Proc. malac. Soc. Lond. (1969) **38**, 431.

STUDIES ON *CRUCIBULUM SPINOSUM* (SOWERBY)*

MARTHA L. ULBRICK†

Department of Zoology, University of Hawaii, Honolulu, Hawaii

The molluscan fauna of the Kaneohe Bay, Oahu, Hawaii, offered an opportunity to study the biology of a population of *Crucibulum spinosum* (Sowerby) living far from south California, the only habitat described previously (Coe, 1938). The limpet is found clinging to stones, dead coral and other solid substrata in protected areas below the low tide mark. The low conical shell with posterior apex has an internal cup-like projection for the attachment of the columellar muscle; hence, it is commonly called the cup-and-saucer shell.

The members of the Calyptraeidae are noted for their protandric hermaphroditism. Coe (1938) found that juveniles rapidly maturing to the male phase seek attachment to the anterior right of the females' shells. These mated males and the older individuals in the female phase he observed to be sedentary. He stated that other individuals, 'presumably less endowed with genetic factors for maleness', remain solitary throughout the male phase, and these, as well as the immature young, move around freely.

The principal object of this study is to elucidate certain aspects of the biology of another population of *Crucibulum*. Observations on shell shape, growth and movements of the mollusks are presented. A mating pattern not ascribed to *Crucibulum* by Coe is described and feeding mechanisms are discussed.

HABITAT

Most of the *Crucibulum* used in this study were found on pieces of dead coral or basalt rocks dredged from sand and rock bottom at 15–25 ft in Kaneohe Bay. This habitat allows good circulation without high turbulence. The rock is frequently encrusted with algae, bivalves, barnacles, tubiculous forms and notably with *Hipponix grayanus* (Menke). Within the bay *Crucibulum* is also found on sea walls and experimental trays put out for oyster spat; these may be enclosed in metal cages. These trays were in protected coves where there is good circulation, light fish grazing, little silt and substratum not disturbed by tidal fluctuations.

* Contribution No. 331, Hawaii Institute of Marine Biology.

† Present address: M. U. Gillette, Department of Zoology, Scarborough College, University of Toronto, Toronto, Canada.

On a single dredged rock, individuals of all sizes and stages of maturity may occur. A maximum of twenty-two individuals ranging from 3 to 22 mm in length was found on the top and sides of a basalt rock (maximal dimensions: 9·6 × 8·0 × 5·8 cm) heavily encrusted with *Hipponix*, barnacles and algae. On other rocks individuals may also be found on the bottom close to the substratum; however, if any part of a rock is inhabited, it is most frequently the upper surface.

There appears to be no pattern of orientation of individuals on the substratum, suggesting that *Crucibulum* does not orient towards the current. Nor does the mollusk appear to be affected by the close proximity of its neighbors, since individuals may be only a few millimeters apart.

Crucibulum may leave a scar after remaining for some time in one position on the substratum. On dead coral this may be an area cleared, presumably by rasping, of encrusting material. However, on basalt rock, *Crucibulum* appears to have dissolved that part of the rock beneath it so that it sits in a slight ovoid depression.

OBSERVATIONS ON THE SHELL

The coiled protoconch forms the apex of the shell on which radial and spiral striae intersect, and where these meet knob-like projections are formed which may be produced into tubular spines in the older parts. The shell shows slight dextral coiling.

Shape and ornamentation of the shell vary with the habitat. If individuals are crowded or amongst *Hipponix*, the apical angle of the shell is less than where they are well spaced on smooth surfaces in well-protected situations. This applies to *Crucibulum* settling on oyster spat trays protected from high silting and turbulence: their shells are thin and their spines long and delicate. Individuals growing on exposed, encrusted rocks tend to have thick, encrusted shells with moderate ornamentation. Thick shells with almost no ornamentation characterize individuals living on unencrusted basalt rock or dead coral.

