gelatinous sheath encases the extruded protoplasm and forms a template for the new chamber. Incipient calcification takes place in patches on the inside of the sheath and is marked by whitish areas (Fig. 6b, c). These are presumably concentrations of minute calcite crystallites (Angell 1980; Hemleben *et al.* 1986; de Nooijer *et al.* 2009). The striate ornament, as occurs in previous chambers, is already imprinted in the transparent sheath (Fig. 6c). As suggested by Parker (2017), ornament in the miliolid foraminifers is a genetic function of wall formation, rather than added afterwards.

The presence of abnormal *V. striata* living on *Posidonia* has been observed throughout the year. On *Posidonia australis* leaf segments with few epiphytes collected during May 2020, living *V. striata* was present at frequencies of 0.5 specimens per cm^2 , but on leaf segments with dense epiphyte growth the frequencies were six specimens per cm^2 , comparable to frequencies found in our January 2022 observations (Table 1). This suggests that the maximum abundance of *V. striata* occurs when there is a heavy epiphyte load on the *Posidonia* leaves.

Examination of mainly discarded *V. striata* tests in sediments from Mangles Bay yielded 4–60 specimens per cm^3 (Table 2). The highest abundances are in the shallow (<2 m) western parts of the seagrass meadow, and the lowest in deeper (>4 m) on the outer edges. Within the sediment, bifurcate and trifurcate specimens are rare, with only two specimens per cm^3 encountered in samples

