Nest Building in the Bivalve Genera *Musculus* and *Lima*

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(Plates 9 to 11)

The adaptations of bivalve mollusks are numerous. Many species burrow into soft muds and sands,fewer into harder substances only. Others can crawl, leap, and swim, and some live as commensals or parasites. There are sedentary species which attach themselves, temporarily or permanently, to objects by means of byssal threads which they secrete. Among the latter a number of species have developed the process of byssus spinning to the point where they enclose themselves in capsules, or "nests."

Bivalves have two principal methods for constructing nests. One method involves the agglutination of foreign particles with mucus produced by the animal. According to Haas (1942, 1943) these are the main ingredients used in building the nests of *Diplodonta orbella* (Gould, 1851) and *Cooperella subdiaphana* (Carpenter, 1864). The second method, which utilizes byssal threads as the principal constituent, is far more common among nest builders and has been studied most extensively in the case of *Lima* and *Musculus*.

The process of nest building has been observed for *Lima hians* (Gmelin, 1791) by Robertson (*in* Jeffreys, 1863), Gilchrist (1897), and others, but no one, to our knowledge, has kept *Musculus discors* (Linnaeus, 1767) in aquaria and observed the early stages of nest building.

Recently a large number of specimens of *Musculus discors* was acquired during dredging operations of the U. S. Bureau of Commercial Fisheries research vessel *Delaware* (Cruise 62 - 6). These specimens were found in nests, fouling the upper valve of the sea scallop, *Placopecten magellanicus* (Gmelin, 1791), and usually well camouflaged among other fouling growth. They were taken from the Northeast Peak of Georges Bank, off Massachusetts (Lat. 41° 57.2′ N; Long. 66° 16.7′ W), on June 1, 1962, at a depth of 44 fathoms, and were held aboard ship in tanks with running sea water. In the laboratory, specimens of various sizes were removed from their nests and placed in individual aquaria, supplied with running sea water (Plate 9, Figure 1), to see if they would construct new nests. After several days some did. The early phases of construction were observed closely and documented with a series of photographs.

In this paper the process of nest building of *Musculus discors* is described and illustrated; and for comparison, the process for *Lima* is reviewed. In a final section, the adaptive significance of nest building in the two genera is discussed and compared.

NEST BUILDING IN *MUSCULUS*

During the early stages of nest building *Musculus discors* tends to weave a compact structure entirely of byssal threads which it attaches to the substrate. In waters off Cape Cod, Massachusetts, however, the completed nest later becomes well camouflaged, for stolons of hydroids grow into it, small bivalves and annelids nestle among the outer threads, and colonies of bryozoans often overgrow it completely. MacGinitie (1959) described similarly the completed nest of the Pacific variety of this species. Forbes & Hanley (1853) remarked that those in English waters are found "enveloped in nests formed of fragments of *Flustra foliacea* [a colonial bryozoan] and masses of sand agglutinated together and combined by byssal threads." Stimpson (1853) observed that the nests of specimens from the vicinity of New Brunswick are formed of various marine substances. Thus, it would seem that, in a given area, the composition of the completed nest depends in part on the composition of the substrate and on the organisms closely associated with the nest builder.

Musculus discors has no permanent openings in the byssal capsule for water currents to pass through. Rather, the byssal threads radiate from their point of attachment to the animal, and surround the shell in all directions, completely concealing the resting animal. Only when the shell valves are open are the byssal threads separated and the siphons exposed for feeding and respiration.

The foot (Plate 9, Figure 2), in conjunction with special glands, is used in the formation of byssal threads. This highly specialized organ is capable of great extension. When contracted it is short and tongue-shaped, but when fully extended it becomes slender and strap-shaped. The means by which the Mytilidae form and attach threads of conchiolin have been carefully described by White (1937). In essence, the foot has a groove on the posterior side which, at the base, is continuous with the byssal aperture. Secretions issue not only from glands of the byssogenous cavity but also from those lining the groove of the foot. The groove, which terminates in a depression or sucker at the distal end of the foot, is closed during the process of secretion. The sucker is rounded in *Mytilus edulis* (Linnaeus, 1758), but somewhat triangulate in *Musculus discors*. Other glands emit a cement-like secretion into the sucker which forms the adhesive disc at the point of attachment of the thread. To fix a thread the foot extends to the object of attachment, cements the adhesive disc in place, then opens its groove, allowing sea water to enter and harden the white, transparent thread. To see a newly produced thread is not easy because of its transparency, but a bright light shined over an area where the foot has been observed at work will pick up a thread by its reflection. In time, chemical reaction causes the thread to darken; the color becomes light yellow the first day and changes later to progressively darker shades of brown. The threads of *Musculus* are thin and flexible, unlike the thick, stiff ones of *Mytilus*.

