Extremely slow feeding in a tropical drilling ectoparasite, *Vitularia salebrosa* (King and Broderip, 1832) (Gastropoda: Muricidae), on molluscan hosts from Pacific Panama

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ABSTRACT

This study documents one of the slowest feeding behaviors ever recorded for a muricid gastropod in one of the most biotically rigorous regions on the planet. In Pacific Panama, *Vitularia salebrosa* attacks mollusks by drilling through their shells. The duration of attacks estimated by isotope sclerochronology of oyster shells collected during attacks in progress ranges from 90 to 230 days, while experimental observation of interactions documented one attack greater than 103 days. The prolonged nature of attacks suggests that *V. salebrosa* is best characterized as an ectoparasite than as a predator, which is the ancestral condition in the Muricidae. An ectoparasitic lifestyle is also evident in the unusual interaction traces of this species, which include foot scars, feeding tunnels and feeding tubes, specialized soft anatomy, and in the formation of male-female pairs, which is consistent with protandrous hermaphroditism, as is typical in sedentary gastropods. To delay death of its host, *V. salebrosa* targets renewable resources when feeding, such as blood and digestive glands. A congener, *Vitularia miliaris* from the Indo-Pacific, has an identical feeding biology. The origin and persistence of extremely slow feeding in the tropics challenges our present understanding of selective pressures influencing the evolution of muricid feeding behaviors and morphological adaptations. Previously, it has been suggested that faster feeding is advantageous because it permits predators to spend a greater proportion of time hiding in enemy-free refugia or to take additional prey, the energetic benefits of which could be translated into increased fecundity or defenses. The benefits of exceptionally slow feeding have received little consideration. In the microhabitat preferred by *V. salebrosa* (beneath boulders), it is possible that prolonged interactions with hosts decrease vulnerability to enemies by reducing the frequency of risky foraging events between feedings. Ectoparasitic feeding through tunnels by *V. salebrosa* may also reduce competitive interactions with kleptoparasites (e.g., crabs, snails) that steal food through the gaped valves of dead or dying hosts.

Additional keywords: *Vitularia miliaris*, ectoparasite, foot scar, feeding tube, sclerochronology

INTRODUCTION

Predatory species of the neogastropod family Muricidae generally attack prey by slowly drilling a hole through the wall of the prey's shell, a process that can take from several days to just over a week (Palmer, 1990; Dietl and Herbert, 2005; Peharda and Morton, 2006). During this time, muricids are left exposed and vulnerable to attacks from their own enemies and to theft of food by competitors attracted to the chemical scent of drilling or the injured prey (Paine, 1963; Morissette and Himmelman, 2000; Ishida, 2004). Thus, several authors have argued that natural selection should favor the evolution of offensive weapons and behaviors (e.g., edge drilling, kleptoparasitism, toxins, shell grinding) that accelerate or completely replace slower styles of attack (Vermeij and Carlson, 2000; Herbert, 2004; Dietl et al., 2004). Faster feeding allows animals to spend more time in enemy-free refugia or to take additional prey, the energetic benefits of which could be translated into increased reproduction or defenses (e.g., large size, thicker shell, speed, toxins, etc.). Selection for faster feeding should be particularly important in "biotically rigorous" environments, where predation and competition pressures are most intense (Dudley and Vermeij, 1978; Vermeij and Currey, 1980; Vermeij, 1987, 2004).

The present study focuses on the feeding ecology of *Vitularia salebrosa* (King and Broderip, 1832), a muricid that is relatively common in rocky intertidal habitats beneath boulders in Pacific Panama where it feeds on other mollusks. We document the unexpected occurrence of one of the slowest feeding behaviors ever recorded for a muricid in one of the most biotically rigorous regions on the planet, the tropical Pacific. Our finding on the duration of attacks together with information on the feeding traces, specialized anatomy and reproductive behavior of *V. salebrosa* are consistent with

an ectoparasitic rather than a true predatory mode of life. We also compare and contrast alternative hypotheses to explain the environmental conditions surrounding the rare evolutionary transition between a temporary intimate predator-prey interaction to a persistent ectoparasite-host interaction.

MATERIALS AND METHODS

STUDY AREA: Mollusks were collected from under boulders in the exposed rocky intertidal around Venado Island, in the Gulf of Panama, near Panama City, Panama (8°52′ N, 79°35′ W) in August 2005 and January 2006. This island is approximately 1.6 km offshore but accessible by foot during extreme low tides. Upwelling of cold, nutrient-rich water in late winter/early spring and freshwater runoff during the summer rainy season affect surface water conditions in this region, with average annual temperature and salinity in near-surface waters (top 20 m) of the Gulf of Panama ranging from 19.3 to 27.7°C and 29.3 to 34.3‰, respectively (Smayda 1965, 1966; Wyrtki, 1966, 1981; Geary et al., 1992). A more detailed description of the oceanographic and hydrographic regime of the Gulf of Panama is found in Bemis and Geary (1996). The dominant rock-encrusting macrofauna at Venado Island includes bryozoans and suspension-feeding mollusks, including the oysters *Pinctada mazatlanica* (Hanley, 1856), *Spondylus calcifer* Carpenter, 1857, *Chama* sp., and *Ostrea* cf. *fisheri* Dall, 1914, a vermetid gastropod *Tripsycha (Eualetes) tulipa* (Chenu, 1843 ex Rousseau, MS), and the calyptraeid gastropods *Crucibulum (Crucibulum) spinosum* (Sowerby, 1824) and *Bostrycapulus calyptraeformis* (Deshayes, 1830). This rocky intertidal site also includes abundant predatory gastropods, octopods, and crabs.

HOST PREFERENCES AND FEEDING TRACES: Twenty-three individuals of *Vitularia salebrosa*, with shell lengths ranging from 40.5 to 54.1 mm, were observed under boulders at Venado Island in August 2005. Fourteen of these, all females, were found to be actively feeding on molluscan prey, which was determined by observing whether the proboscis could be seen extending through a hole in the host's shell as the predator was lifted away. All fourteen *V. salebrosa* and their hosts were collected and preserved in 75% ethanol. Five host shells (three oysters and two vermetids) were cut with a rock saw to view predation traces in cross-section. All figured material is housed in the Paleontological Research Institution (PRI) in Ithaca, NY. Non-figured material associated with experiments in this study (see below) is in the collection of the third author (HF). All other field-sampled material discussed herein is reposited in the collections of the first two authors (GSH and GPD).

DURATION OF INTERACTIONS WITH MOLLUSCAN HOSTS: We estimated the duration of interactions between *V. salebrosa* and its hosts using two independent methods. The first, stable isotope sclerochronology, provides an indirect estimate but measures interactions with hosts under natural conditions in the field. The second approach, a long-term feeding experiment in the laboratory, cannot fully simulate natural conditions in the field but provides the only practical means of obtaining direct observations for attacks lasting months or longer. The two approaches together are much stronger than either alone. In this study, they yielded similar results on the estimated duration of species interaction.

Stable Isotope Sclerochronology: Stable isotope sclerochronology is a powerful tool for aging molluscan shells. The ratio of ^{18}O to ^{16}O isotopes in individual growth increments of shell $CaCO_3$ is determined by the environmental conditions in which shell precipitation occurs. In general, more positive/negative $\delta^{18}O_{carbonate}$ values correspond to cooler/warmer temperatures. The specific relationship between temperature and $\delta^{18}O_{carbonate}$ values has been empirically derived, with a change in isotope values of 1‰ being roughly equivalent to a temperature change of 4°C (Epstein et al., 1951; Krantz et al., 1987; Wefer and Berger, 1991; Jones, 1998). Salinity may also influence $\delta^{18}O_{carbonate}$ values via riverine input to coastal areas during the rainy season, which introduces freshwater that is relatively depleted in ^{18}O (Epstein et al., 1951; Surge et al., 2001, 2003).

When a shell is sampled serially across any axis of accretionary growth (e.g., umbo to ventral margin or across laminae of a thickened shell lip, etc.), the $\delta^{18}O$ values of those samples plotted against growth distance should exhibit near-sinusoidal variation resulting from seasonal changes in temperature and salinity over a year (Grossman and Ku, 1986; Wefer and Berger, 1991; Kirby et al., 1998). In the tropical eastern Pacific, where the rainy season coincides with warm summer temperatures, temperature and salinity effects on $\delta^{18}O_{carbonate}$ values reinforce one another and exaggerate the amplitude and distinctiveness of annual cycles in the profile (Geary et al., 1992). Annual cycles in oxygen isotope profiles can be counted to reconstruct a minimum estimate of lifespan and an absolute duration of shell growth. Here, we use the technique to age only new shell growth in bivalve hosts spanning the time between the initiation of an attack by *V. salebrosa* and the time the attack was disrupted when we collected the interacting species pair in the field.

