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THE UNIVERSITY OF ALBERTA

A NEW SPECIES OF *HAMINOEA* (MOLLUSCA: OPISTHOBRANCHIA): SYSTEMATICS, DEVELOPMENT, AND COMPARATIVE REPRODUCTIVE ENERGETICS.

by

(C) Glenys Dianne Gibson

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE OF
Master of Science

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

(FALL) (1987)

ISBN 0-315-40916-9

THE UNIVERSITY OF ALBERTA

RELEASE FORM

NAME OF AUTHOR: Glenys Dianne Gibson

TITLE OF THESIS: A NEW SPECIES OF *HAMINOEA* (MOLLUSCA: OPISTHOBRANCHIA): SYSTEMATICS, DEVELOPMENT, AND COMPARATIVE REPRODUCTIVE ENERGETICS.

DEGREE: Master of Science

YEAR THIS DEGREE GRANTED: 1987

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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled A NEW SPECIES OF *HAMINOEA* (MOLLUSCA: OPISTHOBRANCHIA): SYSTEMATICS, DEVELOPMENT, AND COMPARATIVE REPRODUCTIVE ENERGETICS submitted by Glenys Dianne Gibson in partial fulfilment of the requirements for the degree of Master of Science.

F. A. Chew
(Supervisor)

A. V. Spencer

Robert Burke

Date: 12 August 1987

ABSTRACT

Haminoea is a genus of shelled opisthobranch molluscs that is common in muddy bays worldwide. In this thesis, I describe a new species of *Haminoea*, *H. callidegenita*, based on diagnostic features selected through an analysis of morphological characters in the genus. In addition, I describe and compare the developments of *H. callidegenita* and the sympatric species, *H. vesicula*.

Taxonomic characters in *Haminoea* have not been well defined; therefore, most species are poorly known. Morphological features are compared both intra- and inter-specifically in three species of *Haminoea* from the Pacific Northwest: *H. callidegenita*, n. sp., *H. vesicula* Gould 1855, and *H. virescens* Sowerby 1833. Morphological descriptions in the literature were also compared in attempts to define diagnostic characters that are universal in the genus. Structures suggested as diagnostic are: external pigmentation, shape of the cephalic shield, Hancock's organ, the penial complex, and gizzard plate papillae. Historically cited characters, such as the shell and radular morphologies, are of limited value as they may vary intra-specifically.

Haminoea callidegenita n. sp. is found in Washington State, U.S.A.. They are reddish-brown with a deeply bifurcate cephalic shield. Additional diagnostic features are: tubular Hancock's organ, unilobular prostate, and the presence of pointed papillae on the medial ridges of the gizzard plates.

The development of *Haminoea callidegenita* is unusual in that both lecithotrophic veligers and juveniles hatch simultaneously from the same egg mass. The egg mass jelly is suggested as being influential in determining the veliger : juvenile ratio at hatching

through promotion of intra-capsular metamorphosis.

H. vesicula produces planktotrophic veligers with a lengthy pelagic period. *H. vesicula* has a much greater fecundity than does *H. callidegenita*, and *H. callidegenita* eggs contain more organic carbon. The annual life-cycles are compared between these two species.

This thesis makes two contributions to the biology of *Haminoea*. The first is a general review of *Haminoea* taxonomy and the definition of some diagnostic features. The second is the description and comparison of development and life-cycles of two sympatric species of *Haminoea* . One contribution relevant to opisthobranchs in general is the potential role of the egg mass jelly in determining the developmental stage at hatching.

ACKNOWLEDGEMENTS

I wish to thank my supervisor Dr. Fu-Shiang Chia for his support. The financial support and numerous travel opportunities which he [redacted] were invaluable to my research, but even more so were his helpful discussions and [redacted] enthusiasm. I also wish to thank my committee members, Drs. J. Holmes, A. Spencer, R. Burke for their advice, comments and criticisms. I also thank Dr. R. E. Peter, Chairman, Department of Zoology, University of Alberta, Dr. R. E. Foreman, Director, Bamfield Marine Station, and Dr. A. O. D. Willows, Director, Friday Harbor Laboratories for the provision of support and facilities. I gratefully acknowledge the staff at Bamfield Marine Station, where most of this research took place, and in particular Joan Glazier for her assistance and enthusiasm.

I am grateful to the following people who provided me with access to specimens: W. Dewey, Rock Point Oyster Company, Samish Bay, P. Scott, Santa Barbara Museum of Natural History, C. Hertz, San Diego Natural History Museum, K. Way, British Museum (Natural History), and Dr. R. Garthwaite, George M Gray Museum, Marine Biological Laboratory, Woods Hole. I sincerely thank Dr. T. Thompson, University of Bristol, for the use of his *Haminoea* collection, his advice, and his insight on cephalaspideans.

I thank R. Mandryk and G. Braybrook for technical assistance. Also R. Koss, whose advice and friendship is deeply appreciated. I also thank several researchers and graduate students for their technical

and not so technical advice: Drs. S. Rumrill and L. McEdward, P. Dunn, P. Marino, C. J. Gratto, N. McFadden, S. Hatfield, T. Turtle, M. Weiss. The companionship of Qian Peiyuan during field work and in the lab were greatly appreciated.

In conclusion, I wish to thank two people who have been instrumental in instigating my graduate career. First, Dr. S. Bleakney for instilling in me a deep-rooted affection and respect for opisthobranch molluscs. Finally, Dr. M. A. Gibson for encouraging and directing my appreciation and curiosity of how things live.

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CHAPTER 1

GENERAL INTRODUCTION.

The genus *Haminoea* (Opisthobranchia: Cephalaspidea) is characterized by an oblong body of which approximately $^2/_3$ is covered by a fragile shell, an elongate cephalic shield posterior to the head, and 3 pallial lobes (2 lateral, 1 posterior) partially covering the shell (Adams, 1855; Rudman, 1971a). This group of opisthobranchs typically inhabits the intertidal zones of muddy bays and lagoons, often in association with eelgrass beds. At least one species has been described from rocky intertidal areas (Morris *et al.*, 1980), and a few species are found subtidally on coral reefs (Heller and Thompson, 1983). Although feeding processes are not well understood in this genus, some species are believed to graze epiphytes, a trait which is probably widespread, if not universal, throughout the genus (Rudman, 1971b).

Since Leach's (1847) designation of the type for the genus, approximately 121 species of *Haminoea* have been described worldwide. As with most taxonomic malacology of the 19 th century, the majority of *Haminoea* species were described on the basis of shell characteristics only (Reeve, 1868; Pilsbry, 1893, 1917). Many species are still known only by the type descriptions. Attempts have been made to subdivide the genus based on shell characteristics (Pilsbry, 1917; Habe, 1952).

Recently, descriptions have been made on the morphology of the soft tissues of a few *Haminoea* species (Rudman, 1971 a and b; Thompson and Brown, 1976). However, descriptions are not available for a sufficient variety of species to indicate if these data will

support the subdivision of the genus, as proposed on the basis of shell characteristics. Also, the possibility of intra- and interpopulation variability in characters considered diagnostic has not been examined.

Although *Haminoea* species are widespread and often locally abundant, their biology is not well understood. Perhaps the most widely examined component has been embryology, of which comprehensive observations have been made of 3 species (Berrill, 1931; Usuki, 1966; Harrigon and Alkon, 1984), and egg mass descriptions made of another 4 species (Leonard, 1918; Richards, 1921, 1923; Ostergaard, 1950; Davis, 1967; Hurst, 1967).

The purpose of this study is to examine taxonomic problems within the genus *Haminoea* and to describe a new species, *H. callidegenita*. Also, *H. callidegenita* development will be described and compared with that of *H. vesicula* Gould.

A population of *Haminoea* was identified in Spencer's Spit, Lopez Island, Washington, by the late Professor R.L. Fernald of the University of Washington. Individuals from this population had a different pattern of development from that observed in individuals known to be *H. vesicula*, a sympatric and morphologically similar species. Closer examination revealed that not only was the Spencer's Spit population a distinct species, but that *Haminoea* taxonomy was in a state of disarray.

In Chapter 2, I evaluate *Haminoea* taxonomy, through an examination of characteristics considered important as diagnostic features in the genus. Species descriptions and subsequent species reports in the literature were reviewed and compared with my observations on 3 species of *Haminoea* found along the Pacific

Northeast coast (*H. vesicula* Gould, *H. virescens* Sowerby, and *H. callidegenita*, n.sp.). Features historically considered diagnostic are re-examined both inter- and intraspecifically, and new characteristics are suggested.

In Chapter 3, I use the diagnostic features examined in Chapter 2 to describe a new species of *Haminoea* , named *Haminoea callidegenita*, from Spencer's Spit, Lopez Island, Washington.

In Chapter 4, the development of *H. callidegenita* , n.sp., is described. In this species, the pattern of development is characteristic of other opisthobranchs (Thompson, 1958, 1967; Rao, 1961; Smith, 1967; Chia, 1971; Bridges, 1975; Switzer-Dunlap and Hadfield, 1977; Chia and Koss, 1978; Clark, *et al.*, 1979), with the exception of the developmental stage at hatching. From each *H. callidegenita* egg mass, some individuals hatch as pelagic larvae, whereas others metamorphose within the embryonic capsule and hatch as juveniles. Although temporal and spatial variability in patterns of larval development are not uncommon among opisthobranchs (Mileikovsky, 1971; Clark, *et al.* , 1979; Eyster, 1979; West, *et al.*, 1984), this is the first report of a species having 2 developmental stages hatching simultaneously from the same egg mass. The effects of 3 factors (temperature, oxygen, and egg mass jelly) were considered as potentially influencing the hatching stages are examined and discussed.

In Chapter 5, I continue to examine *Haminoea* development with a brief, descriptive account of development in the planktotrophic species, *H. vesicula* Gould, a species common in both the San Juan Islands, Washington, and the Barkley Sound, British Columbia.

In Chapter 6, I compare the developmental patterns in 2 species of *Haminoea* : *H. callidegenita* (lecithotrophic) and *H. vesicula* (planktotrophic). These 2 species co-exist in the same habitat, and are morphologically and, it appears, ecologically similar. Relative fecundity, energetic content of the eggs, population size structure, and length of the reproductive season are compared.

Concluding remarks of the thesis as a whole are given in Chapter 7.

This thesis was written in a format suitable for publication as separate reports, as the most efficient presentation of data on related, yet discrete lines of thought.

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CHAPTER 2

A TAXONOMIC REVIEW OF THE GENUS *HAMINOEA* LEACH (OPISTHOBRANCHIA: CEPHALASPIDEA: HAMINOEIDAE).

INTRODUCTION :

Haminoea is a genus of shelled opisthobranch molluscs with a worldwide distribution which are generally found intertidally in muddy lagoons and bays. Since the genus was introduced by Leach (*in* Gray, 1847), approximately 125 species have been described. Most type designations were based solely on shell descriptions and, for many *Haminoea* species, are currently the only descriptions available. This profusion of poorly- known species has created much confusion in the systematics of the genus.

A population of *Haminoea* was discovered in Spencer's Spit, Lopez Island, Washington, by the late Professor R. L. Fernald, and some of his graduate students. These *Haminoea* were considered unusual because they differed developmentally from individuals of the superficially similar sympatric species, *H. vesicula* Gould 1855. A study was undertaken to determine if the Spencer's Spit population was *H. vesicula* by comparing the morphologies of animals from the Spencer's Spit population with individuals known to be *H. vesicula* . Not only was the Spencer's Spit population distinct from *H. vesicula*, but a review of the literature indicated that it was an undescribed species.

In identifying and describing the Spencer's Spit population, I realized that revision is necessary in the genus *Haminoea* . Not only are the majority of type descriptions based only on shells, but many of the characters used appear to be unreliable.

In this chapter, diagnostic characters are introduced, including

a comparison of the descriptions available in the literature with my observations on 3 species of *Haminoea* found in the Pacific Northeast (*H. vesicula* Gould 1855, *H. virescens* Sowerby 1833, and *H. callidegenita*, n. sp.) in an attempt to isolate reliable characteristics that are diagnostic at the species level. In Chapter 3, these diagnostic characters are used in a description of a new species, *Haminoea callidegenita* , features of which are included in the present chapter for comparative purposes.

MATERIALS AND METHODS:

All of the known *Haminoea* species were reviewed through an examination of the literature. A morphological comparison was made between specimens of *Haminoea vesicula*, *H.virescens*, and *H.callidegenita* . Both fresh (7% MgCl anaesthetized) and fixed (10 % phosphate buffered formalin) specimens of *H. vesicula* and *H. callidegenita* , and fixed specimens only (10 % formalin with hexamene) in the case of *H. virescens* were used unless otherwise indicated. *H. vesicula* was collected from Grappler and Bamfield Inlets, Bamfield, British Columbia, and from False and Fisherman's Bays in the San Juan Islands, Washington. *H. callidegenita* , was collected from Spencer's Spit, Lopez Island, and from Rock Point, Samish Bay, Washington. Specimens of *H. virescens* were borrowed from the Santa Barbara Museum of Natural History, Santa Barbara, California (wet specimens; No. B3212, collected from Goleta, Coal Oil Point, California), and from the San Diego Society of Natural History, San Diego, California (shells; No. 29020, collected from Laguna Beach, California, No. 29021 from San Pedro, California, No. 2667 from Ocean Beach, California, and, No. 18880 from San Diego, California). Shells of *H. solitaria* Say 1822, an Atlantic species

included for comparative purposes, were borrowed from the Gray Museum (No. 10001 and 10004), Marine Biology Laboratory, Woods Hole, Massachusetts.

Sketches and measurements of morphological features (including Hancock's organ, the penis complex, gizzard plates, and shells) were made with a camera lucida. Each structure was examined in a minimum of 10 specimens for each population examined. Radulae from specimens fixed in 10 % formalin were prepared for examination by scanning electron microscopy by removing the investing tissue layers with 6 % sodium hypochlorite, followed by rinsing with distilled water, and air-drying onto stubs.

Gizzard plates were dissected from fresh specimens, rinsed in seawater followed by 15 s sonication, and then immediately fixed in 2.5 % glutaraldehyde in seawater, followed by 2 % osmium tetraoxide in Millonig's phosphate buffer. The gizzard plates of *H. virescens* had been previously fixed in formalin, then secondarily fixed in 2 % osmium tetraoxide (2 h). Further processing of gizzard plates from all 3 species consisted of dehydration to 70 % ethanol, re-sonication (15 s), then dehydration to amyl acetate, and critical point drying. Gizzard plates and radulae were examined with a stereoscan 100 at the University of Alberta.

Shell length and width were measured with a camera lucida in 30 specimens for each of 4 *Haminoea* species (*H. callidegenita, H. vesicula, H. virescens*, and *H. solitaria*). Measurements were taken at the points of maximum length and width of each shell.