Crucibulum is observed to lift the shell from the substratum and remain in this position for some time. It is then that the limpet may be sucked off by fish or taken by a crab or carnivorous mollusk; these are natural predators of the population. A sudden increase in water current or tactile stimulation causes *Crucibulum* to contract the columellar muscle fully and clamp down tightly. A close conformation between shell edge and substratum, together with the strength of the columellar muscle, gives protection.

Even when the shell is held to the rock, *Crucibulum* is able to filter feed, for there is a slight upward curvature at the left anterior edge of the shell through which the inhalant current passes to the mantle cavity. Filter feeding also occurs when no part of the shell edge is accurately fitting the substrate; in fact, an animal with an uneven shell will continue to feed when placed on glass.

Shell growth appears to occur regularly until the male phase is attained. Typically the shell has an ovoid aperture and shows little variation in general shape or sculpture. However, among individuals approaching the female phase the angle of growth changes to give a broadening of the shell aperture and so a ledge is formed; sculpturing

becomes more pronounced and the shell edge irregular. This irregularity is particularly marked in older females where the shell may fit the contour of the rock surface precisely. Frequently these females are brooding eggs.

Crucibulum can add rapidly to the shell edge. Females of 17–21 mm in length with irregular shell bases were placed in a mesh-walled polyethylene container under good circulation in the sea water system. Within 2 days new shell material up to 2 mm from the old shell edge had been laid around the peripheries of the shells establishing good conformation with the smooth walls of the container.

MOVEMENT IN ADULT STAGES

In order to verify Coe's statement that only immature individuals and unmated males move, *Crucibulum* on rocks were labelled with numbers sealed on the shell with Dekophane. The location of each individual was recorded by measuring its distance from three reference points on the rock. The animals were observed in three environmental conditions.

TABLE I. Movement of *Crucibulum spinosum* as it relates to the day–night cycle

Size of individual (mm) length × max. breadth	Length of experimental period (in 24-hr days)	No. of occasions on on which movement was recorded			Distance moved on each occasion (mm)		
		Day	Night	Time of movement not recorded	Day	Night	Time of movement not recorded
20 × 17	4·5	1	3	–	4·5	5·0, 3·0, 4·5	
17 × 15	4·5	2	1	–	3·0, 13·0	8·0	
16 × 13	3·0	–	2	–		Changed rocks twice	
16 × 12	4·5	1	1	–	3·0	22·0	
15 × 12	4·5	2	1	–	1·5, 2·0	3·0	
14 × 12	4·5	1	–	–	Changed rocks		
10 × 8	3·0	–	1	–		Changed rocks	
9 × 7	43·5	–	5	–		2·5, 3·0, 2·0, 92·0, 83·0	
9 × 7	12·5	(2)		2	5·0, 3·0		32·0, 36·0
9 × 6·5	30·5		(2)	1		3·5, 48·0	68·0
8 × 5·5	35·5	(1)	(1)	2	2·2	66·0	90·0, 13·0
7 × 6	2·0	1	–	–	25·0		
7 × 5	21·5	–	4	–		8·0, 3·5, 3·0, 35·0	

Firstly, the rocks were placed in $\frac{1}{4}$ in. and 1 in. mesh wire cages and lowered off a pier 8 ft to the bottom of the bay. There was little silting and good circulation with current fluctuating from 2 to 6 cm/sec or more when boats passed near. The positions of the mollusks were examined morning and evening for $4\frac{1}{2}$ days. On each occasion the cages were hauled on to the pier and rocks examined out of water.

During the $4\frac{1}{2}$ days, 33% of the population of fifty-seven individuals was observed to change position at least once. Of those that moved, nearly half (42%) were in the female phase, but not brooding eggs; 11% of the population moved from their rock

over the transite floor of the cages and attached themselves to another rock, 50% of these being in the female phase. In one case a young female travelled to another rock, remained several days, returned to her original rock, and then spawned. Twenty-one per cent of the initial population was lost, presumably to predation.