Of the host-types available for this study, the stable isotope technique works best for determining duration of interactions with the oyster *Ostrea* cf. *fisheri*. *Vitularia salebrosa*'s edge drilling attacks on this oyster fortuitously mark the surface of the thickened lip. The $\delta^{18}O$ values of shell deposited between this point and subsequently formed growth increments at the lip record the duration of the attack. If attacks by *V. salebrosa* last roughly a week, as is typical of most muricid predators, there should be few or no growth increments formed by the host after the edge attack is initiated. Furthermore, the $\delta^{18}O$ profile of samples collected across any growth increments that did form should show little or no variation, consistent with the rate of environmental change

expected over a week. In contrast, if the duration of interactions are on the scale of months or longer, there should be numerous growth increments formed after the attack is initiated, and the $\delta^{18}O$ profile should exhibit a roughly sinusoidal trend with a range of values expected of seasonal to annual variation. The two oysters selected for analysis were collected *during* an attack in progress by *V. salebrosa* in August 2005. This eliminated any ambiguity over the provenance of the feeding traces. However, because the attack was interrupted, isotope profiles of these shells yield only a minimum estimate of the duration of predatory interactions by *V. salebrosa*.

The predicted annual range of $\delta^{18}O_{aragonite}$ for shells precipitated in nearsurface waters (top 20 m) of the Gulf of Panama is roughly –0.5 to –3.0‰, with an amplitude of 2.5‰ (Geary et al., 1992). Because oyster shell laminae are composed of calcite, a mineral form that differs in its isotopic composition from aragonite by a –1.0‰ offset (Bohm et al., 2000), the predicted annual range of oyster $\delta^{18}O_{calcite}$ for near surface waters of the Gulf of Panama is closer to –1.5 to –4.0‰. Measured $\delta^{18}O$ values from a gastropod *Strombus gracilior* collected at a tidally exposed beach near Venado Island have a larger amplitude of 4.5‰ for the strombid's first year of growth (Geary et al., 1992). For intertidal oysters at Venado Island (a slightly deeper site than the tidally exposed beach), the amplitude of annual change in the $\delta^{18}O$ profile should fall between 2.5 and 4.5‰, but probably closer to the latter.

Prior to sampling, oyster shells were soaked in a concentrated solution of bleach for 30 minutes, scrubbed with a soft brush, and sonicated in deionized water to remove organic contaminants, sediment, and encrusting organisms. Powdered carbonate samples were collected by abrading the edges of individual laminae exposed at the outer lip with a modified 0.5 mm bit attached to a hand-held Dremel drill. Samples were also taken from laminae visible along the less exposed inner surface of the lower valve 1–2 mm from the edge of the outer lip. Powdered carbonate samples ranged from 50 to 80 μg in size, with an average spatial resolution of 0.5 mm.

Stable isotope measurements were made on a ThermoFinnigan Delta+XL IRMS in dual-inlet mode coupled to a Kiel-III carbonate preparation system housed at the University of South Florida College of Marine Science. All values are reported in standard delta (δ) notation relative to the VPDB isotopic standard, where $\delta = [R_{sample}/R_{standard} - 1] \times 1000$ and R_{sample} and $R_{standard}$ are the oxygen isotopic ratios of the sample and the Pee Dee Belemnite (V-PDB) standard, respectively, in ‰ units. Stable isotopic precision, based on daily measurements of laboratory standards (N > 500) over the past 12 months, is ±0.06 ‰ (1 sigma) for oxygen, ±0.03 ‰ (1 sigma) for carbon.

Long-term Laboratory Observation of Feeding: An informal feeding experiment was conducted at the Smithsonian Tropical Research Institute (STRI) marine lab at Naos, Panama by one of us (HF) to determine whether attacks last longer than one to two weeks. Three 37.9 liter aquaria with flow-through seawater dripped in from above were partitioned into equal quadrants with plastic netting. Three quadrants of each aquarium were used to house *V. salebrosa* and potential molluscan hosts, and the fourth quadrant contained a pipe for outgoing water. Each quadrant held one *V. salebrosa* and one host.

Each aquarium was a replicate of the other two in terms of the host type offered in each quadrant. *Vitularia salebrosa* in quadrant I of each aquarium were offered only the byssate oyster *Pinctada mazatlanica;* the vermetid *Tripsycha (Eualetes) tulipa* was the sole host type offered in quadrant II; and either of the cementing oysters *Spondylus calcifer* or *Chama* sp. were offered in quadrant III, depending on availability. All four species are commonly found in the natural habitat of *V. salebrosa*. The experiment began April 18, 2006 and was terminated September 4, 2006. Observations were made roughly biweekly during this period. Hosts killed were replaced immediately with a single individual of the same species. Three *V. salebrosa* that died during the experiment were also replaced, but none died during attacks in progress. Twelve *V. salebrosa* were used in all.

RESULTS

ECTOPARASITISM FEEDING TRACES: We observed fourteen *V. salebrosa* feeding on the following molluscan hosts during two low tides at Venado Island in August 2005: the oyster *Ostrea* cf. *fisheri* (n = 8), the calyptraeid gastropod *Crucibulum (Crucibulum) spinosum* (n = 2), and the vermetid gastropod *Tripsycha (Eualetes) tulipa* (n = 4). In nine instances, a large female *V. salebrosa* was joined by a single smaller male, which sat directly adjacent to the female (Figures 1–2). We observed only females feeding. Adjacent males were not situated over separate feeding holes.

OYSTER HOSTS (FIGURES 3–11): The following are general characteristics of interaction traces associated with the eight *Ostrea* collected from the field: *Vitularia salebrosa* was situated on the left, cemented valve, near the ventral commissure, with its proboscis extended through a straight-sided, 1 mm diameter hole that penetrated into the lip of the left, cemented valve at an angle parallel to the commissural plane. The lower half of the hole (the half closest to the rock substrate) cuts through multiple oyster lamellae, as if formed by a drilling attack, while the upper half (the half closest to the commissural plane of the oyster) does not. Instead, the roof of the hole is formed by a single curved lamina, apparently as the oyster deposited new shell over the feeding proboscis. The attack, therefore, must have initiated as an edge drilling attack at an older (ontogenetically earlier) commissure.