RESULTS:

TYPE DESIGNATION AND SUBSEQUENT DESCRIPTIONS OF THE GENUS:

The genus *Haminoea* was introduced by Leach in his

" Classification of the British Mollusca " (*in* Gray, 1847). This manuscript was written in 1818, but not published until 1847 when, after Leach's death, Gray brought it into the literature. The delay in publication has produced some confusion, because in the interim Turton and Kingston (1830) referenced 2 species in the genus with the result that they have been considered as the original authorities by many authors (Abbott, 1954; MacPherson and Gabriel, 1962; Marcus and Marcus, 1967; Humfrey, 1975). Turton and Kingston (1830) did not describe the genus, nor did they refer to Leach's unpublished manuscript, or to any other previous references concerning the genus. They did, however, redescribe *H. navicula* DaCosta 1778 and *H. hydatis* Linneus 1758 from their original placement in the genus *Bulla* Klein. Leach (1847) included 4 species in *Haminoea* , but he did not describe or illustrate these species. The first description of the genus was provided by Adams (1855, p.557), based on Leach's (1847) designated type (*H. hydatis* Linneus 1758) and is as follows :

> Body oblong. Head broad, depressed, elongated, posteriorly bilobed; eyes sessile on the middle of the head. Mantle with the right or external part greatly dilated, thickened, truncated and extending beyond the shell. Foot short, subquadrate, with two large swimming lobes, which nearly cover the shell.
>
> Shell convolute, thin, horny, transversely grooved, destitute of columella or spire.

Pilsbry (1893) extended this description of the genus to include more detailed information regarding the specifics of shell morphology, and some information on the external characteristics of the animal, gizzard plates, and radulae within the genus *Haminoea* . He also reviewed the 43 species known at that time, and included shell descriptions, illustrations, and references. Since the genus was

first brought into the literature , approximately 121 species (Table 1) have been described worldwide, with at least 24 varieties (some considered as subspecies by subsequent authors), and an additional half dozen " variations " (eg. *angustata* and *angusta* A. Adams 1850, *rotundata* and *rotunda* Adams 1850, and *pemphis* and *pemphix* Philippi 1847) which are the cause of some confusion in the literature. Of these 121 species, 24 have been referred to as synonoms of a previously described species, although some discrepancies exist in descriptions and arguments of the authors (Table 2).

Pilsbry considered the only useful subdivision of the genus to be a geographical one, although he did state that in the shell, "the different modes of insertion of the outer lip at the vertex offers a good character" (Pilsbry, 1893, p. 352). In 1920, Pilsbry divided the genus into 3 groups based on structure of the columella. Pilsbry's (1920) descriptions of these 3 groups were as follows : "section" Haloa, with a deeply concave columella, and a crescentric, reflected margin separated from the body whorl by a furrow, type *H. crocata* Pease; "subgenus" Liloa, with a cylindrical shell and an umbilicate, slightly concave columella that is little reflected, type *H. tomaculum* Pilsbry ; and "section" Haminoea proper, columella concave and broadly reflected, thin at the edge appressed to whorl, type *H. hydatis*

An attempt has been made to subdivide the genus by promoting Pilsbry's subgenera to genera (Habe, 1952; Hamatani, 1961; Kuroda and Habe, 1961; Burn, 1966; Usuki, 1966; retained as subgenera by Zilch, 1959). Although the characteristics of the columella are useful taxonomically, I do not think they are sufficiently encompassing to warrant division of *Haminoea* into several genera. At this time, there is not enough known at the species level, let alone of the entire

genus, to indicate other morphological features that may support this division. The columella appears to be well defined in the species examined by Pilsbry (1920) when designating these " sections ". However, in many species this is not the case. In the majority of *Haminoea* species, the only taxonomically informative reference(s) are restricted to shell descriptions. In many of these descriptions, information on the columella was either incomplete, the columella was not distinctive (Table 3), or it was variable intraspecifically (Fig. 1).

Designation of these species into new genera would depend on a re-examination of the shells, but type locales were often not specified in the older literature. Intraspecific variation necessitates that a large number of individuals be examined, and as the majority of *Haminoea* species and their distributions are poorly known, this task would be extremely difficult if not impossible. Also, it appears that while shell characters are valuable taxonomically, morphological examination of the entire animal is more reliable and indeed necessary in characterizing a species. Most species (80 %) are known by the shell only. Descriptions of the other species are brief and only a dozen contain useful morphological detail (Table 4). Many type descriptions are based on one or a few shells only. Given the overlap in characteristics and potential intraspecific variation, it is probable that as data are accumulated, many of these species will be shown to be synonyms. As the available data are largely incomplete, I suggest that the genus *Haminoea* remain intact until the morphologies of several different species are more thoroughly understood.

SHELL MORPHOLOGY:

Historically, the majority of type descriptions did not include information on the animal, as the material was probably not available.

In those types where the animal was examined, excluding those of recent years, descriptions were brief and were mainly concerned with external features. Recent descriptions (Marcus and Burch, 1965; Heller and Thompson, 1983) and re-examinations of established species (Marcus, 1957; MacNae, 1962; Marcus and Marcus, 1967; Rudman, 1971 a and b; Kay, 1979; Appendix 1) contained a greater variety of information, but the problem remained of definition of the relevent characteristics. Unfortunately, there are still approximately 86 species that are known solely by shell descriptions, and only a dozen species for which extensive whole animal descriptions have been made, in some cases through the works of several authors. Although the type specimens of those species known only by the shell were, for the most part, described by excellent conchologists, there are problems inherent with this approach, because the shells of all *Haminoea* species are similar (see Reeve, 1868). The most frequently used characteristics are summarized below, including the problems and inconsistencies which I have noticed while reading the type descriptions or examining shells.

A. Shell Shape:

Haminoea shells fall into 3 shapes (Table 3), each of which has become associated with one of Pilsbry's (1920) subgenera ; globose (Haminoea proper), ovate (Haloa) and cylindrical (Liloa). Another feature is truncation of the shell, either anteriorly or more frequently posteriorly. A major problem associated with using shell shape as a primary characteristic is that morphometric changes can be associated with growth and environmental conditions. Such morphometric variability is important when one considers that many of the original type descriptions were based frequently on one, or at best a few shells. Shell morphology among the Mollusca (Clark,

1978), especially in the Mesogastropoda (Kemp and Bertness, 1984) and the Pulmonata (Clark, 1973), is infamous for its high degree of variablility with growth and environmental influences (Gould, 1966). Although there are no published accounts of variable shell morphology in the Opisthobranchia, my observations on 3 west coast species of *Haminoea* (*H. callidegenita* , *H. vesicula* , and *H. virescens*) indicated that there was intraspecific morphological variability (Fig. 1). Given the interspecific similarity typical of *Haminoea* species (Reeve, 1868; and others), such intraspecific variability must be addressed in future taxonomic studies.

Shell shape variability was also apparent in an examination of the length:width ratio in shells of a range of sizes for 4 species of Haminoea (Fig. 2; *H. callidegenita, H. vesicula, H. virescens,* and *H. solitaria).* There was sufficient intraspecific variation within shells of both similar and different size groups to indicate that this characteristic needs a detailed examination for a variety of species before shell shape can be used confidently as a major systematic feature.

B. Shell Colour:

Colour is another commonly cited taxonomic character. *Haminoea* shells are all very pale, but many species have a characteristic tint that appears to be reliable in some species (as long as the shell described was not sunbleached, as was frequently the case in descriptions made from specimens that were found washed up on a beach). Whether these tints are environmentally or genetically determined has not been examined. Specimens from certain widespread species collected from a variety of locales have been described as being the same colour (eg. *H. navicula* DaCosta 1778, with a yellowish shell whether collected from England, Spain,

or the Mediterranean Sea, *in* Pilsbry, 1893, or *H. antillarum* d'Orbigny 1844, which was always described as being greenish-yellow, regardless of collection site in the Gulf of Mexico, *in* Humfrey, 1975, or the West Indies, *in* Abbott, 1954). However, *H. elegans* Gray 1825, a common species along the West Atlantic coast from Florida to Texas and throughout the West Indies, seems to be highly variable. Humfrey (1975) recorded shells that were greenish-yellow, brown, and white, and Marcus (1957) reported variations ranging through white, ivory, yellow, and brown, to reddish and greenish grey.

Although colour intensity may be slightly variable, I have not observed interpopulation differences in *H. callidegenita* (shells reddish-white, collected from Spencer's Spit and Rock Point, Washington) or in *H. vesicula* (shells pale yellowish-green, collected from Bamfield and Grappler Inlets, British Columbia, and from False Bay and Fisherman's Bay, Washington). *Haminoea* shells are typically lightly pigmented, do not show pigment patterns, and there is considerable overlap in colour between species.

C. Shell Vertex:

The shape of the shell vertex is also a commonly cited character. In the literature, shell descriptions ranged from having a vertex that is flattened, impressed, or perforate. Unfortunately, " perforation " has been variously interpretated by different authors, often dependent on the location of the point of insertion of the outer lip of the aperture. Pilsbry (1893) thought the mode of insertion of the outer lip might provide a good systematic character (p. 352). In his monograph, Pilsbry (1893) included excellent descriptions of a number of species that indicated that this might be the case (eg, *H. elegans* Gray 1825, *H. glabra* Adams 1850, *H. petitii* d'Orbigny 1842, and *H. zelandiae* Gray 1843, all show a characteristic morphology

that readily distinguishes them from other species; Table 3). The diagnostic importance of the point of insertion of the apertural lip has been supported by the descriptions of other authors, including Baker and Hanna's (1927) description of *H. angelensis*, Marcus and Burch's (1965) description of *H. musetta* , and Abbott's (1954) key to the west Atlantic species. My observations on the 3 *Haminoea* species found in the Pacific Northwest indicated that the point of insertion seemed to be consistent within a species, and was distinctive between them (Fig. 3). Pilsbry (1917, 1920) dropped this character from his later examination of the genus. Although included by some authors (Marcus, 1961; Marcus and Marcus, 1967), the apertural lip was not commonly described in useful detail. The extent of the callous associated with the shell in the region of the vertex may be misleading as, although callous thickness usually is consistent throughout a species, the extent of the callous over the body whorl is variable among individuals. Marcus and Marcus (1967, p. 21) observed that "the extension of a callous and the insertion of the outer lip of the aperture to the right or to the left of the apex may depend on secondary calcification" and concluded that the characteristic was unreliable.

D. Columella and Callous:

In the literature, descriptions of the columella indicated interspecific and where examined, intraspecific variations in the degree of curvature and reflection of the callous (Table 3). My observations on a range of sizes of shells of *H. callidegenita*, *H. vesicula* , and *H. virescens* indicated that a variety of curvatures were possible within one species (Fig. 1). The variability observed in columella shape seemed broad enough to encompass curvatures considered species-specific by other authors (Reeve, 1868; Kobelt,

1896; Pilsbry, 1893, 1917). Pilsbry (1920) subdivided *Haminoea* into 3 sections, based on the curvature, reflection, and sculpturing of the columella in 9 species. Although the columella of these 9 species does lend itself to Pilsbry's division, an examination of shells of other species revealed so much overlap that it is difficult to group many of them into his sections (Table 3).

If the shape of the columella is accepted as the diagnostic character used to identify a specimen to genus, some *Haminoea* species would have to be moved to other, long-established genera. For example, *H. virescens* have strongly truncated shells in which the columella resembles that of *Philine*. However, morphological differences of the animals make it difficult to accept so close a phylogeny (Rudman, 1971a; this paper). Reeve (1868) has noted that shell shape (from his illustrations, it appears that the columella was often the most strongly expressed feature) in *H. sinensis* Adams 1850 (now *H. exarata* Philippi 1849, *in* Pilsbry, 1893) "so much resembles the shells of *Philine* that it is only placed in this genus on the authority of Mr. Adams, believed to be based on a knowledge of the animal ". Reeve (1868) also noted a strong resemblance between the shells of *H. ambigua* Adams (now *H. arthuri* nom. n. Finlay 1927; *in* Finlay 1927) and those of *Atys* species. Reflection of the callous appears variable intraspecifically as well. Given the intraspecific variation, and the similarity between species, it seems that the columella should not support the subdivision of the genus, as has been suggested by Pilsbry (1920), and accepted by other authors (either as subgenera, *in* Zilch, 1959, or as genera, *in* Habe, 1952; Hamatani, 1961; Kuroda and Habe, 1961; Burn, 1966; Usuki, 1966).

Two other features of the columella were often recorded; the presence of folds or twists, usually occurring anteriorly (eg. *H.*

angustata Adams 1850, *H. grisea* Smith 1875, *H. peruviana* d'Orbigny 1837; all *in* Pilsbry, 1893), or an umbilicate chink (*H. olopana* Pilsbry 1920, *in* Pilsbry, 1920, *H. perrieri* Morlet 1889, *in* Morlet, 1889, and *H. petiti* d' Orbigny 1842, *in* Pilsbry, 1893 ; and Table 3, this chapter). Neither *H. callidegenita* , *H. vesicula* , nor *H. virescens* had umbilicate shells. *H. callidegenita* , and *H. vesicula* showed characteristic folds in the columellar callous (Fig. 3), the extent and depth of which being variable with curvature and projection of the body whorl.

E. Surface Sculpturing:

Two forms of shell sculpturing were visible in the majority of species; growth lines and spiral striae. The former are generally visible, and are interesting in that they have been reported to show interspecific variation in the extent to which they are defined. Whether environmental conditions influence definition has not been examined. Characteristics of the spiral striae are more useful because more variation occurs among species, and they are probably less subject to environmental influences than are growth lines. Spacing, regularity, and straightness of the striae are all commonly cited as taxonomic characters (Table 3) and are probably useful for the majority of species. In some cases, species are recorded as not having striae, or reports differ between authors. Striae in these species are probably present but are so finely carved that observation requires the use of magnification. Also, striae may be lost or rendered inconspicuous by loss of the periostracum as shells are washed about by the tide. Although the striae are useful and seem to remain consistent throughout a species, records vary with technique of observation and condition of the specimen when collected, and reports of many species indicate similar if not

identical configurations (Table 3). For many species there is only one description thorough enough to include details of the striae, or in some cases two contradictory descriptions. Within these limitations, striae appear to be a useful characteristic.

The majority of *Haminoea* species were first described, and still are known, by shell characteristics only. The original types were described in great detail, but were often based on one or a few shells. Shells of all the species in this genus are very similar and descriptions based on shell characteristics are not reliable. Nonetheless, shell morphology can be useful when comparing a limited number of species, as in the case of sympatric species. There appears to be no single shell character, or combination of a few characters, that is sufficiently encompassing and consistent to provide a universal basis for species description.

ANIMAL MORPHOLOGY:

Although the shell was valuable historically, aspects of animal morphology are more useful taxonomically. The most commonly decribed characteristics are details of Hancock's organ and the morphology
of the penis complex (Table 4). In species where they have been examined, these structures seem consistent intraspecifically, and provide sufficient interspecific variation to offer diagnostic features. Other characteristics, such as number of uncini in the radula and the number of ridges on the gizzard plates, are useful but are not diagnostic on their own as they vary with the size of the specimen.

A. External Morphology:

A.1. Pigmentation and Cephalic Lobes:

External features (Table 4), such as colour and the distribution

of pigment spots, are valuable in live material but the details are lost with fixation. Rudman (1971b) noted that species inhabiting temperate waters are usually brown and grey in colour (eg. *H. antillarum* d'Orbigny 1841, and *H. zelandiae* Gray 1843; *in* Rudman, 1971b; and, supported by my observations of *H. callidegenita* and *H. vesicula*). On the other hand, tropical species are typically much more colourful, as, for example, *H. cymbalum* Quoy and Gaimard 1835 which are lime green with orange and purple (Rudman, 1971b) and *H. cyanomarginata* Heller and Thompson 1983, which are green with yellow and blue (Heller and Thompson, 1983). Bifurcation of the cephalic shield and extension of the epipodial and posterior pallial lobes over the shell are also characteristic, but again, examination of live material is necessary as *Haminoea* are capable of almost complete retraction into the shell.