Observations reveal a pattern of sporadic movement: a migration of 2–92 mm during one 12-hr interval is followed by a sedentary period ranging from days to weeks. The distance travelled over the rock was greater for males than females. Most of those which moved did so at night. There may be minor movements, for frequently when a snail clamps down on the rock after having had the shell raised, it is within a few millimeters of its original position.

Next the rocks were moved from the cages, others with *Crucibulum* added to give a population of fifty-one, and all placed in a quiet lagoon (current: 0–2 cm/sec) with a very sandy bottom and high water turbidity. They were directly on the substratum 2–3½ ft deep. During the 13 days in this environment it was necessary to move the rocks under water only occasionally, and a film of sand particles and algal growth accumulated on them.

Results of underwater observations showed that 8% of the population moved. One individual (2%), a female, changed rocks, moving about 70 mm to a rock previously buried in the sand. Several individuals were observed to lay down new shell edges enabling them to seal their soft parts from the environment. During this period, 31% of the population was removed.

Finally, the animals were observed in conditions as nearly natural as possible. The same rocks and others with *Crucibulum* to make a population of fifty were placed near the same location as the first, but on the sea floor (6–8 ft deep) and not in cages. Here *Crucibulum* is normally found settled on oyster spat trays, rocks and the lower edge of the sea wall nearby. All investigations were made under water.

TABLE 2. Summary of information gathered on individuals during the experimental period (44 days)

	No. remaining stationary	No. exhibiting movement	Total
Individual living at end of experimental period	20	15	35
Individual lost to predation	28	14	42
Individual with egg capsules	8	4	12
Individual which changed rocks		9	9
Total	48	29	77

Of the initial population 19% moved during the 19-day period, at least 67% of those moving being females. One member (12·0 × 10·5 mm) of the experimental population changed rocks. Two of the local population (15·5 × 12·0 mm, 13·0 × 9·5 mm) moved on to experimental rocks. In less than 3 days the larger of these changed position and laid down 1·5–2·0 mm in new shell; examination of the gonad revealed that it was a mature female. Thirty per cent of the population was lost, probably taken by predators.

Looking at the whole experimental period 38% of the seventy-seven individuals moved at some time during the period of observation; 12% changed rocks. At least

52% of those moving were females, the largest of which measured 20 × 15 mm, and 5% of these settled and laid eggs. One female (18 × 14 mm) changed rocks twice before settling and laying eggs.

For the figures presented on movement of females, a criterion of length greater than 15 mm (Coe, 1938) was set for females not sexed by examination. This is probably a conservative figure for the Kaneohe population as marine life commonly matures more rapidly in the tropics than in more temperate waters. This is supported by the fact that functional males and females smaller than the minimal lengths stated by Coe were found. One individual 9 mm long had a reduced penis and oocytes were found in the gonad. This suggests that a larger percentage of individuals in the female phase were moving than is reported above.

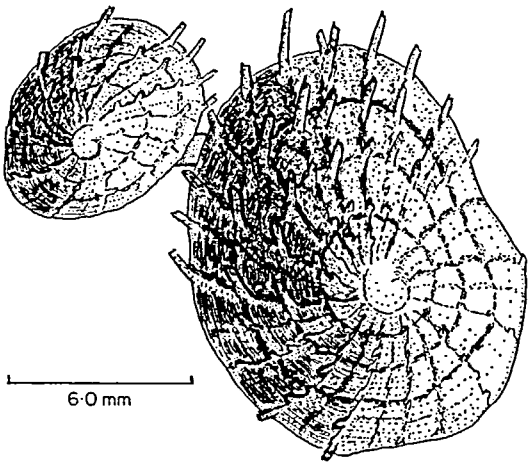

FIG. 1. Male *Crucibulum spinosum* (on left) with penis inserted in inhalant opening of female.

MATING BEHAVIOR

According to Coe (1938), mating behavior is similar to that in *Crepidula fornicata*, consisting of the male settling on the right anterior side of the female's shell with the right edges of both shells in close proximity. The long penis is inserted into the female genital opening and sperm are transferred to the seminal receptacle. He found a large portion of females with a scar on the shell where a male once sat.

