The Morphology, Reproduction and Ecology of the Commensal Bivalve *Scintillona bellerophon* spec. nov. (Galeommatacea)

by

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Abstract. *Scintillona* **bellerophon** spec. nov. is ectocommensal with the holothurian *Leptosynapta clarki* (Heding, 1928) in Sooke Harbour, Vancouver Island, British Columbia. It is similar in form and habit to *Scintillona zelandicus* (Odhner, 1924) and is a simultaneous hermaphrodite with a fecundity of up to 3000 eggs. The young are brooded in the suprabranchial chamber and released as D-veligers. Following a planktotrophic stage, settlement and subsequent attachment to the host species occurs. In aquaria, attached animals locate deeper in the sediment than unattached specimens. Individuals may live up to 4 years. Another galeommatacean bivalve, *Mysella tumida* (Carpenter, 1864), and two polychaete species are associated with *L. clarki* in Sooke Harbor. Both *S.* **bellerophon** and *S. zelandicus* are relatively less specialized than related bivalves ectocommensal on holothuroids.

INTRODUCTION

THE SUPERFAMILY Galeommatacea contains numerous species that live in association with a large diversity of host species. Some members of the genera *Entovalva, Devonia, Cycladoconcha, Montacuta,* and *Scintillona* occur on or in synaptid holothurian hosts (BOSS, 1965). In September 1982, an intertidal population of an unidentified bivalve was found in Sooke Harbour, Vancouver Island, British Columbia. Specimens recovered were attached externally to the synaptid holothuroid *Leptosynapta clarki* (Heding, 1928). The bivalve was identified as a new species of *Scintillona,* and is the first record of this genus on the Pacific coast of North or South America. It is similar in form and habit to *S. zelandicus* (Odhner, 1924), but differs in details of the shell, foot and mantle. *Scintillona zelandicus* occurs off New Zealand to depths of 90 m (ODHNER, 1924) and intertidally as an ectocommensal attached to the synaptid *Trochodota dendyi* Mortensen (MORTON, 1957). Its morphology has been described from preserved specimens by ODHNER (1924) and from live animals by MORTON (1957), who also made behavioral observations. *Scintillona stigmatica* (Pilsbry, 1920) has been recorded off Hawaii (PILSBRY, 1920), and attached to the echinoid *Brissus lateracarinatus* (Leske) off Japan (YAMAMOTO & HABE, 1974).

Galeommataceans exhibit a wide variety of reproductive specializations and are generally considered to have the most complex reproductive patterns in the Bivalvia (DEROUX, 1961; JENNER & McCRARY, 1968; MORTON, 1976; OCKELMANN & MUUS, 1978). There is no available information concerning reproduction in *Scintillona*. Therefore, aspects of the reproduction of *S.* **bellerophon** spec. nov., as well as the morphology and ecology, are described.

MATERIALS AND METHODS

Animals were sampled intertidally at Woodward Point in Sooke Harbour (Figure 1). Sampling was carried out monthly during spring tides from October 1982 to April 1983 as well as in June and September 1983. All specimens of *Leptosynapta clarki* encountered were removed from their burrows and examined in the laboratory with a dissecting binocular microscope. Specimens of *Scintillona* **bellerophon** were removed from the holothuroids, measured with an ocular micrometer, and checked for the occurrence of brooding. Individuals were fixed for light-microscope histology in 4% glutaraldehyde (biological grade), dehydrated in ethanol, embedded in Poly Bed 812, sectioned at 1 μm and stained with Richardson's stain (RICHARDSON & JARRET, 1960). For scanning electron
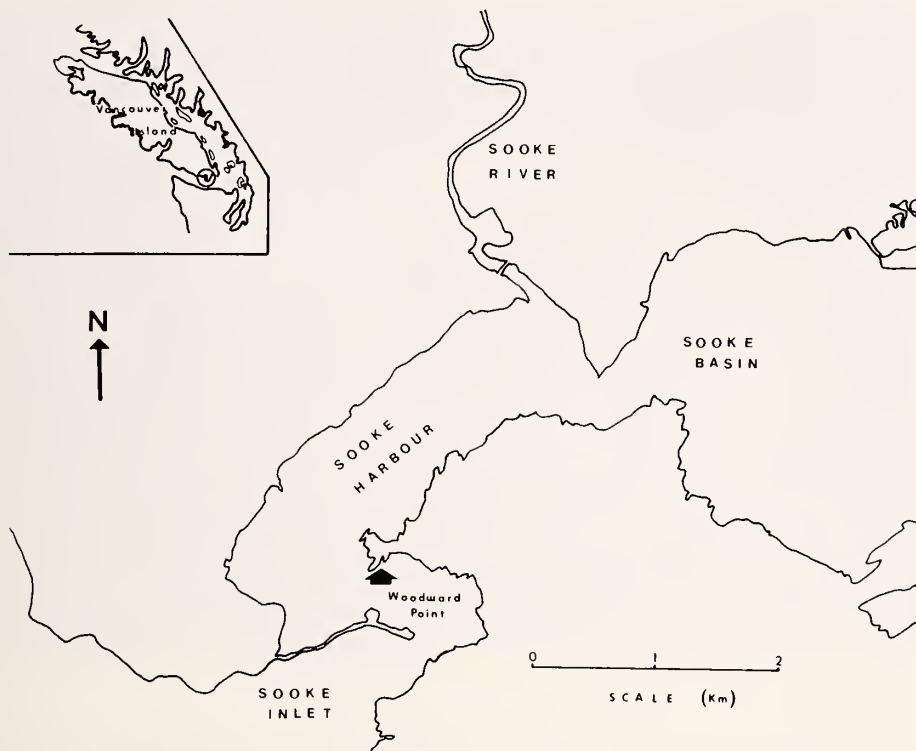
Figure 1

