The biology of sympatric species of Scintillona (Bivalvia: Galeommatoidea) commensal with Pilumnopeus serratifrons (Crustacea: Decapoda) in Moreton Bay, Queensland, Australia, with a description of a new species

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ABSTRACT

Two species of the galeommatid genus Scintillona, S. cryptozoica and S. daviei sp. nov. are sympatrically associated with the gallery-building pilumnid crab Pilumnopeus serratifrons inhabiting clumps of the mussel Trichomya hirsuta on a seagrass-covered intertidal mudflat at Myora Springs, North Stradbroke Island, Queensland, Australia. The new species is described and compared with S. cryptozoica. Sympathy is not total: of the 100 galeommatid clusters examined, 40 of S. cryptozoica and 27 of S. daviei were species specific, and 33 were sympatric. Clusters of S. cryptozoica and S. daviei ranged in numbers from 1–25 and 1–7 individuals, respectively. Both species appear to be protandric consecutive hermaphrodites: the male component of the ovotestis dominated at shell length sizes of 1–3 mm (S. cryptozoica) and 1–2.5 mm (S. daviei), respectively; females ranged in shell length from 5–10 mm and 3–7.5 mm, respectively. Both species brood fertilised eggs in the outer demibranchs of their ctenidia at shell lengths of between 6.5–8.0 mm and 3.5–6.0 mm. The relationship of both species with their host crab appears to be related to protection within its gallery and the provision of respiratory and feeding currents by virtue of its activities, and can thus be defined as commensalism.

Fourteen species of mangroves occur in south-eastern Queensland (Duke 2006), though only seven reach as far south as Moreton Bay, which is the southern limit for most species (Davie 1998). At Myora Springs on the northwest coast of North Stradbroke Island, the coastal fringe of mangroves mostly comprising Avicennia marina, Aegiceras corniculatum and Rhizophora stylosa gives way to an extensive area of mud that is colonised at mid-tidal levels by the seagrasses Zostera capricorni, Halodule uninervis and Halophila ovalis. As the tide recedes, the seagrass beds are seen to be dotted with clumps of the hairy mussel Trichomya hirsuta (Lamarck, 1819), up to ~15 cm in diameter. This large, up to 65 mm shell length, mussel has a wide distribution encompassing South Australia, Tasmania and New South Wales to as far north as northern Queensland (Lamprell & Healy 1998). The mussel clumps sit in shallow depressions in the mud, and when turned over, sometimes possess small groups of white, translucent bivalves. Two species of the genus Scintillona Finley, 1927 [formerly attributed to Varotoga (Iredale, 1931)]
(Galeommatoidea Gray, 1840) occur sympatrically beneath the mussel clumps. From the clumps have been recorded a number of other species of invertebrates, including an alpheid shrimp, but their bases are almost exclusively occupied by the pilumnid crab *Pilumnopeus serratifrons* (Kinahan, 1856). This crab creates galleries in its mussel clumps, and it is to the roofs of these that the two bivalves attach.

*Scintillona cryptozoica* (Hedley, 1917) has been recorded from New South Wales, but its sympatric congeneric is undescribed. This study is therefore a description of the new bivalve species as well as a study of the biology of the two species, including basic anatomy, the extent and intimacy of their sympatry, reproduction and the relationship with their host crab *Pilumnopeus serratifrons*.

The Galeommatoidea comprises a highly diverse group of miniature, commensal bivalves that are associated with an equally wide range of marine invertebrate hosts (Boss 1965a) (although *Cycladoconcha amboinensis* (Spärck, 1931) is possibly parasitic within the oesophagus of synaptid holothurians). Galeommatoids can also be members of quite complex communities, for example, the tiny (1.7 mm shell length) *Jousseaumella concharum* shares a gastropod shell with a sipunculan and a polychaete (Knudsen 1944). They are, however, rarely recorded as associates of crabs although they do live with, similarly commensal, pinnotherids in often highly complex associations with larger invertebrate hosts (Manning & Morton 1987; Morton 1988). The association between the two species of *Scintillona* to be described herein with *Pilumnopeus serratifrons* is thus of especial interest, particularly with regard to their sympatry, the morphological adaptations they have, particularly of the mantle, and their expressions of sexuality that equip them for such a lifestyle.

**Abbreviations.** Institutions: Queensland Museum, Brisbane, Queensland (QM); Australian Museum, Sydney, New South Wales (AM); The Natural History Museum, London, UK. (NHM).

Shell and anatomical structures: A, Anus; AA, Anterior adductor muscle (or scar); ADT, Antero-dorsal tentacle; AT, Anterior tentacles; B, Byssal thread; DD, Digestive diverticula; ES, Exhalant siphon; F(H), ‘Heel’ of foot; F(T), ‘Toe’ of foot; H, Heart; HT, Hinge tooth; I, Intestine; ID, Inner demibranch; ILP, Inner labial palp; K, Kidney; L, Ligament; LP, Labial palp; OD, Outer demibranch; OLP, Outer labial palp; OVT, Ovotestis; PA, Posterior adductor muscle (or scar); PDT, Postero-dorsal tentacle; PS, Pigment spot; PT, Posterior tentacles; R, Rectum; RM, Reflected mantle; S, Socket; SUBC, Supra-branchial brood chamber; U, Umbo.