The hole through which *Vitularia salebrosa* feeds travels into the lower valve as a tunnel, curving gradually until it erupts at the inner surface some distance from the lip. From there, the tunnel continues in a straight
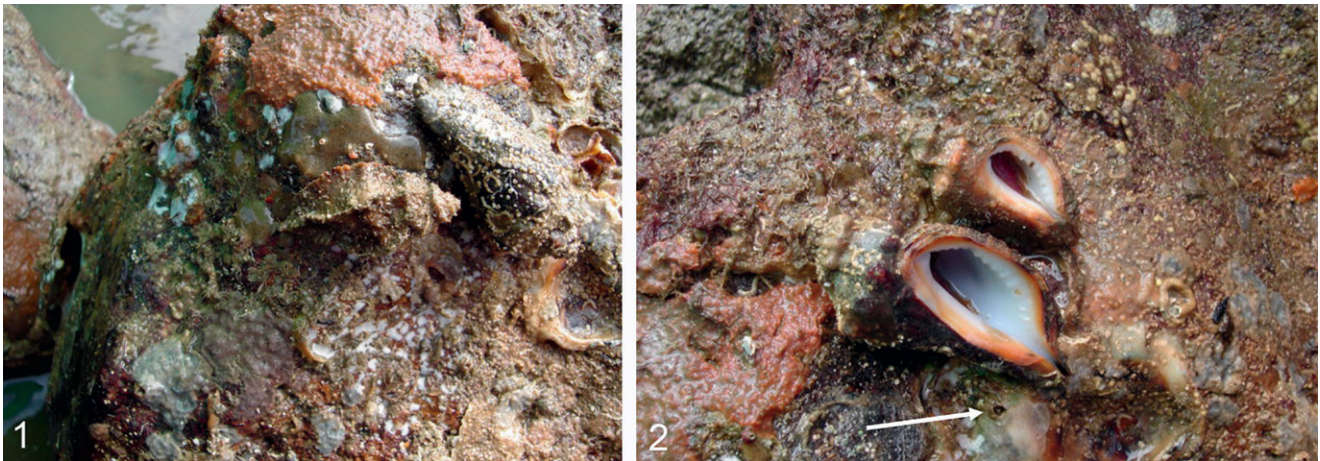
Figures 1–2. Large female *Vitularia salebrosa* with smaller male on overturned boulder. Female was feeding on an oyster heavily encrusted with bryozoans and sponges. Figure 2 shows hole (arrow) leading to feeding tunnel and characteristic foot scar left by female (etched area around hole). Adjacent male was not feeding.
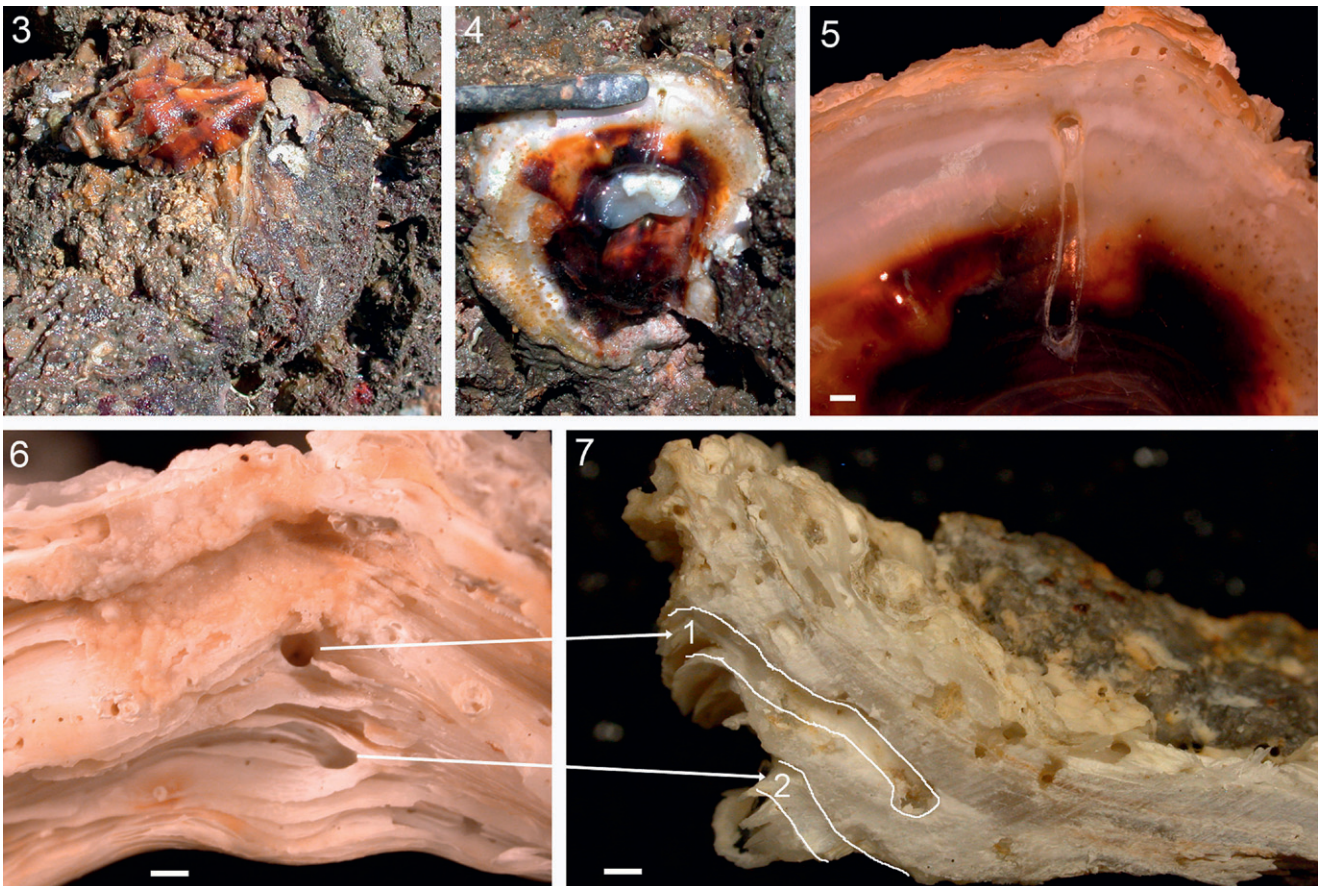
Figures 3–7. Ectoparasitism traces left by *Vitularia salebrosa* feeding on the oyster *Ostrea* cf. *fisheri* (PRI 8743). **3.** Female ectoparasite feeding on oyster attached to intertidal boulder. **4.** Left valve of oyster host showing opening of feeding tunnel (hole near screwdriver tip) and feeding tube extending from hole to adductor muscle. **5.** Close-up of hole and feeding tube. **6.** Close-up of left valve showing calcite foot scar (top, left of center) and holes leading to two feeding tunnels. Valve is oriented with commissure at bottom of image. **7.** Cross-section of oyster shell revealing two feeding tunnels. Only the second tunnel provided access to the interior of the hosts shell at the time of collection. Scale bars = 1 mm.
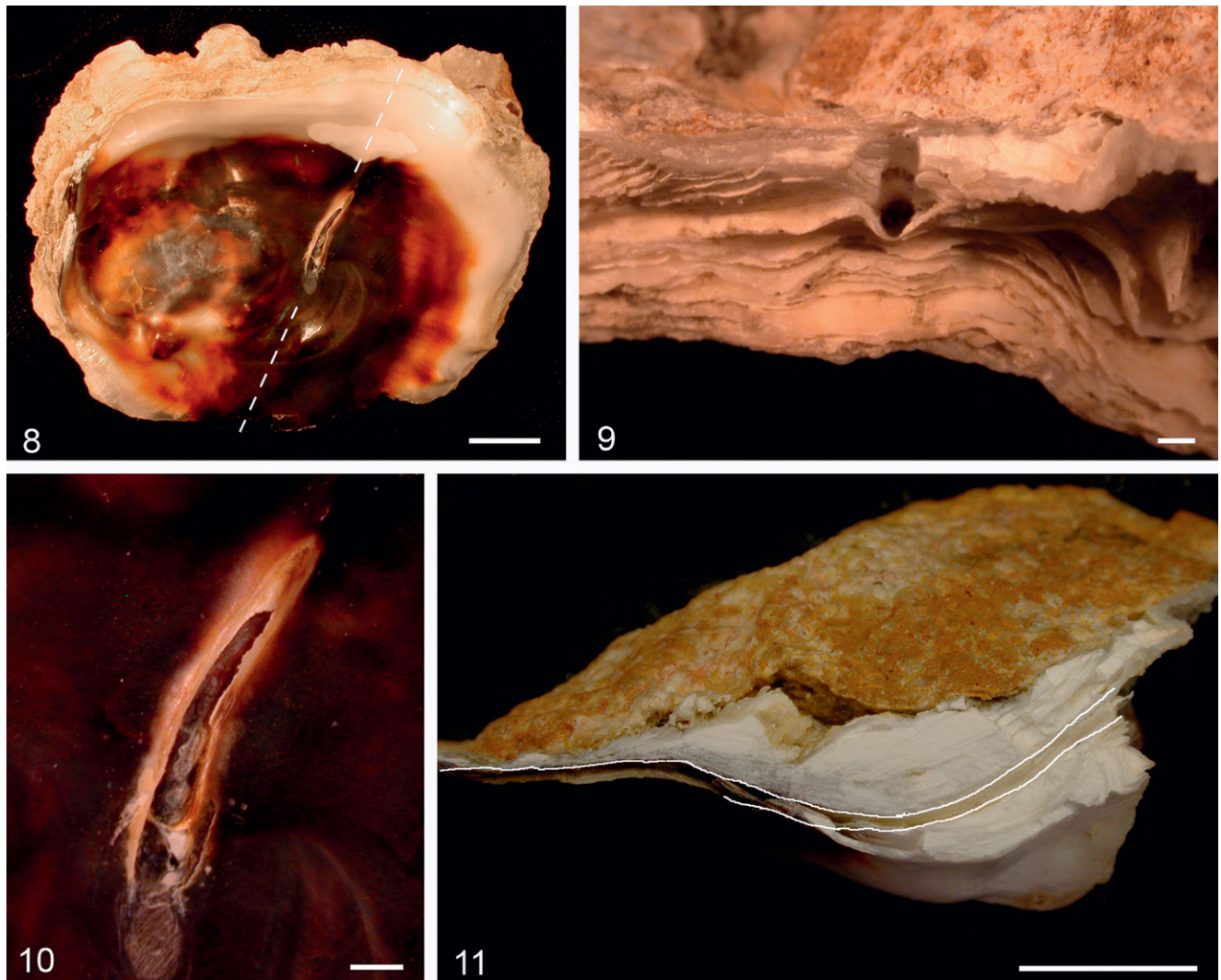
Figures 8–11. Ectoparasitism traces left by *Vitularia salebrosa* feeding on the oyster *Ostrea* cf. *fisheri* (PRI 8744). **8.** Left valve of oyster prey showing feeding tube leading towards adductor muscle. Dotted line depicts cut made for cross-section in figure 11. **9.** Close-up of external hole showing upper lip of hole excavated by drilling and lower lip formed by undulating shell laminae deposited by oyster. **10.** Close-up of feeding tube on interior of oyster. **11.** Cross section of oyster shell revealing a single, long feeding tunnel winding through shell. Outer lip of oyster is to the right of the image. Scale bars in figures 8 and 11 = 5 mm. Scale bars in figures 9 and 10 = 1 mm.

line as a closed tube or open channel with low walls. The tube/channel structure extends up to 25 mm along the inner surface stopping just inside the margin of the adductor muscle scar. There was no sign of feeding on the adductor muscle itself, although some muscles exhibited a localized whitened region that could represent scar tissue or inflammation.