Location of Woodward Point, Sooke Harbour, British Columbia, type locality and study area of *Scintillona **bellerophon*** spec. nov.

microscopy, specimens were fixed in a 3:1 mixture of 4% glutaraldehyde and 1% osmium tetroxide in 3% NaCl (SMITH, 1983), dehydrated in acetone, critical point dried, gold coated, and viewed with a JEOL JSM-35 scanning electron microscope.

SYSTEMATICS

Family GALEOMMATIDAE Gray, 1840

Genus *Scintillona* Finlay, 1927

Small shells, being rounded at both ends. Small tubercular cardinal tooth in right valve; oblique cardinal in left, extending into a thin lamella. Resilium has a prominent nymph (CHAVAN, 1969).

Type species: *Scintillona zelandicus* (Odhner, 1924) (by original designation, *Spaniorinus zelandicus* Odhner, 1924).

Scintillona bellerophon
Ó Foighil & Gibson, spec. nov.

(Figures 1 to 14)

Specific characteristics: Umbone slightly posterior, midmantle fold extended posterodorsally as three pairs of retractable flaps; distal part of foot has prominent longitudinal ciliated grooves.

Type location: Woodward Point, Sooke Harbour, Vancouver Island, British Columbia, Canada (48°21'49"N; 123°42"54°W).

Holotype: British Columbia Provincial Museum, Victoria, British Columbia (BCPM) 983-1617-1. **Paratypes:** BCPM 983-1617-2, National Museum of Natural Sciences, Ottawa (NMNS) 86701 and NMNS 86702 (Table 1).

RESULTS

Morphology

The valves are broadly elliptical (Figure 2) ranging up to 4.4 mm in length. They are equivalve and non-equi-

Table 1

Shell dimensions (mm) of holotype and paratypes of *Scintillona **bellerophon*** spec. nov.

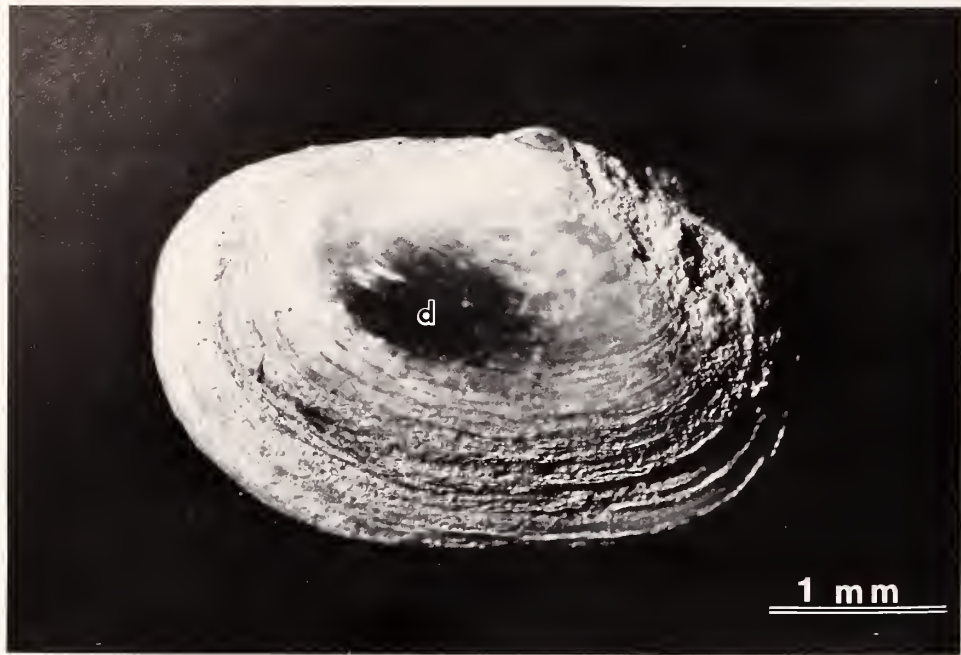| Specimen	Length	Height	Width
Holotype BCPM 983-1617-1	4.2	2.7	1.7
Paratype BCPM 983-1617-2	2.1	1.5	0.7
Paratype NMNS 86701	3.7	2.4	1.2
Paratype NMNS 86702	3.3	2.2	1.1