**MATERIALS AND METHODS**

From 9–24 February 2005, daily visits were made during periods of falling tides to the mud flats at Myora Springs, Moreton Bay, North Stradbroke Island, Queensland. Here, the seagrass covered mud flats are dotted with byssally bound clumps of the mussel *Trichomya hirsuta*. On each visit, the clumps were picked up, turned over and examined for the galeommatid bivalves of the genus *Scintillona*. Where these were seen, all individuals were collected and put into pre-numbered vials of seawater. The clumps were then broken apart gently and any other animal species associated with the *Scintillona* individuals collected and placed in numbered tubes. On return to the laboratory, the *Scintillona* individuals were separated into species, that is, *S. cryptozoica* and a sympatric new species. Shell lengths of all individuals were measured. All individuals of all species collected in association with the mussel clumps, and the two species of *Scintillona* were identified to the highest taxonomic category.

Both *Scintillona* species were examined anatomically. Some individuals were drawn, others were dissected to expose details of shell and hinge structure, and general anatomy. The ciliary currents of the organs of the mantle cavity of both species were examined under a binocular microscope and elucidated using carmine dissolved in seawater. Finally, all individuals were sexed into one or other of four categories, that is: i) females brooding fertilised eggs in their ctenidia; ii) unfertilised females; iii) individuals of indeterminate sex; and iv) males. Subsequently, two individuals of the new species of *Scintillona* were, following routine processing and gold sputter coating, examined using a scanning electron microscope (Jeol 820) at the University of Cambridge.
HABITAT NOTES

The clumps of *Trichomya hirsuta* have as their basis an empty oyster shell, *Saccostrea glomerata* (Gould, 1850), a valve of *Pinctada cf. fucata* (Gould, 1850), or *Isognomon ephippium* (Linnaeus, 1758) or that of a conspecific. The mussel clump so attached may comprise >30 individuals, and the hair-like periostracum that covers the posterior region of each individual’s valves creates a matted covering to the byssally bound, compact mass. The bowl of mud in which each mussel clump sits, is not anaerobically black, but clearly aerated. When each mussel clump is turned over, typically the most obvious co-residents are the galeommatid bivalves. Other inhabitants of the galleries included the near ubiquitous occurrence of *Pilumnopeus serratifrons*, and either one or two individuals each of: i) *Alpheus cf. pacificus* Dana, 1852 (Caridea: Alpheidae); ii) *Phascolosoma cf. arcuatum* (Gray, 1828) and *P. cf. dunwichi* Edmonds, 1956 (Sipuncula); iii) *Paralepidonotus cf. ampulliferus* (Grube, 1878) (Annelida: Polynoidae); iv), *Favonigobius cf. lateralis* (Macleay, 1881) (Pisces: Gobiidae) and v) occasional representatives of four other species of Galeommatoidea (the latter all sent to Dr. P. Middlefart, Australian Museum, Sydney).

NOTES ON THE *PILUMNOPEUS SERRATIFRONS* POPULATION

A total of 78 individuals of *Pilumnopeus serratifrons* was collected comprising 45 males (57.7%) and 33 females (42%). Nine females were gravid (27.3%). The mean carapace widths of male and female individuals of *P. serratifrons* were 7.3 mm and 9.2 mm, respectively. Interestingly, although all collected individuals were relatively small (ranging in carapace width from 3.5–14.5 mm), this species can reach about 28.0 mm in carapace width (Davie 1989). However, much of the material recorded by Davie (1989: 130) in his taxonomic revision of the species was of similar size to that recorded here. It would seem possible that smaller individuals preferentially inhabit mussel clumps as well as other narrow cavities such as in rotting logs and amongst oysters (Davie, pers. comm.). The broader habitat of this species is ‘in the lower estuary or on sandy mud flats, living under stones and debris resting on the substrate, from about half tide level to low water’ (Davie 1989).

The majority of individuals (32 males and 26 females occurred singly, although five male/female, four male/male and one female/female pairs were identified. Of the nine gravid (egg bearing) individuals collected, seven occurred singly while two were partners in the male/female pairs (Table 1). Morton & Lutzen (2008) report upon the rhizocephalan *Loxothylacus spinulosus* Boschma, 1928, parasitising *P. serratifrons* in the *Trichomya* clumps.

**TAXONOMY**

Hedley (1917, pl. xvi, fig. 1[animal]; pl. ii, fig. 40 [shell]) erected a new name, *Solecardia cryptozoica*, for a gregarious galeommatid species that lives in ‘companies of a dozen or so’ (p. 685) individuals underneath stones at low water in Middle Harbour, Sydney. Iredale (1931: 206) proposed the generic name *Varotoga* for this species, as he felt *Solecardia* was being too broadly used ‘for any glassy oval shell’. Subsequently, Iredale (1936) described a second galeommatid occupying the burrows of the prawn *Crangon* from Bottle and Glass Rocks, Watson’s Bay, Sydney. This was called *Ambuscintilla praemium* gen. nov., sp. nov., although the illustration (pl. xxi, fig. 4) is clearly identical with that of

<table>
<thead>
<tr>
<th></th>
<th>Numbers</th>
<th>Mean carapace width (mm)</th>
<th>Range in carapace width (mm)</th>
<th>Nos of single individuals</th>
<th>Nos of M:F pairs</th>
<th>Nos of M:M pairs</th>
<th>Nos of F:F pairs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males</td>
<td>45</td>
<td>7.3</td>
<td>3.5 – 14.5</td>
<td>32</td>
<td>5</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Females</td>
<td>33</td>
<td>9.2</td>
<td>5.5 – 14.0</td>
<td>26</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Gravid females</td>
<td>9 (of 33)</td>
<td>8.7</td>
<td>7.5 – 10.0</td>
<td>7</td>
<td>2</td>
<td>–</td>
<td>–</td>
</tr>
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</table>

Table 1. Data on the population structure of *Pilumnopeus serratifrons* inhabiting the mussel (*Trichomya hirsuta*) clumps on the shore at Myora Springs, Moreton Bay, North Stradbroke Island, Queensland.
Varotoga cryptozoica (Hedley, 1917, pl. ii, fig. 40). Dr P. Middelfart (pers. comm.) believes that Iredale probably did collect specimens of a new species (of Varotoga) but that he also appears to have mixed them with at least one specimen of V. cryptozoica which was used for the published figure. As the deposited type specimen in the Australian Museum also belongs to V. cryptozoica, Ambuscintilla praemium must be treated as a junior synonym of V. cryptozoica.

