

## Some Aspects of the Biology, Population Dynamics, and Functional Morphology of *Musculista senhausia* Benson (Bivalvia, Mytilidae)<sup>1</sup>

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THE MYTILACEA with the Dreissenacea are perhaps the most specialized and most successful heteromyarian bivalves. Their similarity is probably not phylogenetic, as suggested by Purchon and Brown (1969), but is the result of convergence and the adoption of similar habits (Yonge and Campbell 1968). Thus, the European dreissenid *Dreissena polymorpha* and the Asian mytilid *Limnoperna fortunei* have both adopted a mode of life involving the colonization of hard surfaces in fresh waters (Morton 1969a in press).

The evolution of the heteromyarian condition in these bivalve lines probably proceeded from different isomyarian ancestors, with the neotenus retention of the larval byssus by the adult (Yonge 1962). This process, occurring in shallow coastal waters, must have enabled the ancestors of modern-day species initially to colonize the intertidal zone. Here the Mytilacea have been extremely successful and inhabit rocky shores the world over. Other mytilids may be found sublittorally, e.g., *Crenella* (Soot-Ryen 1955); in estuaries, e.g., *Xenostrobus* (Wilson 1967); in fresh waters, e.g., *Limnoperna* (Morton, in press); and even as highly specialized commensals, e.g., *Fungiacava* (Goreau et al. 1969). The Dreissenacea by contrast have not undergone this extensive adaptive radiation and are restricted to estuaries, e.g., *Congeria* (Wolff 1969) and fresh waters, e.g., *Dreissena* (Morton 1969a). Within their spheres of influence, however, both of these bivalve lines cause problems as fouling organisms, e.g., *Dreissena* (Morton 1969c) and *Mytilus* (Haderlie 1968).

In Asia *Musculista senhausia* Benson is also a fouling organism (Kawahara 1961) and has been introduced into the United States (Smith 1944, Hanna 1966). In China the species serves as a source of food and attempts have been made to culture them artificially (Cheung et al. 1962). Little information, however, is available in the published literature on the biology of this animal. Accordingly, a study has been undertaken of the functional morphology of the animal and the biology and population dynamics of a colony occurring in Tai Tam Bay, Hong Kong. The results of this investigation are reported here.

### DISTRIBUTION AND HABITS

*Musculista senhausia* forms large colonies in intertidal mud flats in many parts of the Far East. The type locality is Chusan, China. Cheung et al. (1962) reported it as being of very wide distribution in the western Pacific and recorded it from the South China Sea, the East China Sea, the Yellow Sea, and the Sea of Japan. It has been reported from Japan and Singapore by Kira (1961) and Chuang (1961), respectively.

In Tai Tam Bay, Hong Kong, the animal was found in a dense colony at around mid-tide level in numbers of up to 2,500/m<sup>2</sup>. The animal lies buried vertically in the mud, anchored in position by a well-developed byssus. The byssus is also woven into a nest in which the animal is almost completely enclosed (Fig. 1). Such a habit is unusual in the Bivalvia, although it occurs in a few other mytilid genera such as *Modiolus* and *Amygdalum* (Soot-Ryen 1955). The process of nest building in *Musculus* and *Lima* has been reported upon by Merrill and Turner (1963). The similarity of the nest of *Musculista* to that of *Musculus* suggests that

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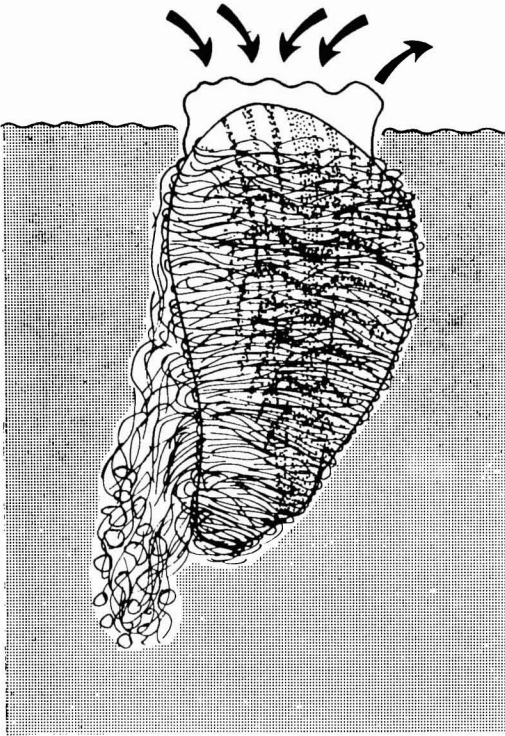


FIG. 1. *Musculista senhausia*. A diagrammatic representation of the animal in its nest in the mud. The positions of the inhalant and exhalant currents are also indicated.

they are constructed in a similar manner. The byssal threads are not attached to the shell but initially to sand grains, thereby forming an anchor. Thereafter, further byssal threads are wrapped around the shell and attached to sand grains, thereby forming the nest itself. Unlike the nest of *Musculus* (Merrill and Turner 1963), that of *Musculista* has a permanent posterior aperture.

The shores of Tai Tam are characteristically composed of coarse sand. A few centimeters below the colony a similar coarse sand is found. Only the surface material is composed of fine mud. There was no evidence of empty shells of past generations of *Musculista*, either bound up in the colony or in the underlying sand. The colony was probably a newly formed one and mucus-bound feces and pseudofeces produced by the colony were likely responsible for the creation of the mud flat. The byssal nest

serves as a matrix stabilizing the particles.

In Hong Kong the same species has colonized wooden test panels suspended 3 to 4 meters in the sea. Such animals did not build a nest as do their littoral counterparts. Significantly, Hanna (1966) found specimens with no nests living attached to pilings in San Francisco Bay. Furthermore, the related *Musculus discors* has been reported to be an intertidal species by Tebble (1966), whereas Merrill and Turner (1963) have reported it as living sublittorally.

#### FUNCTIONAL MORPHOLOGY

##### *Shell and Ligament*

The shell of *Musculista senhausia* (Fig. 2) is equivalve and heteromyarian. It is a dull olive green in color but above the umbonal keel is delicately patterned with 15 to 16 radiating brown stripes, originating at the umbo. One of the central stripes is typically thicker than the others. Irregular vertical bands of brown pigment also pattern the shell. Internally the same patterning can be distinguished. The blue-white nacre of the interior is uniformly distributed.