Figure 2

Right valve of *Scintillona* **bellerophon** spec. nov. showing deposit (d).
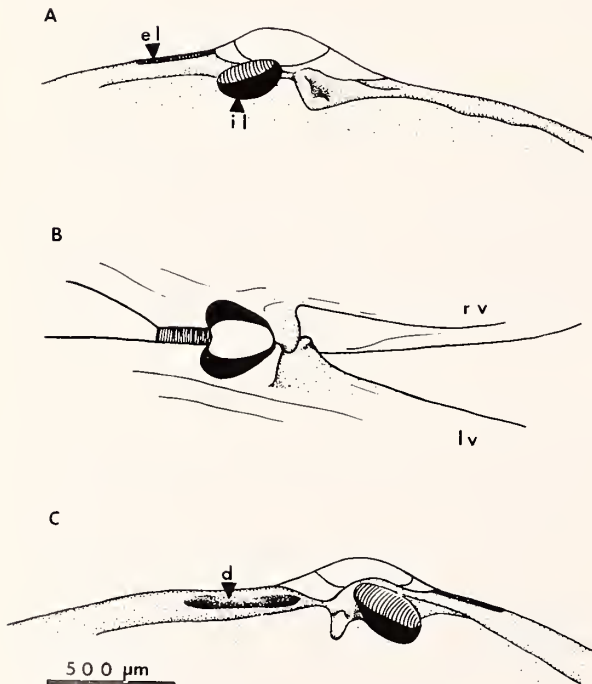

Figure 3

Scintillona **bellerophon** spec. nov.: A. Hinge of left valve; B. Ventral view of hinge; C. Hinge of right valve. d, depression; el, external ligament; il, internal ligament; lv, left valve; rv, right valve.

lateral, the orthogyrous umbone being slightly posterior ($\frac{3}{5}$ of the total shell length from the anterior) and having a prominent, rounded prodissoconch-2. The valve margins are excurved, particularly anterodorsally and to a lesser extent posterodorsally. As a result, the valves cannot be firmly apposed.

The outer shell surface appears slightly nacreous and is usually whitish in color. Fine concentric lines are present on the other outer shell surface, and in some individuals distinct growth checks are present. Many individuals display a prominent patch of dark brown or purple deposit (Figure 2) similar to that occurring on numerous other galeommataceans commensal with burrowing hosts (GAGE, 1966; KAWAHARA, 1942; MORTON, 1957; PILSBRY, 1920; PONDER, 1968). A prominent periostracal edge is present, especially anteriorly. Numerous pits (visible at × 40 magnification) occur on the inner surface of the shell. The pallial line is entire, and the anterior and posterior adductor muscle scars are of a similar size.

The external ligament is weak and posterior, and the internal ligament is moderately developed and has a marked nymph. In the left valve, a single, more robust anterior tooth occurs, and is connected to a lateral ridge (Figure 3A) that articulates with a corresponding shallow depression in the right valve (Figure 3C). A single peg-like tooth is present in the right valve (Figure 3C), the base of which is continuous with a weak ridge delineating the shallow depression. Both teeth are cyclodont and interlock across the hinge line (Figure 3B).
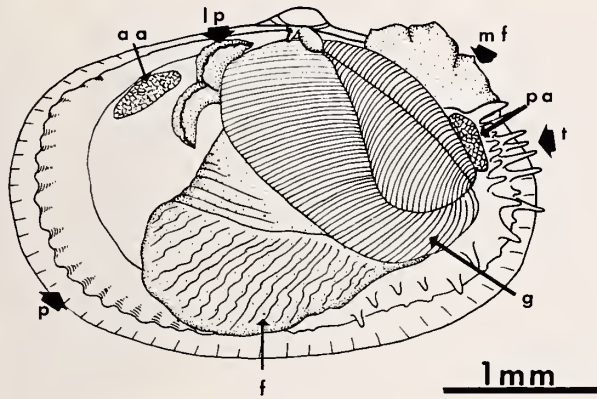
Figure 4

*Scintillona **bellerophon*** spec. nov. General morphology (left valve and left mantle fold removed). aa, anterior adductor muscle; f, foot; g, gill; lp, labial palps; mf, mid-mantle fold extension; p, periostracum; pa, posterior adductor muscle; t, inner mantle fold tentacles.