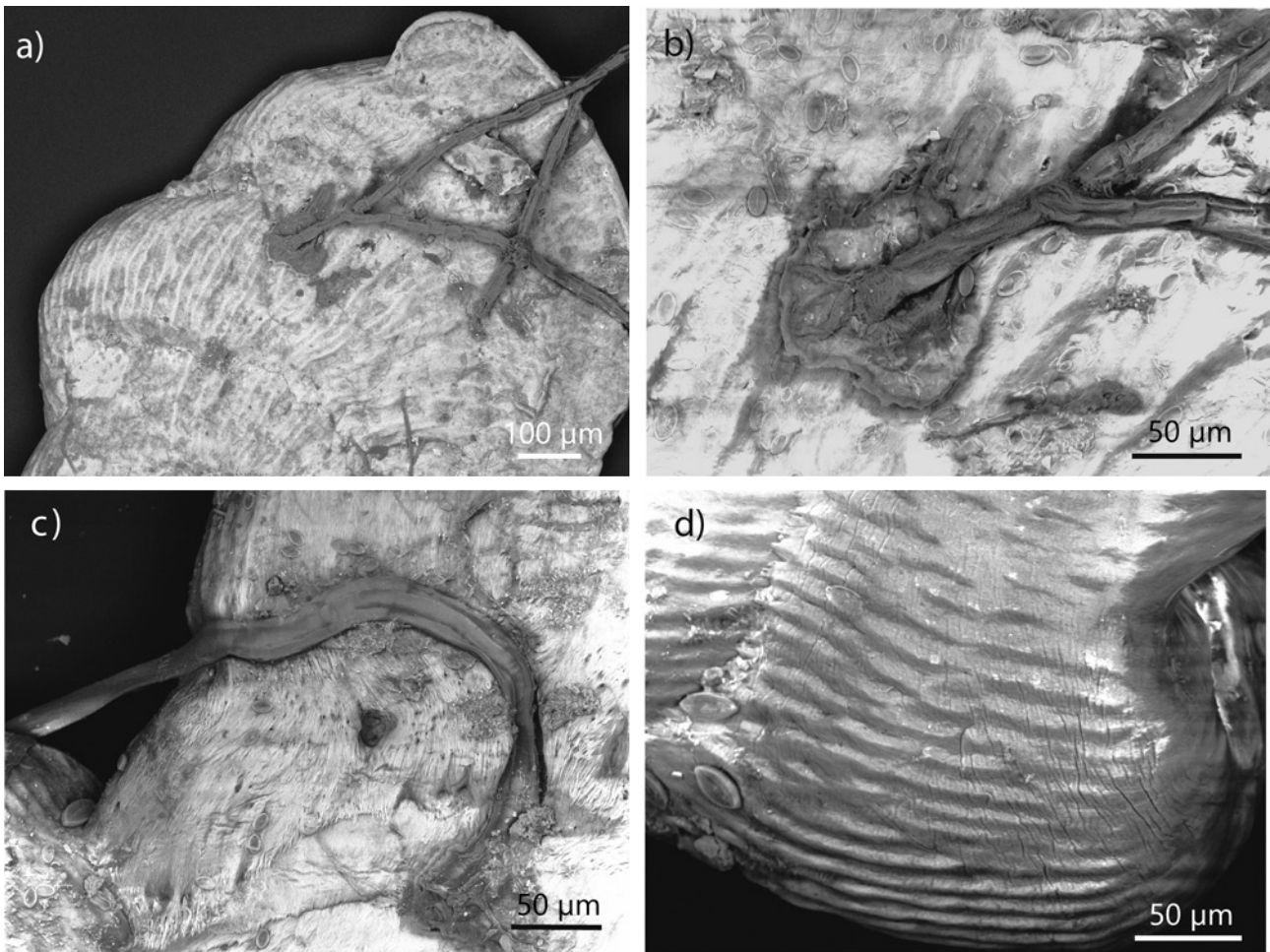


Figure 5. *Vertebralina striata* with thalli of *Sphacelaria* and abnormal surface microstructure; SEM micrographs taken of uncoated specimens in an environmental scanning electron microscope. a, b) lateral views of UWA181398 (Fig. 3a); b) closeup view of the base of a protruding thallus; c) lateral views of UWA181400 (Fig. 2c); and c, d) lateral view of UWA181404 (Fig. 3g). Note long thin irregular marks that are perpendicular to the striate ornament. Diatoms are common on most of the tests.

with the highest abundances of *V. striata*—at the same locality as the observed abundance of abnormal *V. striata* living amongst *Sphacelaria*. Minor deformities, such as indentations and the propensity to uncoil, can make up to >50% of the adult population in the sediment.

INFLUENCE OF SPHACELARIA ON GROWTH IN *V. STRIATA*

On *Posidonia* leaves, *V. striata* are common in small, enclosed spaces among the tufted *Sphacelaria* (Fig. 2). They are much more common around *Sphacelaria* growths than on younger leaves and lower parts of leaves that lack a dense epiphytic community. In normal growth position, *V. striata* lives with its broad flat umbilical side downwards on the substrate. In Mangles Bay, they are commonly found on the surface of *Posidonia* leaves—an observation that contrasts with that of Langer (1993) who suggested *Posidonia* rarely hosts *V. striata* in meadows within the Mediterranean. The aperture, through which food is ingested, is normally just above the leaf surface enabling pseudopodia to gather diatoms and other

very fine organic detritus, and to stream this material to the internal cytoplasm. However, where there are dense *Sphacelaria* thalli on the *Posidonia*, this life position is impossible to maintain. The confinement to small inter-thalli spaces impedes the normal addition of new chambers. This is evident in the observed relationship between *V. striata* and *Sphacelaria* tufts on *Posidonia* leaves, i.e. the tufts occur within shallow grooves in the peripheries of tests, between bifurcating and trifurcating branches, extending through narrow holes in the test, and growing attached to first-formed parts of large mature *V. striata*.