A cross-section of the oyster in Figure 3 shows two separate tunnels, although just one penetrated the inner surface of the valve. The termination point of the earlier tunnel (tunnel #1 in Figure 7) occurs at precisely the same growth line that the newer tunnel (tunnel #2 in Figure 7) begins. Feeding activity by *V. salebrosa* on this host is interpreted to have been more or less continuous, with the second tunnel beginning almost immediately after abandonment of the first tunnel. Adjacent to the outer hole leading to tunnel #1 is a cap of bubbly calcite cement, which was formed underneath the foot of the predator (a foot scar). No other oyster valves were found with a foot scar.

CALYPTRAEID GASTROPOD HOSTS (FIGURES 12–17): Two *Crucibulum (Crucibulum) spinosum* were found with a single *V. salebrosa* sitting on top of the host shell with its proboscis extending through a 1 mm diameter, straight-sided hole roughly 7.5 mm from the shell lip. No foot scars on the outer surface of the host shells were observed. The hole, which is perpendicular to the shell surface, erupts ventrally as a tube that runs along the inner surface of the shell, adjacent to the cup, for about 5 mm. The distal, open end of the tube exits between

the shell and mantle in the region just posterior to the host's head and gills but continues as a low-sided channel extending another 5 mm. Dissection of both individuals revealed a cavity in the digestive gland roughly 2 mm in diameter and 5 mm in length, apparently representing the region of the gland consumed by *V. sale-*

brosa. The cavity did not break through the digestive gland but terminated within it. A second drill hole that was repaired and is not associated with a tube is present on one of the shells, although the driller responsible for this hole is not known. No foot scars were found on any calyptraeid shells.
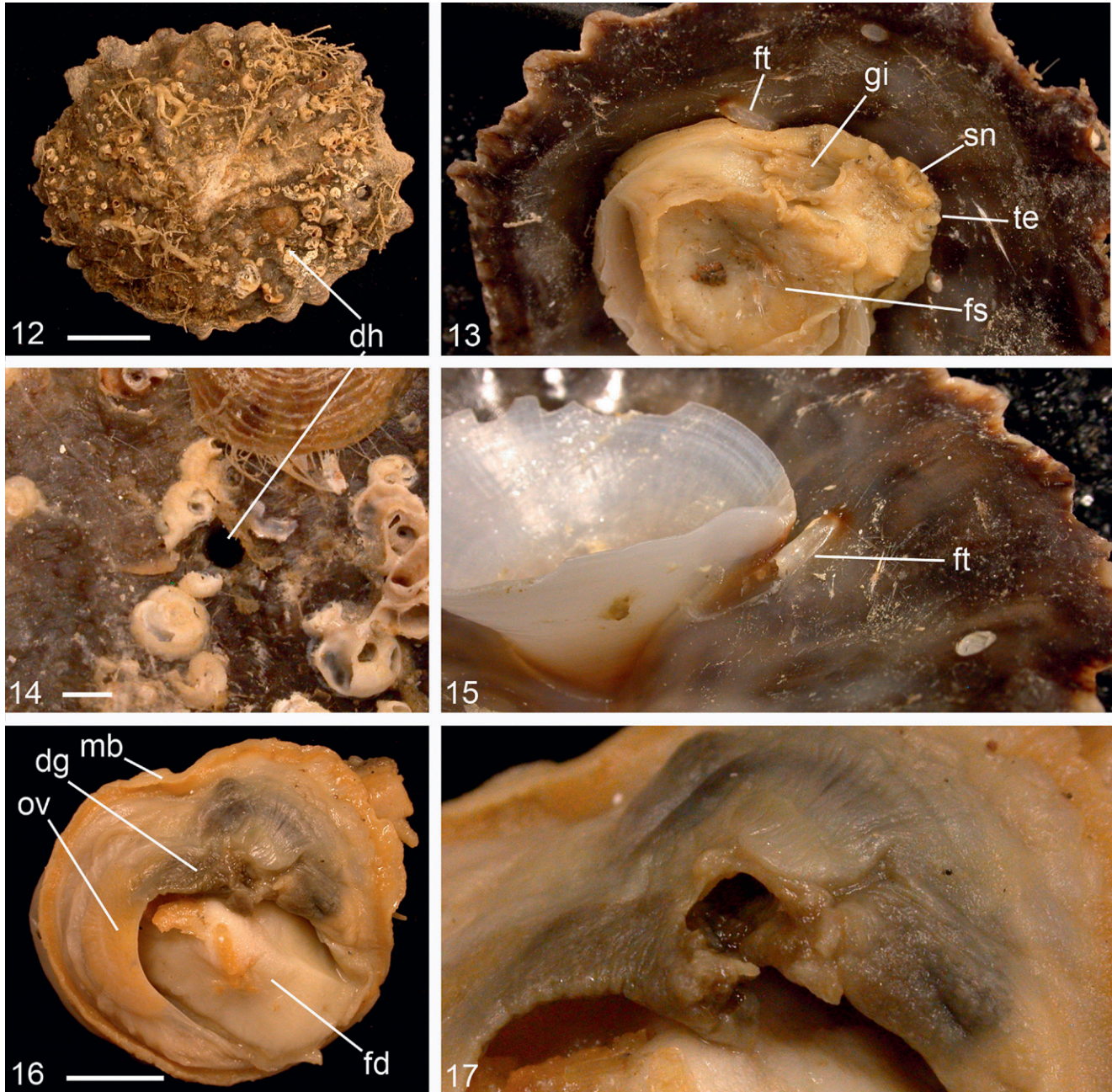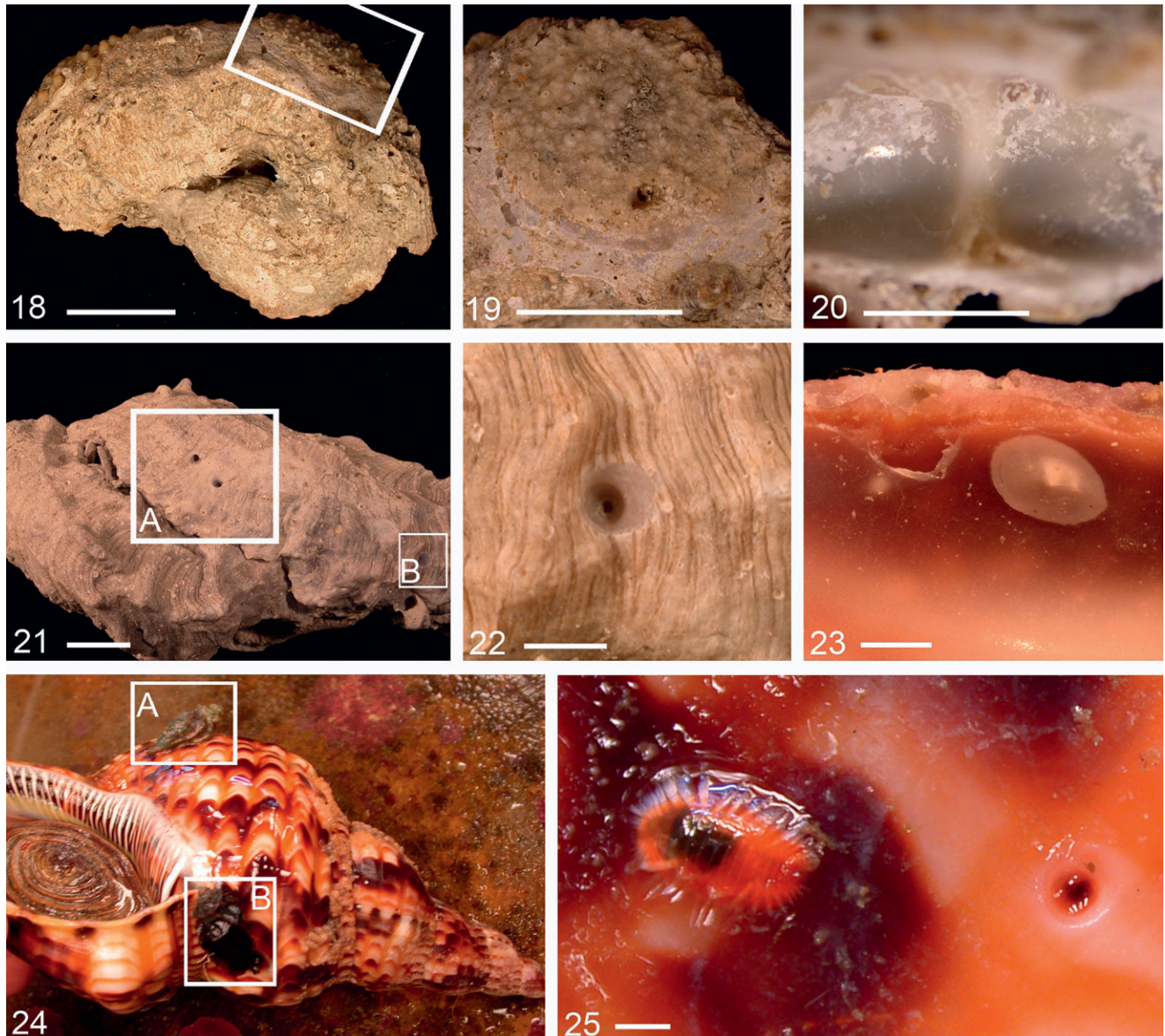