The inner fold of the mantle is fused posteroventrally to separate an anterior pedal (inhalent) opening from a narrow, slit-like posterior exhalent siphon. Anterior to the fusion, the inner fold has a scalloped margin. Numerous tentacles (20–30) are present on the region of fusion and surrounding the exhalent siphon. The edge of the mid-mantle fold bears small papillae, except dorsoposteriorly. Here the mid-fold is hypertrophied into three flaps on either side which, when relaxed, extend to cover the shell surface dorsal to the exhalent siphon. Ridges are present on the inner face of these flaps, but they do not display ciliary activity. The outer mantle fold is small and is attached to the periostracal edge.

The homorhabdic eulamellibranchiate ctenidia cover the visceral mass, with the gill axis (orientated at approximately 45° to the long axis) extending from under the umbone to the exhalent opening (Figure 4). Inner and outer demibranchs are present, as in other galeommatids (POPHAM, 1940); the outer demibranchs, however, are much reduced in size, especially anteriorly. A food groove is present in the inner demibranch only.

Ascending and descending lamellae are present in both demibranchs. In the outer demibranch, the ascending lamellae extend dorsally to fuse with the mantle above the gill axis. The inner demibranchs fuse behind the foot. Few interlamellar junctions occur, and these are restricted to the extreme posterior of the gill.

Gill ciliation is similar to that described for other galeommatids (JUDD, 1971; POPHAM, 1940). Particles are passed ventrally along the ascending lamellae of the outer demibranchs and dorsally via the descending lamellae to the gill axis. Here the particles are propelled anteriorly and then ventrally toward the labial palps. Ciliary currents on both lamellae of the inner demibranchs pass par-

ticles to the ventral food groove, and hence to the labial palps.

The foot is large and laterally compressed, and has two distinct parts (Figure 4). The distal portion is thickened and opaque, and has a pleated surface with 20–30 longitudinal, densely ciliated grooves. The proximal part is thinner, smooth-surfaced, and more translucent. The cilia in the distal grooves become active only when the foot is engaged in locomotion. Particles are passed dorsally along these grooves, bound in a mucous sheet, and pushed over the outer mantle fold when the foot contracts. A byssal gland is present at the posteroventral end of the distal section of the foot.

Locomotion is achieved as in *Scintillona zelandicus* (MORTON, 1957). The distal part of the foot is extended and applied laterally to the substratum. This is followed by serial contractions of the anterior, then posterior, pedal retractor muscles, which rock the rest of the body forward onto the foot. Byssal attachment is accomplished by adopting an upright position, contact with the substratum being made by the slender base of the foot onto which the byssal gland opens.

Waste particulate material in the mantle cavity is expelled anteriorly by valve contractions, or ventrally by mantle ciliary rejection tracts between the foot and the region of mantle fusion. Fecal pellets and brooded veliger larvae exit via the exhalent siphon.

The gonad develops along the ventral and posterior margins of the digestive gland. *Scintillona **bellerophon*** is a simultaneous hermaphrodite, with sperm and eggs developing within separate follicles (Figure 5). In individuals less than 2.5 mm in length, the gonad is predominantly male. The ovotestis is connected to the suprabranchial chamber by a pair of ciliated gonoducts, one on each side. Some specimens contained a few sporocysts of an unidentified helminth parasite embedded in the gonad.

Reproduction

Fertilization occurs in the suprabranchial chamber and embryos are brooded there until they have reached the D-veliger (straight hinge) stage of development. They are then released and assume a planktotrophic existence until settlement. It is not known if *Scintillona **bellerophon*** self-fertilizes.

Brooding individuals were observed in the November 1982 and February–September 1983 samples, with the highest frequency of brooders in March and April of 1983 (38% and 10% respectively). Samples from the other months showed less than 2% of the animals brooding.

Uncleaved eggs observed in the gill chamber had undergone two reduction divisions (Figure 7) and are about 70 μm in diameter ($\bar{x}$ = 69.9 ± 1.1 SE, n = 40). The fecundity of three specimens examined ranged from 1965 (2.95 mm valve length) to 2912 (3.5 mm valve length).