A. 2. Hancock's Organ :

Hancock's organs are 2 elongate organs located on either side of the head and are believed to be sensory in function (Rudman, 1971a). *H. callidegenita*, *H. vesicula*, and *H. virescens* all showed characteristic morphologies of Hancock's organ (Fig. 3) without intraspecific variability within or among populations. An examination of the literature revealed two basic forms: an elongate, tubular organ, (as in *H. callidegenita, H. cymbalum* Quoy and Gaimard 1833, *H. zelandiae* Gray 1843), and an elongate organ that is lamellated dorsally and ventrally (*H. vesicula*, *H. virescens*, *H. antillarum* d'Orbigny 1841, *H. elegans* Gray 1825, and others, Table 1.4). If lamellated, Hancock's organ contains lamellae that are characteristic in number, arrangement (*i.e.*, number of dorsal *vs.* ventral pairs), and shape (some species, such as *H. linda* Marcus and Burch 1965, have lamellae that are pinnate). If tubular, Hancock's

organ can be interspecifically variable in size, both in length (as a proportion of body size) and in diameter.

B. Internal Anatomy:

Rudman (1971 a and b) examined the mantle cavity and associated organs, reproductive and digestive systems, and the major ganglia in 4 species of *Haminoea* (*H. crocata* Pease 1860 and *H.cymbalum* Quoy and Gaimard 1835, both from Hawaii; *H. solitaria* Say 1822, from the eastern North Atlantic; and *H. zelandiae* Gray 1843, from Auckland), and reported a similar morphology throughout, although a few organs were interspecifically variable. I examined the 3 species found on the Pacific Northeast coast and found similar results; the major organ systems seem to be comparable between species, with a few structures being consistently diagnostic (penis complex, gizzard plates, and in some cases, radulae and jaws; Table 4).

B.1. Penis Complex:

In the literature, the penis/ prostate complex is an important diagnostic character (Table 4). *H. callidegenita*, *H. vesicula*, and *H. virescens* also show species-specific morphologies (Fig. 3) which are consistent within a population, and in the cases of *H. callidegenita* and *H. vesicula*, among two or more populations. Diagnostic features include the number of lobes composing the prostate and their relative sizes, size of the penis sheath, the presence of spines or other forms of armature inside the penis sheath (as in *H. elegans* Gray 1825, *in* Marcus, 1957), and the presence of any additional structures (such as the " muscle sac " of *H. virescens* , *in* Marcus, 1961). If live or wet specimens are available, the penis complex is a nice diagnostic feature because it is easily dissected and observed, and differences between species are readily apparent.

B.2. Radula Morphology:

In all species of *Haminoea* where it has been examined, the radula formula is the same (n.1.1.1.n, sometimes listed as n.1.n, depending on the characteristics or technique of examination of the first row of laterals), with the rachidian and first lateral teeth showing characteristic sculpturing in some species (Table 4). Intrapopulation variation in the nature of the sculpturing was not observed in *H. callidegenita* (n=10), but size and shape of the rachidian tooth was slightly variable between the 2 study populations (n=5 individuals / population; Fig. 4). Considerable interpopulation variation was apparent in 3 populations of *H. vesicula* (n=10 individuals / population) in an examination of unworn teeth from corresponding regions of the radular ribbon (Fig. 4), although intrapopulation differences were not apparent. Radulae from only one population of *H. virescens* (n=10) were available for examination. The details agreed with Marcus' (1961) description of this species, although appearing slightly shrunken, possibly because of the fixation (Fig. 4).

B.3. Jaw Shape:

Haminoea have small, chitinous jaws which are used to grasp and hold food while the radula rasps up particles. The jaws are flat, with a broad, crescentric outline, and are covered with a fine etching of lines in a cross-hatch pattern. They did not seem to be an important diagnostic feature, as with few exceptions, there is little interspecific variation. *H. virescens* have jaws that are pointed anteriorly, while those of *H. callidegenita* and *H. vesicula* are rounded (Chapter 3, Fig. 7, 8, and 9).

B.4. Gizzard Plate Morphology:

The number of ridges on the gizzard plates has been commonly cited as diagnostic (Table 4) but they are variable in *H. callidegenita* , *H. vesicula* , and *H. virescens* . The number of ridges per plate increases with specimen size, ans also varies among animals of the same body length (eg. in *H. callidegenita*, ridge number ranges from 10 to 16 in 23-24 mm long animals). Examination of the details of the surface of the gizzard plates with the S.E.M. revealed the presence of papillae, and their distribution may prove to be significant: In *H. virescens*, papillae cover both the ridges and troughs that make up the medial surface of each plate, while in *H. callidegenita* and *H. vesicula* papillae are restricted to the ridges. *H. callidegenita* have pointed papillae and *H. vesicula* have rounded, finger-like papillae (Fig. 5). The sizes of the papillae are difficult to compare, as the orientation of some papillae suggests that they are capable of slight contractions and extensions. The only previous report of these papillae was by Rudman (1971a), who includes them as " chitinous rods " in a figure on gizzard plate formation (Fig. 18, p. 672) and his only description of them in the text is that the ridges are " weakly denticulate" (p. 671). These papillae are of interest in that they may reveal the function of the gizzard plates to include sorting and/or secretion, rather than just crushing, as has commonly been assumed (Rudman, 1971a).

NATURAL HISTORY:

A. Diet and Habitat:

In addition to morphological data, it is important to record information on natural history. *Haminoea* are typically intertidal or shallowly subtidal animals, inhabiting bays and lagoons with fine, silty or sandy substrata. They are usually found in association with eelgrass beds. Some species are found in other habitats, such as coral

rubble

(*H. cyanocaudata* Heller and Thompson 1983 and *H. cyanomarginata* Heller and Thompson 1983; both *in* Heller and Thompson, 1983), or intertidal rocky pools (*H. virescens* Sowerby 1833; *in* Morris *et al.*, 1980 , and *H. gracilis* Sowerby 1833, *in* Kilburn and Rippey, 1982). Diet is unknown, but *Haminoea* are considered to be epiphytic grazers. *H. brevis* Quoy and Gaimard 1835 (MacPherson and Gabriel, 1962) and *H. hydatis* Linne 1758 (Thompson and Brown, 1976) have been reported to prey on small bivalves.

B. Development:

Berrill (1931) studied the development of *H. hydatis* , a lecithotrophic species, and Richards (1921, 1923) briefly examined cleavage in *H. virescens* , a planktotrophic species. Development of *H. solitaria* Say 1822 (Smallwood, 1904 a and b; Harrigan and Alkon, 1984), and of *H.* (*Haloa*) *japonica* Pilsbry 1895 (Usuki, 1966), both lecithotrophic species, have been examined.

C. Additional Natural History Observations:

Locomotion is through ciliary action on a continually secreted mucous tube (*H. antillarum* d'Orbigny 1841, *in* Olmsted, 1917, and *H. zelandiae* Gray, 1874, *in* Rudman, 1971b). Edlinger (1982) found that *H. navicula* DaCosta 1778 are able to change colour from nearly white to black over a period of 9 d, through melanophore contraction and migration. *H. crocata* , Pease 1849 were described as having 17 bivalent chromosomes (Natarjan, 1970). Swimming was described in *H. hydatis* Linne 1758 (Clark, 1855), although this observation has not been reported by others working on this or other species.

DISCUSSION :

The genus *Haminoea* Leach (Opisthobranchia : Cephalaspidea)

currently contains approximately 96 species (excluding synonyms; Table 2). The majority of these species were described, and still are known by shell characteristics only. Many of these data were repetitive, as many authors when reviewing a species or the genus as a whole merely referenced the original work or re-examined the type specimen (shell) only. Characteristics historically considered diagnostic are based on the shell, and include: shell shape, colour, surface sculpture (spiral striae), features of the vertex and the associated point of insertion of the outer apertural lip, and the curvature of the columella with its reflexed callous (Table 3). Most of the early species were described and are known on the basis of one or a few shells only. An examination of a range of shells of different sizes in 3 species of *Haminoea* (*H. callidegenita*, n.sp. (described in Chapter 3), *H. vesicula* Gould 1855, *H. virescens* Sowerby 1833) revealed that many of these characters are not as specific or as reliable as was formerly considered. None of them seemed sufficiently encompassing to support the subdivision of this genus, as has been proposed (Pilsbry, 1920) and accepted by some other authors (Habe, 1952; Hamatani, 1961; Kuroda and Habe, 1961; Burn, 1966; Usuki, 1966; not by Zilch, 1959). However, these features may be useful in distinguishing between sympatric species as there should be no merging of characters through hybridization if they are distinct species, and the relative sparsity in the number of species found in one geographic area may allow universally subtle shell characters to be diagnostic.

Morphological features other than shell characteristics are essential both in new species descriptions and in the re-examinations of established species. My examination of three species of Northeast Pacific *Haminoea* suggest a number of characters that appear reliable

to effect a clear separation of species. These characters are: Hancock's organ and the penis complex, as well as external features, such as pigment pattern, cephalic shield, and the epipodial and posterior pallial lobes (Table 4). Morphology of the radula was variable between populations, yet patterns of dentition and sculpturing appear species-specific (Fig. 4). Gross morphology of the gizzard plate was not a reliable character, but the distribution and shape of the surface pa[illegible]ae may prove to be diagnostic.

As in all taxonomic work, it is necessary in this genus to examine the morphology of a number of specimens, preferably from more than one population. Descriptions of certain structural features are required (ie., Hancock's organ, penis and prostate, and external features), while other structures are useful if discretion is used in assessing their importance for each species (ie., radula, gizzard plates, and shell). Structures included in the second group show some intraspecific variability, but are nonetheless valuable for several reasons. Hard parts are useful because they can be used in animals which have been poorly fixed. Also, some features are diagnostic even though variable; for example, the sculpturing and dentition of the radulae are characteristic, although the size and arrangement of the teeth may be variable. If examined in a number of specimens, from more than one population, the patterns of variation can be recorded and anticipated in other populations, and confidence in certain features may be maintained. The shell is valuable because it provides the only data currently available for the majority of species. Descriptions based solely on shell morphology should not be disregarded until sufficient information has been accumulated to reveal these species as discrete or as synonymous entities. Although *Haminoea* species are widespread and seasonally abundant animals,

their natural history is poorly understood, and such contributions would be valuable to further systematic work.

It is probable that many *Haminoea* species will prove to be synonyms. Many *Haminoea* species have not been recorded since their original shell-based description. However, genera of herbivorous molluscs are often composed of many species (Marcus and Marcus, 1967), so it seems equally possible that many of the poorly-known species are actually discrete.

It is evident that most *Haminoea* species need to be re-examined in order to prepare more complete descriptions. Revision may be necessary, and may include subdivision of the genus. Such subdivision will probably not follow Pilsbry's (1920) criteria based on structure of the columella alone, unless strucytural features other than the shell are supportive.

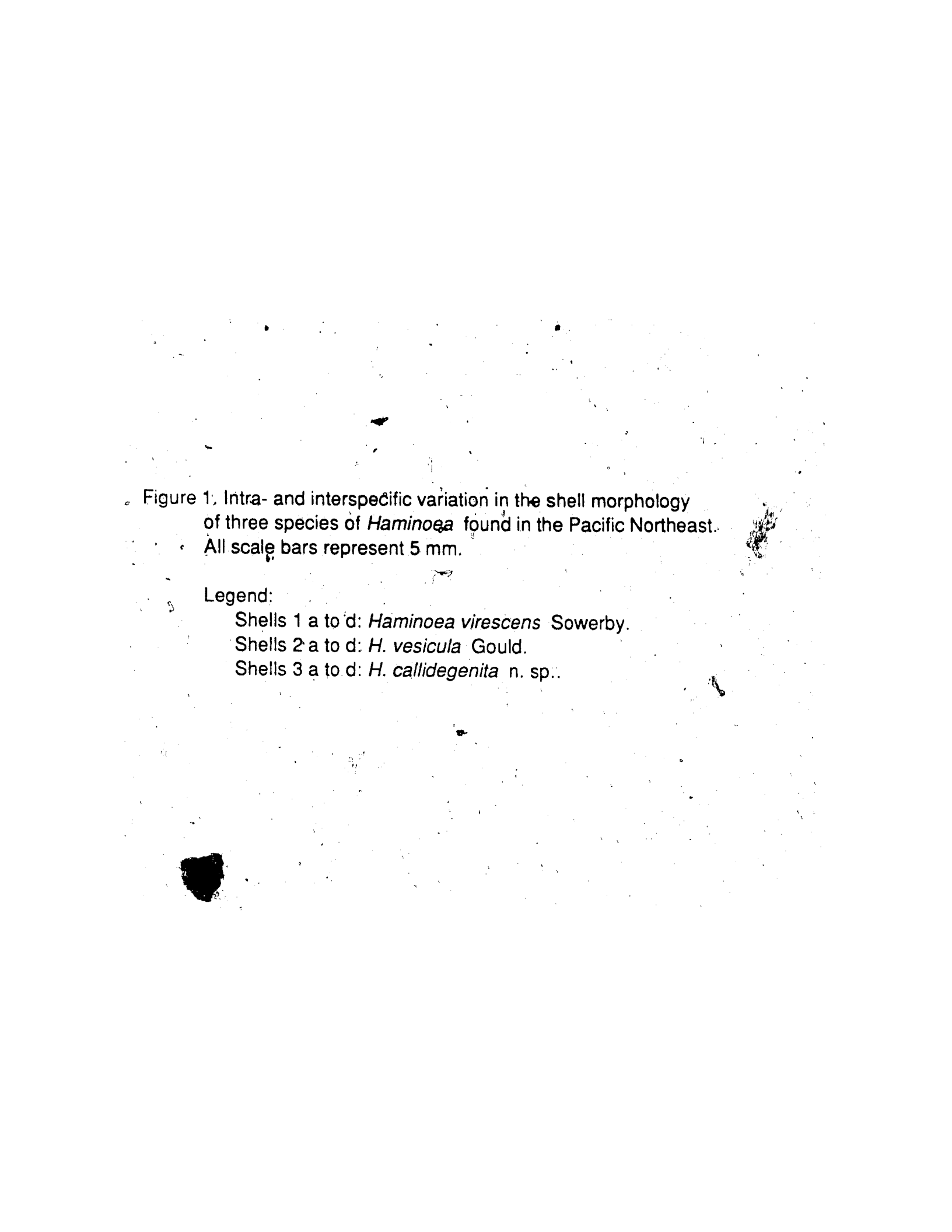

Figure 1. Intra- and interspecific variation in the shell morphology of three species of *Haminoea* found in the Pacific Northeast. All scale bars represent 5 mm.

Legend:

Shells 1 a to d: *Haminoea virescens* Sowerby.
Shells 2 a to d: *H. vesicula* Gould.
Shells 3 a to d: *H. callidegenita* n. sp..