The outer periostracal layer of the shell is smooth, shiny, and thin. The umbones are subterminal and the dorsal ligamental margin is straight or at most only slightly curved. The ventral margin of the shell is slightly concave. The anterior region of the shell is somewhat inflated, rounded, and distinctly crenulate. There are no hinge teeth and no byssal notch.

The internal opisthodontic ligament (Fig. 2B, L) commences anterior to a number of weak crenulations reminiscent of the much more pronounced crenulations of *Septifer* (Yonge and Campbell 1968). The ligament is composed of two layers with similar staining reactions to that of *Mytilus edulis* (Trueman 1950, Beedham 1958). The outer layer stains red and the inner layer blue with both Mallory's triple stain and Masson's trichrome. Other mytilids—for example, *Modiolus*, *Lithophaga* (Yonge 1955), *Septifer* (Yonge and Campbell 1968), and *Limnoperna* (Morton, in press)—also pos-

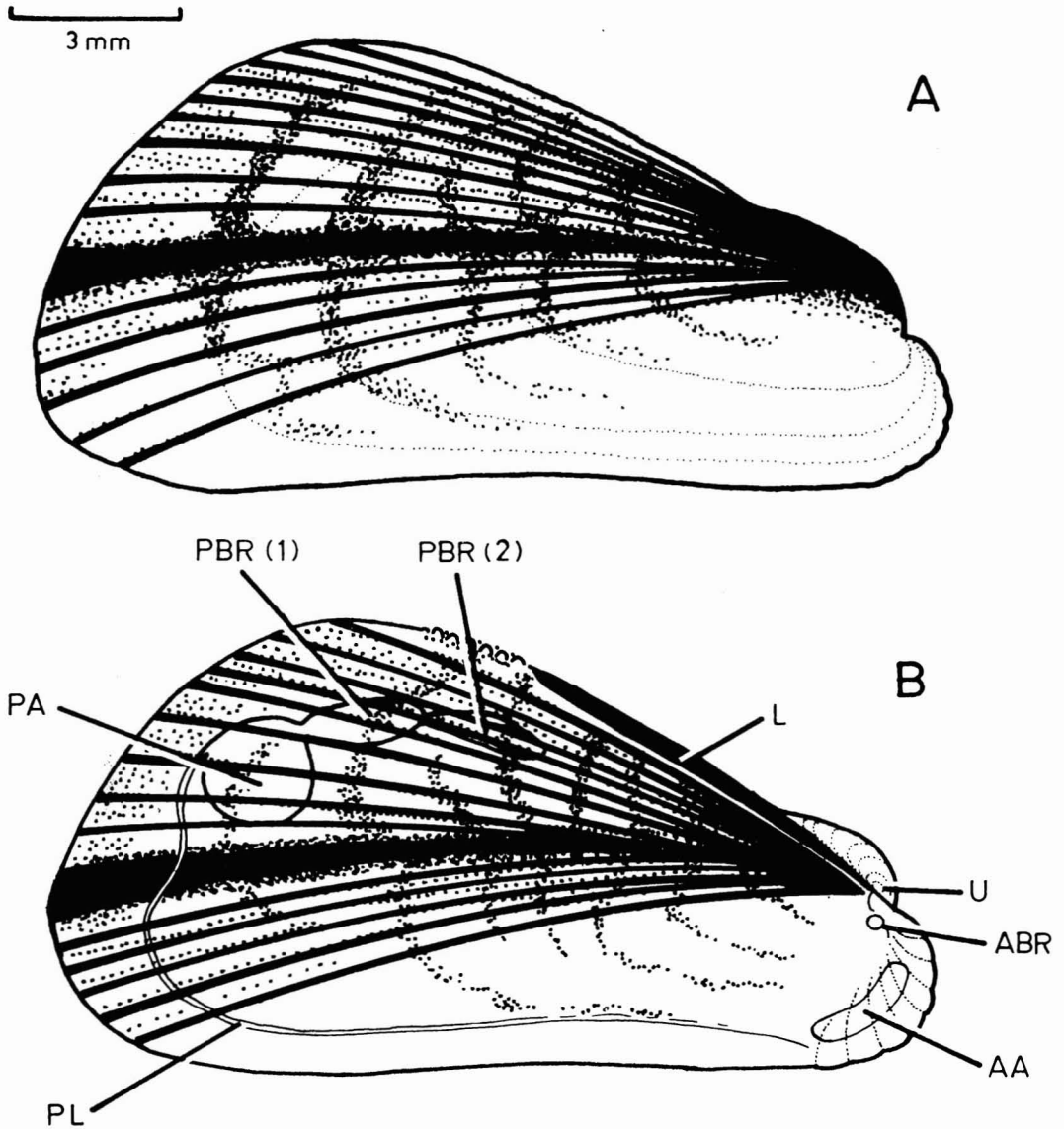


FIG. 2. *Musculista senhausia*. External and internal views of A, the right shell valve and B, the left shell valve, respectively.

ABBREVIATIONS USED IN FIGS. 2, 4, 5, 6, AND 7: A, a cell layer of style sac; AA, anterior adductor muscle; ABR, anterior byssal retractor muscle; AP, appendix; AU, auricle; B, byssus; B<sub>1</sub>, B<sub>1</sub> cell layer (minor typhlosole) of style sac; BG, byssal gland; BS, branchial septum; C, C cell layer of style sac; CI, cilia; CS, crystalline style; D, D cell layer of style sac; DD, digestive diverticula; DDD 1-5, ducts of the digestive diverticula opening into the stomach; DH, dorsal hood; DHT, dorsal hood tract; DS, dorsal septum; ES, exhalant siphon; F, foot; FC, food-sorting cecum; GS, gastric shield; GU, gutter of style sac; IA, inhalant aperture; ID, inner demibranch; IG, intestinal groove of major typhlosole; IP, inner labial palp; L, ligament; LP, left pouch; LT, left duct tract; MF, point of ventral mantle fusion; MG, midgut; MIG, intestinal groove of minor typhlosole; MM, mantle margin; MT, minor typhlosole; O, oesophagus; OD, outer demibranch; OP, outer labial palp; OV, ovary; PA, posterior adductor muscle; PBR (1) (2), posterior byssal retractor muscles; PL, pallial line; PPR, posterior pedal retractor muscle; R, rectum; RP, right pouch; RT, right duct tract; SP, sensory papillae; SS, style sac; T, major typhlosole; U, umbo; US, unsolidified style material; V, ventricle.

sess a ligament with a similar structure; it is significant that in all of these genera and in *Musculista senhausia* the periostracum extends over the ligament. Such an arrangement must, therefore, be typical of the Mytilacea in general.