Figures 12–17. Ectoparasitism traces left by *Vitularia salebrosa* feeding on the calyptraeid gastropod *Crucibulum (Crucibulum) spinosum* (PRI 8745). **12.** Dorsal view of *Crucibulum* shell. 13. Ventral view of *Crucibulum* showing position of feeding tube relative to animal. **14.** Close-up of external opening of drill-hole. **15.** Close-up of feeding tube with animal removed; feeding tube (not including etched area beyond tube) is roughly 5 mm in length. **16.** Dorsal view of *Crucibulum* anatomy showing damaged digestive glands. **17.** Close-up showing hollowed-out digestive glands. Abbreviations: **dg,** digestive glands; **dh,** drillhole; **fd,** foot, dorsal side; **ft,** feeding tube; **fs,** foot, sole; **gi,** gills; **mb,** mantle border; **ov,** ovaries; **sn,** snout; **te,** tentacle. Scale bar in figure 12 = 10 mm; scale bar in figure 14 = 1 mm; scale bar in figure 16 = 5 mm.

VERMETID GASTROPOD HOSTS (FIGURES 18–23): All four *Tripsycha (Eualetes) tulipa* hosts were attacked by drilling through the shell wall. Drillholes are roughly 1 mm in diameter and conical in vertical cross-section. Figures 18 (box) and 19 show an attachment scar from the foot consisting of a broad halo of heavy shell dissolution capped by a smaller region of reprecipitated calcite cement. Sectioning of this shell revealed that the hole on the outer surface was connected to a tube on the inner surface (Figure 20). Vermetids were observed with as many as seven complete and incomplete holes. Figure 21 shows a shell that had seven holes, although only three are visible from a single angle (two in box A, and one in box B); all but one of the holes are incomplete or repaired (Figures 22–23).

OTHER MOLLUSCAN HOSTS (FIGURES 24–25): In a holding tank used for teaching at the STRI marine lab at


Figures 18–25. Ectoparasitism traces left by *Vitularia salebrosa* on the vermetid gastropod *Tripsycha (Eualetes) tulipa* (PRI 8746: figures 18–20; PRI 8747: figures 21–23) and the ranellid gastropod *Charonia tritonis*. **18.** Top-down view of vermetid shell; foot scar highlighted in box. **19.** Close-up of foot scar and drillhole. **20.** Close-up of feeding tunnel on interior surface of sectioned vermetid shell. **21.** Second vermetid shell showing three drillholes (2 in box A, 1 in box B). **22.** Close-up of drillhole in box B. **23.** Close-up of interior surface of sectioned vermetid shell showing internal shell repair of two holes corresponding with drillholes in figure 21, box A. **24.** Large *Charonia tritonis* gastropod attacked by two *V. salebrosa* predators in a holding tank at STRI marine lab, Naos, Panama. **25.** Close-up of two drill holes. Ectoparasite in figure 24, box A observed feeding through smaller, rounded hole on the right side of the figure (see text for details). Scale bar in figure 18 = 10 mm; scale bars in figures 19–21 = 5 mm; scale bars in figures 22–23 and 25 = 1 mm.

Naos, Panama, a large *Charonia tritonis* gastropod was attacked by two *V. salebrosa*. One individual was removed to reveal two adjacent drillholes and its long proboscis extending through one of them. The hole is round in plan view and conical in vertical cross-section. The second hole is irregular, having a round inner edge but a strongly ovate outer edge. Additionally, the wall of the second hole is heavily gouged with what appear to be radular scrape marks. We do not know when these attacks started or if they resumed at a later date. *Charonia tritonis* generally occurs in slightly deeper waters than *V. salebrosa* and is almost certainly a novel host.

STABLE ISOTOPE SCLEROCHRONOLOGY: The first oyster analyzed (PRI 8743: same shell as in Figures 3–7) was

sampled along the axis of lip thickening, with sample 1 corresponding roughly to the point at which feeding tunnel #1 was initiated by drilling, sample 4 corresponding to the initiation of tunnel #2, and sample 17 (the last sample) corresponding to the most recently deposited shell lamina, closest in time to when the attack was interrupted by our collection of both ectoparasite and host (Figure 26). Nearly constant isotope values between samples 1–4 suggest that abandonment of tunnel #1 and initiation of tunnel #2 occurred over a very short period of time and, thus, without any significant break in feeding activity.

The isotope profile of this first set of samples shows a single, complete cycle, with values beginning at –2.6‰ (sample 1) followed by a warming/freshening trend with
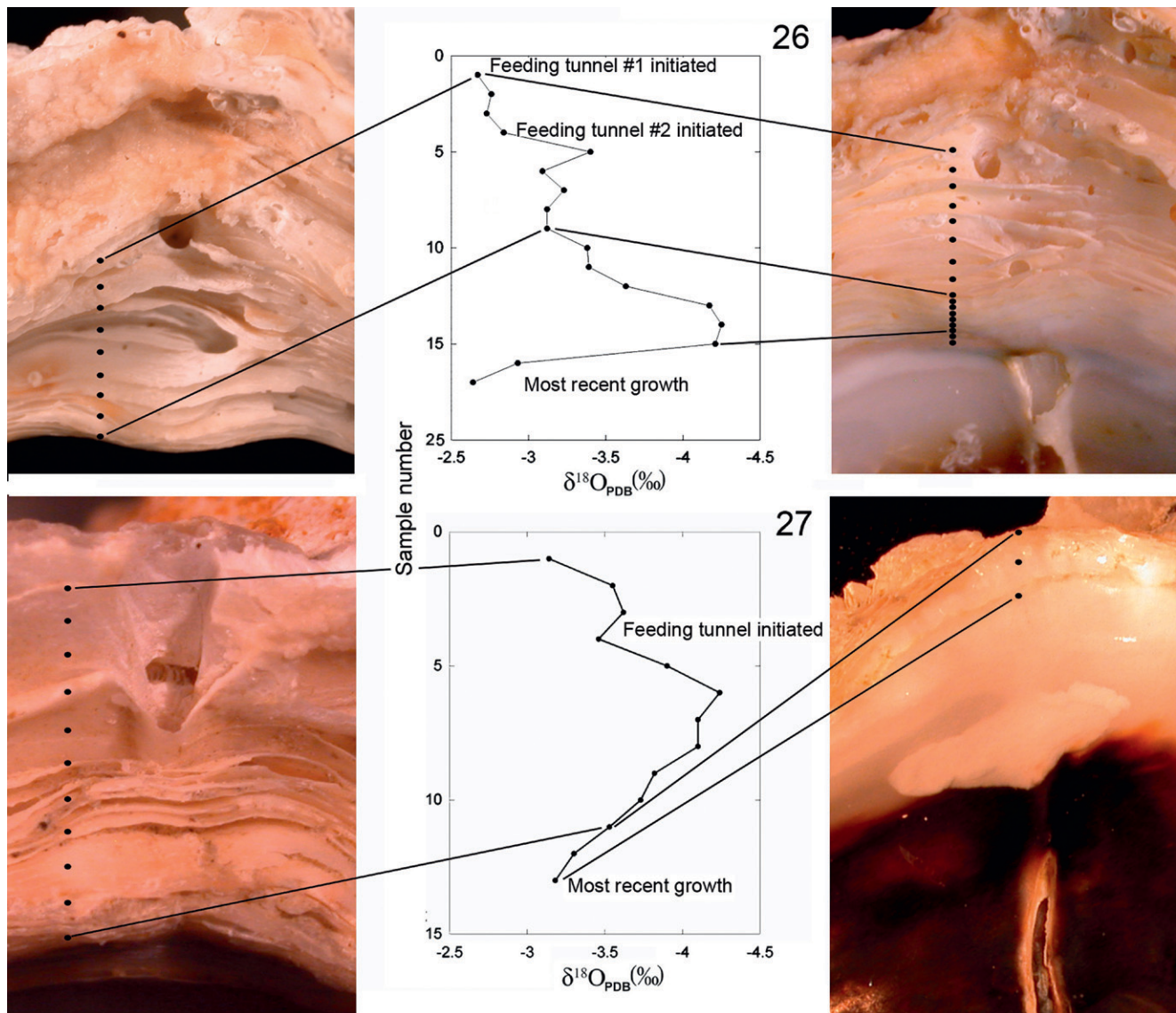
Figures 26–27. Oxygen stable isotope sclerochronology profiles of two oyster shells (*Ostrea* cf. *fisheri*) parasitized by *Vitularia salebrosa*; Images to the right and left of each profile show approximate spacing and position of samples taken from each oyster. Figure 26 shows same oyster as in figures 3–7 (PRI 8743). Figure 27 shows same oyster as in figures 8–11 (PRI 8744). See text for details.