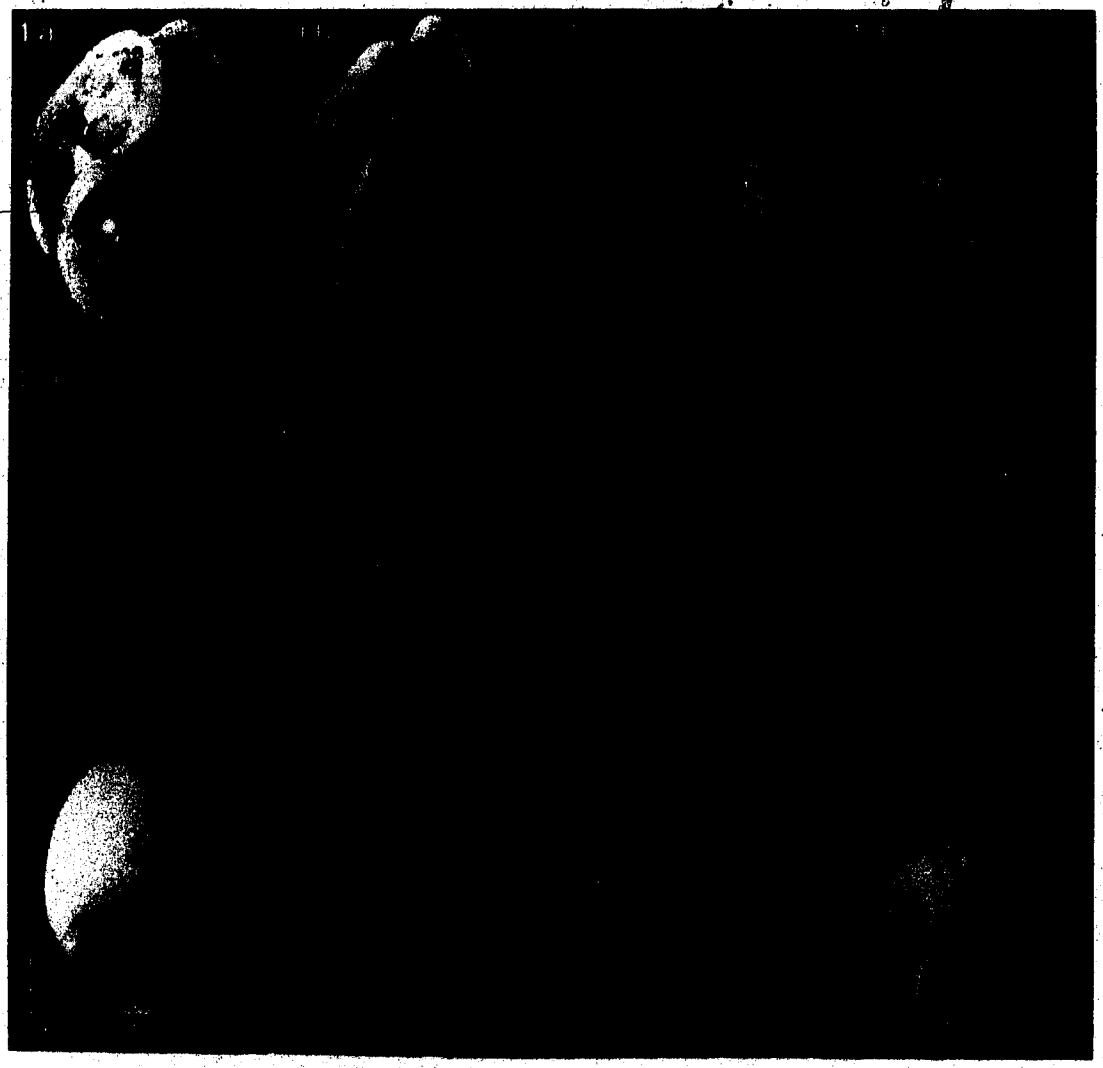

Figure 2. Variation in the shell shape of four species of *Haminoea*, expressed as a comparison of length:width ratios (n = 30 shells/species).

Legend:

- ▫ *Haminoea callidegenita*.
- ◆ *H. vesicula*.
- ■ *H. virescens*.
- ◇ *H. solitaria*.

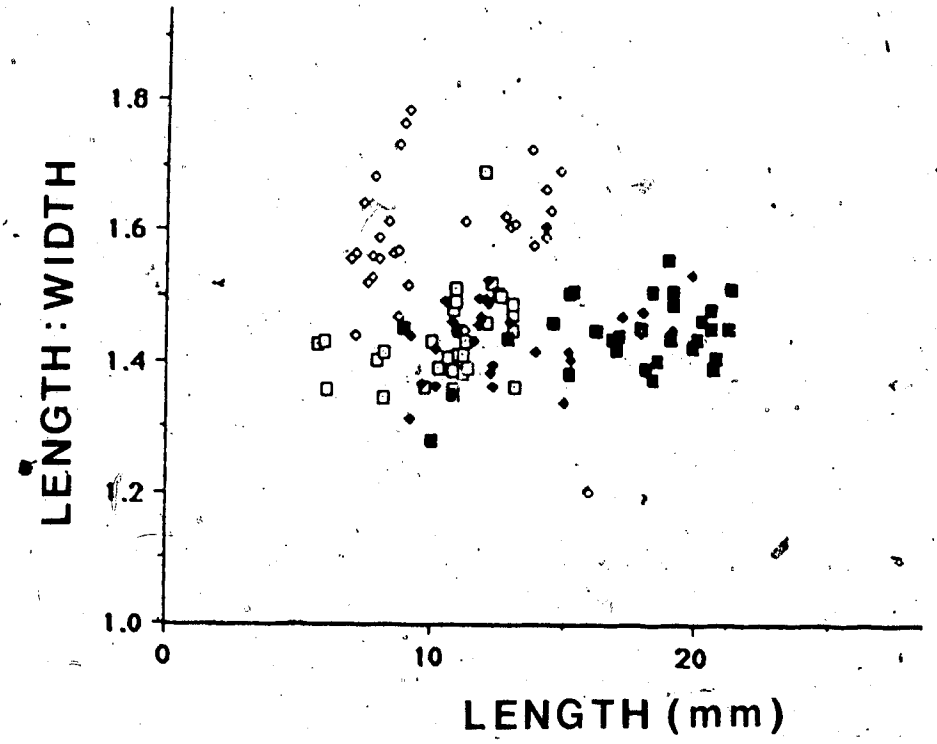
LENGTH : WIDTH
1.8
1.6
1.4
1.2
1.0
0
10
20
LENGTH (mm)

Figure 3: Summary of some diagnostic features of three *Haminoea* species found in the Pacific Northeast.

Legend:

Species:

1. *Haminoea callidegenita.*
2. *H. vesicula.*
3. *H. virescens.*

Structures:

a. shell. Scale bars represent 5 mm.
b. shell vertex. Scale bars represent 3 mm.
c. Hancock's organ. Scale bars represent 0.5 mm.
d. penis complex. Scale bars represent 1 mm.

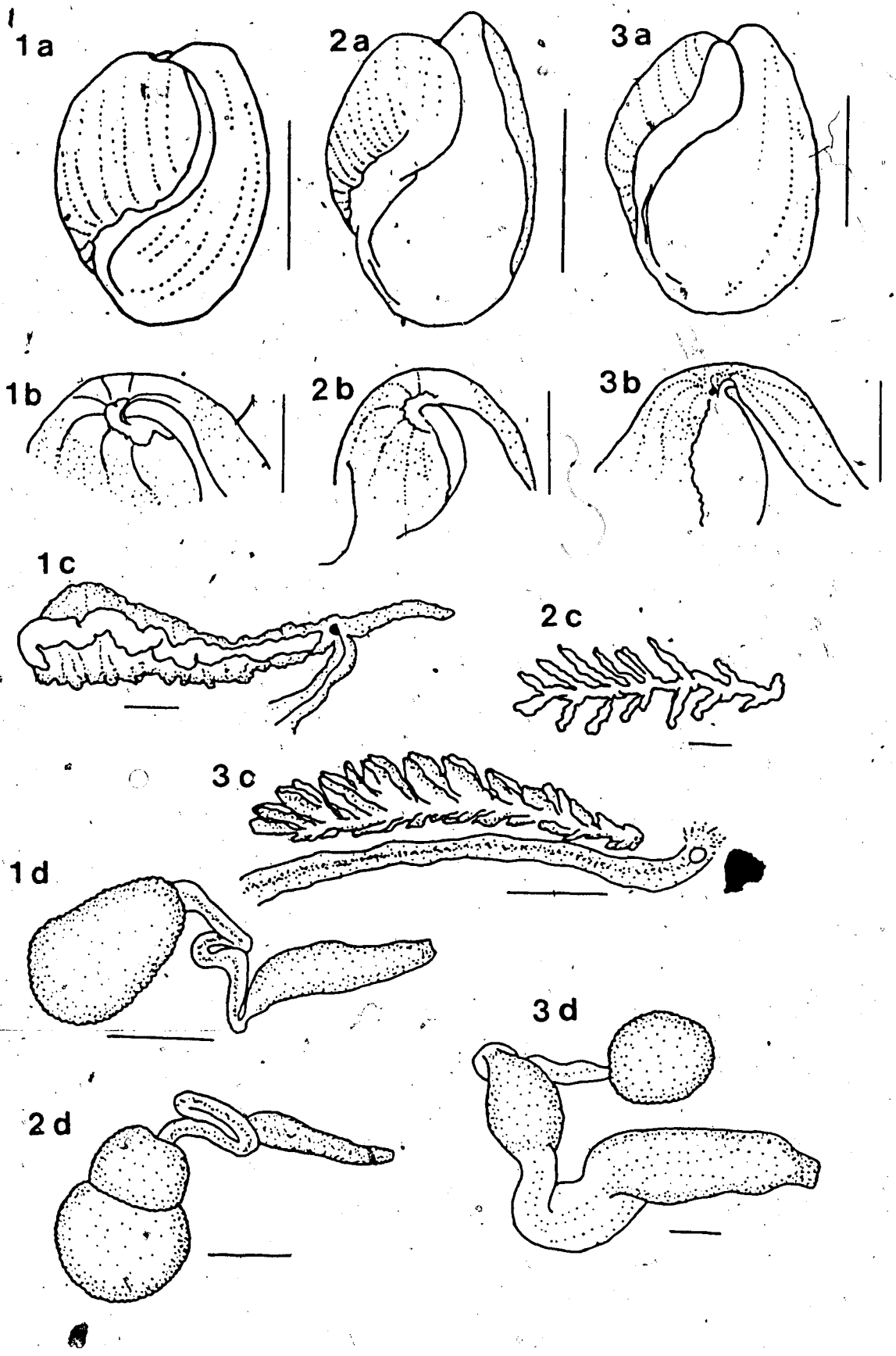
1a
2a
3a
1b
2b
3b
1c
2c
3c
1d
3d
2d

Figure 4. Intra- and interspecific variation in the radula morphology of three species of *Haminoea* found in the Pacific Northeast.

Legend:

1. *Haminoea callidegenita*, collected from:
   a) Spencer's Spit. Scale bar represents 50μm.
   b) Rock Point. Scale bar represents 50μm.

2. *H. vesicula*, collected from:
   a) Grappler Inlet. Scale bar represents 25μm.
   b) Rock Point. Scale bar represents 25μm.
   c) Santa Barbara. Scale bar represents 25μm.

3) *H. virescens*, collected from:
   a) Santa Barbara. Scale bar represents 25μm.

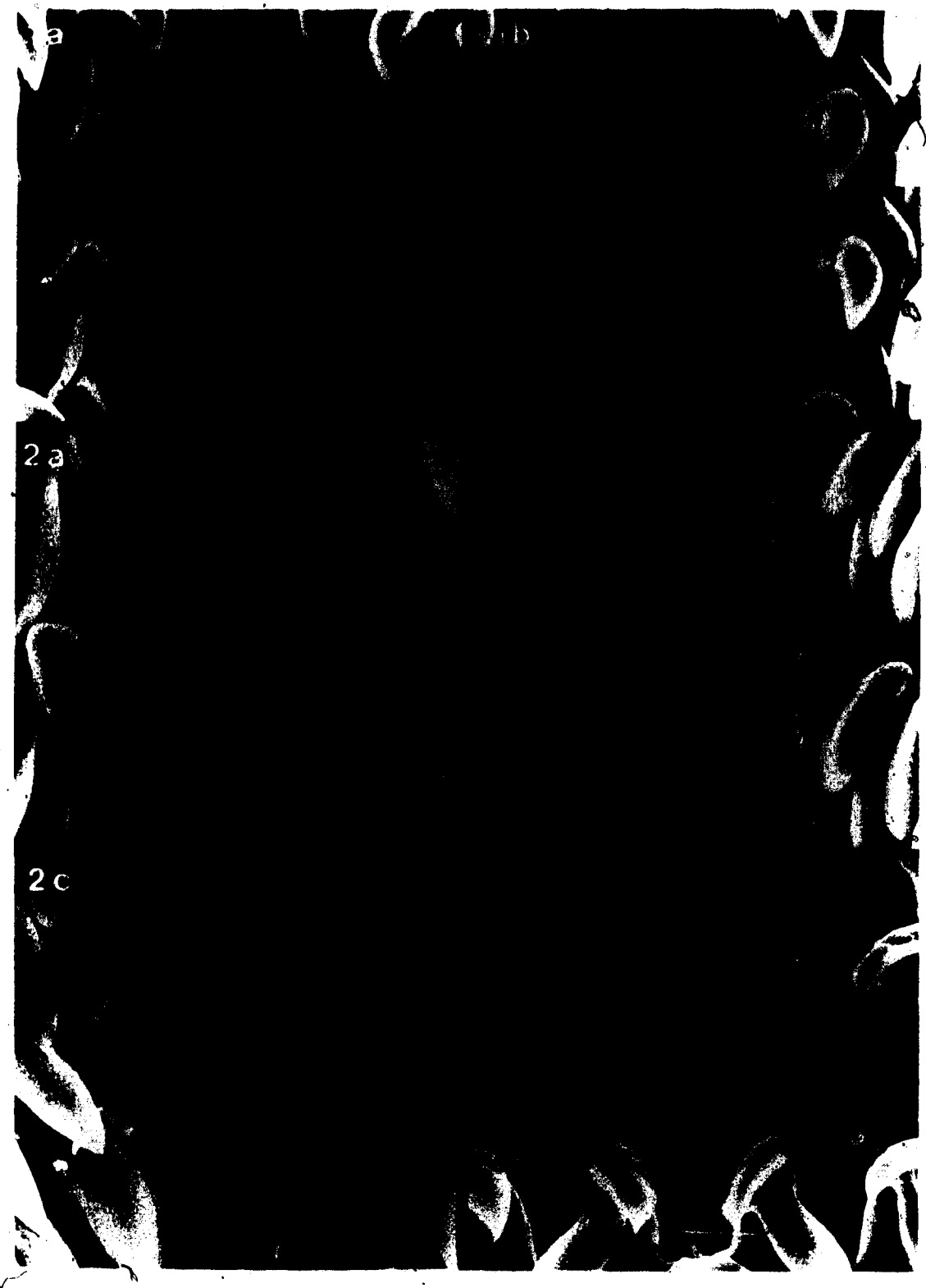
a
2a
2c

Figure 5: Photomicrographs of the medial ridges of the gizzard plates in three species of *Haminoea*. All scale bars represent 50μm.

Legend:

1. *Haminoea callidegenita*.
2. *H. vesicula*.
3. *H. virescens*.

Table 1. A list of the described *Haminoea* species, including location of type specimen (if known) and sites of collection.