The overall dimensions of the shell are regular for the population of *M. senhausia* sampled from Tai Tam Bay, a fact which is most clearly demonstrated by the ratio of width : height : length, which is:  $1 : 1.28 \pm 0.15 : 2.65 \pm 0.35$ . The ratios of shell width : length, shell height : length and shell width : height have been calculated as being  $0.38 \pm 0.04$ ,  $0.49 \pm 0.04$ , and  $0.78 \pm 0.08$ , respectively.

The shell of *M. Senhausia* is thin as compared with a number of other Hong Kong mytilids from a variety of habitats (Table 1). In relative terms the shell is only one-half the thickness of *Limnoperna fortunei*, an inhabitant of fresh waters, and only one-quarter of the thickness of *Septifer bilocularis*, an inhabitant of exposed rocky shores.

### Mantle

Mantle fusions are of the inner folds only and, thus, are of type A (Yonge 1957). Mantle fusions occur dorsally above the exhalant siphon and between the exhalant siphon and the inhalant aperture. The mantle also fuses anteroventrally and here an elongate adductor muscle (AA) links the two valves.

The outer mantle fold is small and the periostracum that is secreted by the inner surface of the outer mantle fold is composed

of three layers. The outer layer achieves a thickness of  $7.5 \mu$  and stains pink in Mallory's triple stain and Masson's trichrome. The middle layer is only  $5 \mu$  in thickness and is composed of a yellowish substance that is unaffected by the routine stains used in this study. An inner laminated layer ultimately achieves a thickness of  $25 \mu$  and stains blue with Masson's and Mallory's stains. The structure of the periostracum and of the epithelium that secretes the component layers bears a close similarity to those possessed by *Mytilus* (Beedham 1958) and *Limnoperna* (Morton, in press).

The dorsal region of each mantle lobe contains, as in other mytilids, much of the gonadial tissue. The sexes are separate, and spawning in the population inhabiting Tai Tam Bay occurs from January to March or April. Spat were first observed in the population in mid-January (Fig. 3). In northern China the species breeds in July and August (Cheung et al. 1962).

### Siphons

Only the siphons protrude through the mud to the water above (Fig. 1). The exhalant siphon (Fig. 4, ES) is formed by tissue fusion between the inner mantle folds only, this being type A (ii) (Yonge 1957). The inhalant aperture (IA) is not separated from the pedal/byssal aperture by mantle fusions and thus cannot be regarded as a siphon. The exhalant siphon is devoid of tentacles, though the inhalant aperture bears on each lobe a number of somewhat branched papil-

TABLE 1  
A COMPARISON OF THE THICKNESSES OF THE SHELLS OF FOUR SPECIES  
OF HONG KONG MYTILIDS

SPECIES	MAXIMUM RECORDED SHELL LENGTH (MM)	MAXIMUM SHELL THICKNESS (MM)	RATIO OF SHELL THICKNESS : SHELL LENGTH (%)
<i>Musculista senhausia</i> Benson	28	0.25	0.97
<i>Limnoperna fortunei</i> (Dunker)	37	0.65	1.70
<i>Brachidontes atratus</i> Lischke	16	0.35	2.27
<i>Septifer bilocularis</i> Linnaeus	58	2.05	3.53