a minimum value of –4.3‰ (sample 14) and a return to cooler/drier values around –2.6‰ (sample 17). This pattern, together with the 1.7‰ magnitude of variation between isotopic maxima and minima, is consistent with seasonal change, probably on the scale of months. To refine this estimate of the duration of the attack, we divided the observed amplitude of the oyster profile (1.7‰) by the predicted annual amplitude of 2.5‰ for near-surface waters of the Gulf of Panama (see Materials and Methods). By this comparison, the observed data encompass roughly 65% of the expected annual range, or 7.8 months.

A more conservative estimate of the attack duration can be obtained by dividing the amplitude of the oyster profile (1.7‰) by the larger annual amplitude (4.5‰) reported for the isotope profile of a strombid gastropod collected at Venado Beach, a more exposed site than Venado Island that has greater environmental extremes of temperature and salinity (Geary et al., 1992) (see Materials and Methods). By this estimate, the amplitude of isotopic variability in the oyster profile is roughly 38% of the observed annual amplitude in the strombid profile, or 4.6 months.

The isotope profile of the second oyster (PRI 8744: same shell as in Figures 8–11) shows a similar full-cycle but a lower amplitude (1.0‰) due to truncation of isotopically heavier values at the beginning and end of the profile (Figure 27). The amplitude of this second oyster profile is roughly 40% of the annual range predicted for near surface waters of the Gulf of Panama, or 5.0 months. If this profile is compared to the observed annual range of 4.5‰ for the Venado Beach site, the estimate for the duration of the attack is a more conservative 2.6 months.

LONG-TERM FEEDING EXPERIMENT: We observed a total of 8 long-term interactions between *V. salebrosa* and its hosts (0 attacks on *Pinctada mazatlanica,* 1 attack on *Spondylus calcifer,* 3 attacks on the vermetid gastropod *Tripsycha (Eualetes) tulipa*, and 4 attacks on *Chama* sp; Table 1). The average duration of attacks that were completed (i.e., ending in the death of the host) was 46 days (n = 7). The shortest attack recorded was on *Chama*, lasting 21 days. The longest attack, also on *Chama*, lasted 103 days and was still in progress at the termination of the experiment. The longest attack on a vermetid lasted 69 days. The only attack on *Spondylus* lasted 44 days. *Vitularia salebrosa* were observed to move on and off of their host in half of the observed encounters. In one case, an attack on *Tripsycha* was abandoned for a month before resuming at the same position. In a 97-day attack on *Chama,* two *V. salebrosa* sat side by side on a single host and fed from a single hole (one snail had climbed over the experimental partition in the tank).

DISCUSSION

In this study, we show that a typical interaction between *Vitularia salebrosa* and its molluscan hosts is initiated by wall- or edge-drilling and lasts several months. Estimates from isotope sclerochronology of two *Ostrea* hosts collected in the field during attacks in progress indicate that the interactions had already lasted between a minimum of two and a maximum of eight months when we collected the species pairs. Had the attacks not been interrupted, they might have lasted considerably longer. In our laboratory-based feeding experiments, we observed an attack lasting 103 days, which ceased only because the experiment was terminated at this time. Both estimates of feeding times for *V. salebrosa* exceed a 29-day long attack recorded for the drilling muricid *Trophon* in the Antarctic (Harper and Peck, 2002) and are on par with the nearly half-year long attacks recorded in the laboratory for the muricid *Genkaimurex varicosa* (Kuroda, 1953), which has been regarded as ectoparasitic or commensal on scallops in deep waters off Japan (Matsukuma, 1977). Although we did observe some mortality of hosts due to attacks by *V. salebrosa* in our laboratory experiment, death was in all cases delayed well beyond the initiation of feeding. Table 1 shows that *Spondylus* and *Tripsycha* hosts survived, on average, for 44 days after feeding began, while *Chama* survived for an average of 63 days. By contrast a typical predatory muricid consumes its entire prey within hours after feeding begins, and drilling attacks rarely last longer than a week (Dietl and Herbert, 2005; Herbert, unpublished experimental observations). Combined with field data and isotope results, these observations suggest that *V. salebrosa* is best characterized as an ectoparasite than as a predator.

Ectoparasite as used here refers to an organism that lives on the exterior of and takes resources from another organism in a lasting, intimate interaction that may or may not be lethal. Ectoparasites that have the capacity to move between hosts minimize the fitness losses associated with

Table 1. Results of Long-Term Feeding Experiment

Species	Number of Attacks	Mean Duration of Attacks (days)	Minimum Duration of Attacks (days)	Maximum Duration of Attacks (days)
Pinctada mazatlanica	0	-	-	-
Spondylus calcifer	1	44	44	44
Tripsycha tulipa	3	44	31	69
Chama sp.	4	63	21	103*

*experiment terminated before death of prey/host

intense use of host resources and host death (Lehmann, 1993; Ewald, 1995). This generalization may help explain why the majority of hosts offered in our experiments were ultimately over-exploited (killed) by *V. salebrosa.*

In the following sections, we discuss the interaction traces, specialized anatomy, and reproductive behavior of *V. salebrosa* relative to other predatory Muricidae that are also suggestive of an ectoparasitic lifestyle.

INTERACTION TRACES OF AN ECTOPARASITIC MURICID: FOOT SCARS, FEEDING TUNNELS, AND FEEDING TUBES: The foot of *Vitularia salebrosa* frequently forms an attachment scar on the host shell that consists of a circular calcareous deposit (or "carbonate foot pad" of Bromley and Heinberg, 2006) or a region of substrate etching. Such scars are exclusive to gastropods that have a sedentary existence on molluscan hosts or rock substrates (e.g., herbivorous limpets: Bromley and Heinberg, 2006; capulid gastropods: Matsukuma, 1978; Ward and Blackwelder, 1975; Bongrain, 1995; suspension feeding calyptraeid gastropods: Walker, 1992; Simone, 2002; Santos et al., 2003; detritivorous hipponicid gastropods: Noda, 1991; Vermeij, 1998; Simone, 2002; Santos et al., 2003; and ectoparasitic muricids, including *Genkaimurex* and some coralliophilines: Matsukuma, 1977; Massin, 1987). The mechanism of attachment likely explains the formation of the scars. In general, scar formation is a function of organic adhesives secreted by the gastropod foot that contain a high concentration of proteins with acidic or basic residues (Smith et al., 1999; Smith, 2001; Pawlicki et al., 2004; Bromley and Heinberg, 2006). The low or high pH of these residues produces etching or secondary calcite deposition, respectively. The formation of foot scars by *V. salebrosa* suggests that it, like *Genkaimurex*, has evolved the capacity to secure itself to host shells and has a sedentary life habit, both of which are highly unusual for the Muricidae.