#	SPECIES	VARIETY	AUTHOR	TYPE LOCALE	COLLECTION SITE(S)
1	H. callidegenita, n. sp.		Gibson, 1987		Spencer's Spit & Rock Point
2	H. adamsii		Dunker, 1861		Hawaii ?
3	H. aequistriata		Smith, 1872		Suez
4	H. alfredensis		Bartsch, 1915	#186656 USNM	South Africa
5	H. ambigua		A. Adams, ? by 1855		New Ireland.S.P.
6	H. angelensis		Baker & Hanna, 1927	#2517 US NatMus	dredged, California
7	H. angusta		A. Adams, 1850		Japan
8	H. angustata		A. Adams, 1850		China & Japan
9	H. antillarum		d'Orbigny, 1841		Jamaica, Florida, Bermuda
		quadalapensis	Sowerby, 1853		Bermuda to Brazil, W. Indies
10	H. aperta		Pease, 1868	#57575 ANSP	Tahiti
		oahuensis	Pilsbry, 1917	#117072 ANSP	Hawaii
11	H. articensis		Addicott, 1966	#649136 USNatMus	Oregon, Tertiary period
12	H. arthuri		Finlay, 1927		New Zealand ?
13	H. barakai		Abbass, 1975		Egypt, Upper Eocene
14	H.binotata		Pilsbry, 1895		Eniwetok Atoll, W. Pacific
		japonica	Pilsbry, 1895		Japan
15	H. brevis		Quoy & Gaimard, 1832		New South Wales, AUS, N Z
16	H. brevissima		A.Adams, 1862		Japan
17	H. cairnsiana		Melvill & Standen, 1895		Lifu ?
18	H. callosa		Preston, 1908		Eniwetok Atoll, W. Pacific
19	H. canalis		Dall, 1912	#214355,US NatMus	Panama & Costa Rica
20	H. castanea		A. Adams, 1850		N.Zealand
21	H. cerina		Menke, 1853		West Indies
22	H. cingulata		Muenster, 1835		
23	H. constricta		A.Adams, 1850?		Philippines & Japan
24	H. cornea		Lamarck, 1822		
25	H. corticata		Beck, 1842		
26	H. crocata		Pease, 1860	#1916119, BM(NH)	Hawii, Pakistan, N.S.Wales
27	H. curta		A.Adams, 1850		Fiji, Hawaii, Red Sea

#	SPECIES	VARIETY	AUTHOR	TYPE LOCALE	COLLECTION SITE(S)
		tomaculum	Pilsbry, 1917		
28	H. cuticulifera		Smith, 1872		New Zealand
29	H. cuvieri		Leach, 1852		
30	H. cyanocaudata		Heller & Thompson, 1983		Red Sea
31	H. cyanomarginata		Heller & Thompson, 1983		Red Sea
32	H. cymbalum		Quoy & Gaimard, 1833		Hawaii
33	H. cymbiformis		Carpenter, 1853 , '56 ?		Mazatlan, W.Centr.America
34	H. dalli		Bartsch, ? by 1933		
35	H. decora		Brazier, 1878	Macleay Mus,#A102	N - NE AUS
36	H. diaphana		Coutherier, 1849		
37	H. dilata		Leach, 1847		Great Britain
38	H. dilatata		Leach, 1847		Great Britain
39	H. dubia		Schepman, 1913		Malay Archipelago
40	H. elegans		Gray, 1825		Florida, W. Indies, Texas
41	H. exarata		Philippi, 1849		China
42	H. ferruginea		Chemnitz, ? by 1855		
43	H. flavescens		A. Adams, ? by 1855		
44	H. folliculus		Menke, 1853		unknown
45	H. fulgida		A.Adams, 1862		China
46	H. fusca		A. Adams, ? by 1855		Philipines, 25 fms
47	H. galba		Pease, 1860	BM(NH) #1961194	Hawaii
48	H. gantease		Pruvot-Fol, 1953		
49	H. glabra		A. Adams, 1850		Virgin Isl., W. Indies
50	H. gracilis		Sowerby, 1897		Mozambique, W. Africa
51	H. grandis		Aldrich, ? by 1928		Jackson eocene
52	H. grisea		Smith, 1875		Japan
53	H. guadalapensis		Sowerby, 1868		Guadaloupe
54	H. guildingii		Swainson, 1840		Jamaica
55	H. hydatina		Linne, ?		

#	SPECIES	VARIETY	AUTHOR	TYPE LOCALE	COLLECTION SITE(S)
56	H. hydatis		Linne, 1758		S. England, E. Atlantic, Med
		albescens	Monterosato, ? by 1893		
		cymoelium	Monterosato, 1923		Mediterranean
		globosa	Monterosato, ? by 1893		
		major	Monterosato, ? by 1893		
		media	Monterosato, ?		
		miocoenica	Berger, 1953		Tertiary Vienna
		minor	Monterosato, ? by 1893		
		oblonga	Monterosato, 1884		
		violacea	Monterosato, ? by 1893		
		virescens	Monterosato, ? by 1893		
57	H. incincta		Mighels, 1844		
58	H. insculpta		Totten, 1835		North Pacific
59	H. labrea		Olsson, 1928		Peru, extinct
60	H. linda		Marcus & Burch, 1965	U. Hawaii, U. Michegan	Eniwetok Atoll, S. Pacific
61	H. lucida		A. Adams, 1862		China
62	H. luticola		C. B. Adams, ? by 1858		
63	H. malleata		Smith, 1872		
64	H. maltzani		Thiele, 1925		
65	H. maugeansis		Burn, 1966		S. Australia
66	H. mauritaniae		White, 1957		Mauritania, W. Africa
67	H. musetta		Marcus & Burch, 1965	U Hawaii, U Michegan	Eniwetok Atoll, S. Pacific
68	H. natalensis		Kr[illegible]		Port Natal, Mauritius
69	H. navicula		Da[illegible]		Atl fr England to Spain, Med.
		albina	Monterosa[illegible]		
		glaucescens	Monterosato, ? by [illegible]		
		expansa	Monterosato, ? by [illegible]		
		ferruginosa	Monterosato, ? by 1893		
		globosa	Jeffrey, ? by 1893		
		globosa major	Monterosato, ? by 1893		Venice
		subquadrata	Monterosato, ? by 1893		
70	H. nigropunctata		Pease, 1868		Polynesia
71	H. novi eboraci		Sowerby, 1868		New York ?

#	SPECIES	VARIETY	AUTHOR	TYPE LOCALE	COLLECTION SITE(S)
72	H. obesa		Sowerby, 1868		New Zealand ?
73	H. olgae		Dall, 1919	#216812 US	Orcas to Cal., USA
74	H. olopana		Pilsbry, 1920		Hawaii
75	H. orbignyana		Ferrussac, 1820		France, Canary Isl.,S.Engl, Ire
76	H. oryza		Totten, 1835		Massachusetts
77	H. ovalis		Pease, 1868		Tahiti
78	H. ovoidea		Quoy & Gaimard, 1833		Guam
79	H. padangensis		Thiele, 1925		
80	H. papyrus		Salis, 1793		Borneo
81	H. parallela		Gould, 1848		
82	H. paulae		Nardini, 1933		Indian Ocean
83	H. pemphis		Philippi,1847		Red Sea
84	H. pemphix		Philippi, 1847		Red Sea
85	H.perforata		Philippi, 1847		Manila
86	H. perplexa		Smith, 1872		unknown
87	H. perrieri		Morlet, 1889		Siam
88	H. peruviana		d'Orbigny, 1837		Peru
89	H. petersi		von Martens, 1879		Mozambique
90	H. petitii		d' Orbigny, 1842		Florida, W. Indies, Brazil
91	H. postangulata		Clark & Woodford, 1927	#31246 UCMInverts	California
92	H. pusilla		Pease, 1860	#1962754 BM(NH)	Hawaii
93	H. pygmoea		A. Adams, 1862		Japan
94	H. quebradillica		Maury, 1920		Tertiary Porto Rico
95	H. rotunda		A. Adams, 1850		
96	H. rotundata		A. Adams, 1850		
97	H. rugosa		Smith, 1872		Persian Gulf
98	H. sandwichensis		Sowerby, 1868		Hawaii
99	H. savignyana		Gray, 1825		Red Sea
100	H. serica		Smith, 1872		unknown

#	SPECIES	VARIETY	AUTHOR	TYPE LOCALE	COLLECTION SITE(S)
101	H. simillima		Pease, 1868		Tahiti, Zanzibar
102	H. simpsonensis	as Huminea	Stephenson, 1941		Cretaceous Texas
103	H. sinensis		A. Adams, 1850		
104	H. solaria		Olsson, 1928		Peru, fossil
105	H. solitaria		Say, 1822		Massachusetts - Carolinas
106	H. strigosa		A. Adams, 1862		Japan
107	H. strongi		Baker & Hanna, 1927	#2518 Mus Cal.Acad.S	San Diego, S. California
108	H. subcylindrica		Sowerby, 1897		S. Africa
109	H. subpellucida		H. Adams, 1869		Lisbon
110	H. succinea		Conrad, 1846		W. Florida
		solidior	Vanatta, 1901	#57900 Acad.Sci Phil	West Indies, Yucatan
111	H. tenella		A. Adams, 1850		
112	H. tenera		A.Adams, 1850		NSW, AUS., Suez-dredged
113	H. tomaculum		Pilsbry, 1920		Honolulu, 8 FA
114	H. ventripotens		Cossman, 1913		Martinique, Miocene
115	H. vesicula		Gould, 1855		California
		virgo	Pilsbry, ? by 1893		
116	H. virescens		Sowerby, 1833		California
		rosacea	Spicer, 1933		San Diego, CA
117	H. virginalis		Thiele, 1925		
118	H. vitrea		A.Adams, 1850		Philipines, Suez
119	H. wallisii		Gray, 1825		Naw Holland, near AUS
120	H. zanzibarica		Vanatta, 1901	#57552 AcadSci Phil	Zanzibar
121	H. zelandiae		Gray, 1843		N. New Zealand

Table 2. A list of possible synonomous species of *Haminoea* including pertinent references.

SPECIES	AUTHORITY	VALID ?	SYNONYMS	REFERENCE	PROBABLE ? (Y, N)
H. callidegenita, n.sp.	Gibson, 1987	*			
H. adamsii	Dunker, 1861		crocata Pease, 1860	Pilsbry, 1893	Y
				Kay, 1979	Y
H. aequistriata	Smith, 1872		now curta Adams, 1850	Pilsbry, 1893	Y
				Cooke, 1886	Y
			Atys isseli (H. Adams1872)	Pilsbry, 1893	Y
H. alfredensis	Bartsch, 1915	*	natalensis Krauss, 1868	Kilb&Ripp, 1982	uncertain
H. ambigua	A. Adams, ? by 1855		now arthuri	Finlay, 1927	Y
H. angelensis	Baker&Hanna,1927	*			
H. angusta	A. Adams, 1850	*			
H. angustata	A. Adams, 1850		really angustata Gould, ?	Pilsbry, 1893	Y
			Sowerby adds -ta	Smith, 1872	Y
H. antillarum	d'Orbigny, 1841	*	cerina Menke, 1853	Kobelt, 1896	Y
			guadalapensis Sby, 1853	Pilsbry, 1893	Y
H. ant guadalapensis	Sowerby, 1853		separate species	Kobelt, 1896	Y
			variety guadalapensis	Leigh,1953,Pils1893	Y
			subspecies guadalapensis	Marcus&Marcus,'67	Y
H. aperta	Pease, 1868	*			
H. aperta oahensis	Pilsbry, 1917		now cymbalum Q & G,1835	Kay, 1979	Y
H. articensis	Addicott, 1966	*			
H. arthuri	Finlay, 1927	*	nom.n. for ambigua		
H. barakai	Abbass, 1975	*			
H.binotata	Pilsbry, 1895	*			
H. brevis	Quoy&Gaimard, 1832	*	B. brevis, Q & G	Pilsbry, 1893	Y
			H. brevis Sby	Pilsbry, 1893	Y
			B.ovoidea Mke1844	Pilsbry, 1893,Kobelt,1896	Y
			B. ovoidea Q&G	Pilsbry, 1893	N
H. brevissima	A. Adams, 1862	*			
H. cairnsiana	Mel & Standen, 1895	*			
H. callosa	Preston, 1908	*			
H. canalis	Dall, 1912	*			
H. castanea	A. Adams, 1850	*	also of Sowerby	Pilsbry, 1893	Y

SPECIES	AUTHORITY	VALID ?	SYNONYMS	REFERENCE	PROBABLE ?
					(Y, N)
H. cerina	Menke, 1853		antillarum d'Orbigny,1841	Pilsbry, 1893,Kobelt,1896	Y
H. cingulata	Muenster, 1835	*			
H. constricta	A. Adams, 1850 ?	*	B.(H.) constr.A.Ad	Pilsbry, 1893	Y
			also constricta of Sby.	Pilsbry, 1893	Y
H. cornea	Lamarck, 1822	*	H. cornea Monterosato	Lemche, 1948	Y
			= navicula DaCosta 1778	Pilsbry, 1893	Y
			nav not cornea Lamarck	Pilsbry, 1893	Y
H. corticata	Beck, 1842	*			
H. crocata	Pease, 1860		galba	Pilsbry, 1920	possibly
			galba	Kay, 1965	N
			H. adamsii, Dkr., 1861	Pilsbry,1893,Kobelt,1896	Y
			now cymbalum Q & G, 1885	Kay, 1979	Y
H. curta	A.Adams,1850	*	aequistriata Smith, 1872	Pilsbry,1893,Cooke,1886	Y
			B. curta, A.Adams	Pilsbry, 1893	Y
			H. curta Martens	Pilsbry, 1893	Y
			H. curta tomaculum Pilsbry	Kay, 1979	Y
			H. olopana Pilsbry,1921	Kay, 1979	Y
			H. tomaculum Pils,1921	Kay, 1979	Y
			Atys isseli H. Adams1872	Pilsbry, 1893	Y
H. cuticulifera	Smith, 1872	* ?	tenera (Adams, 1850)	Mac&Gab,1982	
			tenera	Pilsbry, 1893	N
H. cuvieri	Leach, 1852		now navicula	Pilsbry, 1893,Lemche,1948	Y
H. cyanocaudata	Heller & Thompson,1983	*			
H. cyanomarginata	Heller & Thompson, 1983	*			
H. cymbalum	Quoy & Gaimard, 1833	*	similima, Pease, 1868	Kay, 1979	Y
				Pilsbry, 1893	N
			B. cymbalum Q&G	Pilsbry, 1893	Y
			H. cymbalum Sowb.	Pilsbry, 1893	Y
			aperta oahuensis Pils 1921	Kay, 1979	Y
			crocata Pease, 1860	Kay, 1979	Y
H. cymbiformis	Carpenter, 1853 , '56 ?		virescens Sby, 1833	Morris et al., 1980	Y
			type unidentfiable	Pilsbry, 1893	Y