Under current usage, Varatoga is considered a junior synonym of Scintillona Finlay, 1927 (see Lamprell & Healy 1998: 152). Dr Peter Middelfart is currently undertaking a revision of the Galeommatoidea, and believes there are good reasons to maintain Varatoga as a separate taxon. However, until his revision is published it seems more appropriate to use Scintillona for the present work.

GALEOMMATOIDEA Gray, 1840
Galeommatidae Gray, 1840

Scintillona Finlay, 1927
Scintillona Finlay, 1927: 465 [type species: Spaniorinus zealandica Odhner, 1924].

Scintillona daviei sp. nov.
(Figs 1, 2, 3, 4, 5 & 6)

Material Examined. HOLOTYPE: QM-MO77617, shell length 4.5 mm, sand flat in front of Myora Springs, Moreton Bay, North Stradbroke Island, Queensland, 9–24,02, 2005, B. Morton. PARATYPES: QM-MO77618, shell length 4.0 mm, AM-C.454645, shell length 5.0 mm, AM-C.454646, shell length 5.0 mm, NHM 20060145, shell length 4.0 mm, NHM 20060146, shell length 4.5 mm, data as for holotype.

Etymology. The species is named after Peter Davie, Senior Curator (Crustacea), Queensland Centre for Biodiversity, Queensland Museum, Brisbane, Queensland, Australia, in gratitude for his endeavours in organising the workshop during which the material was collected.

Description. Small (< 7.5 mm shell length), approx. equilateral and equivalved. Holotype: shell 4.5 mm in length; almost as tall (4.0 mm) as long and laterally plump. Posterior valve face more inflated and pointed than the more marginally rounded anterior. Hinge line purple with an internal opisthodetic ligament and small anterior hinge teeth on both valves interlocking in a medial socket. Shell translucent with purple hinge.

Remarks. Scintillona daviei sp. nov. has a distinctive array of tentacles and papillae adorning the middle mantle folds that are reflected to mostly cover the shell except apically (Fig. 1). The mantle margin is dark red around the exhalant siphon and yellow/orange around the inhalant aperture. There are antero- and postero-dorsal tentacles above the inhalant aperture and exhalant siphon, respectively. There are two pairs of other tentacles anteriorly and one pair posteriorly. Smaller papillae adorn the outer (actually the inner) surface of the reflected middle mantle fold. All the tentacles and papillae are coloured a deep red/purple apically. Such an arrange-

FIG. 1. Scintillona daviei sp. nov.: holotype (QM-MO77617) illustrated in life from the left side.
ment of tentacles and the purple hinge identifies the species.

According to Lamprell and Healy (1998) two species of *Scintillona* occur in Australian waters. These are *S. hyalina* (Deshayes, 1856) and *S. cryptozoica* (Hedley, 1917). The former is known only from the holotype in the collections of the Natural History Museum, London (BMNH 196791) and was collected in the Torres Strait but from an unknown habitat (see Lamprell and Healy, 1998, fig. 395). It is 14 mm long, equilateral and is elongately oval with a straight hinge line. It is clearly different from the much smaller, rounded, plump *S. daviei* sp. nov. *Scintillona daviei* also differs from the only other known Australian species, *S. cryptozoica* (but with which it is sympatric, as this study will show), in a number of distinctive ways (Table 2). Firstly, not only is *S. daviei* smaller (<7.5 mm shell length) than *S. cryptozoica* (10 mm shell length), but it is also plumper, that is, the shell length to height ratio is 1:0.75, versus 1:0.69. Secondly, the hinge line and plate of *S. daviei* is always a distinctive purple and the arrangement of the hinge teeth between the two species is subtly different. There are, thirdly, distinctive differences in the arrangement of the tentacles and pallial papillae, but *S. daviei* also possesses a distinctive pigment spot in the foot whereas *S. cryptozoica* does not. Differences between the species are further detailed more extensively under the headings ‘Shell Structure and Anatomy’ following.

**Distribution.** Known only from the type locality; sand flats in front of Myora Springs, Moreton Bay, North Stradbroke Island, Queensland, Australia.

**SHELL STRUCTURE AND ANATOMY OF SCINTILLONA DAVIEI**

The shell of *Scintillona daviei* sp. nov. is illustrated as a SEM image from the left side in Fig. 2A. It is translucent and covered in a thin (2 μm) periostracum. The umbo is tall and prosogyrous. The posterior face is more inflated and pointed than the narrower and more rounded anterior. Nevertheless, the species is approx. equilateral and equivalent. Internally (Fig. 3A), the anterior (AA) and posterior adductor (PA) muscles are of approximately equal sizes and are situated below the anterior and posterior hinge lines, respectively. The purple hinge plate is illustrated in Figs 2B, C and 3B, C. The ligament (Fig. 3, L) is situated posterior to the umbo (U) and there is an anterior hinge tooth (HT) in the left valve (Figs 2B & 3B). There is a similar hinge tooth in the right valve (Figs 2C, 3C, HT) and both abut each other but do not