We suggest that morphological abnormalities present in mature specimens of *V. striata* living on *Sphacelaria*-encrusted leaves, are the result of *Sphacelaria* thalli obstructing the flexible transparent sheath (Fig. 6) that forms the template for the new chamber. Figure 7 shows a model for adult chamber addition. Normal development (Figs 3d, i; 6a–c) takes place where no thalli are present in the area where the new chamber is forming (Fig. 7a, b). Bifurcations (Fig. 3 c, h, j) and trifurcations (Fig. 3f, g) develop where *Sphacelaria* thalli impede the normal development of the transparent sheath encasing the

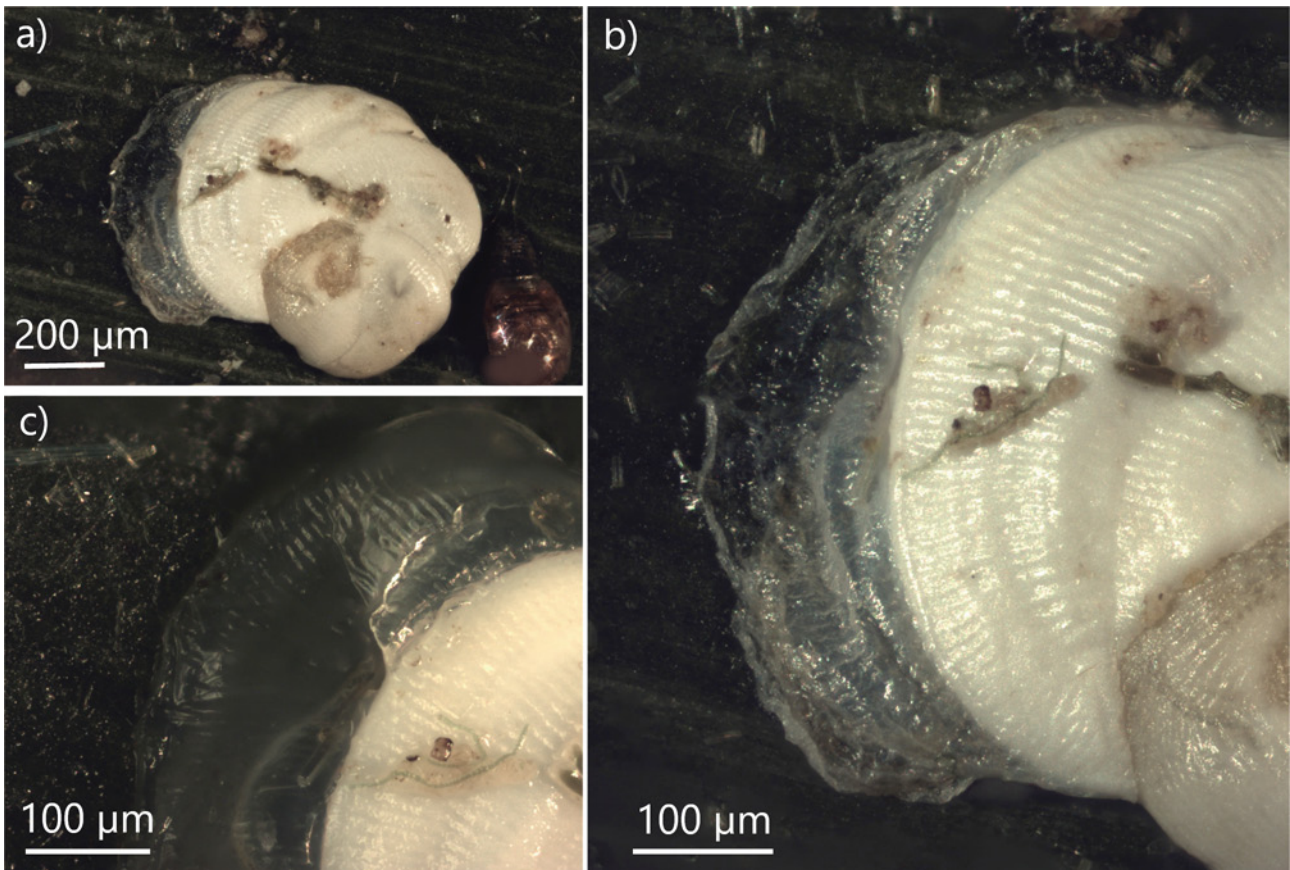


Figure 6. The addition of a new uniserial chamber in *Vertebralina striata* living on a *P. australis* leaf free of dense epiphytic algae. Note: (1) cytoplasm is enveloped by a transparent sheath that outlines the position of the new chamber; (2) striate ornament is already present in the transparent sheath before calcification; (3) white areas on the sheath indicate incipient concentrations of minute calcite crystallites that form the mineralised wall. Specimen collected from Mangles Bay seagrass meadow in 2018.