Careful examination of 202 adult *Crucibulum* from the Hawaiian population revealed eight pairs mated in the position Coe describes, one female with two males attached to the anterior part of the shell, nine shells with definite scars and seven with possible scars. Even including shells with possible scars, only in 17% of the males and females examined was there evidence of this type of mating; this figure is significantly less than Coe suggests. A number of females with egg capsules showed no evidence of the mating scar.

While movement of inviduals on a rock was being studied, a male limpet was found settled on the rock alongside a female with the penis inserted in the left (inhalant) side of the mantle cavity (Fig. 1). The two were separated only with difficulty. If this is a position of copulation, as is assumed from this observation, then entry of the penis into the mantle cavity is possible either on the inhalant or exhalant side.

That this is so is supported by other observational evidence. Two undisturbed individuals orientating with respect to one another were observed for some time on the sea wall. After some minutes, they settled in the same relative positions as the pair described above. They were then removed and were found to be a mature male and female.

During observations on the experimental animals, several males were observed to move across the rock and remain for some days beside large females, then move on without being observed to mount the females' shells. At the end of the experimental period twelve females were brooding eggs; of these, only two had males sitting on

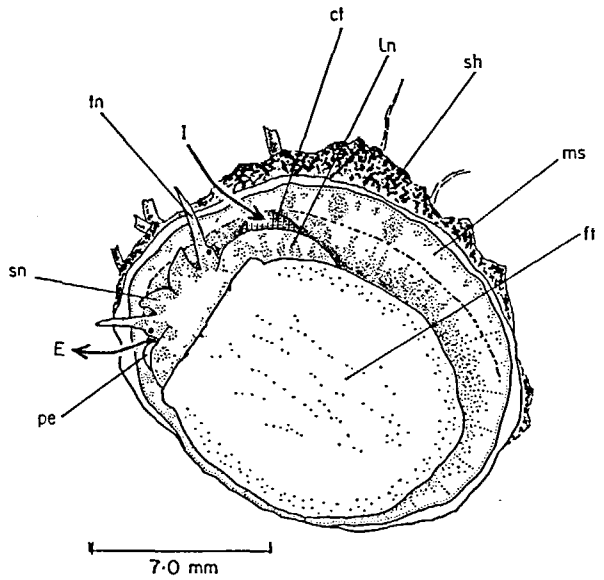

FIG. 2. *Crucibulum spinosum* filter feeding while attached to glass. ct, Ctenidium; E, exhalant; ft, foot; I, inhalant current; ln, left neck lobe; ms, mantle skirt; pe, penis; sh, shell; sn, snout; tn, tentacle.

the shell. It is possible that others of the twenty females remaining stationary during the observation did brood eggs which hatched before the animals were disturbed. None of the experimental females had mating scars and some females' shells had tall spines which would make it difficult for a male to settle, these observations supporting an alternative method of copulation to that described by Coe.

FEEDING MECHANISMS

Like other members of the Calyptraeidae, *Crucibulum* is a filter feeder. The extensive ctenidium with its elongate filaments arches to the right behind the head and follows the semi-circular course of the mantle cavity which lies around the cupule of the shell. Currents established by the lateral cilia of the filaments pass through a restricted inhalant area to the mantle cavity. This area is limited anteriorly by a pallial fold in front of the head and posteriorly by the pallial fold forming the floor of the gill chamber.

Incoming particles are trapped by a mucous sheet secreted by the endostyle on to the ctenidium and moved to the tips of the filaments which lie in the food groove. Here, as in *Crepidula* (Werner, 1953), cilia roll the mucus with food particles into a strand and advance it to a point between the neck lobe and tentacle. The radula pulls the strand into the buccal cavity. A large bolus may accumulate near the anterior end of the neck lobe before the snail drags it in. *Crucibulum* was observed to swing the head to the left and clean particles from the anterior filaments of the ctenidium.