The sperm heads are rodlike in shape and are 10 μm
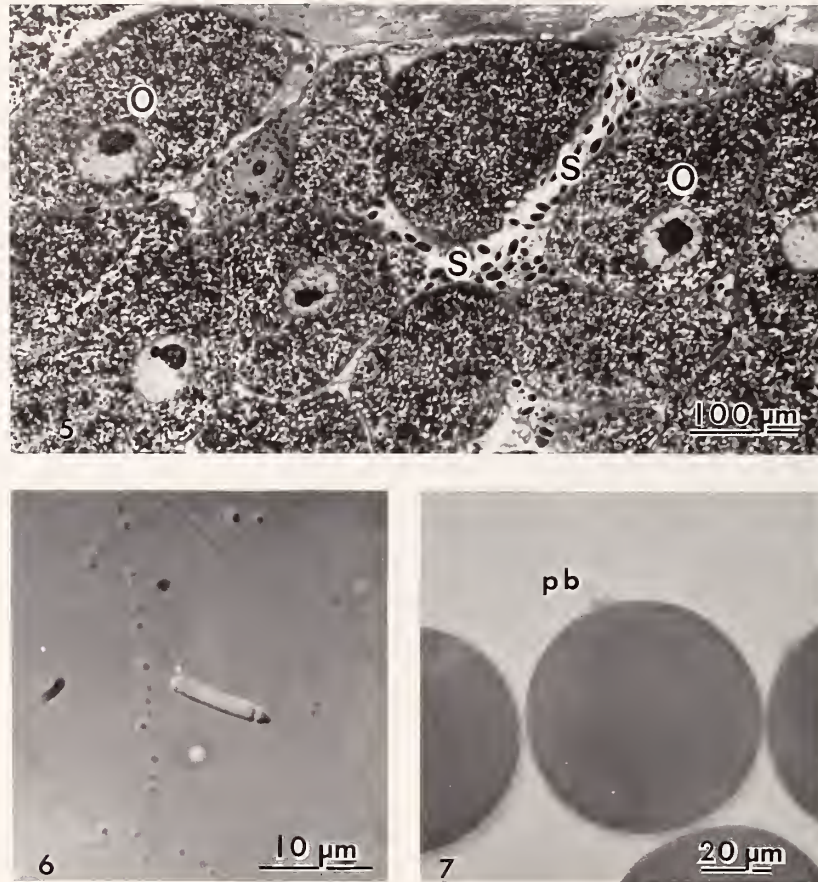
Explanation of Figures 5 to 7

*Scintillona **bellerophon*** spec. nov. Figure 5. Light micrograph of the ovotestis. o, oocyte; s, spermatids. Figure 6.
Light micrograph of sperm. Figure 7. Light micrograph of ovum. pb, polar bodies.

in length (Figure 6). They are generally similar to, though considerably shorter than, the eupyrene sperm of *Mysella bidentata* (Montagu, 1803) (OCKELMANN & MUUS, 1978). The sperm aggregate when removed from the gonad, forming large spherical masses as reported in *M. bidentata* by OCKELMANN & MUUS (1978).

Embryonic development from early cleavage stages to larval release took 12 days at 10°C in aquarium-held specimens (ambient water temperature in March 1983 was 10.3°C). No encapsulating fertilization membrane was apparent in early embryos (Figure 8). Ciliation appears at the trochophore stage (Figure 9), and the embryos are capable of weak swimming movements when removed from the gills. Early developmental stages are circulated by the adult around the gill chamber. As the embryos grow and develop valves, the gills become distended, inhibiting further embryo movement. Mature D-veligers have a rust-colored hinge line, which gives brooding animals a pink internal coloration as in *Montacuta percompressa* Dall, 1899

(CHANLEY & CHANLEY, 1970). The prodissoconch-1 of *Scintillona **bellerophon*** has a pitted surface (Figure 10). It also shows faint radial lines towards the margin as described by REES (1950) for the Galeommatacea (Erycinacea) and Lucinacea.

Mature D-veligers (Figure 11) are released through the exhalent siphon in a few pulses. They immediately commence vigorous swimming. Mean valve length at release was 130 μm ± 2.1 SE, and mean valve height was 97 μm ± 2.5 SE (n = 40) (Figure 11). The duration of the larval stage was not determined.