Other telltale signatures of prolonged feeding by *V. salebrosa* are the calcareous tunnels and tubes through which its long proboscis extends during feeding. One of the first questions we attempted to address was whether tunnels and tubes are formed during feeding by *V. salebrosa,* or whether this ectoparasite simply takes advantage of pre-existing openings in prey shells left by other organisms. It is well known, for example, that calcified infestation tunnels roughly the same diameter as those used by *V. salebrosa* are bored into oysters by spionid polychaetes (Huntley, 2007). Spionid tunnels, however, are u-shaped borings, where the worm penetrates into the shell lip and then turns 180 degrees, emerging at the lip adjacent to the initial boring (Blake and Evans, 1973). These and other organic-walled spionid structures (e.g., Ishikawa and Kase, 2007) are, thus, easily distinguished from the calcareous feeding tunnels and tubes of *V. salebrosa*, which proceed in a direct line from the lip to the targeted tissues or organs. All indications are that the structures used by *V. salebrosa* are formed *during* the interaction between this ectoparasite and its host.

A second question was whether feeding tubes used by *V. salebrosa* and which extrude on the internal surface of some prey shells are made by *V. salebrosa* or its hosts. At least two muricids do, in fact, secrete protective calcareous tubes around their proboscises. In both cases, the muricids [*Reliquiaecava robillardi* (Liénard, 1870) and *Magilus antiquus* Montfort, 1810] are coralliophilines parasitic on corals, and the proboscis is embedded within the host tissues (Massin, 1987; M. Oliverio, personal communication to GSH, 28 Jan. 2008). Feeding tubes associated with *V. salebrosa*, however, are formed by a shell layer that is continuous with the inner surface of the host's shell and presumably formed *by the host* in a process analogous to pearl formation in oysters. The host simply deposits a thin layer of shell over the intruding proboscis in an attempt to seal off the irritant, which results in a straight, calcareous-walled tube.

From time to time, shell repair by the host is effective, with feeding tunnels and drillholes being completely sealed off. In our laboratory feeding experiments, *V. salebrosa* would often leave its host for short intervals, and it may be that successful repair is possible during these breaks in activity. This would force *V. salebrosa* to abandon its host, punch through the repair, or drill a new hole. Some hosts, especially vermetids, have been found still alive with multiple repaired holes. We found one vermetid in the field with six repaired holes and one unrepaired hole (still being used by *Vitularia salebrosa*). Also, at least in edge-drilled oyster hosts, layer after layer of shell may be deposited over the intruding proboscis, such that the original edge-drilled hole is displaced 5 mm from the new commissure.

Persistent ectoparasites, however, are clearly able to maintain open feeding tunnels even after intense efforts by the host at internal shell repair. Tubes that are kept open even with thick shell layers deposited over most of the length of the proboscis by the host become tunnels *through* the prey shell. How tunnels are kept open is unknown. An unusually long accessory boring organ (ABO) peduncle could be used to maintain internal openings in some tubes. Our initial study of *V. salebrosa*'s anatomy found that it does indeed possess a relatively narrow and long ABO (Simone et al., 2009). However, this solution is unlikely to work for some of the longer tunnels, which can reach nearly 25 mm in length. It is also problematic for radular rasping alone to maintain the opening. Carriker and Van Zandt (1972) found that muricid drillers that have had their ABO's amputated cannot excavate deep holes in shells until the ABO has regenerated. Herbert et al. (2008), however, showed that *V. salebrosa* sometimes forms a robust, elephant-tusk shaped radula that is different from its typical radular morphology and unique within the Muricidae. It is possible that this unusual morphology could function more effectively as a drilling implement in the absence of ABO secretions, particularly when host scars are newly formed and thin or largely proteinaceous in composition.

A third possible mechanism for preventing host shell repair of deep feeding tunnels is that *V. salebrosa*

produces shell dissolving/loosening secretions from the proboscis itself. This occurs in cassid drillers, for example, which have two large salivary glands that open into the proboscis and trickle acids to the site of boring on echinoid prey (Carriker and Gruber, 1999). *Vitularia salebrosa* has several glands that could potentially function in this manner, including the salivary glands, the gland of Leiblein, the glandular part of the valve of Leiblein, and the gland of the posterior esophagus (Simone et al., 2009). A precedent for specialized boring glands of the proboscis already exists in coralliophiline and some rapanine muricids, which can penetrate the epidermis of cnidarian prey with proteolytic enzymes secreted from a single salivary duct opening into the mouth (Ward, 1965; Fankboner, 1970). At least one coralliophiline muricid, *Reliquiaecava robillardi*, reportedly uses secretions of the proboscis to bore holes through the aragonitic skeletons of coral hosts (Massin, 1987). Future histological work will be needed to test these ideas.

Anatomical Specializations for Ectoparasitic Feeding on Molluscan Hosts: Preliminary data on the anatomical specializations for an ectoparasitic mode of life suggest that *V. salebrosa* has a reduced buccal mass and radula, an elongate proboscis, and a highly simplified foregut relative to other members of the Muricidae. These aspects of the soft anatomy are documented and discussed in detail in a companion paper (Simone et al., 2009). All are consistent with specialized feeding on host fluids. In addition, Herbert et al. (2008) reported that few individuals of *V. salebrosa* (one in nine) collected in the field from museum collections actually possess a radula, an observation also made by D'Attilio (1991). All individuals we collected in August 2006, however, possessed a complete and functional radula (Simone et al., 2009). A similar situation occurs in *Genkaimurex varicosa*, with some studies reporting that this species possesses a radula (Matsukuma, 1977) and others reporting that it does not (Kuroda, 1953). It is possible that these ectoparasitic muricids only form a radula when necessary to initiate attacks by drilling, perhaps just once a year and perhaps seasonally. The radula could then be reabsorbed as the animal begins suctorial feeding. The only other muricids known definitively to lack a radula are ectoparasitic coralliophilines, which feed suctorially on cnidarians (D'Attilio, 1972). The muricine muricid *Pterymarchia martinetana* (Röding, 1798) may also lack a radula (D'Attilio and Myers, 1985), although nothing is known of this species' ecology.

However, prior reports that *V. salebrosa* lacks a radula are based on a potentially error-prone technique that involves not dissection but dissolution of head-region tissues of dried animals in concentrated potassium hydroxide. This technique is useful for extracting radulae from dried and poorly preserved museum specimens, but it is often impossible to determine whether such specimens are complete. Incomplete specimens are likely in the case of *V. salebrosa,* because the proboscis is long, extruding deep into the host shell, and might be severed during collection as the animal is pulled from the substrate.

Host Consumption by *Vitularia salebrosa* Targets Renewable Resources: In general, parasites must target renewable and energetically profitable food resources of a host in order to sustain a long-term interaction. *Genkaimurex*, for example, does not damage its scallop host's tissues and presumably feeds suctorially on replenishable "fluids" (Matsukuma, 1977), such as blood. Gastropods of the muricid genus *Vexilla* are ectoparasites on much larger echinoids and graze the epidermis, which may regenerate (Kay, 1979; Vaïtilingon et al., 2004). Coral ectoparasites of the muricid subfamily Coralliophilinae feed preferentially at the margins of coral colonies due to the tendency for renewable photosynthetic products to flow towards energy sinks at the colony margins (Oren et al., 1998). In short, wherever there is evidence of parasitic feeding by a muricid, there is evidence that the parasites target renewable resources of the host.

In this study, we found that *V. salebrosa* feeding tubes in oyster hosts stop just inside the outer margin of the adductor muscle scar, in the approximate location of a major blood vessel. We did not observe damage to oyster tissues, including the adductor muscle, and it is reasonable to conclude that *V. salebrosa* pierces these blood vessels and feeds suctorially. Direct feeding on the adductor muscle itself by *V. salebrosa* would be immediately lethal to the oyster, as the oyster would no longer be able to close its shell and defend itself from opportunistic predators. The consistency with which this anatomical region of the host was targeted (100% of oysters found with a *V. salebrosa* attached) is evidence that feeding on oyster hosts by *V. salebrosa* is highly specialized. *Vitularia salebrosa* derives nutrition from calyptraeid hosts differently, but some degree of specialization is evident here as well. The feeding tubes of both calyptraeids we dissected led in the direction of the digestive gland, and the organ itself had been partially hollowed out in each case. Digestive glands of Mollusks are commonly attacked by endoparasitic protists (Wardle, 1993; Damborenea et al., 2006; Gonzalez-Moreno and Gracenea, 2006), and some molluscan hosts can survive with infesting parasites occupying as much as 50% of the glands (Tetreault et al., 2000). Moore and Halton (1973) showed that molluscan hosts adapt to digestive gland infections with histochemical changes that increase intracellular digestive processes, which is the same response as in animals that are starved. Thus, digestive glands of calyptraeids constitute a potentially viable source of nutrition for a molluscan ectoparasite.