SPECIES	AUTHORITY	VALID ?	SYNONYMS	REFERENCE	PROBABLE ?
					(Y, N)
H. dalli	Bartsch, ?		cymbiformis Cpter,1853	Grant & Gale,1931	Y
			now virescens Sby	Pilsbry, 1933	Y
H. decora	Brazier, 1878	*			
H. diaphana	Coutherier, 1849		B. diaphana		
			elegans Gray, 1825	Pilsbry, 1893	Y
			guildingii Swainson, ?	Kobelt, 1896	Y
H. dilata	Leach, 1847		originally dilatata	Pilsbry, 1893	Y
H. dilatata	Leach, 1847		now orbignyana Ferru.1822	Fisher, 1879	Y
				Pilsbry, 1893	Y
			H. dilatata Fisher 1879	Kay, 1979	Y
			B. dilatata Wood, 1839	Lemche, 1948	Y
			H. dilatata Jeffreys, 1858	Lemche, 1948	Y
H. dubia	Schepman, 1913	*			
H. elegans	Gray, 1825	*	B. elegans Gray, 1825	Pilsbry, 1893	Y
			B. diphana Couth., 1849	Pilsbry, 1893	Y
			H. guildingii,Swains., ?	Pilsbry, 1893	Y
			H. succinea Conrad, 1846	Marcus&Marcus,'63	Y
H. exarata	Philippi, 1849	*	B. exarata Philippi, 1849	Pilsbry, 1893	Y
			H. exarata Mke.	Pilsbry, 1893	Y
			H. sinensis A.Ad, Sby.	Pilsbry, 1893	Y
H. ferruginea	Chemnitz, ?		now fusca A.Adams, ?	Pilsbry, 1893	Y
				Smith, 1872	Y
B(A?)ferruginosa	Chemnitz(Gmelin)		genus Cypraea	Pilsbry, 1893	Y
H. flavescens	A. Adams, ?	*	B. flavescens A.Ad	Pilsbry, 1893	Y
			H. flavescens Sby	Pilsbry, 1893	Y
H. folliculus	Menke, 1853		B. folliculus, Menke, 1853	Kobelt, 1896	Y
			now hydatis Linne,1758	Pilsbry, 1893,Kobelt,1896	Y
H.fulgida	A.Adams, 1862	*			
H. fusca	A. Adams, ?	*	B. fusca Adams	Kobelt, 1896	Y
			H. fusca Sby	Kobelt, 1896	Y
			H. ferruginea Chem	Smith,1872,Pilsbry,1893	Y
H. galba	Pease, 1860	*	sandwichensis Sby,1868	Kay, 1979	Y

SPECIES	AUTHORITY	VALID ?	SYNONYMS	REFERENCE	PROBABLE ? (Y, N)
H. gantease	Pruvot Fol, 1953	•			
H. glabra	A. Adams, 1850	•	B. glabra, Adams	Pilsbry, 1893	Y
			H. glabra, Sby.	Pilsbry, 1893	Y
H. gracilis	Sowerby, 1897		now petersi Martens,1879	Kilburn&Rippey,1982	Y
H. grandis	Aldrich, ?	•			
H. grisea	Smith, 1875	•			
H. guadalapensis	Sowerby, 1868	•	antillarum d'Orbigny,1841	Kobelt, 1896	Y
			antillarum d'Orbigny 1841	Marcus&Marcus, 1967	N
H. guildingii	Swainson, 1840		B. guildingiiSwains.,?	Kobelt, 1896	Y
			now elegans Gray, 1825	Pilsbry, 1893	Y
H. hydatina	Linne, ?	•			
H. hydatis	Linne, 1758	•	B. hydatis Linne, 1758	Lemche, 1948	Y
			B. folliculus Menke, 1853	Pilsbry, 1893	Y
			elegans of some authors	Kobelt, 1896	Y
			but not elegans Gray	Kobelt,1896,Pilsbry,1893	Y
H. hydatis cymoelium	Monterosato, ?	•			
H. hydatis miocoenica	Berger, 1953	•			
H. incincta	Mighels, 1844	•			
H. insculpta	Totten, 1835		B. insculpta Totten, 1835		
			and of Gould,Adams, Sby	Kobelt, 1896	Y
			now solitaria	Pilsbry,1893,Kobelt,1896	Y
			novae-eboraci Sby	Smith, 1872	Y
H. labrea	Olsson, 1928	•			
H. linda	Marcus & Burch, 1965	•			
H. lucida	A. Adams, 1862	•			
H. luticola	C.B.Adams, ?	•			
H. malleata	Smith, 1872	•			
H. maltzani	Thiele, 1925	•			
H. maugeansis	Burn, 1966	•			
H. mauritaniae	White, 1957	•			
H. musetta	Marcus & Burch, 1965	•			
H. natalensis	Krauss, 1868	•	H. peruviana d' Orb.	of Sby, Smith,1872	Y

SPECIES	AUTHORITY	VALID ?	SYNONYMS	REFERENCE	PROBABLE ?
					(Y, N)
				of Krauss, Smith	N
			B.natalensis Krauss	Pilsbry, 1893	Y
			H. natalensis Martens	Pilbry, 1893	Y
			B. natalensis A.Ad in Sby	Pilsbry, 1893	N
			H. natalensis Sowb	Pilsbry, 1893	N
				Smith, 1872	Y
			H. antillarum d'Orbigny,184	A.Adams,?	Y
				Pilsbry, 1893	N
			H. orbignyana Ferru.,1822	Sowerby, ?	Y
				Pilsbry, 1893	N
H. navicula	Da Costa, 1778	*	B. navicula DaCosta,1778	Lemche, 1948	Y
			B. ampulla Pennant 1776	Pilsbry, 1893	Y
			B. ampulla Linne, ?	Pilsbry, 1893	N
			B. hydatis of Brug., Sby.,	Pilsbry, 1893	Y
			Forbes&Hanley,Jeffreys	Pilsbry, 1893	Y
			Blainville, Donovan	Kobelt, 1896	Y
			B. hydatis of Linne	Pilsbry, 1893	N
			cornea Lamarck, 1822	Pilsbry, 1893	Y
			cornea Sowerby	Kobelt, 1896	Y
			cuvieri Leach, 1852	Lenche, 1948	Y
			subpellucida H.Adams,1869	Pilsbry, 1893	Y
H. nav. ferruginea	Monterosato, ?	*			
H. nigropunctata	Pease, 1868	*			
H. novi eboraci	Sowerby, 1868		novae eboraceae	Pilsbry, 1893	Y
			insculpta Totten	Pilsbry,1893,Smith,1872	Y
			now solitaria Sby	Smith, 1872	Y
H. obesa	Sowerby, 1868		now zelandiae Gray, 1825	Pilsbry,1893,Kobelt,1896	Y
H. olgae	Dall, 1919		poss vesicula	Pilsbry, 1893	Y
			virescens Sby, 1833	Abbott, 1954	N
H. olopana	Pilsbry, 1920	*	now curta A.Adams,1850	Kay, 1979	Y
H. orbignyana	Ferrussac, 1820	*	B. orbignyana Ferru.,1822	Pilsbry, 1893	Y
			H. dilatata Leach	Lemche, 1948	Y

SPECIES	AUTHORITY	VALID ?	SYNONYMS	REFERENCE	PROBABLE ?
					(Y, N)
H. oryza	Totten, 1835	*	B. oryza Totten	Smith, 1872	Y
H. ovalis	Pease, 1868	*			
H. ovoidea	Quoy & Gaimard, 1833	*	B. ovoidea Q&G	Pilsbry, 1893	Y
H. padagensis	Thiele, 1925	*			
H. papyrus	Salis, 1793	*			
H. parallela	Gould, 1848	*			
H. paulae	Nardini, 1933	*			
H. pemphis	Philippi, 1847	*	H. tenella Adams	Pilsbry, 1893	Y
H. pemphix	Philippi, 1847		zelandiae Gray, 1825	Pilsbry,	Y
			zelandiae Gray, 1825	Smith, 1872	N
H: perforata	Philippi, 1847	*	B. perforata [illegible]847	Pilsbry, 1893	Y
			B. elegans [illegible]	Pilsbry, 1893	Y
			B. elegans Gray, 1825	Pilsbry, 1893	N
H. perplexa	Smith, 1872	*			
H. perrieri	Morlet, 1889	*			
H. peruviana	d'Orbigny, 1837	*	natalensis Krauss	Pilsbry, 1893	N
			natalensis, Sowerby	Pilsbry, 1893	Y
H. petersi	von Martens, 1879	*	gracilis Sby, 1897	Kilburn&Rippey, 1982	Y
H. petitii	d' Orbigny, 1842	*	B. petitii d'Orbigny	Pilsbry, 1893	Y
			H. petitii Morch	Pilsbry, 1893	Y
H. postangulata	Clark & Woodford, 1927	*			
H. pusilla	Pease, 1860		Mnestia pusilla	Kay, 1965	Y
H. pygmoea	A. Adams, 1862	*			
H. quebradillica	Maury, 1920	*			
H. rotunda	A. Adams, 1850		H. rotundata	Pilsbry, 1893	Y
H. rotundata	A.Adams, 1850	*	B.rotundata Ad	Pilsbry, 1893	Y
			Sowb drops last ta	Pilsbry, 1893	Y
H. rugosa	Smith, 1872	*			
H. sandwichensis	Sowerby, 1868		now galba Pease, 1860	Kay, 1979	Y
H. savignyana	Gray, 1825	*			
H. serica	Smith, 1872	*			
H. simillima	Pease, 1868		now cymbalum Q&G, 1835	Kay, 1979	Y

SPECIES	AUTHORITY	VALID ?	SYNONYMS	REFERENCE	PROBABLE ?
					(Y, N)
H. [illegible]ensis	Stephenson, 1941		as Huminea		
H. sinensis	A. Adams, 1850		now exarata Phil.,1849	Pilsbry, 1893,Kobelt,1896	Y
H. solaria	Olsson, 1928				
H. solitaria	Say, 1822		B. insculpta	Pilsbry, 1893	Y
			H. insculpta Totten, 1835	Lemche, 1948	Y
			B. solitaria Say,1822	Pilsbry, 1893	Y
			H. novae-eboraceae	Smith, 1872	Y
			H. novi-eboraci Sby	Lemche, 1948	Y
H. strigosa	A. Adams, 1862				
H. strongi	Baker & Hanna, 1927	?	virescens	Morris et al.,1980	Y
				Pilsbry, 1933	N
H. subcylindrica	Sowerby, 1897				
H. subpellucida	H. Adams, 1869		now navicula DaCosta,1778	Pilsbry, 1893	Y
H. succinea	Conrad, 1846		B. succinea	Pilsbry, 1893	Y
			H. succinea, Sby.	Pilsbry, 1893	Y
			now elegans Gray, 1825	Marcus&Marcus,63	Y
H. succ. solidior	Vanatta, 1901				
H. tenella	A. Adams, 1850				
H. tenera	A.Adams, 1850		cuticulifera Smith, 1872	MacPh & Gabr.,1962	Y
			vitrea Adams, 1850	Pilsbry, 1893	N
			vitrea	Cooke, 1886	Y
H. tomaculum	Pilsbry, 1920		B. curta tomaculum Pilsbry	Kay, 1979	Y
			now curta Adams, 1850	Kay, 1979	Y
H. ventripotens	Cossman, 1913				
H. vesicula	Gould, 1855		olgae Dall 1919	this paper	Y
H. virescens	Sowerby, 1833		cymbiformis Carp.,1853		
			strongi Baker & Hanna	Abbott, 1954	Y
			strongi Baker & Hanna	Pilsbry, 1933	N
			olgae Dall 1919	Abbott, 1954	Y
			olgae Dall, 1919	this paper	N
			dalli Bartsch, ?	Pilsbry, 1933	Y
H. virescens rosacea	Spicer, 1933				

SPECIES	AUTHORITY	VALID ?	SYNONYMS	REFERENCE	PROBABLE ?
					(Y, N)
H. virginalis	Thiele, 1925	•			
H. vitrea	A.Adams, 1850	•	tenera Adams, 1850	Pilsbry, 1893	N
				Cooke	Y
H. wallisii	Gray, 1825	•			
H. zanzibarica	Vanatta, 1901	•			
H. zelandiae	Gray, 1843	•	B. zelandiae Gray	Pilsbry, 1893	Y
			H. zeland. Hutton	Pilsbey, 1893	Y
			H. obesa Sowb.	Pilsbry, 1893	Y
			B.(H) pemphis Phil.	Pilsbry, 1893	Y
			H. pemphix Phil.,Sby	Pilsbry, 1893	Y
			B. pemphis Phil.	Pilsbry, 1893	N

Table 3. A summary of shell characteristics in the genus *Haminoea* compiled from the literature (references listed). Characteristics included are: shape, size, length:width ratio, colour, vertex, striae, columella, and callous.

SPECIES	AUTHOR	REFERENCE	SHELL SHAPE	SIZE (mm)	RATIO (L:W)
H. callidegenita, n.sp.	Gibson, 1987	this paper	ovate	11 x 7.8	1.41 : 1
H. aequistriata	Smith, 1872	Smith, 1872	cylindric oblong	12 x 6	2.0 : 1
H. alfredensis	Bartsch, 1915	MacNae,1962	ovate, pear-sh.	19, 12.4x10	1.24 : 1
H. ambigua	A. Adams, ?	Kobelt, 1896	ovate-cylindrical	8	
H. angelensis	Baker & Hanna, '27	B & H , 1927	globose, narr.above	7.2 x 5.6	1.29: 1
H. angustata	A. Adams, 1850	Pilsbry, 1893	ovate-cylindrical	6 x 4	1.5 : 1
H. antillarum	d'Orbigny, 1841	Pilsbry, 1893	globose,narr.above	10 x 7.5	1.22 : 1
H. aperta	Pease, 1868	Pease, 1868	ovate	15 x 9	1.67 : 1
H. aperta oahensis	Pilsbry, 1917	Pilsbry, 1917	ovate,swollen	14.5 x 10	1.45 : 1
H. articensis	Addicott, 1966	Addicott, 1966	sub-cylindr.	8.3 x 5.4(brk)	1.54 : 1 (br)
H. binotata	Pilsbry, 1895	Marc&Burch,1965			
H. brevis	Q & G ,1833	Kobelt, 1896	cylindrical	10 x 6	1.67 : 1
H. cairnsiana	Mel & Standen, 1895	Mel & Stdn, 1895	cylindr,trunc.postly	8.5 x 6	1.42 : 1
H. callosa	Preston, 1908	Marc&Burch,1965	ovoid ?		
H. canalis	Dall, 1912	Dall, 1912	cylindrical	4 x 2	2.0 : 1
H. castanea	A. Adams, 1850	Kobelt, 1896	oblong-ovate	26 x ?	
H. constricta	A.Adams, 1850	Kobelt, 1896	oblong-ovate	30 x ?	
H. corticata	Beck, 1842	Pilsbry, 1893	laterally convex	25 x ?	
H. crocata	Pease, 1860	Pilsbry, 1893	ovate-elongate	13 x 8.5	1.52 : 1
H. curta	Adams, 1850	Pilsbry, 1893	cylindrical	12 x 6	2.0 : 1
H. cuticulifera	Smith, 1872	Pilsbry, 1893	elong-cylindrical	14 x 6.5	2.25 : 1
H. cyanocaudata	Heller & Thompson,1983	H & T, 1983	ovate		
H. cyanomarginata	Heller & Thompson, 1983	H & T, 1983	ovate	4	
H. cymbalum	Q & G, 1833	Kobelt, 1896	globose	15 x 10	1.4 : 1
H. cymbiformis	Carpenter, 1853 , '56 ?	Pilsbry, 1893	inflated	1.75 x 1.25	1.4 : 1
H. decora	Brazier, 1878	Brazier, 1878	cylindr-ovate	1.5 x 1.25	1.2 : 1
H. elegans	Gray, 1825	Pilsbry, 1893	cyl-ovate,trunc.abv	20.5 x 16	1.28 : 1
H. exarata	Philippi, 1849	Pilsbry, 1893	ovate, truncate	8 x 6	1.33 : 1