Settlement occurs when the larvae are between 300 and 375 μm in length. Newly metamorphosed juveniles with little or no dissoconch growth were found attached to *Leptosynapta clarki* (Figure 12). In aquaria, dislodged juveniles were frequently picked up by the feeding tentacles of the holothuroid and passed onto the host's body surface. Many of these reattached by byssal threads at the base of the tentacles. This is in contrast to *M. percompressa* where
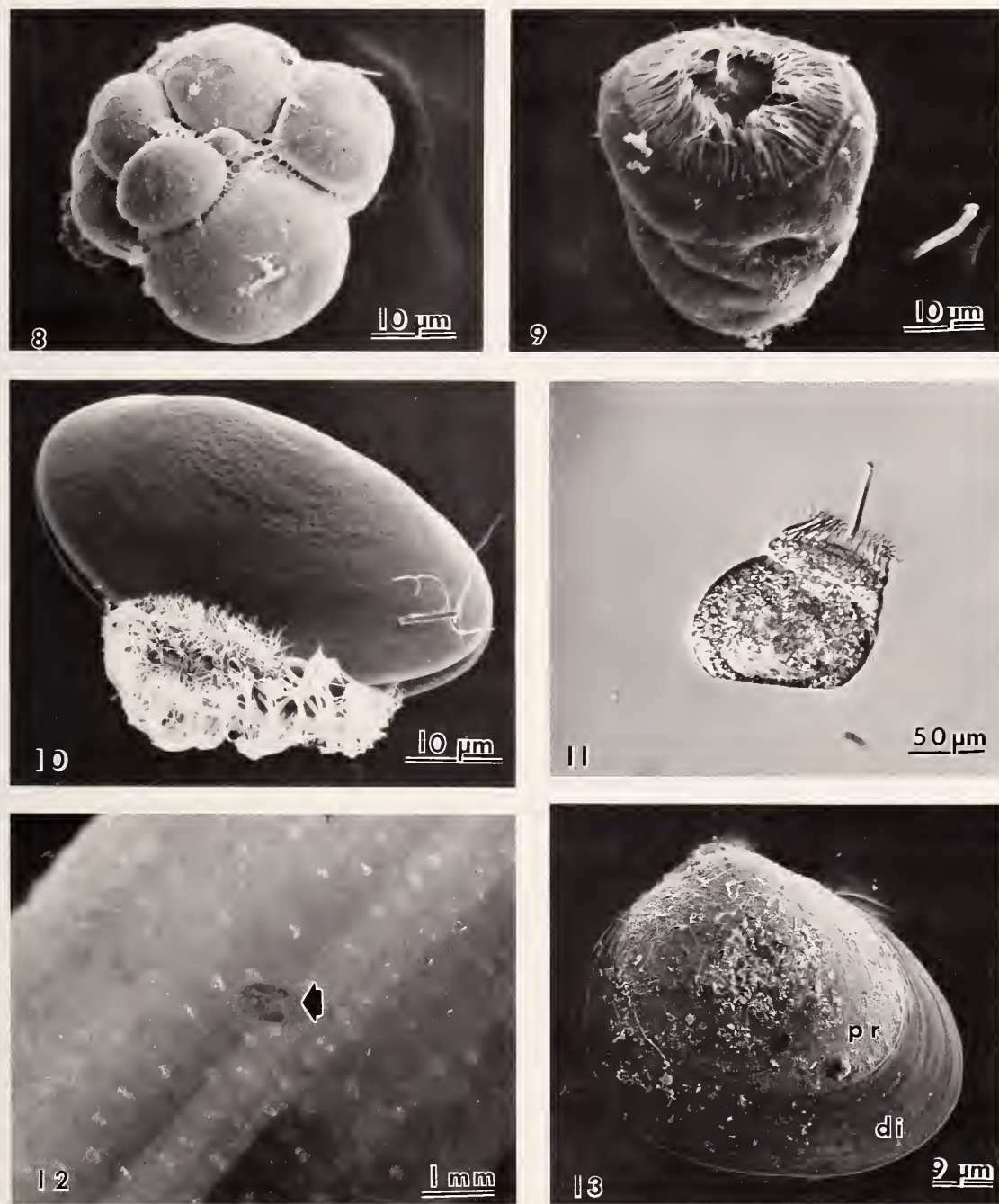
Explanation of Figures 8 to 13

Scintillona **bellerophon** spec. nov. Figure 8. Scanning electron micrograph (SEM) of early morula. Figure 9. SEM of trochophore. Figure 10. SEM of D-veliger, before release. Figure 11. Light micrograph of newly released D-veliger. Figure 12. Newly settled *Scintillona* **bellerophon** attached to *Leptosynapta clarki*. Figure 13. SEM of juvenile. di, dissoconch; pr, prodissoconch.
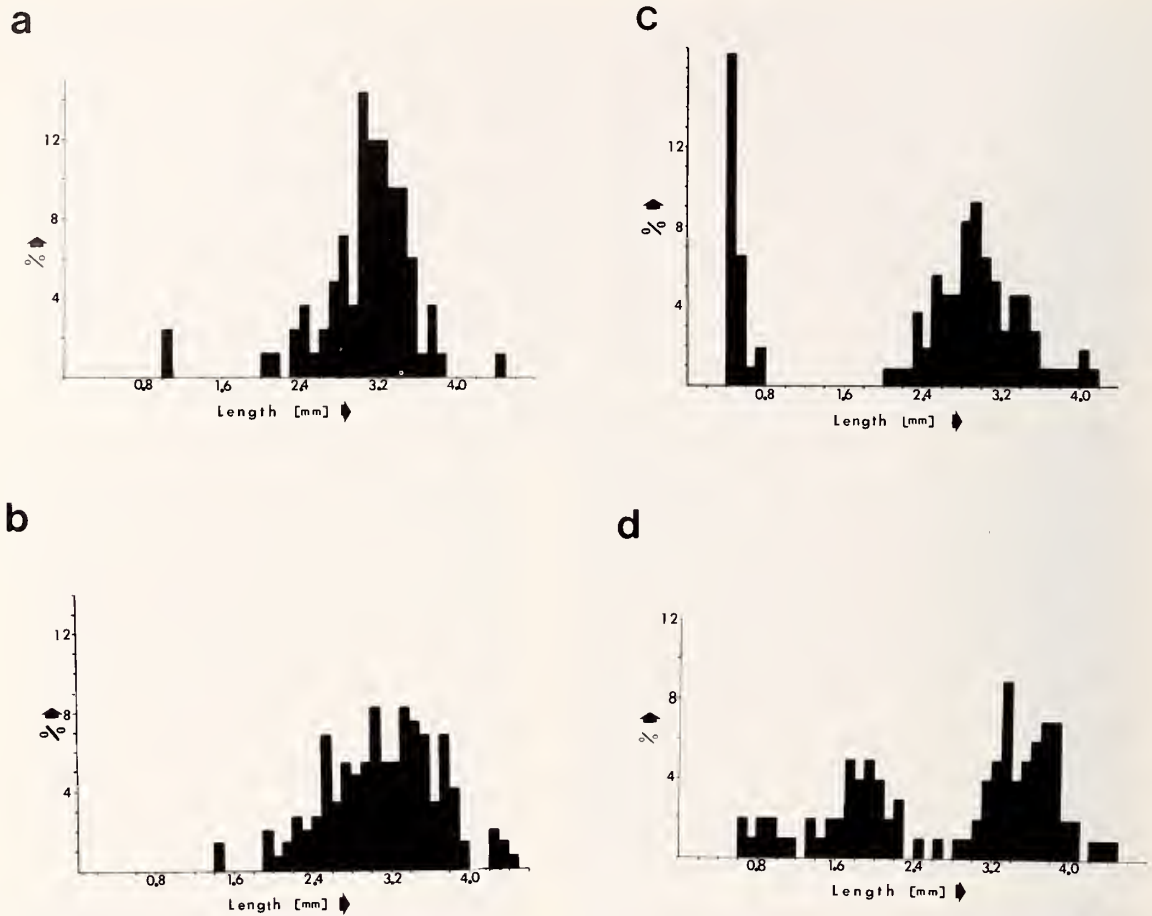
Figure 14