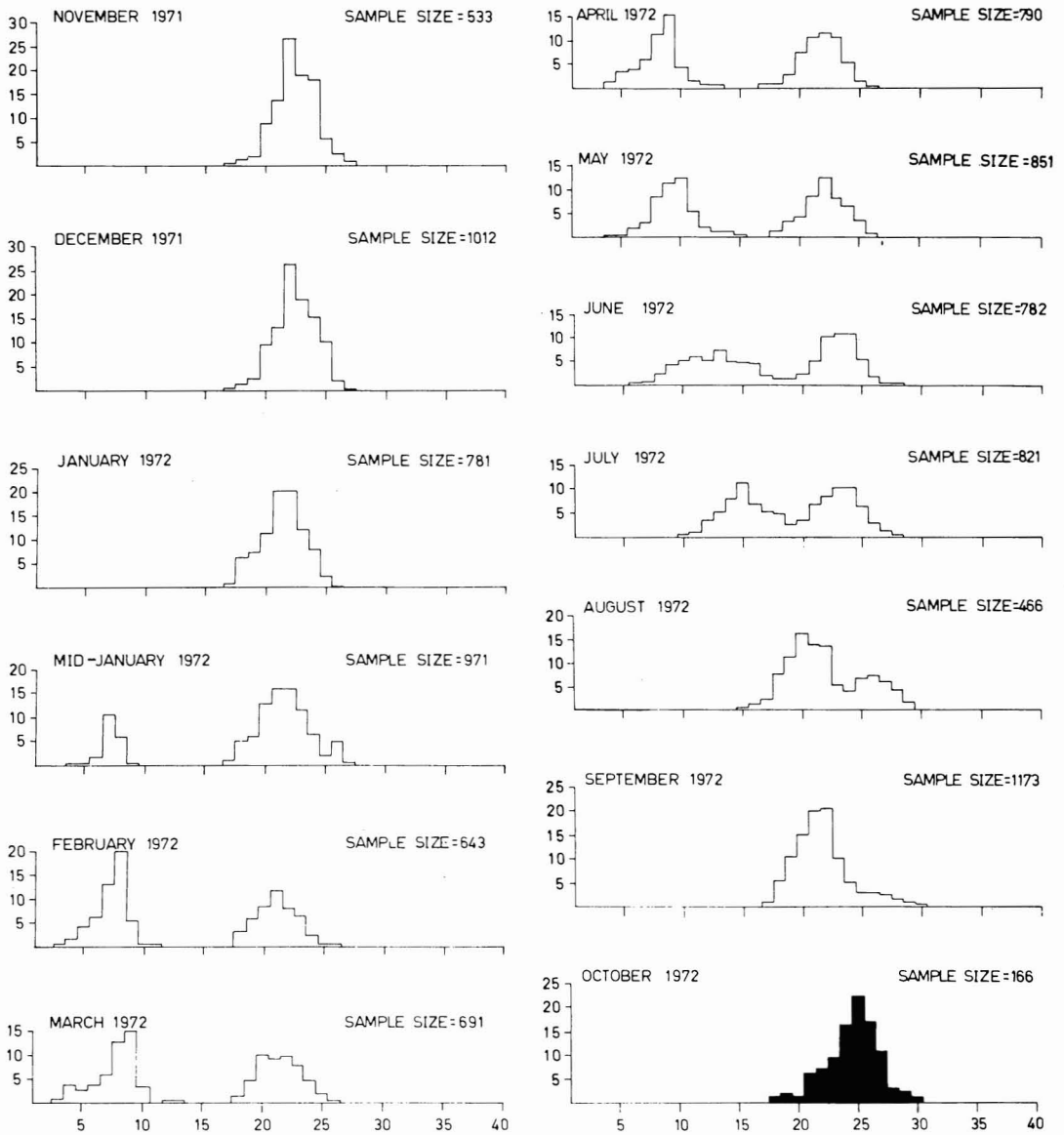


FIG. 3. Length-frequency histograms showing the composition of monthly samples of the population of *Musculista senhausia* at Tai Tam Bay. Open histograms represent live animals, black histograms empty shells. The x axis represents shell length in millimeters; the y axis represents the number of animals of a given size expressed as a percentage of the total sample.

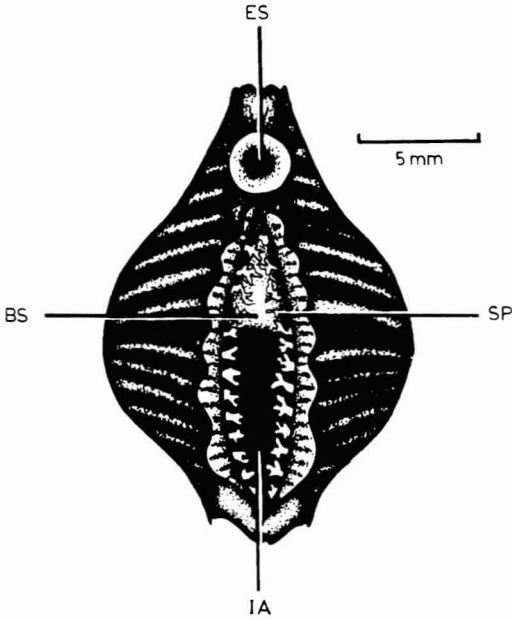


FIG. 4. *Musculista senhausia*. A posterior view of the animal when actively filtering clean seawater. (See legend for Fig. 2 for abbreviations.)

lae (SP). Each mantle lobe is cream colored and patterned by radiating brown bands with small patches of white pigment. This is particularly noticeable around the inhalant aperture. A large branchial septum (BS) restricts the size of the inhalant aperture and (Fig. 5, BS) connects the ctenidia (ID, OD) to the mantle at the point of fusion separating the exhalant siphon from the inhalant aperture and, thus, the suprabranchial from the infrabranchial chambers.

*Musculature*

The anterior adductor muscle (Fig. 5, AA) is relatively large and elongate and is located on the anteroventral floor of the shell valves. It is thus in a similar position to that of *Limnoperna* (Morton, in press), *Xenostrobus* (Wilson 1967), and *Mytilus* (White 1937). The anterior byssal retractor muscles (ABR) are very small and originate on the anterodorsal roof of the shell valve just underneath the umbo (U). The posterior adductor muscle (PA) is approximately

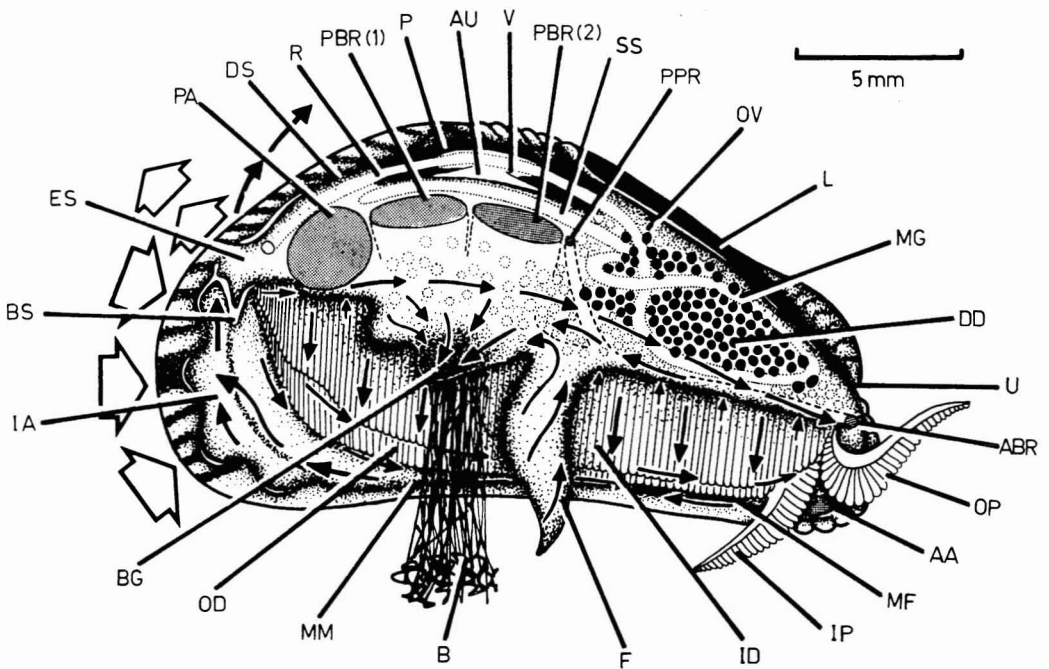


FIG. 5. *Musculista senhausia*. The organs of the mantle cavity. The right shell valve, mantle lobe ctenidium, and labial palps have been removed. (See legend for Fig. 2 for abbreviations.)



twice the size of the anterior adductor muscle and is located posterodorsally. The posterior byssal retractor muscle is large and is divided into two component units (PBR[1], PBR[2]) as in *Limnoperna* (Morton, in press) and *Xenostrobus inconstans* (Wilson 1967). There is a small posterior pedal retractor (PPR).