protoplasm of the new chamber (Fig. 7c, d). Small cavities and depressions, and peripheral grooves are also formed where the transparent sheath encloses or is indented by *Sphacelaria* thalli (Fig. 7e, f). The effects of algal filaments that encrust on the wall surface, other than indentation of the test wall, require further study (Fig. 5).

DISCUSSION

Morphological aberrations in *V. striata*, similar to those reported here, have been described in the Gulf of Izmir, northern coast of Karaburun Peninsula, Turkey by Meriç *et al.* (2009, 2012, 2019). Their specimens were collected from sand near a thermal spring, but the living habitat was not described. Several studies conducted around the same locality have described prolific shallow-water seagrass meadows, where *Posidonia oceanica* is abundant (Dural *et al.* 2012, 2013). The epiphytic community on *P. oceanica* comprises brown macroalgae including *Sphacelaria* (Taşkin & Öztürk 2013; Taşkin 2014). The assemblage in sand likely includes many dead specimens from many generations of the species. Some of the *V. striata* tests figured by Meriç *et al.* (2019, e.g. figs 2, 4a, b, c), appear to have scars on the walls caused by embedded algal thalli. The morphology may not be related to influences on the environment by thermal

springs as this would cause noticeable deformities in the tests throughout ontogeny. Based on our observations in Mangles Bay of *V. striata* with similar deformities, we suspect that the Turkish deformed assemblages of *V. striata* may also be the result of interaction with *Sphacelaria* epiphytes on *Posidonia*.

Consorti *et al.* (2020) suggested that abnormal test development in *Peneroplis planatus* from Pete's Pond at Lake McLeod, Western Australia, was linked to cyanobacterial growth. They postulated that *P. planatus* gets entangled in fine cyanobacterial filaments growing on mangrove roots inhibiting growth, forcing the foraminifers to adapt the shape of new chambers around the filaments. This results in bifurcation and trifurcation of chambers. As in *Vertebralina*, such deformities were only observed in the later chambers of adult specimens. At Mangles Bay, the association of *V. striata* with the brown algae thalli appears to be similar and results in wide variations in the shape of adult chambers. On the examined seagrass leaves, deformed *V. striata* were observed abutting other less common epiphytes, such as other algae and bryozoans. The interactions were not as striking as observed with the denser *Sphacelaria*, but overall, our observations demonstrate that by deforming its chambers during growth, *V. striata* is able to successfully compete for living space amongst other epiphytic organisms.