Size-frequency distributions from pooled monthly samples of *Scintillona* **bellerophon** spec. nov. at Woodward Point. A. October, November, and January 1982 (n = 147); B. January, February, and March 1983 (n = 84); C. April and June 1983 (n = 108); D. September 1983 (n = 99).

laboratory-raised juveniles did not attach to their synaptid host (CHANLEY & CHANLEY, 1970).

Ecology

The sediment at Woodward Point is a coarse silt (McDERMID, 1983) and has a prominent algal cover of *Ulva* in summer months. A narrow spit projects across the mouth of Sooke Harbour (Figure 1), and protects the study site from direct wave action (McDERMID, 1983). Specimens of *Leptosynapta clarki* were present from mid to low tide levels, and, in November 1982, occurred in a mean density of 78/0.1 m² (estimated from 13 randomly taken 5.5-cm diameter cores). The holothuroids were found to a depth of 8–10 cm in the sediment, and occupied semi-permanent burrows as they moved slowly through the substratum. In September 1983, 57% of the *Leptosynapta* recovered (n = 68) had ≥1 attached *Scintillona* **bellerophon**. The mean number of bivalves per host was 1.69 ±

1.05 SE (n = 39), and the maximum occurrence on a single holothuroid was 6. Typically *S.* **bellerophon** attached to the anterior half of *Leptosynapta* in a forward-facing orientation. Adhesion was achieved either by fine byssal threads, or more loosely by the lateral apposition of the extended foot to the integument of the host.

In aquaria, bivalves removed from their hosts usually reattached to any available *Leptosynapta*. Specimens of *Scintillona* **bellerophon** placed in aquaria without holothuroids remained at the surface or burrowed superfically in the sediment (mean depth = 4 mm ± 0.2 SE, n = 10). Upon the introduction of *Leptosynapta* and subsequent attachment, individuals of *S.* **bellerophon** were found at significantly greater depths ($\bar{x}$ = 18 mm ± 6 SE, n = 8, P < 0.001), probably as a result of the holothuroid's burrowing activity. The burrowing and ventilating activities of the holothuroids increased the depth of the lighter colored (oxygenated) sediment zone from 2–3 mm to 45–50 mm.

Three other invertebrate species were frequently found in *Leptosynapta clarki* burrows. Two were polychaetes, *Harmathoe lunulata* (delle Chiaje) and *Pholoe minuta* (Fabricius, 1780); the third was another galeommatacean bivalve, *Mysella tumida* (Carpenter, 1864). Both polychaetes were free in the burrow and tended to cling to the host holothurian. *Mysella tumida* was never seen to attach to the host, but occurred in the oxidized sediment layer immediately surrounding the burrow.

Some of the larger individuals of *Scintillona bellerophon* exhibited 3 growth-arrest rings on their valves, indicating that they may live up to 3–4 years of age. The first growth-arrest ring is formed at a valve length of 1.8–2.6 mm, the size attained by the first year class (Y_0) by their first winter (Figure 14). In 1983, settlement commenced in April, peaked in June, and continued at a reduced rate throughout the summer (Figure 14). By September, individuals recruited in April/June had grown by approximately 1.3 mm in length to reach 1.6–2.1 mm. It would appear that they reach sexual maturity the following spring at a length of 2.4–3.0 mm.