#### *Ciliary Currents of the Mantle, Visceral Mass, and Foot*

The ciliary currents of the mantle, visceral mass, and foot are all rejectory in nature. Those of the mantle pass unwanted material posteriorly to be ejected via the inhalant aperture (Fig. 5, IA). Such material is not ejected by the rapid phasic adduction of the adductor muscles as in many eulamellibranchs but by cilia passing it dorsally to be finally ejected by the outward flow of water from the exhalant siphon (ES). In this respect *Musculista senhausia* is very similar to *Limnoperna* (Morton, in press) and *Adula* (Fankboner 1971).

The ciliary currents of the visceral mass similarly pass unwanted material posteriorly, where it accumulates at a point immediately posterior to the byssal gland (BG). From this point it falls on to the mantle for rejection by the mantle cilia.

The foot (F) is long, lanceolate, and very active. The ciliary currents on the surface of the foot pass material dorsally. The foot constructs the nest.

#### *Ctenidia and Labial Palps*

The ctenidia comprise two somewhat subequal demibranchs of which the outer (Fig. 5, OD) is the longer. They are not as long as those of *Limnoperna* (Morton, in press). The ctenidia are flat, homorhabdic, and filibranchiate; and at their dorsal edges the ascending lamellae of both the inner and outer demibranchs are attached to the visceral mass and to the junction of the visceral mass and mantle, respectively, by ciliary fusions. Filamentary cohesion is achieved, as in all mytilids, by ciliary discs. The ciliary currents of the ctenidia are of type B(1) (Atkins 1937), in which acceptance tracts lie in

the ventral marginal food grooves of both demibranchs, the ctenidial axis, and at the junctions of the dorsal edges of the ascending lamellae of the inner and outer demibranchs.

The ctenidial/labial palp junction is of type I (Stasek 1963), and the mechanism by which material arriving at the ctenidial termini of the food grooves is sorted is essentially the same as that described by Morton (in press) for *Limnoperna*. In *Limnoperna*, however, the anterior filaments of the inner demibranch are shorter than are those of the outer demibranch. In *Musculista* the filaments of the outer demibranch are the shorter. However, this modification fulfills the same function in both species. Material arriving at the labial palps on the crests of both ventral marginal food grooves is thus presented to the sorting surfaces of both labial palps. Such a modification thereby dramatically increases the sorting potential of the labial palps.

As noted by Fankboner (1971) for *Adula*, the outer demibranch of *Musculista senhausia* is some 4 to 5 filaments shorter anteriorly than is the inner demibranch. This adaptation, apparently characteristic of all mytilids, further enhances the sorting mechanism described above.

The labial palps of *M. senhausia* are comparatively large. Other burrowing species living in soft mud, such as members of the Tellinacea (Yonge 1949), also possess large labial palps. The ciliary currents of the labial palps bear a close resemblance to those of *Adula* (Fankboner 1971) and thus can be considered to be of the typical mytilid type.

The lips of the mouth are large and fleshy; they possess ciliary currents similar to those of *Dreissena polymorpha* (Morton 1969a) and serve a rejectory function. They can be classified as "simple" (Bernard 1972).

#### *Alimentary Canal*

The stomach is located under the anterodorsal margin of the shell and is surrounded by the dark digestive diverticula (Fig. 5, DD).

The oesophagus enters at the anterior end of the stomach, whilst from the posterior end arises the midgut (MG) and a separate style sac (SS). The style sac passes backward between the posterior byssal retractor muscles (PBR [1] [2]) and terminates dorsal to the posterior adductor muscle (PA). The midgut does not, as it does in other mytilids, e.g., *Mytilus* (White 1937) and *Limnoperna* (Morton, in press), pass between the byssal retractors conjoined to the style sac. Before reaching them the midgut turns upon itself, loops on the right side of the body, passes under the posterior edge of the stomach, and then penetrates the ventricle (V) of the heart, extending posteriorly as the rectum (R) and terminating in an anus posterior to the posterior adductor muscle.

The style sac when seen in transverse section (Fig. 6) is very different from that of the typical mytilid as exemplified by *Mytilus*

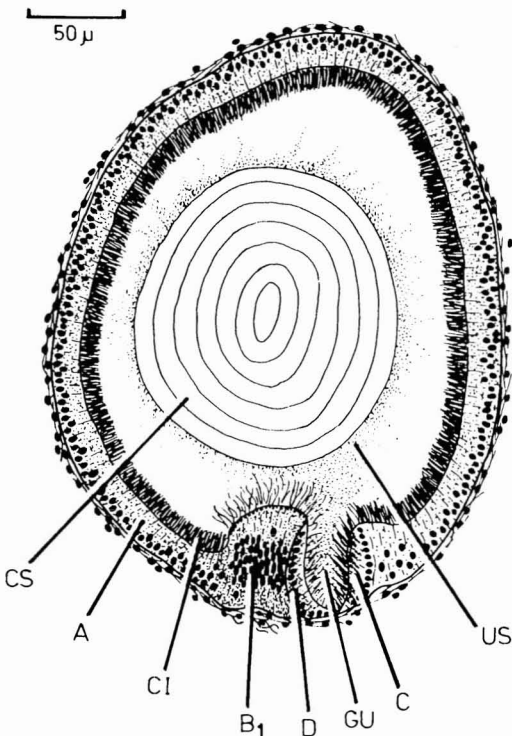


FIG. 6. *Musculista senhausia*. A transverse section through the style sac with crystalline style showing the distribution of the different epithelia. (See legend for Fig. 2 for abbreviations.)

*Galloprovincialis* (Giusti 1971). In *Mytilus* the style sac and midgut are conjoined but in *Musculista senhausia* the style sac is separated by a fusion of the minor typhlosole with the epithelium of the midgut. The major typhlosole of the stomach passes directly into the midgut. Such an arrangement results in a style sac with a structure that is similar to, but convergent with, the separate style sac of many of the Eulamellibranchia, e.g., *Dreissena polymorpha* (Morton 1969a). Kato and Kubomura (1954) have described the structure of various bivalve style sacs and recognize that the epithelium constituting the sac is divisible into a number of zones which they have termed A, B, and C. A further zone, D, was recognized by Morton (1969a) and regarded as the secretory region of the major typhlosole. In *Musculista senhausia* the same zones can be recognized, although because the typhlosole is the minor typhlosole the term B<sub>1</sub> has been used. The cells of the A cell layer are 25  $\mu$  tall and possess a dense ciliary border of length 15  $\mu$ . The cells of the B<sub>1</sub> cell layer are 70  $\mu$  tall with a somewhat less dense and shorter ciliary border between 12 to 14  $\mu$  tall. The cells of the C cell layer are 20  $\mu$  tall with short (5  $\mu$ ) cilia arranged in distinct groups. Internally the ciliary rootlets are discernible. The cells of the D cell layer are 12  $\mu$  tall and possess cilia 10  $\mu$  long.