Crucibulum also feeds by rasping the substratum. Both male and female adults were placed in transparent moist chambers covered by an algal film. While viewed from the ventral side, they were seen rasping the alga. This method of feeding may be used by the limpet to clear the area of rock on which it settles. Such a cleared area is obvious on encrusted rock, especially when the female broods the eggs.

DISCUSSION

The elongate gill filaments, the presence of an endostyle, and the sedentary habits of *Crucibulum spinosum* and *Crepidula fornicata* are all indications of successful filter feeders. However, unlike *Crepidula*, the present study shows that *Crucibulum* can move about and rasp a substratum, though Coe working on a Californian population did not observe this. Indeed, it is not evident unless marked individuals are studied.

One important difference between *Crucibulum* and *Crepidula* is the shell shape, which reflects differences in the attachment of the columellar muscle. In *Crepidula* the attachment is across the transverse shelf of the shell, and the foot is used as a sucker to attach the animal to the shell beneath; the snail loses the ability to creep at an early age (Fretter and Graham, 1962). In *Crucibulum* the attachment is to the cupule beneath the shell's apex from which the muscle fibers radiate to the foot and allow considerable freedom of movement. The shell can be raised 2–3 mm from the substratum during feeding.

The fact that *Crucibulum* can creep over the rocks would also account for differences in mating behavior between the two genera. Like *Crepidula*, *Crucibulum* can copulate with the male attached to the female's shell. However, because *Crucibulum* can move about, it is possible that the male can crawl up to a female, and without

mounting the shell position himself so that the penis enters the inhalant or exhalant pallial opening during copulation.

In *Crucibulum* females can move and apparently do so until they are ready to lay eggs. From observations on the rate of shell growth, and from the fact that there is an increasing tendency towards irregularity in the shell edge with increase in age of the female and that the shell of a brooding female fits tightly to the irregularities of the rock, the following hypothesis can be made: when a female is about to lay eggs, she rapidly lays down a new shell margin establishing good conformation with the rock and so creates a potentially well sealed brooding chamber. Within this chamber the eggs are laid and attached to the rock beneath the propodium. Here they lie in the inhalant stream of water, well protected by the mother's shell.

The ability to rasp must also be associated with mobility in *Crucibulum*. *Crepidula* attaches at an early age and remains fixed whereas *Crucibulum* moves about sporadically and before it settles on a site uses the radula to clear the area of rock. The results of experiments show that *Crucibulum* may move four to five times in a month.

ACKNOWLEDGMENTS

The author wishes to express her gratitude to Dr Vera Fretter, The University, Reading, England, for her guidance and patience, to Dr Philip Helfrich, Director of the Summer Training Program, and to the staff of the Hawaii Institute of Marine Biology for use of the facilities. This work was supported by the National Science Foundation, Grant No. GB6134.

SUMMARY

The population of this protandric hermaphrodite in Kaneohe Bay, Oahu, occurs on solid substrata swept by a moderate current. The angle of slope of the shell increases with shelter. Although remaining stationary for some days, young and older individuals move about. The distances travelled were greater for males than females, most individuals moving at night; movement in the male is chiefly associated with finding a mate, in the female with spawning. The mollusks collect food in suspension and also rasp it from the substratum. At copulation the penis may be passed through the inhalant or exhalant pallial opening. In the former case the male rests on the substratum on the left of the female; in the latter it may be either on the substratum or on the right side of the female's shell.

REFERENCES

Coe, W. R., 1938. Sexual phases in the gastropod *Crucibulum spinosum*. *J. Morph.* **63**, 345–361.

Fretter, V. and Graham, A., 1962. *British Prosobranch Molluscs*. London, Ray Society.

Hyman, L. H., 1967. *The Invertebrates, Mollusca I*, Vol. VI. McGraw-Hill, New York.

Werner, B., 1953. Über den Nährungserwerb der Calyptraeidae (Gastropoda Prosobranchia) Morphologie, Histologie und Funktion der am Nährungserwerb beiteiligten Organe. *Helgoländ. wiss. Meeresunters.* **4**, 260–315.