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<tr>
<th>Character</th>
<th>Scintillona cryptozoica</th>
<th>Scintillona daviei</th>
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<tr>
<td>Maximum shell length</td>
<td>10.0 mm</td>
<td>7.5 mm</td>
</tr>
<tr>
<td>Shell length to height ratio</td>
<td>1 : 0.69</td>
<td>1 : 0.75</td>
</tr>
<tr>
<td>Hinge area</td>
<td>Translucent white</td>
<td>Purple</td>
</tr>
<tr>
<td>Hinge teeth</td>
<td>Single anterior tooth in left valve</td>
<td>Single anterior teeth in left and right valves</td>
</tr>
<tr>
<td>Anterior tentacle area</td>
<td>Anterior tentacle red plus two other pairs</td>
<td>Anterior tentacle purple/red plus three other pairs</td>
</tr>
<tr>
<td>Posterior tentacle area</td>
<td>Posterior tentacle red plus three other pairs</td>
<td>Posterior tentacle purple/red plus two other pairs</td>
</tr>
<tr>
<td>General mantle papillae</td>
<td>Numerous: scattered all over reflected mantle</td>
<td>Reflected mantle with inner ring of 12 pairs plus outer postero-ventral ring of five pairs</td>
</tr>
<tr>
<td>Pedal pigment spot</td>
<td>Absent</td>
<td>Present</td>
</tr>
<tr>
<td>Shell length of mature females</td>
<td>Females mature at &gt; 5 mm</td>
<td>Females mature at &gt; 3 mm</td>
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**Table 2. Scintillona cryptozoica and Scintillona daviei: a comparison of anatomical characters.**
interlock. There is a medial socket (S) directly beneath the umbo.

A mature individual of *Scintillona daviei* is illustrated in life position in Fig. 4. The shell, as described above, is almost wholly obscured, except apically at the umbo (U), by the reflected and enlarged middle mantle folds (RM). The outer surface of this fold is actually the inner (because the fold as a whole is reflected) and possesses a number of tentacles and papillae. The inhalant aperture is long, extending from the antero-dorsal tentacle (ADT) to the mid point of the posterior margin of the shell. Inhalant currents (solid arrows) can enter the mantle cavity at all points of this aperture. Conversely, the exhalant flow (open arrow) is confined to a discrete siphon (ES) located beneath the posterior dorsal tentacle (PDT) and is formed by fusion of the inner mantle folds only, that is, type A (Yonge 1982). Anteriorly, where the main inhalant current is located, are three pairs of anterior tentacles (AT) whereas posteriorly there is only one pair (PT). The outer surface of the mantle is adorned by two cycles of papillae above each valve. The outermost cycle approximately tracks the location of the postero-ventral valve margins. The inner cycle defines the mantle edge apically. Also seen in Fig. 4 is the extended foot, comprising a posterior ‘heel’ (F(H)) and a much longer anterior ‘toe’ (F(T)) within which is a distinctive red pigment spot (PS). The foot allows *S. daviei* to crawl effectively.

The anatomies of the organs of the mantle cavity of *Scintillona daviei* are illustrated from the left side in Fig. 5. Once again, the inhalant flow is indicated by closed arrows and the exhalant by an open arrow. The homorhabdic, eulamellibranchiate ctenidia are the largest struc-
Biology of Scintillona

FIG. 4. *Scintillona daviei* sp. nov: individual illustrated from the left side showing the inhalant (closed arrows) and exhalant (open arrow) currents (see Abbreviations section earlier).

FIG. 5. *Scintillona daviei* sp. nov: structure and ciliary currents of the ctenidia and labial palps, as seen from the left side. Also shown are the inhalant (closed arrows) and exhalant (open arrow) currents (see Abbreviations section earlier).

FIG. 6. *Scintillona daviei* sp. nov: diagrammatic transverse section through the right ctenidium showing the ciliary currents and the oral-ward currents (●) (see Abbreviations section earlier).

Features in the mantle cavity and each comprises an inner (ID) and an outer demibranch. The pattern of ciliation on the ctenidia is of type C(1) (Atkins 1937) and thus bears a close resemblance to those of *Galeomma turtoni* (Sowerby, 1825) (Popham 1940), *Divariscintilla maoria* Powell, 1932 (Judd 1971) and *Galeomma takii* (Kuroda, 1945) (Morton 1973a). That is, only the inner demibranch bears a ventral marginal food groove, although there are other oralward currents in the ctenidial axis and where the ascending lamellae of the inner and outer demibranchs unite with the visceral mass and mantle, respectively. The outer demibranch does not achieve anterior contact with the labial palps. Rather, accepted material passes onto the inner demibranch to be transported to the labial palps. Such a ctenidial-labial palp configuration is typical of the Galeommatoidea and is of Category 3 (Stasek 1964). The labial palps (LP) located anteriorly below the anterior adductor muscle (AA) possess ciliary currents on their grooved inner surfaces that are responsible for the sorting, selection and either acceptance or rejection of potential ctenidially-collected food particles. Rejected material is evicted as pseudofoeces from the infra-branchial chamber of the mantle cavity posteriorly below the exhalant siphon (ES).

The structure and ciliation of the left ctenidium of *Scintillona daviei* are illustrated in transverse section in Fig. 6. The outer demibranch (OD) only, enclosing this component of the supra-branchial chamber (SBC) is modified for the brooding of fertilised eggs and larvae. The longer inner demibranch (ID) is hence the main ciliary potential food transporting structure in *S. daviei*. 
The shell of Scintillona cryptozoica has a maximum length of 10 mm and is longer relative to shell height than S. daviei. The shell is uniformly translucent white and covered by a very thin (2 μm) periostracum. The shell is also more equilateral than S. daviei but is similarly equi-valve. The internal structure of the shell is illustrated in Fig. 7A. The anterior (AA) and posterior adductor (PA) muscles are of approx. equal size and are situated below the anterior and posterior hinge lines, respectively. The hinge plate is illustrated in Fig. 7B & C. The ligament (Fig. 7, L) is situated posterior to the umbo (U) and there is an anterior hinge tooth (HT) in the left valve only (Fig. 7B). There is not a similar hinge tooth in the right valve as there is in S. daviei. There is, however, a medial socket (S) directly beneath the umbo.