The stomach of *M. senhausia* (Fig. 7) is elongate and bears a close resemblance to the stomachs of other mytilids, e.g., *Lithophaga* (Purchon 1957, Dinamani 1967), *Mytilus* (Graham 1949, Reid 1965), *Perna* (Dinamani 1967), *Adula* (Frankboner 1971), and *Limnoperna* (Morton, in press) and thus belongs to type III (the Gastrotriteia) and section I of the stomach types elucidated by Purchon (1957) and Dinamani (1967), respectively. The nomenclatural systems of Purchon (1957) and Reid (1965) are adopted here.

The structure of the stomach of various members of the Mytilacea seems to be remarkably constant and in this description only those points in which *Musculista senhausia* differs from the others will be commented upon. The stomach of *M. senhausia* possesses a distinct appendix, as



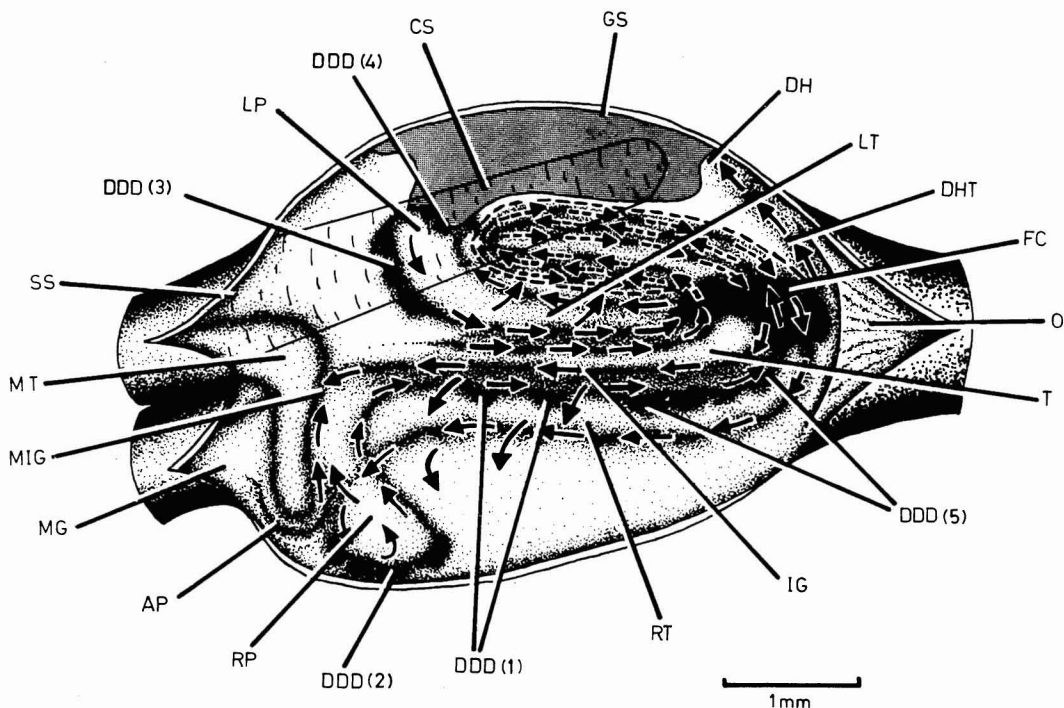


FIG. 7. *Musculista senhausia*. The interior of the stomach viewed from the right side after having been opened by a horizontal incision. The ciliary currents of the stomach (dark arrows) and of the food sorting cecum (broken arrows) are indicated. (See legend for Fig. 2 for abbreviations.)

does *Mytilus* (Reid 1965). In other mytilids this structure is not so well developed (Purchon 1957) and may be vestigial or absent. Lying next to the appendix are a group of ducts which communicate with the digestive diverticula (DDD 2) located at the termination of what Reid (1965) has termed the right duct tract (RT). On the left side of the stomach the left duct tract (LT) terminates in the ducts of the digestive diverticula (DDD 3, DDD 4) constituting the left pouch (LP) into which a spur of the gastric shield (GS) is located. It would seem reasonable to call the ducts on the right side of the body, the right pouch (RP). Associated with the right duct tract are other ducts of the digestive diverticula (DDD 1, DDD 5) which are also present in other mytilids, e.g., *Lithophaga* (Purchon 1957) and *Mytilus* (Reid 1965), although in *Adula* (Fankboner 1971) and *Limnoperna* (Morton, in press) some of these ducts (DDD 5) are to be found just inside the

food-sorting cecum. In *Musculista senhausia* the food-sorting cecum (FC) is small and terminates under the left pouch. In other mytilids it is long and in such genera, e.g., *Limnoperna* (Morton, in press), it is thought that a long cecum gives greater efficiency to the processes of collection and sorting of food material. The ciliary tracts of the food-sorting cecum are similar to those described for *Mytilus* (Reid 1965) and *Limnoperna* (Morton, in press).

#### POPULATION DYNAMICS

It has been shown earlier that the shell dimensions of *Musculista senhausia* are relatively constant. It was, therefore, decided to attempt to establish the number of age groupings within the population by means of a length-frequency histogram. Such histograms have been used successfully in the past for the analysis of populations of other molluscs, e.g., *Monodonta lineata* (Desai

1966), *Monacha cantiana* (Chatfield 1968), and *Dreissena polymorpha* (Morton 1969b). Accordingly, a large sample of animals was collected from Tai Tam Bay in early November 1971 and the shells were measured along their greatest length to the nearest 1 mm (Fig. 3). In November the population comprised a single age grouping of mean length 22 mm. Such a result finds accord with an earlier conclusion that the colony was a new one, this conclusion having been reached because of an absence of empty shells within the population. Similar samples of 500 to 1,000 animals collected in the first weeks of December 1971 and January 1972 showed a similar population structure. By mid-January 1972 a spatfall had occurred on the fringes of the existing colony and young individuals had already established themselves in nests. In subsequent monthly samples the new age group assumed increasing importance. In the summer of 1972 they grew very rapidly. Their parents grew at a slower rate. By September 1972 the primary adult age group had all but died out. This was evidenced by the occurrence of very many empty shells within the population. In early October 1972 it was found that the entire population had died. The shell of *Musculista senhousia* is extremely thin, so that even after such a short period of time most of the empty shells had been broken up. However, a small sample of intact valves was collected and when measured revealed that the young animals had died when 25 mm in mean length. Perhaps significantly the primary adult population had also died when approximately this size earlier in August to September.