The nest is composed of a soft, flexible network of threads which may be likened to a hollow ball of twine. The threads, however, all emanate from a single point, the byssal aperture; and it is only at this point that the animal is attached to its nest, for none of the threads is ever attached to the shell itself. Thus the animal is suspended within the nest, in a manner allowing freedom of movement when opening the valves during feeding and respiration. The animal controls the opening of the nest by the action of the byssal retractor and the two adductor muscles of the shell. When these three muscles are relaxed and the valves open, the byssal aperture becomes situated nearer the shell edges. This extension of the byssal attachment point relieves the tension on the threads and allows them to separate, forming an oval aperture in the posterior-ventral region through which the siphons protrude. When fully extended, the valves open to a considerably wider angle than those of the unprotected species of the mytilids we have observed. Closing of the nest aperture is accomplished by simultaneous contraction of the adductor muscles and of the byssal retractor muscle. As a result, the threads over the ventral margin of the shell are drawn into the mantle cavity; this causes the remaining portion of the nest to be brought into closer contact with the shell, completely hiding it.

Several specimens were observed in the process of nest building and all proceeded in the same fashion. They attached themselves to some object so that they were free of the bottom and could wrap threads completely around themselves in all directions. The specimen described here (Plate 10, Figures 1 and 2) first attached itself high on the side of the aquarium with the right valve towards the glass and the ventral margin uppermost. The first threads attached were directly above the shell and the next were placed in front and behind it. Then the very extensible foot reached out and over the left valve to attach threads on the glass below it. Once these initial "guy ropes" had been put in place, the animal proceeded to strengthen its position by producing several series of threads. Each series was composed of 5 to 12 threads arranged in straight lines. The first series was placed directly above the shell, while others occupied various points around the periphery until 40 or more separate threads had been produced. After this the animal extended its foot around the left valve of the shell and attached threads to those already produced on the opposite side. The first of these threads were placed directly around the central part of the shell,

Explanation of Plate 9

Musculus discors Linnaeus, 1767

Figure 1: Specimen removed from the nest, lying on the right valve and partially opened, showing the incurrent (left) and excurrent siphons (about 4 x) Figure 2: Specimen with foot extended and the tip appressed against the side of the aquarium. Note the byssal groove extending the length of the posterior surface and terminating in the sucker near the tip (about 4 x)

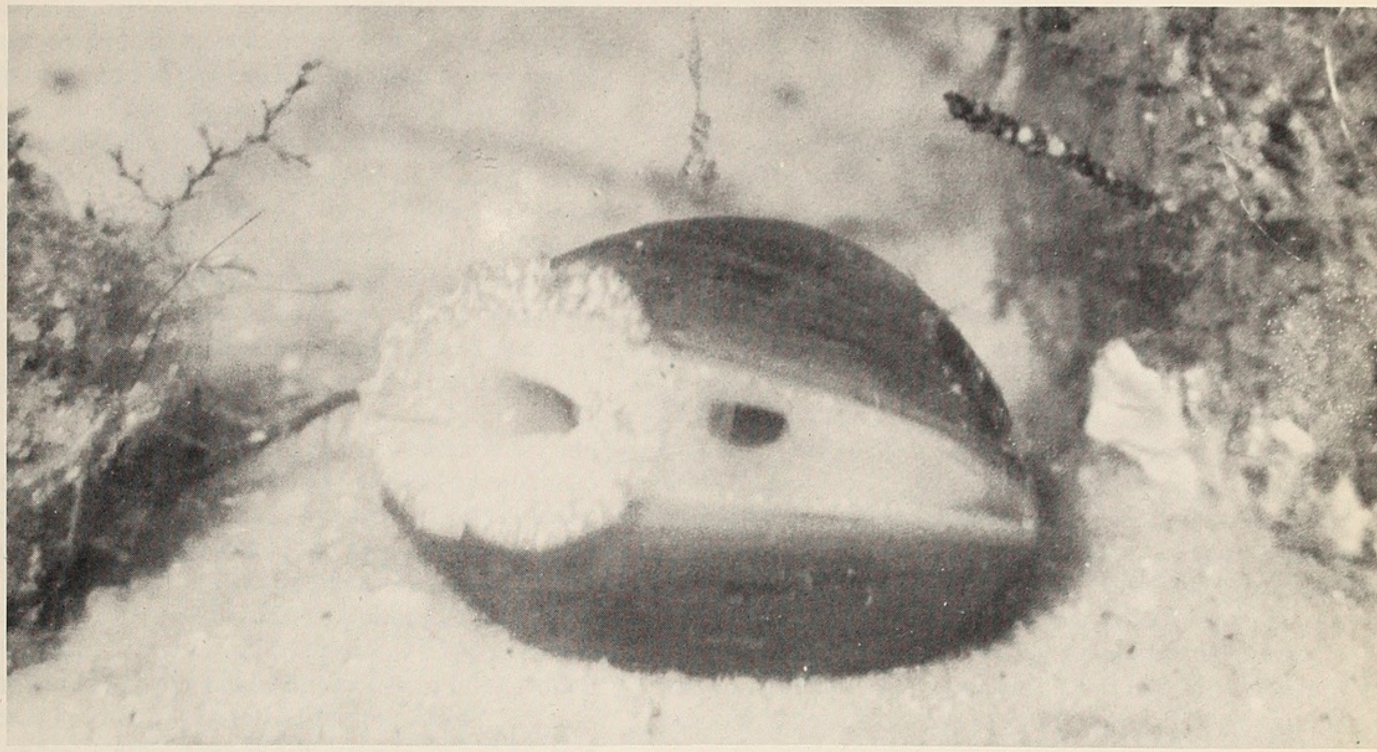

Figure 1

Figure 2

but thereafter they were wrapped diagonally or centrally about the shell. During this stage the remarkable agility and extensibility of the foot were most noticeable. It was also noticed that the foot always extended over the left valve and around itself, but never went in the opposite direction between the right valve and the glass except for purposes of strengthening its position of attachment.