A mature individual of Scintillona cryptozoica is illustrated in life position in Fig. 8. It is suspended by a single byssal thread (B) from the roof of the crab gallery in the mussel clump. The shell is almost wholly obscured, except apically at the umbo (U), by the reflected and enlarged middle mantle folds (RM). As in S. daviei, the outer surface of this fold is actually the inner and possesses a number of tentacles and papillae all of which are tipped deep red. The inhalant aperture is long, extending from the antero-dorsal tentacle (ADT) to the mid point of the posterior margin of the shell. Inhalant currents (solid arrows) can enter the mantle cavity at all points along this aperture. Conversely, the exhalant flow (open arrow) is confined to a discrete siphon (ES) located beneath the posterior dorsal siphon (PDT) and is formed by fusion of the inner mantle folds only, that is, type A (Yonge 1982). Anteriorly, where the main inhalant current is located, are two (three in S. daviei) pairs of anterior tentacles (AT) whereas posteriorly there are four (only one in S. daviei sp nov.) pairs (PT). The outer surface of the mantle is adorned by an array of numerous papillae. Also seen in Fig. 8 is the posterior ‘heel’ of the foot (F(H)). The foot allows S. cryptozoica to crawl.

Scintillona cryptozoica, like S. daviei, has a distinctive array of tentacles and papillae adorning the middle mantle folds that are reflected to mostly cover the shell except apically (Fig. 9). The mantle edge is a light red around the exhalant siphon and yellow around the inhalant aperture. There are antero- and postero-dorsal tentacles above the inhalant aperture and exhalant siphon, respectively. In addition, there are two pairs of other tentacles anteriorly and four pairs posteriorly. Smaller papillae adorn the outer (actually the inner) surface of the reflected middle mantle fold. All the tentacles and papillae are coloured a deep red apically. Such an arrangement of tentacles and papillae, the translucent hinge and the absence of a pigment spot in the foot of S. cryptozoica, distinguishes it from S. daviei.

The anatomies of the organs of the mantle cavity of Scintillona cryptozoica are illustrated from the left side in Fig. 10. Here, the inhalant flow is indicated by closed arrows and the
exhalant by an open arrow. The homorhabdic, eulamellibranchiate ctenidia are the largest structures in the mantle cavity and each comprise an inner (ID) and an outer demibranch. The outer demibranch is much reduced in comparison with the inner, as in *S. daviei*. Similarly, the ctenidial-labial palp configuration is of Category 3 (Stasek 1964) and the labial palps (LP) located anteriorly below the anterior adductor muscle (AA) possess ciliary currents on their grooved inner surfaces that are responsible for the sorting, selection and either acceptance or rejection of potential ctenidially-collected food particles.

The ciliary currents of the inner surface of the mantle and the visceral mass of *Scintillona cryptozoica* are illustrated in Fig. 11. When viewed from the left side, the ciliary currents of the visceral mass move particles in an anticlockwise direction. That is, dorsally particles are moved by an oralward current that approximates the position of a similarly directed current in the junction of the ascending lamella of the inner demibranch with the visceral mass. Material is then circulated downwards and backwards, to eventually fall from the visceral mass posteriorly and be captured by the currents of the mantle. These move particles in a similar anticlockwise direction on the inner surface of the right mantle lobe (but of course in a clock-
wise direction on the left) circulating material from the postero-dorsal region of the mantle cavity forwards but then backwards ventrally. When such a flow arrives posteriorly, held and other captured material rejected by the visceral mass, is discharged from the mantle cavity as pseudofaeces at a point just below the exhalant siphon.

**POPULATION STRUCTURES OF SCINTILLONA DAVIEI AND SCINTILLONA CRYPTOZOICA**

Of the 100 clusters of *Trichomya hirsuta* that possessed the commensal galeommatids, 40 comprised groups of only *Scintillona cryptozoica*, 27 comprised groups of *S. daviei* and 33 were sympatric. That is, the sympathy is neither 100% nor, obviously, obligatory. Clusters of *S. cryptozoica* and *S. daviei* contained numbers of individuals ranging from 1 to 25 and 1 to 7, respectively.

Figure 11 shows the position of the ovotestis (OVT) in the visceral mass of *Scintillona cryptozoica*. This has not been examined histologically, but it develops primarily postero-ventrally around the intestine (I). Both species appear to be protandric consecutive hermaphrodites, with the male component of the ovotestis dominating shell length sizes of 1–3 mm (*S. cryptozoica*) and 1–2.5 mm (*S. daviei*), respectively. Females of the two species ranged in shell length from 5–10 mm and 3–7.5 mm, again respectively. Both species brood fertilised eggs in the outer demibranchs only of their ctenidia at shell lengths of between 6.5–8.0 mm and 3.5–6.0 mm (Fig. 12). It seems that in both *S. cryptozoica* and *S. daviei*, the colour (and its intensity) of the tips of the mantle tentacles and papillae change (and are enhanced) with size which is also related to both age and stage of sexual development (Table 3).