SPECIES	AUTHOR	VERTEX	STRIAE	COLUMELLA	CALLOUS
H. callidegenita, n.sp.	Gibson, 1987	impressed	many, fine	concave	thick,reflexed
H. aequistriata	Smith, 1872	depressed	~36,irregular	curved	reflexed
H. alfredensis	Bartsch, 1915		fine, close		
H. ambigua	A. Adams, ?		present		
H. angelensis	Baker & Hanna, '27	impressed	minute, wavy	str. curved	heavy,reflexe
H. angustata	A. Adams, 1850	subperforate	present	straight,folded	present
H. antillarum	d'Orbigny, 1841	impress.,imperf.	fine, close or absent	very concave	light
H. aperta	Pease, 1868	imperforate	fine,irregular	very concave	str. reflexed
H. aperta oahensis	Pilsbry, 1917	imperforate	none	arcuate	
H. articensis	Addicott, 1966	imperf ?, shallow	~100, wavy		
H. binotata	Pilsbry, 1895				
H. brevis	Q & G ,1833	imperf,impressed	20 anteriorly		
H. cairnsiana	Mel & Standen, 1895		regular		
H. callosa	Preston, 1908				
H. canalis	Dall, 1912	impressed	sharp,wide intersp.		
H. castanea	A. Adams, 1850	umbilicate	fine, close		
H. constricta	A.Adams, 1850		fine		
H. corticata	Beck, 1842				
H. crocata	Pease, 1860	impressed,imperf.	wavy	concave	reflexed
H. curta	Adams, 1850	depressed	present	curved	reflexed
H. cuticulifera	Smith, 1872	thick	at base	straight	thin,reflexed
H. cyanocaudata	Heller & Thompson,1983		none		
H. cyanomarginata	Heller & Thompson, 1983		none	concave	anteriorly
H. cymbalum	Q & G, 1833	impressed,imperf.			
H. cymbiformis	Carpenter, 1853 , '56 ?		small, close		
H. decora	Brazier, 1878		16, deep	straight	umbilicate
H. elegans	Gray, 1825	concave,perforate	fine, straight	arcuate	thin, white
H. exarata	Philippi, 1849		widely separated	arcuate	

SPECIES	AUTHOR	COLOUR	SIMILAR TO	FIGURED IN
H. callidegenita, n.sp.	Gibson, 1987	reddish		this paper
H. aequistriata	Smith, 1872	white	rugosa	not figured
H. alfredensis	Bartsch, 1915	gr- yellow	natalensis	Bartsch, 1815, MacNae, 1962
H. ambigua	A. Adams, ?	white	Atys	Adams, 1855, Kobelt, 1896
H. angelensis	Baker & Hanna, '27	gr-yellow	cymbiformis	Baker & Hanna, 1927
H. angustata	A. Adams, 1850	gr-yellow		Pilsbry, 1893, Kobelt, 1896
H. antillarum	d'Orbigny, 1841	greenish		Pilsbry, 1893, Kobelt, 1896
H. aperta	Pease, 1868	white	cymbalum	Pease, 1868, Pilsbry, 1893
H. aperta oahensis	Pilsbry, 1917	white	aperta	Pilsbry, 1917
H. articensis	Addicott, 1966			Addicott, 1966
H. binotata	Pilsbry, 1895	colour pattern		
H. brevis	Q & G ,1833	white w br	ovoidea	Pilsbry, 1893, A.Adams, 1855
H. cairnsiana	Mel & Standen, 1895	white	papyrus	Melvill & Standen, 1895
H. callosa	Preston, 1908		musetta	
H. canalis	Dall, 1912		papyrus	not figured
H. castanea	A. Adams, 1850	white w brown		A.Adams, 1855, Kobelt, 1896
H. constricta	A.Adams, 1850			A.Adams, 1855, Pilsbry, 1893
H. corticata	Beck, 1842	yellow	grisea	not figured
H. crocata	Pease, 1860	yellow		Annandale, 1924, Kobelt, 1896
H. curta	Adams, 1850	white		Pilsbry, 1893, Adams, 1855
H. cuticulifera	Smith, 1872	white	papyrus	Pilsbry, 1893
H. cyanocaudata	Heller & Thompson,1983	white		not figured
H. cyanomarginata	Heller & Thompson, 1983	white		Heller & Thompson, 1983
H. cymbalum	Q & G, 1833	white		Adams, 1855, Pilsbry, 1893
H. cymbiformis	Carpenter, 1853 , '56 ?	white	imperfect shell	unfigured
H. decora	Brazier, 1878	white	Atys	not figured
H. elegans	Gray, 1825	br-yellow,gr		Pilsbry, 1893, Marcus, 1957
H. exarata	Philippi, 1849	white		Pilsbry, 1893, Kobelt, 1896

SPECIES	AUTHOR	REFERENCE	SHELL SHAPE	SIZE (mm)	RATIO (L:W)
H. ferruginea	Chemnitz, ?	Reeve, 1868	ovate		
H. flavescens	A.Adams, ?	Kobelt, 1896	suboval,trunc:post	8	
H. fulgida	A. Adams, 1862	Pilsbry, 1893	elongate, truncate		
H. fusca	A. Adams , ?	Kobelt, 1896	globose-ovate	26 x 16	1.63 : 1
H. galba	Pease, 1860	Pilsbry, 1893	ovate		
H. glabra	Adams, 1850	Pilsbry, 1893	ovate, trunc.above	9 x 6	1.5 : 1
H. gracilis	Sowerby, 1897	Kilb & Ripp,1982	oblong	19	
H. grisea	Smith, 1875	Pilsbry, 1893	cylindrical	6 x 3	2.0 : 1
H. guadalapensis	Sowerby, 1853	Kobelt, 1896	globose,trunc. above	18 x 14	1.29 : 1
H. guildingii	Swainson, 1840	Kobelt, 1896	ovately oblong	20 x 16	1.25 : 1
H. hydatis	Linne, 1758 (66?)	Pilsbry, 1893	oblong-oval	11 x 8	1.38 : 1
H. insculpta	Totten, 1835	A.Adams, 1855	oval		
H. labrea	Olsson, 1928	Olsson, 1928	ovate	44 x 34	1.29 : 1
H. linda	Marcus & Burch, 1965	M & B, 1965	ovoid	10 x 7.5	1.33 : 1
H. lucida	A.Adams, ?	Pilsbry, 1893	cylindric-ovate		
H. malleata	Smith, 1872	Pilsbry, 1893	quadrate-ovate	12 x 8	1.5 : 1
H. musetta	Marcus & Burch, 1965	M & B, 1965	ovoid,swollen	8 x 5	1.51 : 1
H. natalensis	Krauss, 1868	Kobelt, 1896	ovate-globose	9 x 6.8	1.33 : 1
H. navicula	Da Costa, 1778	Pilsbry, 1893	oblong-cylindrical	23 x 16	1.44 : 1
H. nigropunctata	Pease, 1868	Pilsbry, 1893	suboval	16 x 10	1.6 : 1
H. obesa	Sowerby, 1868	Reeve, 1868	subglobose		
H. olgae	Dall, 1919	Dall, 1920	inflated	27 x 16	1.69 : 1
H. olopana	Pilsbry, 1920	Pilsbry, 1920	cylindric	7.8 x 3.3	2.36 : 1
H. orbignyana	Ferrussac, 1820	Pilsbry, 1893	oblong-oval	12	
H. oryza	Totten, 1835	A. Adams, 1855	suboval		
H. ovalis	Pease, 1868	Pilsbry, 1893	obliquely oval	9 x 6	1.5 : 1
H. ovoidea	Q & G, 1833	Kobelt, 1896	ovate	12.5 x 8	1.5 : 1

ECIES	AUTHOR				
		VERTEX	STRIAE	COLUMELLA	CALLOUS
H. ferruginea	Chemnitz, ?	umbilicate	clear, fine	str.arched	
H. flavescens	A.Adams, ?		close, minute		
H. fulgida	A. Adams, 1862		close, minute	arcuate, acute	
H. fusca	A. Adams, ?		irreg., wavy	arched	
H. galba	Pease, 1860		fine	arched	reflexed
H. glabra	Adams, 1850	concave, perforate	few, unequal spced	very concave	narrow
H. gracilis	Sowerby, 1897	narrowly perf.	fine, spiral		
H. grisea	Smith, 1875		minute, close	oblique,twisted	
H. guadalapensis	Sowerby, 1853	imperforate	fine, close, wavy	very concave	white,folded
H. guildingii	Swainson, 1840		few, well spaced		
H. hydatis	Linne, 1758 (66?)	imperf.,sl.concave	minute, close	short,straight	reflexed
H. insculpta	Totten, 1835		minute, close		
H. labrea	Olsson, 1928	concave	none ?		
H. linda	Marcus & Burch, 196	perforate	none	str.concave	low,broad
H. lucida	A.Adams, ?		throughout	arcuate	thin
H. malleata	Smith, 1872	flat	delicate	arcuate	reflexed
H. musetta	Marcus & Burch, 196	sunken	fine	concave	furrowed
H. natalensis	Krauss, 1868	impressed,imperf	none ?	arcuate	
H. navicula	Da Costa, 1778	imperf,concave,wh	many, fine, spiral	very concave	thin,reflexed
H. nigropunctata	Pease, 1868	imperforate	close	arched	laminate
H. obesa	Sowerby, 1868		"wrinkled above"	arched	umbil.,broad
H. olgae	Dall, 1919	imperf	minute, close		thin
H. olopana	Pilsbry, 1920	perforate	26, fine	sl. concave	umbilicate
H. orbignyana	Ferrussac, 1820				
H. oryza	Totten, 1835	depressed,imperf.	few		
H. ovalis	Pease, 1868	imperforate	none ?		lower only
H. ovoidea	Q & G, 1833		in front	umbilicate	

SPECIES	AUTHOR	COLOUR	SIMILAR TO	FIGURED IN
H. ferruginea	Chemnitz, ?	reddish		Reeve, 1868
H. flavescens	A.Adams, ?	yellow		Pilsbry, 1893,Adams, 1855
H. fulgida	A. Adams, 1862	white	curta	not figured
H. fusca	A. Adams , ?	fawn		Adams, 1855, Pilsbry, 1893
H. galba	Pease, 1860	yellowish	crocata	Pilsbry, 1893
H. glabra	Adams, 1850	greenish	elegans	Adams, 1855, Pilsbry, 1893
H. [illegible]cilis	Sowerby, 1897	olive-yellow		Kilburn & Rip,1982,MacNae,1962
	Smith, 1875	blue-white		
H. [illegible]is	Sowerby, 1853	gr-yellow	antillarum	Pilsbry, 1893, Kobelt, 1896
	Swainson, 1840	rufescent		Adams, 1855, Kobelt, 1896
	Linne, 1758 (66?)	gr-yellow	corticata	Adams, 1855, Kobelt, 1896
	Totten, 1835	blueish-wh.		Adams, 1855, Reeve, 1868
H. labrea	Olsson, 1928		grandis	Olsson, 1928
H. linda	Marcus & Burch, 1965	white		Marcus & Burch, 1965
H. lucida	A.Adams, ?	glassy	brevissima	
H. malleata	Smith, 1872	white		
H. musetta	Marcus & Burch, 1965			Marcus & Burch, 1965
H. natalensis	Krauss, 1868	gr-yellow		Pilsbry,1893, Adams, 1855
H. navicula	Da Costa, 1778	wh - yellow	hydatis	Pilsbry, 1893, Kobelt, 1896
H. nigropunctata	Pease, 1868	chestnut		Pilsbry,1893,Kobelt,1896
H. obesa	Sowerby, 1868	pale fulvous	pemphix	Reeve, 1868
H. olgae	Dall, 1919	y - gr, red-br	vesicula	not figured
H. olopana	Pilsbry, 1920	white	curta	Pilsbry, 1893
H. orbignyana	Ferrussac, 1820	gr-yellow	hydatis	
H. oryza	Totten, 1835	white		A.Adams, 1855
H. ovalis	Pease, 1868	greenish		Pilsbry, 1893,Kobelt, 1896
H. ovoidea	Q & G, 1833	white		Pilsbry, 1893, Kobelt, 1896

SPECIES	AUTHOR	REFERENCE	SHELL SHAPE	SIZE (mm)	RATIO (L:W)
H. papyrus	Salis, 1793	Kobelt, 1896	cylindrical	15 x 8.5	1.76 : 1
H. pemphis	Philippi, 1847	Kobelt, 1896	subglobose,rotund	15 x 11	1.27 : 1
H. perforata	Philippi, 1847	Pilsbry, 1893	ovate-rotund	8 x 5.5 lines	1,45 : 1
H. perplexa	Smith, 1872	Pilsbry, 1893	ovate-cylindrical	14 x 7.5	1.87 : 1
H. perrieri	Morlet, 1889	Morlet, 1889	ovate-oblong	16 x 9	1.78 : 1
H. peruviana	d'Orbigny, 1837	Pilsbry, 1893	oval	20	
H. petersi	von Martens, 1879	Pilsbry, 1893	oblong	19 x 13	1.46 : 1
H. petitii	d' Orbigny, 1842	Pilsbry, 1893	cyl-oval, trunc abv	9 x 6	1.5 : 1
H. postangulata	Clark & Woodford, 1927	C & W, 1927	subovate	26 x 19	1.37 : 1
H. pusilla	Pease, 1860	Pilsbry, 1893	cylindr-ovate		
H. rotundata	A. Adams, 1850	Kobelt, 1896	ovate	11.5 x 8	1.44 : 1
H. rugosa	Smith, 1872	Pilsbry, 1893	cylindrical	6 x 3	2.0 : 1
H. sandwichensis	Sowerby, 1868	Kobelt, 1896	ovate,pointed ends	15	
H. savignyana	Gray, 1825	Pilsbry, 1893	ovate-oblong	12.5	
H. serica	Smith, 1872	Pilsbry, 1893	rotundly-ovate	11 x 9	1.22 : 1
H. simillima	Pease, 1868	Pilsbry, 1893	oval	8 x 6	1.33 : 1
H. sinensis	A. Adams, 1850	A.Adams, 1855	oval		
H. solaria	Olsson, 1928	Olsson, 1928	subspherical	65 x 59	1.1 : 1
H. solitaria	Say, 1822	Pilsbry, 1893	sub-cyl,concave sds	10 x 6.5	1.54 : 1
H. strigosa	A.Adams, 1862	Pilsbry, 1893	cylindr-ovate		
H. strongi	Baker & Hanna, 1927	B & H, 1927	narrow base	14.1 x 10.2	1.38 : 1
H. subcylindrica	Sowerby, 1897	MacNae, 1962	subcylindrica		
H. subpellucida	H.Adams, 1869	Adams, 1869	ovate	17 x 11	1.55 : 1
H. succinea	Conrad, 1846	Pilsbry, 1893	cyl, wide base	10 x 5.66	1.79 : 1
H. tenella	A. Adams, 1850	Pilsbry, 1893	oval,trunc.above		
H. tenera	Adams, 1850	Kobelt, 1896	obliquely ovate	13 x 8.5	1.53 : 1
H. tomaculum	Pilsbry, 1920	Pilsbry, 1920	cylindrical	12.4 x 5.5	2.25 : 1
H. ventripotens	Cossman, 1913	Cossman, 1913	ovate	11 x 8.5	1.29 : 1