As the nest is being produced bits of mucus and detritus collect between the threads which tend to mat the whole together. Literally thousands of threads are laid down before the nest is completely and securely matted together. After the nest is compact and well established, the animal occasionally passes its foot over and around stationary organisms which have attached to the nest, incorporating these in the outer fringes of the nest (Plate 11, Figures 1 and 2).

One animal, although disturbed intermittently for observational purposes, produced 300 to 400 threads in 8 days. Another, left undisturbed for a period of 2 weeks, had constructed a rather complete but loose nest of perhaps 1000 threads. A third specimen, observed after it had put out 5 or 6 threads, added another 24 strands in the next 2 days, 50 or 60 more during the succeeding 2 days, and over 100 the following 2 days, totaling about 200 threads in a week (Plate 10, Figures 1 and 2).

The animal works sporadically at weaving. The foot will attach several threads industriously and then retire for an indefinite period. Hours may pass before the foot is observed at work again. One animal was seen applying the tip of the foot to the glass side of an aquarium. The spot was marked on the outside of the glass, the slight jar causing the foot to retire. Twenty minutes later, six more adhesive discs, lined in a row, were noticed beside the marked one.

During the early stages of nest building mucus is produced by the mantle glands. As the threads come in contact with the mucus small globules are picked up, collecting like beads on the threads and aiding in the accumulation of adherent detritus, all of which give texture to the partially built nest (Plate 10, Figure 1).

In the field, the size of the smallest specimen of *Musculus discors* which we observed encased completely in its own nest was 8.1 mm. However, specimens up to 18.0 mm were occasionally without nests, but usually specimens over 15.0 mm had at least a rudimentary covering about themselves, and some were already housed in fairly elaborate capsules.

Adult specimens of *Musculus discors* lay egg-strings inside their nests where the embryos develop without any pelagic stage (see Thorson, 1935; MacGinitie, 1955; and Ockelmann, 1958 for further details). The young postlarvae remain in the nest near the edge of the adult shell, feeding from the currents produced by the parent. Even larger juveniles are found close to the siphonal area of the parent still clinging in the outer fringes of the nest. It is not unusual to see several small specimens drawn into the mantle cavity of the parent along with the threads to which they are attached when the parent contracts its byssal muscles while closing its valves. According to Suter (1913), a number of specimens of *Modiolaria* [=*Musculus*] *impacta* (Hermann, 1782) are usually found in the same nest. Cohabitation of offspring in the nests of their parents is one plausible interpretation of this communal relationship.

Thorson (1935) illustrated the East Greenland form of *Musculus discors* which had drawn together blades of *Fucus* or *Laminaria* by means of byssal threads as part of its encasement. This was reported also for *Modiolaria* [=*Musculus*] *marmorata* (Forbes, 1833) by Jeffreys (1836); incidentally, both Robertson (1897) and Gilchrist (1897) mentioned this very phenomenon for *Lima hians*: ". . .nest found with its occupant securely lodged in the folded frond of a sea weed." We have not seen this type of nest construction in *M. discors,* perhaps only because the area in which we found the species did not include appropriate sea weed among its biota. All the specimens we have observed, however, make nests in natural crevices when possible, attaching threads loosely to various places on the substrate before fixing threads about themselves.

NEST BUILDING IN *LIMA*

The nests of several species of *Lima* have been described by a number of authors. Gilchrist (1897) observed specimens of *Lima hians* (Gmelin, 1791) held in aquaria, and reported the process of nest building for this species. In essence, *L. hians* and presumably other nest building *Lima* construct nests by attaching byssal threads to available fragments of shell, stone, and other debris. It does this by applying the tip of the foot to some object lying nearby, to which it attaches and draws off a fine thread. This process continues, and threads are attached repeatedly to and about nearby fragments. Gradually the nest is bound together by a constant repetition of this process. The internal feltwork is smeared with a slimy secretion from the glandular tentacles which fringe the mantle edge.

Lima hians interlaces byssal threads with nullipores [coralline algae] if they are present (Robertson, 1897), but if building material is lacking, it is capable of making a latticework completely of byssal threads (Gilchrist, 1897). One specimen which Robertson presented with glass beads fabricated a beautiful nest out of them.

MacGinitie & MacGinitie (1949) mentioned that *Lima dehiscens* [of authors, *non* Conrad (=*hemphilli* Hertlein & Strong, 1946)] builds nests in cavities by attaching byssal threads to the surrounding surface in a