The compositions of the clusters of *Scintillona cryptozoica* are identified in Table 4. Cluster composition ranged from solitary individuals (x 23) to 25 individuals (x 1). Most individuals were thus in clusters of more than one and an average of 8.7. Solitary individuals comprised but 8.2% of the total population and most of these (16) were in the intersex stage. Significantly, brooding females were never solitary and were recorded from clusters comprising 2, 9 and 14 individuals. That is, they are associated with one or more males which are presumably required to effect fertilisation. The greatest numbers of individuals in the clusters were at the intersex stage and, except for one case of clusters of 14 individuals, these always outnumbered females by a factor of > 2:1 and more often by ~ 6:1. That is, each cluster of more than one individual of *S. cryptozoica* usually comprised a female plus a number (1–6) of intermediate-sized intersex individuals. If a brooding female was also present in the cluster there was also usually a male present. Thus, of the total of 73 clusters of *S. cryptozoica* examined, the average
A cluster of between 8–9 individuals comprised a ratio of 0.30 males: 2.66 intersex individuals: 1.09 females and 0.12 brooding females.

The compositions of the clusters of *Scintillona daviei* are identified in Table 5. Cluster composition ranged from solitary individuals (x 23) to 7 individuals (x 1). Most individuals (61%) were thus in clusters of more than one and an average of 4. Solitary individuals comprised 16.0% of the total population and most of these (12: 52.2%) were in the intersex stage. Brooding females were never solitary and were recorded from clusters comprising 1–6, but not 7 individuals. Similarly, all cluster sizes, save those comprising 4 and 7 individuals, possessed at least one male. That is, one or more males was always associated with clusters containing mature and brooding females, suggesting, as for *S. cryptozoica*, that a male is required for fertilisation. Also as for *S. cryptozoica*, the greatest numbers of individuals (83: 57.6%) in the clusters were at the intersex stage and always outnumbered

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**Table 3. Variations in colour with size in *Scintillona cryptozoica* and *Scintillona daviei*.**

<table>
<thead>
<tr>
<th>Reproductive stage</th>
<th><em>Scintillona cryptozoica</em></th>
<th><em>Scintillona daviei</em></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>~Shell length range (mm)</td>
<td>~Shell length range (mm)</td>
</tr>
<tr>
<td>Male</td>
<td>1.0–3.0</td>
<td>Both tentacles pale</td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.0–2.5</td>
</tr>
<tr>
<td>Intersex</td>
<td>2.0–8.5</td>
<td>Both tentacles pale yellow</td>
</tr>
<tr>
<td></td>
<td></td>
<td>2.0–6.0</td>
</tr>
<tr>
<td>Female</td>
<td>5.0–10.0</td>
<td>Posterior tentacle red: anterior paler</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.0–7.5</td>
</tr>
<tr>
<td>Brooding female</td>
<td>6.5–8.0</td>
<td>Both tentacles bright red</td>
</tr>
<tr>
<td></td>
<td></td>
<td>3.5–6.0</td>
</tr>
</tbody>
</table>

---

**Table 4. The composition of the clusters of *Scintillona cryptozoica*.**

<table>
<thead>
<tr>
<th>Cluster size (Nos of individuals)</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>8</th>
<th>9</th>
<th>11</th>
<th>14</th>
<th>18</th>
<th>25</th>
</tr>
</thead>
<tbody>
<tr>
<td>Numbers of such clusters</td>
<td>23</td>
<td>14</td>
<td>9</td>
<td>7</td>
<td>4</td>
<td>1</td>
<td>2</td>
<td>5</td>
<td>1</td>
<td>1</td>
<td>4</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Total no. individuals</td>
<td>23</td>
<td>28</td>
<td>27</td>
<td>28</td>
<td>20</td>
<td>6</td>
<td>14</td>
<td>40</td>
<td>9</td>
<td>11</td>
<td>56</td>
<td>18</td>
<td>25</td>
</tr>
</tbody>
</table>

**Cluster composition**

| Male               | 1 | 2 | 3 | 3 | – | – | – | 1 | 1 | – | 5 | 2 | 4 | 22 |
| Intersex           | 16| 14| 16| 20| 17| 6 | 10| 33| 5 | 8  | 15 | 16 | 18 | 194|
| Female             | 6 | 7 | 8 | 5 | 3 | – | 4 | 6 | 2  | 3   | 33 | – | 3 | 80 |
| Brooding females   | – | 5 | – | – | – | – | – | 1 | – | 3   | – | – | – | 9 |

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**Table 5. The composition of the clusters of *Scintillona daviei* sp. nov.**

<table>
<thead>
<tr>
<th>Cluster size (Nos of individuals)</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
</tr>
</thead>
<tbody>
<tr>
<td>Numbers of such clusters</td>
<td>23</td>
<td>12</td>
<td>11</td>
<td>5</td>
<td>5</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Total numbers of individuals</td>
<td>23</td>
<td>24</td>
<td>33</td>
<td>20</td>
<td>25</td>
<td>12</td>
<td>7</td>
</tr>
</tbody>
</table>

**Cluster composition**

| Male               | 3 | 1 | 1 | – | 2 | 3 | – | 10 |
| Intersex           | 12| 9 | 25| 10| 15| 5 | 7 | 83 |
| Female             | 7 | 7 | 4 | 9 | 3 | 3 | – | 33 |
| Brooding females   | 1 | 7 | 3 | 1 | 5 | 1 | – | 18 |
females by an average factor of 2.5:1 and males by often ~8:1. That is, each average cluster of more than one individual usually comprised a female plus a number (~3) of intermediate-sized intersex individuals. If a brooding female was also present in the cluster then so was a male. Of the total of 59 clusters of *S. daviei* examined, therefore, the average cluster of four individuals comprised a ratio of 0.7 males: 0.58 intersex individuals: 0.23 females and 0.12 brooding females.