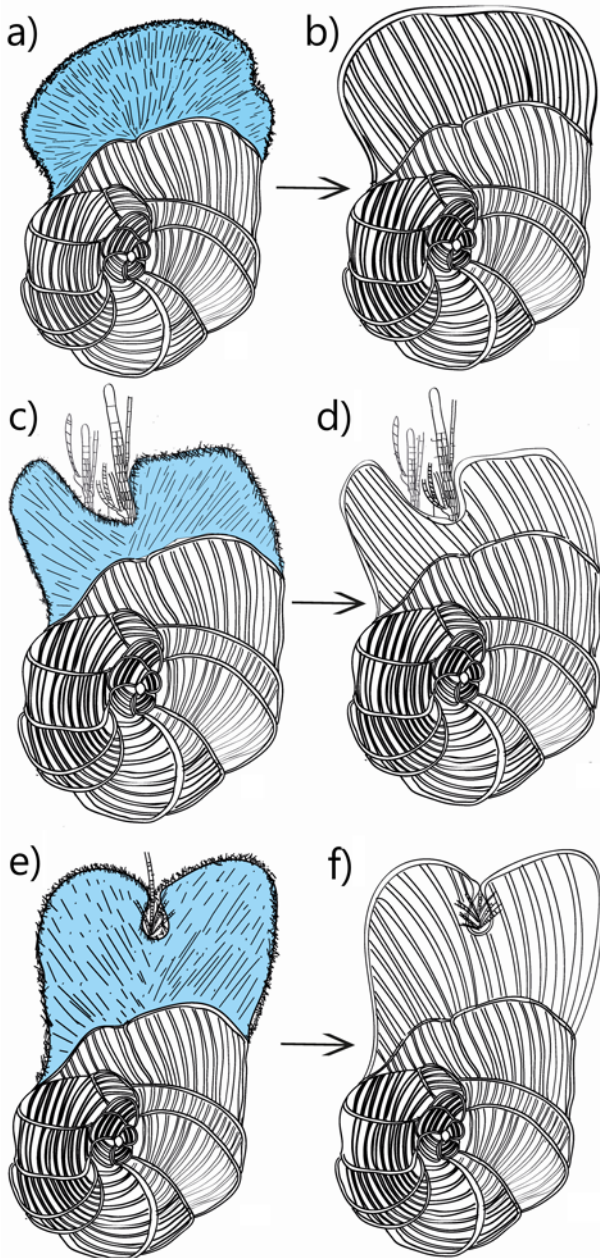


Figure 7. Diagrams showing possible scenarios for development of morphological abnormalities in *Vertebralina striata*. The blue areas shown on a, c, e) are cytoplasm extruded from the aperture covered by a transparent flexible sheath (Fig. 6) that forms the template for the new chamber; a, b) normal unimpeded growth; c, d) chamber addition when dense tufted *Sphacelaria* causes bifurcation of the final chamber; e, f) initial chamber divergence around *Sphacelaria* thalli is repaired leaving the thalli protruding through the test.

We suspect that the seasonal shedding of leaves by *Posidonia* (Silberstein 1985) and changes in intensity of *Sphacelaria* incrustation (Trautman & Borowitzka 1999) results in the seasonal variation in the abundance of deformed tests of *Vertebralina* and possibly of other foraminifers. As *Posidonia* sheds leaves in Autumn (April–May) and the build-up of *Sphacelaria* reaches a maximum density in Summer (December–February), the maximum

number of deformed tests would be expected during Summer. This also suggests that there may be increased abundances of dead deformed tests in sediment where seagrass wrack is deposited, which could be away from meadows. However, investigation of these is outside the scope of the present study, and demonstrations of seasonal and transported increases in the abundance require further study.

CONCLUSIONS

Up to 80% of mature specimens of *Vertebralina striata* in the fauna described here, living among the brown tufted algae *Sphacelaria* on *Posidonia* leaves, show abnormalities in their adult chambers. During chamber addition, due to obstruction mainly by thin cylindrical algal thalli, deformities occur in the growth of the flexible transparent sheath that forms a template for the new chamber. Thus, after calcification, some specimens have bifurcated or trifurcated final chambers, and/or have embedded thalli in the chamber walls forming depressions or cavities. The abnormalities are mainly in the adult chambers of mature specimens; juvenile stages show normal growth patterns.

This study demonstrates that some foraminiferal species, when competing for space with epiphytic algae, can adapt the shape of new chambers to deflect around or accommodate the epiphyte, resulting in structural abnormalities in the test that need not be linked to pollution. It also shows an increase in *V. striata* with deformed tests may be linked to seasonal growth patterns in both *Posidonia* and its epiphytic *Sphacelaria*. More detailed studies of living *V. striata* on *Posidonia* should include: (1) sampling and examination of the meadows and their epiphytes at short regular intervals through the year to chart seasonal variations in more detail; (2) determine if the abundance of foraminiferal species such as *V. striata* is linked to abundance of food particles (e.g. diatoms) in the dense *Sphacelaria* growths; and (3) recording abnormalities in other foraminifers living in Cockburn Sound, particularly in other habitats.

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