Leptosynapta clarki occurs off the Pacific coast of North America from the Queen Charlotte Islands to Pacific Grove, California (BROOKS, 1973). *Scintillona bellerophon* is, to date, known only from Sooke Harbour. Two nearby sites with dense populations of the holothuroid, Bamfield Inlet (Vancouver Island) and False Bay (San Juan Island, Washington State), apparently do not contain this species (A. Gibson, personal observation, and R. D. Burke, personal communication, respectively). In an ecological study carried out on the Sooke population of *Leptosynapta* in 1973, BROOKS (1973) did not encounter any *S. bellerophon*. This implies that the bivalve colonized this site 4–10 years ago and has since built up a considerable population density.

DISCUSSION

Scintillona bellerophon is similar to *S. zelandicus* in both morphology and mode of life. At least three distinct morphological differences, however, exist between the two (based on ODHNER's (1924) and MORTON's (1957) descriptions and the examination of three specimens of *S. zelandicus*); these are sufficient to give *S. bellerophon* a separate species designation. In *S. bellerophon* the (A) umbone is slightly posterior, the anterodorsal margin being as a result higher than the posterodorsal margin (in *S. zelandicus* the umbone is slightly anterior (personal observation) and the posterodorsal margin is higher), (B) mid-mantle fold is extended posterodorsally into three retractable flaps on either side (not extended in *S. zelandicus*), (C) distal part of the foot contains numerous and prominent longitudinal ciliated grooves (present in reduced form in *S. zelandicus*).

Of the four species found with *Leptosynapta clarki*, *Scintillona bellerophon* is probably the most intimately associated. To the other species, the burrow may only serve as a temporary refuge or feeding site. *Pholoe minuta* was frequently found outside the burrows, and *Mysella tumida* also occurs as an ectocommensal of the polychaete *Mesochaetopterus taylori* (Ó Foighil, personal observations). *Harmathoe lunulata* has previously been recorded in association with *L. clarki* (BROOKS, 1973) and, in the North Atlantic, with *L. inharens* (O. Fr. Müller) (MORTENSEN, 1927). This is the first record of *P. minuta* and *M. tumida* living as commensals. The ventilating activities of *Leptosynapta* enable these polychaetes and the small, practically siphonless bivalves to live at depth in the substratum by positioning in or around the burrow. This may result in reduced predation pressure (OCKELMANN & MUUS, 1978). *Leptosynapta clarki* does not seem to benefit from the association in any obvious manner.

As well as showing a trend toward commensalism, the members of the Galeommatacea demonstrate various degrees of shell reduction, mid-mantle fold hypertrophy, and reproductive complexity (MORTON, 1976). When *Scintillona bellerophon* and *S. zelandicus* are compared in these respects with other galeommatacean bivalves ectocommensal with synaptid holothurians, they are found to be relatively unspecialized. In *Devonia perrieri* (Malard, 1903), which occurs on *Leptosynapta inharens*, the valves are much reduced, hinge dentition is absent, and the mid-mantle fold extends to almost completely cover the shell surface (ANTHONY, 1916). *Montacuta percompressa*, which also occurs on *L. inharens* (BATESON, 1923), shows secondarily developed sexual dimorphism, in which parasitic, shell-less males occur within the mantle cavity of the female (JENNER & McCRARY, 1968). This hints that, in evolutionary terms, both *S. bellerophon* and *S. zelandicus* are relative newcomers to this particular ecological niche.

For all ectocommensals, adhesion to the host is obviously important. *Scintillona bellerophon* and *S. zelandicus* achieve this by two means, apposition of the laterally compressed foot and ventral attachment by byssus. In the other bivalves ectocommensal on synaptids, foot morphology varies from the relatively unspecialized condition in *Devonia oshimai* (KAWAHARA, 1942) to that of *D. perrieri*. In the latter species, the foot is dorsoventrally compressed and acts as a sucker when attached to the host, *Leptosynapta inharens*. The byssal gland opens ventrally, and the animal may attach by byssus or by foot adhesion (ANTHONY, 1916; POPHAM, 1940). This would seem to be a more efficient situation than that found in *S. bellerophon* and, presumably, in *S. zelandicus*, because changing from foot to byssal adhesion does not involve a re-orientation of the foot. In *S. bellerophon*, contact depends on the relatively narrow, ventral surface until byssal attachment is achieved.

Synaptid holothurians, in common with many other burrow-constructing benthic invertebrates, create micro-environments in sediments that are colonized by a variety of associated species. Several galeommatacean bivalves have been found occurring ectocommensally on synaptid holothurians (BOSS, 1965). In the northeastern Pacific, *Scin-*

tillona **bellerophon** is the representative ectocommensal species, exploiting the ecological niche available in *Leptosynapta clarki* burrows.

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