Both species of *Scintillona* thus appear to be protandric consecutive hermaphrodites, with the male component of the ovotestis dominating shell length sizes of between 1–3 mm (*S. cryptozoica*) and 1–2.5 mm (*S. daviei*), respectively. Females ranged in shell length from 5–10 mm and 3–7.5 mm for *S. cryptozoica* and *S. daviei*. Both species brood fertilised eggs in the outer demibranchs of their ctenidia at shell lengths of between 6.5–8.0 mm and 3.5–6.0 mm, again respectively. It seems that the larvae incubated in the female outer demibranchs of both species of *Scintillona* are released as veligers and after an undefined period of time in the plankton, find a *Pilumnopeus serratifrons* host gallery in the mussel clumps. There, if a female is in residence, such newly settled juveniles become males. If a female is not present they seem to become of undefined sexuality or ‘intersex’ and may await, as they grow, further male discovery when they would become females. Fertilised females of both species were the largest individuals in the clusters and it seems possible that following successful brood hatching they die, allowing the next oldest intersex/putative female to mature. There is thus and, as would be expected in such a pattern of reproduction, a dominance in the clusters of both species by intersex/putative females.

**DISCUSSION**

The two species of *Scintillona* herein described and discussed are not only clearly closely related but also at least partially sympatric. Galeommatoidaean bivalves are well known associates of marine invertebrates, being recorded from a wide range of phyla (Boss 1965a). Although all galeommatoideans are small as a consequence of their symbiotic lifestyles, species of the Galeommatidae show great reduction of the shell valves and reflection of the middle fold of the mantle over them (Morton 1973a, 1975). Adoption of a mode of life that can typically best be defined as ‘commensal’, that is, benefiting from the respiratory currents of the host to facilitate respiration and suspension feeding (Morton 1988) has also been achieved by reproductive specialisation, e.g., the storage (Morton 1980; O’Foighil 1985) of dimorphic sperm (Jespersen et al. 2002); simultaneous and consecutive hermaphroditism (Gage 1968a); sexual dimorphism (Jenner & McCrary 1968); self fertilisation (O’Foighil 1987); and even dwarf males (Morton 1976, 1981). *Mysella tumida* (Carpenter, 1864) produces spermatophores to effect fertilisation (O’Foighil 1985), while Mikkelsen & Bieler (1992, fig. 33) described a form of mating behaviour in their new species *Divariscintilla octotentaculata*. *Turtonia minuta* (Fabricius, 1780) produces egg capsules (Oldfield 1963). In the absence of any facilities for histological sectioning of the two species of *Scintillona* here under consideration, it is unknown if sperm is...
either stored or is dimorphic: notwithstanding, both species appear to be consecutive protandric hermaphrodites, that is, with newly settled males attracted to females which are then fertilised to produce eggs that are incubated within the outer demibranchs. In two cases, two small males (shell lengths of ~1–1.5 mm) were identified (a) inside the mantle cavity and (b) attached to the byssus of females. Incubation is only to the D-veliger stage, however, no brooded crawl-away juveniles ever being seen.

The males of the two Scintillona species are thus not strictly ‘dwarf’ but probably, as proposed for Pseudopythina subsinuata (Lischke, 1871) by Morton (1972), will settle into a clump of adults and become male if an established, maturing female is resident. In the absence of a female, the newly settled individual may become a putative female. This results, as suggested for the present species (Fig. 12), in a surfeit of either putative or intersex females, with each cluster being optimally dominated by one or two mature, possibly gravid or brooding, females. With completion of their life spans, younger females can then assume their places in the cluster hierarchy. Such a pattern of protandric consecutive hermaphroditism has also been identified for Lepton nitidum Turton, 1822 (Pelseener 1925), Arthritica crassiformis Powell, 1833 (Morton 1973b), Montacuta elevata (Stimpson, 1851) (Verrill & Bush 1898) Gage 1968a), Mysella cuneata (Gage, 1968b), Montacutona compacta (Gould, 1861) (Morton 1980).

The situation in Scintillona cryptozoica and S. daviei species closely resembles that seen in Pseudopythina rugifera (Carpenter, 1864). O’Foighil (1985b) described ‘temporary’ dwarf males in P. rugifera, as was postulated for P. subsinuata by Morton (1972), with both authors providing histograms showing small males and larger females.

Morton & Scott (1989) reviewed the commensal, galeommatid bivalves of Hong Kong, identifying 22 species. Lützen & Nielsen (2005), however, recorded 27 species from intertidal reef flats at Phuket (Andaman Sea), Thailand, and over 50 species are known from Japan (Habe 1977, 1981). Very few, however, have been recorded as occurring with crabs. Manning & Morton (1987) reported upon Fronsella ohshimai Habe, 1964 [Pseudopythina nodosa (Morton & Scott, 1989)] and Nipponmysella subtruncata (Yokoyama, 1922) [Barrimusia siphonosomae (Morton & Scott, 1989)] from Hong Kong living with pinnotherids in the burrows of sipunculan worms. Similarly, few galeommatids are recorded as being sympatric with their hosts. Notwithstanding, Morton & Scott (1989) showed that the shallow water holothurian Protankyra bidentata (Woodward & Barrett, 1858) may have three galeommatoideans resident with it in Hong Kong, that is, Pseudopythina ariakensis (Habe, 1959), P. tsurumaru (Habe, 1959) and Entovalva semperi Ohshima, 1930. Similarly, Mikklesen & Bieler (1992) reported upon six species of galeommatoiden bivalves, five of them species of Divariscintilla and Parabornia squillina Boss, 1965 (Boss 1965b), all living in the burrows of Lysiosquilla scabricauda (Lamarck, 1818) in eastern Florida. The five species of Divariscintilla were often collected together (see Mikklesen & Bieler 1992, p. 15 for a description) in a clearly complex sympatric relationship(s). Likewise, in Australian waters, three species of Ephippodonta, that is, E. macdougalli Tate, 1889, E. lunata Tate, 1889 and E. turnbullae (Buick & Bowden, 1951), along with three other species of Myllita, that is, M. tasmanica Tenison-Woods, 1875, M. gemmata Tate, 1889 and M. deshayesi d’Orbigny & Recluz, 1850, as well as an un-named species of Kellia can all be found within the burrows of the mud-lobster Strahlaxius pectoralhymnus (Strahl, 1862) (Tate 1889; Matthews 1893; Woodward 1893; Cotton & Godfrey 1938; Buick & Bowden 1951). Finally, Lützen & Nielsen (2005) report that many of the 27 species of galeommatoideans they collected from reef flats in Phuket, Thailand, occurred in small (undefined) intra- and inter-specific family ‘flocks’.