We have no data on organs, tissues, or fluids of vermetids that might be targeted by *V. salebrosa*. The fact that some vermetid hosts were drilled as many as seven times could mean that this interaction is less specialized than the others. However, unlike other hosts, vermetids can seal off damaged parts of the shell by calcareous septa. Doing so during an attack by *V. salebrosa* might

force the ectoparasite to drill a new hole. Also, formation of septa likely frustrates the drilling process of ectoparasites, which have little information on whether or not they are drilling into an empty chamber. The presence of occasional foot scars and feeding tunnels on vermetid hosts suggests that prolonged, non-lethal interactions with vermetids do occur in nature. In our feeding experiments, interactions between vermetids and *V. salebrosa* ranged from a few weeks to over two months. Shorter interactions may have to do with the relative sizes of ectoparasite and host, with smaller hosts less able to recover from feedings by large *V. salebrosa*. This hypothesis can be tested in the future in an experimental setting.

REPRODUCTIVE CHALLENGES FOR A SEDENTARY ECTOPARASITE: For an animal with internal fertilization, a parasitic and largely immobile existence poses a major problem for finding reproductive partners. Long-term commensals have evolved a variety of adaptations to deal with this challenge. The shrimp *Pontonia margarita*, a symbiont of the oyster *Pinctada mazatlanica* from the Pacific coast of Panama, for example, has evolved a system of social monogamy or mate guarding (Baeza, 2008). Calyptraeid and coralliophiline muricid snails, which are also sedentary, have evolved protandrous hermaphroditism, where new recruits become males in the presence of older females or females in the absence of any other females (Massin, 1990; Collin, 1995; Richter and Luque, 2004). In the case of *V. salebrosa*, many of the snails we observed in the field were in male-female pairs, which is consistent with both social monogamy and protandrous hermaphroditism. We observed a similar pairing behavior in the laboratory. Even though snails were housed individually in separate compartments, they would occasionally crawl out of the water and over barriers to form pairings with snails in neighboring compartments. When pairs did form in the lab, snails would sit side-by-side and occasionally swap positions over a single feeding hole. In the field, we observed only larger females over feeding holes. We also did not find any host shells with more than one foot scar or open feeding hole, suggesting that males are more mobile than females, and that when females and males are together, holes may be "shared."

EVIDENCE FOR ECTOPARASITISM IN THE INDO-PACIFIC CONGENER *VITULARIA MILIARIS*: Through personal communication to the senior author (GSH) in 2007, Anders Warén (Swedish Museum of Natural History) relayed that he has unpublished observations of identical ectoparasite feeding traces and adaptations in *Vitularia miliaris* (Gmelin, 1791), an Indo-Pacific species that feeds on bivalves, including *Isognomon* oysters in Australia and *Pinna* pen shells in the Philippines. Like *V. salebrosa*, *V. miliaris* interactions with bivalves result in the same diagnostic foot scar and feeding tunnel leading to the adductor muscle. Warén also remarked that *V. miliaris* exhibits protandrous hermaphroditism. Dr. Marco Oliverio ("La Sapienza" University Rome, Rome, Italy) has kindly provided photographs of *V. miliaris* collected from Vanuatu, reproduced here, that show a male-female pair and characteristic foot scar on a *Spondylus* host (Figures 28–29). Based on these observations, the origin of ectoparasitism in *Vitularia* dates back to at least the last common ancestor of *V. salebrosa* and *V. miliaris*. Evidence from the fossil record suggests that this ancestor predates the Late Miocene or Early Pliocene, or the approximate time when both species first appear in essentially modern form in the tropical western Atlantic (Vokes, 1977, 1986). It would not be surprising to find *Vitularia*-style interaction traces on oyster, vermetid, or calyptraeid hosts in the Late Oligocene of Europe, which is the approximate age of the earliest known species of *Vitularia* (Vokes, 1977).

EVOLUTION OF ECTOPARASITISM IN THE MURICIDAE: The evolution of ectoparasitism of molluscan hosts in the Muricidae is exceedingly rare, and the *Vitularia* case study provided in this paper is only the second example

Figures 28–29. *Vitularia miliaris* from Vanuatu, Indo-West Pacific, shown in male-female pair feeding on *Spondylus* spiny oyster. Figure 29 shows characteristic ectoparasite foot scar beneath the foot of the female.

ever documented. One reason for its rarity may have to do with the intensity of selection for faster feeding. Especially, in biotically rigorous habitats of the shallow tropics, natural selection often favors the evolution of offensive weapons and attack behaviors that speed up rather than slow down already slow styles of attack, like drilling predation (Vermeij and Carlson, 2000; Herbert, 2004; Dietl et al., 2004). The use of faster, more powerful attack techniques allows predators to spend more time in enemy-free refugia or to take additional prey, the energetic benefits of which could be translated into increased reproduction or defenses (e.g., large size, thicker shell, speed, toxins, etc.).

We hypothesize two evolutionary scenarios to explain the rare transition from predation to ectoparasitism of mollusks in the Muricidae. One hypothesis is that slow feeding on prey may be beneficial during periods of limited or unpredictable prey supply, where the benefits of mere survival outweigh the costs of feeding slowly. During these unfavorable conditions, selection for competitive performance is likely to be less important than selection for stress tolerance or stress avoidance (Parsons, 1996; Stanton et al., 2000; Bijlsma and Loeschcke, 2005; but see Chesson and Huntly, 1997). Stressful abiotic conditions may, thus, stimulate the evolution of resource-conserving traits or behaviors related to metabolic conservatism. For muricids, these environmental stresses would have to be extreme, because some muricids can survive months without feeding (Herbert, unpublished observations), and many muricids are generalist predators capable of exploiting a wide range of prey.

This scenario is appealing on the surface, because it would also explain how a muricid predator might tolerate the potentially greater exposure to enemies during slow feedings. Places and times of low productivity and nutritional stress generally also have lower abundances and diversities of enemies (Vermeij, 1989; Bambach, 1993; Bambach et al., 2002; Valentine et al., 2002). However, this scenario contrasts markedly with the current distribution of *V. salebrosa* in the tropical eastern Pacific, which is resource rich due to seasonal upwelling (Bemis and Geary, 1996) and where there is a relatively high abundance of prey and intense predation (Vermeij and Currey, 1980; Vermeij, 1989). This scenario also contrasts with the current distribution of its ectoparasitic congener, *V. miliaris* in the highly productive Indo-Pacific and with the ancient distributions of some fossil *Vitularia* in the productive tropical western Atlantic (reviewed by Allmon, 2001).

A second hypothesis is that in a dangerous environment, like the one in which species of *Vitularia* occur today and in which likely occurred in the past, ectoparasitism permits individuals to stay for long periods of time on a single prey and under a single boulder rather than to have to forage out in the open between boulders, exposed and unprotected, on a frequent basis. The exposure factor could be significant for *V. salebrosa*, because although the shell is relatively large, it is also remarkably thin and could be easily crushed by most durophagous predators. In a competitive environment, ectoparasitic feeding by *V. salebrosa* through small tunnels in the host shell may also reduce competitive interactions with kleptoparasites (e.g., crabs, snails) that often steal food from muricid drillers through the gaped valves of dead or dying prey.

The energetic costs of ectoparasitism, however, are still severe and probably limiting in terms of population size, growth rates, etc. Whether these costs have limited opportunities for speciation within ectoparasite lineages or opportunities for molluscan ectoparasitism to evolve more times than it has within the Muricidae should be studied further.

It should be noted, however, that muricid ectoparasitism does not involve energetic costs by necessity. For example, coralliophiline muricids that feed ectoparasitically at the margins of coral colonies benefit from the fact that there is a tendency for photosynthetic products from healthy, non-preyed-on corallites to flow towards the colony margins, which are energy sinks due to shading and competition from other corals (Oren et al., 1998). Coralliophilines also tend to feed in aggregations (Ward, 1965; Miller, 1981; Hayes, 1990; Soong and Chen, 1991), and this behavior can also induce the development of new energy sinks even away from coral colony margins (Oren et al., 1998). Still other coralliophilines insert the proboscis into polyp coelenterons to steal food rather than eat and damage the polyp, which may result in a constant high supply of food for the snail (Hayes, 1990). Coralliophilines comprise a diverse subfamily of nearly 200 living species that, as a group, is nearly the same age as the species-poor genus *Vitularia*, which can be traced back to Eocene origins in *Odontopolys* Gabb, 1860. Thus, the degree and nature of constraints of ectoparasitism may depend, in large part, on the type of host that is exploited. Ectoparasitism on large, clonal cnidarian hosts offers access to an abundant and rapidly replenishable supply of food in a way that ectoparasitism on a single bivalve or snail does not.

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