By separately plotting the mean length of the age groups within the population (Fig. 8) as revealed by the length-frequency histogram, one can see that the primary adult age grouping did not grow between the months of November 1971 and May 1972. They did grow, by approximately 4 mm, between the months of June to August 1972 but then died out. By contrast the young age group achieved a high rate of growth in the early months of their life—January to March 1972—but slowed down somewhat in

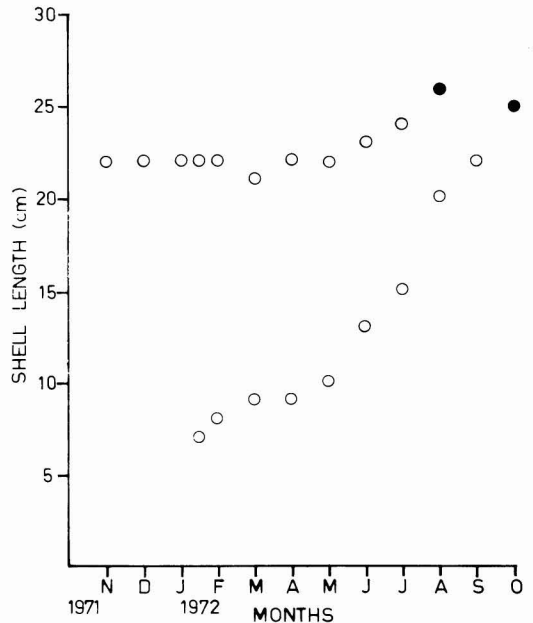


FIG. 8. Average length of each age group in the monthly samples of *Musculista senhousia*. Open circles indicate live animals, black circles empty shells.

March. However, in April the animals started growing again and from then until October 1972 when they had died they grew from 9 mm to 25 mm in length. They achieved in 9 months, i.e., from spatfall to death, a size which it had taken their parents—if one assumes that the time of spatfall for this generation was approximately the same as that of their offspring, i.e., January—20 months to achieve. The adult population had bred after approximately 1 year of life to produce the younger generation; the young generation, however, died before becoming sexually mature and this, together with the death of the primary generation, resulted in the death of the entire colony. This occurred in October 1972. By mid-October that area of beach previously occupied by the *M. senhousia* colony had virtually returned to an ecological condition similar to that of other neighboring unaffected beaches.

#### DISCUSSION

The Mytilacea exhibit a wide degree of adaptive radiation and the more successful

genera such as *Mytilus* and *Modiolus* are to be found on many of the shores the world over. This habit can be related to the evolution of the heteromyarian condition. Other mytilids such as *Crenella* are sublittoral and, judged by their shape, infaunal (Tebble 1966). Perhaps bridging the gap between these two extremes are such animals as *Musculus discors* and *Musculista senhausia*. *Musculus discors* is found living intertidally amongst algae (Tebble 1966), although Merrill and Turner (1963) found the same species living sublittorally. Similarly Hanna (1966) found *Musculista senhausia* without a nest living attached to pilings and this species has also been found attached to test blocks hung 3 to 4 meters in the sea in Hong Kong, again without a nest. Like *Musculus discors*, however, *Musculista senhausia* also occurs intertidally and forms large colonies in estuaries and sheltered bays. The colony inhabiting Tai Tam Bay, Hong Kong, formed a mat developed by the nest-building activities of the colony members. In so doing they also bound themselves to sand grains and, when in large enough numbers, to the nests of each other. The nest completely encloses the animal except for the posterior margin of the shell where the inhalant aperture and the exhalant siphon open to the water above. The gregarious habit of *M. senhausia* results in the colony accumulating around it a fine mud derived from the feces and pseudofeces. Cheung et al. (1962) have suggested that the formation and expansion of a colony dramatically alters the fauna of a sandy shore. This was true in Tai Tam Bay where the colony (Fig. 3) was judged to be newly formed. Typical sandy shore bivalves, e.g., *Cyclina orientalis*, *Paphia euglypta*, and more importantly *Anomalocardia squamosa*, apparently had been unable to compete with the growing *Musculista senhausia* colony. Only empty shells of these species were found. Cheung et al. (1962) report that the layer of *M. senhausia* effectively prevents other bivalves from projecting their siphons through to the water above.

The very wide distribution of this species (Cheung et al. 1962) and its occurrence in a

variety of both intertidal and sublittoral habitats would seem to suggest that it is an opportunist bivalve, settling whenever and wherever it can. Once settled, the animal relies upon the production of a large number of eggs (Cheung et al. 1962) and a rapid rate of growth to colonize quickly all available suitable sites.

In 1971 the colony comprised a single age grouping. A further spatfall, which occurred in January to April 1972, settled on the seaward periphery of the existing colony. Such a habit is almost certainly the way in which such colonies are enlarged. The second age group assumed increasing importance within the population during the course of 1972 and, after the adult age group had died out in August, were the only age group left. By October 1972, however, they too had died. The death of the colony is attributable to the extraordinarily fast rate of growth exhibited by the young generation in 1972, because both adults and young died before producing a further generation. Cheung et al. (1962) record the maximum shell length of animals they examined as 29 mm. Such a figure falls within the normal distribution pattern of the age groupings elucidated in this study as do the maximum figures for shell length of this species recorded by Hanna (1966).

*Musculista senhausia* shows a number of adaptations to its peculiar mode of life. Most important of these is the byssus which, as well as acting as an anchor as in more conventional heteromyarians such as the Pinidae (Yonge 1953), is also woven into an enclosing nest.