Although burrowing anomurans and stomatopods are favoured hosts of galeommatoideans (Boss 1965a; Mikkelsen & Bieler 1989, 1992), there are few reports of them being associated with crabs. Morton & Scott (1989) described Pseudopythina macrophthalmensis Morton & Scott, 1989, attached to the limbs of the burrowing crab Macrophthalmus latreillei (Desmarest, 1817) in Hong Kong, whereas in Okinawa, Japan, it attaches to M. convexus Stimpson, 1858 (Kosuge & Itani 1994). Boyko & Mikkelsen (2002) describe Mysella pedroana Dall, 1899 attached to the spiny
(also burrowing) anomuran sand crab *Blepharipoda occidentalis* Randall, 1840, often inside the branchial chambers. It was initially suggested by Iredale (1936), that *Scintillona cryptozoica* lives in the burrows made by a species of *Crangon* (a species of pistol shrimp in the Alpheidae), however although an alpheid, *Alpheus cf. pacificus*, was twice collected from the mussel clumps herein examined, only the crab *Pilumnopeus serratifrons* was recorded within all the clumps, and it was this species that appeared to be creating the galleries to the roofs of which *S. cryptozoica* and *S. daviei* were attached.

Both species of *Scintillona* are similar to *Ceratobornia cema* (Narchi, 1966) and *Divariscintilla yoyo* (Mikkelsen & Bieler, 1989) and other species of *Divariscintilla* (Mikkelsen & Bieler 1992), in that they hang by a solitary byssal thread from the roofs of the burrows they inhabit, in the latter cases *Callianassa major* Say, 1818, and the stomatopod *Lysiosquilla scabricauda*.

The two species of *Scintillona* herein discussed also possess a complex pattern of large pallial tentacles. The function(s) of the large tentacles are, however, unknown. Such tentacles are absent in some galeommatoidean species, for example, *Scintilla stevensoni* Powell, 1932 (Ponder 1967: fig. 13). In *Rhamphidonta retifera* (Dall, 1899), there are single antero- and postero-dorsal tentacles (Bernard 1975, fig. 2). In the two species of *Galeomma* described by Morton (1973a, 1975), the dorsal tentacles are not only retractable but can autotomise and, in so doing, it was suggested, release a noxious secretion. The complex tentacles of the two species of *Scintillona* are neither retractable nor did they autotomise. Notwithstanding, as with the complex tentacles described for species of *Divariscintilla* Mikkelsen & Bieler (1989, 1992) and for *D. maoria* Powell, 1932, by Judd (1971), they are possibly defensive. That is, they may release a noxious secretion when touched to deter contact from other gallery inhabitants. It is, however, also interesting that the colours of the two species of *Scintillona* deepen with age, and it may be that they also secrete pheromones, as suggested for the yet more complex pallial tentacles of *Chlamydoconcha orcorti* Dall, 1884, by Morton (1981), and in view of the suggestion by Mikkelsen & Bieler (1992) that *Divariscintilla octotentaculata* engages in a ‘mating’ behaviour.

Another interesting point is that galeommatoideans living in close association with or upon crabs (see above), typically do not have a reflected mantle and hence no pallial tentacles. This is not true however for the two species of *Scintillona* herein discussed that live in galleries created and inhabited by *Pilumnopeus serratifrons*, and for their relatives identified above, that live attached to the burrows of anomurans (Boss 1965a). Thus, the possession or lack thereof of pallial tentacles is not wholly related to the category of host, that is, crustacean, worm or other taxon, but to the structure of the galleries or burrows the host creates.

Finally, it is of interest to speculate upon the nature of the relationship between the bivalves and *Pilumnopeus serratifrons*. As described above, the degree of sympathy between the two bivalves is not absolute and thus not obligate. However, the associations between the two bivalves with *P. serratifrons* do appear to be obligate, that is, they have never been recorded from clumps of *Trichomya hirsuta* without the crab (unless the crab escaped during handling, but still leaving a definable gallery behind). The bivalves clearly benefit from the protection, that is, aegism as defined by Morton (1988), afforded by living in a gallery underneath a *Trichomya* clump. However, the crab, by virtue of its activities, must aerate its gallery and, in so doing, bring in suspended particulates that the bivalves can exploit. Both species had such particulates in their mantle cavities and intestines. Grutter & Irving (2007) define such an association as facilitation or commensalism. Morton (1988) defines such an association, identified for a number of similar galeommatoidean/host associations from Hong Kong, as commensalism.

**ACKNOWLEDGEMENTS**

I am grateful to Peter Davie and his colleagues at the Queensland Museum for organising the Thirteenth International Marine Biological Workshop and inviting me to participate. I am also grateful to Lisa Gershwin (James Cook University, Queensland) for allowing me to use her 4-wheel drive vehicle to access the beach herein reported upon. Dr E.M. Harper (University of Cambridge) is thanked for taking the SEM photomicrographs of the *Scintillona* shells. Dr
Peter Middelfart (Australian Museum, Sydney) is thanked for taxonomic advice.

LITERATURE CITED