Other related mytilids also possess this habit: *Musculus* (Merrill and Turner 1963), *Modiolus*, and *Amygdalum* (Soot-Ryen 1955), as well as the unrelated *Lima hians*. In *Lima*, the nest serves a protective function. In *Musculus discors*, which has a thick shell, Merrill and Turner (1963) have suggested that the nest principally protects the eggs which are laid inside the nest. *Musculista senhausia* does not lay eggs within its nest; they are planktonic (Cheung et al. 1962). Compared with such species as *Septifer bilocularis* and *Brachidontes atratus*, *Musculista senhausia* has a very thin

shell (Table 1). The shell is also relatively much thinner than that of *Limnoperna fortunei*, an inhabitant of fresh waters where the calcium content is typically much lower than that of the sea. It would thus seem that the nest that *Musculista senhausia* weaves is essentially a protective device for the adult. The nest serves a subsidiary function in keeping sediment out of the mantle cavity and thus has contributed to the successful exploitation of the soft shore environment by this species. The organs of the mantle cavity are concerned with the processing of large currents of particulate material. As a consequence, the rejectory tracts are well developed. The branchial septum serves as a valve regulating the intake of material, whilst the labial palps and foot are large and the foot, as well as building the nest, also serves to keep the mantle cavity (and perhaps the nest) clean. The ctenidia are relatively small. *Musculista* is thus adapted in a similar manner to other lamellibranchs such as the Tellinacea (Yonge 1949) that are characteristically found in muddy habitats.

Though the stomach is of the typical mytilid type, it, too, is modified. The food-sorting cecum is small. In the Tellinacea, also, the sorting areas of the stomach are reduced (Yonge 1949, Purchon 1960). Also as in the Tellinacea there is a distinct stomach appendix. It would seem that the stomach is adapted to the rapid processing of an abundant food supply rather than with the sorting and abstraction of all available food material.

A major difference between *M. senhausia* and the other mytilids studied (e.g., by Dinamani 1967) is that in the former the style sac is separate from the midgut. In the conjoined style sac and midgut of the typical mytilid such as *Mytilus galloprovincialis* (Giusti 1971), both major and minor typhlosoles are present. In *Musculista senhausia* the major typhlosole passes into the midgut whilst the minor typhlosole penetrates the style sac. The style sac is thus similar to, but convergent with, the style sac of some eulamellibranchs such as *Dreissena polymorpha* (Morton 1969a). In this species the typhlosole of the style sac is a portion of the major typhlosole, whereas in

*Musculista senhausia* it is the minor typhlosole. In other respects the style sac is similar to that of *Dreissena*. The separate style sac serves to keep the large amounts of detrital material passing through the gut away from the style and thus prevents it from returning to the stomach.

*Musculista senhausia* possesses a number of characters that are intermediate between primitive and highly specialized mytilids. The anterior border of the shell is inflated and distinctly crenulate. Weak crenulations, as in *Septifer* (Yonge and Campbell 1968), are also present just posterior to the ligament. Such a condition would seem to be intermediate between the crenulated isomyarian shell of *Crenella* (Tebble 1961) and the noncrenulated extreme anisomyarian shell of more typical mytilids.

The anterior byssal retractor is small and is located almost directly under the umbo. Such a position is intermediate between the condition encountered in *Musculus discors* (Tebble 1961) where the anterior byssal retractor is located anteriorly and the condition in more extreme genera such as *Xenostrobus* (Wilson 1967) where the point of attachment of the muscle is on the posterior border of the shell. The umbo of *Musculista senhausia* is subterminal and thus represents a further example of the intermediate condition exhibited by this species with respect to the extremes seen in *Crenella* (Tebble 1966), *Mytilus* (White 1937), *Xenostrobus* (Wilson 1967), and *Septifer* (Yonge and Campbell 1968). In *Musculista senhausia* the posterior byssal retractor is divided into two blocks. This situation also exists in *Limnoperna* (Morton, in press) and in *Xenostrobus inconstans* (Wilson 1967). Such a development can perhaps be related to the elongation of the posterior border of the shell in the Mytilacea. Significantly, in *Mytilus edulis* (White 1937), which displays extreme heteromyarianism, the posterior byssal retractor is broken up into three units; whilst in *Modiolus* the posterior byssal retractor is divided into many more units (Yonge 1953).

Though in itself highly specialized *Musculista senhausia* may recall an intermediate condition in the evolution of the

heteromyarian condition in the Mytilacea. Significantly, the evolutionary steps envisaged as having occurred in the Dreissenacea (Morton 1970) find a number of parallels with the condition exhibited by *M. senhausia*. Because of the large pallial sinus to the shell, Morton (1970) has suggested that the fossil dreissenid *Dreissenomya aperta* was byssally attached and yet lived an infaunal life. The similarities that exist between *Dreissenomya* and *Musculista senhausia* are attributable to the independent evolution of the heteromyarian condition in these two bivalve phylogenies (Yonge and Campbell 1968). However, the occurrence of *Musculista senhausia* living in intertidal mud may attest to the similarity of the evolutionary process in the Dreissenacea and Mytilacea and perhaps points to some of the changes that have occurred in the evolution of the Mytilacea, namely, that the heteromyarian condition was evolved before the successful exploitation of rocky shores by this group.

#### SUMMARY

The mytilid *Musculista senhausia* Benson forms large colonies in intertidal mud flats in sheltered bays in the Far East.

*M. senhausia* is considered to be an opportunist bivalve with a high reproductive capacity, a fast rate of growth, and an ability to colonize other habitats such as hard sublittoral surfaces. When occurring intertidally it dramatically affects the ecology of the shore. The mud flat is created and maintained as a result of (1) the deposition of feces and pseudofeces and (2) the animals' habit of building a nest which stabilizes the surface mud.

The nest is woven from byssal threads and serves a number of functions: (1) it protects the very thin shell; (2) it prevents the entry of terrigenous material into the mantle cavity; and (3) it anchors the animal into the mud.

The animal also possesses a number of other morphological adaptations that suit it for an infaunal life. These are: (1) a large branchial septum acts as a valve controlling the inflow of large particles into the inhalant

aperture; (2) the ctenidia are relatively short; (3) the labial palps are large; (4) the food-sorting cecum of the stomach is small; and (5) the style sac is uniquely, for a mytilid, separate from the midgut.

Other anatomical characters, particularly of the shell, suggest that *M. senhausia* may recall a transitional stage in the evolution of the heteromyarian condition in the Mytilacea, and that the heteromyarian condition arose in the Mytilacea before the colonization of hard surfaces was achieved.

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