SPECIES	AUTHOR				
		VERTEX	STRIAE	COLUMELLA	CALLOUS
H. papyrus	Salis, 1793		present		
H. pemphis	Philippi, 1847	umbilicated			
H. perforata	Philippi, 1847	umbilicated	fine	umbilicated	
H. perplexa	Smith, 1872	depressed, deep	distant	simple	sl. reflexed
H. perrieri	Morlet, 1889	concave	irregular	concave	umbilicate
H. peruviana	d'Orbigny, 1837			laminated	
H. petersi	von Martens, 1879		sub-vertical		thickened
H. petitii	d' Orbigny, 1842	impressed,imperf	none	staight	umbilicate ?
H. postangulata	Clark & Woodford, 1927		none ?		
H. pusilla	Pease, 1860	perforate	fine	folded at base	
H. rotundata	A. Adams, 1850		very fine		
H. rugosa	Smith, 1872	depressed	distinct	reflexed	chinked
H. sandwichensis	Sowerby, 1868			straight	
H. savignyana	Gray, 1825	imperforate	smooth	subreflexed	
H. serica	Smith, 1872		fine, close	thick,twisted	umbil.,thin
H. simillima	Pease, 1868	imperforate	inconspicuous	arched antrly	present
H. sinensis	A. Adams, 1850		wide apart		
H. solaria	Olsson, 1928	flat,umbilicate	worn ?		
H. solitaria	Say, 1822	impress,subperf.	deeply impressed	concave	thin
H. strigosa	A.Adams, 1862		minute, lots	arcuate	simple
H. strongi	Baker & Hanna, 1927	depressed	very fine		
H. subcylindrica	Sowerby, 1897	sl.umbilicate	dense	straight	
H. subpellucida	H.Adams, 1869	perforated	irregular		
H. succinea	Conrad, 1846	impressed	even + deep	very concave	umbilicate
H. tenella	A. Adams, 1850		irreg.ridges		
H. tenera	Adams, 1850		fine		
H. tomaculum	Pilsbry, 1920		none		
H. ventripotens	Cossman, 1913	perforate			

SPECIES	AUTHOR	COLOUR	SIMILAR TO	FIGURED IN
H. papyrus	Salis, 1793	white		Pilsbry, 1893, Adams, 1855
H. pemphis	Philippi, 1847	reddish	tenella	Pilsbry, 1893, Adams, 1855
H. perforata	Philippi, 1847	white	hydatis, ovoidea	
H. perplexa	Smith, 1872	blueish	Atys	
H. perrieri	Morlet, 1889	greenish		Morlet, 1889
H. peruviana	d'Orbigny, 1837	gr-yellow		Kobelt, 1896
H. petersi	von Martens, 1879	yellow	galba	Pilsbry, 1893
H. petitii	d' Orbigny, 1842	gr yellow	antillarum	Pilsbry, 1893, Kobelt, 1896
H. postangulata	Clark & Woodford, 1927		-	C & W ,1927
H. pusilla	Pease, 1860	white		unfigured
H. rotundata	A. Adams, 1850			Pilsbry, 1893, Adams, 1855
H. rugosa	Smith, 1872	white	brevis	unfigured
H. sandwichensis	Sowerby, 1868	white	galba	Pilsbry, 1893, Kobelt, 1896
H. savignyana	Gray, 1825	buff		unfigured
H. serica	Smith, 1872	whitish	insculpta	
H. simillima	Pease, 1868	white	nigropunctata	Pilsbry, 1893, Kobelt, 1896
H. sinensis	A. Adams, 1850	white		A.Adams, 1855
H. solaria	Olsson, 1928			Olsson, 1928
H. solitaria	Say, 1822	wh-amber		Pilsbry, 1893, Kobelt, 1896
H. strigosa	A.Adams, 1862	white	lucida	not figured
H. strongi	Baker & Hanna, 1927	green	virescens	Baker & Hanna, 1927
H. subcylindrica	Sowerby, 1897	white	brevis	MacNae, 1962
H. subpellucida	H.Adams, 1869	white		Adams, 1869
H. succinea	Conrad, 1846	white	solitaria	Pilsbry,1893,Kobelt,1896
H. tenella	A. Adams, 1850		pemphis	A.Adams, 1855
H. tenera	Adams, 1850	cream	vitrea	Pilsbry, 1893, Adams, 1855
H. tomaculum	Pilsbry, 1920	white	curta	Pilsbry, 1917 (as curta tomac.)
H. ventripotens	Cossman, 1913		elegans, glabra	Cossman, 1913

SPECIES	AUTHOR	REFERENCE	SHELL SHAPE	SIZE.(mm)	RATIO (L:W)
H. vesicula	Gould, 1855	Pilsbry, 1893	globose-oval,rd abv	18 x 13	1.38 : 1
H. virescens	Sowerby, 1833	Pilsbry, 1893	globose-ovate	14 x 10.5	1.33 : 1
H. vitrea	Adams, 1850	Kobelt, 1896	ovate-cylindrical	7.5	
H. wallisii	Gray, 1825	Pilsbry, 1893	oblong-ovate	6.25	
H. zanzibarica	Vanatta, 1901	Vanatta, 1901	subglobose	20 x 14	1.39 : 1
H. zelandiae	Gray, 1843	Pilsbry, 1893	globose-ovate	22 x 19	1.16 : 1

SPECIES	AUTHOR				
		VERTEX	STRIAE	COLUMELLA	CALLOUS
H. vesicula	Gould, 1855	imperf,narrow,dp	close, fine	very concave	narrow
H. virescens	Sowerby, 1833	impress,perforate		dply arcuate	narrow
H. vitrea	Adams, 1850		fine		
H. wallisii	Gray, 1825	imperforate	minute		subreflexed
H. zanzibarica	Vanatta, 1901	impress,imperf.	close, fine	evenly concave	thin
H. zelandiae	Gray, 1843	impress,imperf.	none	concave	reflexed

SPECIES	AUTHOR			FIGURED IN
		COLOUR	SIMILAR TO	
H. vesicula	Gould, 1855	gr,wh,yellow		Abbott, 1954, Pilsbry, 1893
H. virescens	Sowerby, 1833	gr-yellow		Abbott, 1954, Kobelt, 1896
H. vitrea	Adams, 1850	white		Pilsbry, 1893, Adams, 1855
H. wallisil	Gray, 1825	buff		not figured
H. zanzibarica	Vanatta, 1901	pinkish, w ora	zelandiae	Vanatta, 1901
H. zelandiae	Gray, 1843	straw	pemphix	Pilsbry, 1893, Powell, 1979

Table 4. A summary of *Haminoea* adult morphologies, compiled from the literature (references listed). Features included are: body length, colour, cephalic shield, epipodial lobes, Hancock's organ, radula formula, median and first lateral teeth, gizzard plates, and the penis complex.

#	SPECIES	AUTHOR	REFERENCE	LENGTH (mm)	COLOUR	CEPHALIC SHIELD
1	H. callidegenita, n.sp.	Gibson, 1987	this paper	26	brown w. black	bifurcate
2	H. attfedensis	Bartsch, 1915	MacNae, 1962	30	yellow-gr, w red	
3	H. agillarum	d'Orbigny, 1841	Rudman, 1971b	5 to 18	br w bk, wh, orange	slightly bilobed
			Marcus&Marcus,1967		yellow to black	
4	H. brevis	Quoy&Gaimard,1832	Mac & Gabr.,1982		white	
5	H. crocata	Pease, 1860	Annandale, 1924		cinerous	bilobed
			Burn, 1966		yellow w purp,br.	
			Kay, 1979		green w rust*	
			Rudman, 1979b			
6	H. cyanocaudata	Heller & Thompson,1983	H & T, 1983	3.5	wh w purple+green	bifurcate
7	H. cyanomarginata	Heller & Thompson, 1983	H & T, 1983	5.5	gr w wh & cream	bifurcate
8	H. cymbalum	Quoy & Gaimard,1833	Kay, 1979		gr w purple+ oran	1/2 notched
			Rudman, 1971b			
9	H. elegans	Gray, 1825	Marcus, 1957	24	peppar + salt,fawn	not bilobed
10	H. galba	Pease, 1860	Kay, 1979		grey-yellow	bilobed,triangular
11	H. gracilis	Sowerby, 1897	MacNae, 1962	20	gr-yellow	
12	H. hydatis	Linne, 1758	Forbes&Hanley,1853	30	dark	bilobed
13	H. linda	Marcus & Burch, 1965	Marcus&Burch, 1965	17	gr w ora & maroon	bilobed
14	H. musetta	Marcus & Burch, 1965	Marcus&Burch,1965	15	pale gr w dk & bk	bifurcate
15	H. natalensis	Krauss, 1848	MacNae, 1962			
16	H. navicula	Da Costa, 1778	Th & Brown, 1976	70	br w.bk, changes	si bifurcate
17	H. nigropunctata	Pease, 1868	Marc&Burch,1965		bk dots	bifurcate
18	H. ovalis	Pease, 1868	Kay, 1979		gr w wh & ora	bifurcate
19	H. petersi	vonMartens, 1879	MacNae, 1962		yellow-gr,mottled	
20	H. peruviana	d'Orbigny, 1837	Pilsbry, 1893		gr-yellow,w.black	
21	H. simillima	Pease, 1868	Eliot, 1906	15	pale gr w wh & ora	bifurcate
			Rudman, 1971b			
22	H. solitaria	Say, 1822	Rudman, 1971b			
23	H. tenera	Adams, 1850	Burn, 1966		grey w orange	
24	H. vesicula	Gould, 1855	this paper	42	br w bk & wh	not bifurcate
25	H. virescens	Sowerby, 1833	Abbott, 1954	larger than vesicula	dk gr w yellow	
26	H. zelandiae	Gray, 1843	Rudman, 1971a+b	40	grey & br, mottled	small notch

#	SPECIES	AUTHOR	EPIPODIAL LOBES	HANCOCK'S ORGAN	PENIS COMPLEX	GIZZARD PLATES
1	H. callidegenita, n.sp.	Gibson, 1987	cover 1/3 shell	not lamellated	unilobed	~ 24 ridges
2	H. alfredensis	Bartsch, 1915			pr bilobed	
3	H. antillarum	d'Orbigny, 1841		10 d.,12 vtr lamel.	pr bipartite	24 ridges
4	H. brevis	Quoy&Gaimard,1832				deeply toothed
5	H. crocata	Pease, 1860			unarmed	spines & ridges
6	H. cyanocaudata	Heller & Thompson,1983	meet dorsally		not examined	
7	H. cyanomarginata	Heller & Thompson, 1983	do not meet dorsally		elongate prostate	
8	H. cymbalum	Quoy & Gaimard,1833		no leaflets		
9	H. elegans	Gray, 1825	cover most of shell	16 d, 20 vtr lamel.	bipartite prostate	24 ridges
10	H. galba	Pease, 1860				
11	H. gracilis	Sowerby, 1897				
12	H. hydatis	Linne, 1758		12 pr lamellae	unarmed,pr w 3 lobe	3 plates, 6 spines
13	H. linda	Marcus & Burch, 1965		12 lam.,not pinnate	pr globose	17 ridges
14	H. musetta	Marcus & Burch, 1965	cover 1/2 shell	figured	sl lobed, nearly glob	17 ridges
15	H. natalensis	Krauss, 1848				
16	H. navicula	Da Costa, 1778		20 pr lamellae	2 lobes, unarmed	3 lg, 6 small spines
17	H. nigropunctata	Pease, 1868				
18	H. ovalis	Pease, 1868				
19	H. petersi	vonMartens, 1879				
20	H. peruviana	d'Orbigny, 1837				smooth
21	H. similima	Pease, 1868				10 ridges
22	H. solitaria	Say, 1822				
23	H. tenera	Adams, 1850				
24	H. vesicula	Gould, 1855			pr unequally bilobed	16 ridges
25	H. virescens	Sowerby, 1833		18 prs lamellae	pr spherical	18 ridges
26	H. zelandiae	Gray, 1843		slightly folded	segmented	4 ridges

#	SPECIES	AUTHOR	RADULA	TEETH	FIRST LATERAL
			FORMULA	MEDIAN	FIRST LATERAL
1	H. callidegenita, n.sp.	Gibson, 1987	n.1.1.1.n	tricuspid	1 median notch
2	H. alfredensis	Bartsch, 1915	25-30x 50.1.50	long mid.cusp	serr. medially
3	H. antillarum	d'Orbigny, 1841	29 x 23.1.23		
4	H. brevis	Quoy&Gaimard,1832			
5	H. crocata	Pease, 1860	5.1.1.1.5	3 notches	smooth
			40.1.40		
6	H. cyanocaudata	Heller & Thompson,1983	9x 5.1.5	lrg mid cusp	smooth
7	H. cyanomarginata	Heller & Thompson, 1983	20 x 6.1.6	lrg mid cusp	serrated
8	H. cymbalum	Quoy & Gaimard,1833			
			10.1.10,13.1.13		
9	H. elegans	Gray, 1825	35 - 39x 20.1.20	3 notches	sl.notched dist.
10	H. galba	Pease, 1860			
11	H. gracilis	Sowerby, 1897	25x 14.1.14	tricuspid	almost smooth
12	H. hydatis	Linne, 1758	n.1.1.n., n to 36		
13	H. linda	Marcus & Burch, 1965	25 x 8.1.8	mid-lg,serrat	serrated medial
14	H. musetta	Marcus & Burch, 1965	23-35, 10.1.10	lg-med notch	smooth
15	H. natalensis	Krauss, 1848	5.1.5.	lrg. mid cusp	smooth ?
16	H. navicula	Da Costa, 1778	17 x 4-5.1.1.1.4-5		
17	H. nigropunctata	Pease, 1868			
18	H. ovalis	Pease, 1868			
19	H. petersi	vonMartens, 1879	25-30x 12.1.12	long med.cusp	serr. medially
20	H. peruviana	d'Orbigny, 1837			
21	H. simillima	Pease, 1868	32, 35 x 8.1.8	lg median notc	smooth (worn?)
			9.1.9		
22	H. solitaria	Say, 1822	15.1.15		
23	H. tenera	Adams, 1850			
24	H. vesicula	Gould, 1855	30.1.1.1.30	lg med notch	serrated distally
25	H. virescens	Sowerby, 1833	34 x 64.1.64		
26	H. zelandiae	Gray, 1843	16 x 57.1.57	3 notches	smooth, sharp

Table 5. Notes on *Haminoea* natural history, compiled from the literature (references listed), including habitat descriptions.

#	SPECIES	AUTHOR	REFERENCE	HABITAT	NOTES
1	H. callidegenita, n.sp.	Gibson, 1987	this paper	mud, on Chaetamorpha	this paper
2	H. alfredensis	Bartsch, 1915	Kil & Rip, 1982	sandy mud, on Zostera	
			MacNae, 1962	on Zostera & Ruppia	epiphytic grazers
3	H. antillarum	d'Orbigny, 1841	Humfrey, 1975	, mud	uncommon
			Olmsted, 1917		mucous-cliiary locamotion
			Thompson, 1977	soft substratum, 2 m water	
4	H. ant. guadalupensis	Sowerby, 1853	Leigh, 1953	grassy shallow area	infected w. Cercaria
5	H. articensis	Addicott, 1966	Addicott, 1966		Tertiary fossil
6	H. brevis	Quoy&Gaimard, 1832	Burn, 1966	intertidal, & 5 fa, sand-mud	
			Mac&Gab.1962	mud	prey on bivalves
7	H. castanea	A. Adams, 1850	A. Adams, 1855	4 fa, on mud	
8	H. constricta	Adams, 1850	A. Adams, 1855	on sandy mud, low water zone	
9	H. crocata	Pease, 1860	Kay, 1979	in sand on algae on rocks	prey of Conus
			Natarajan, 1970		17 bivalent chromosomes
			Ostergaard, 1950		egg mass described
10	H. curta	A. Adams, 1850	Kay, 1979	12 - 25 m	
11	H. cuticulifera	Smith, 1872	Pilsbry, 1893	2-15 fms (shell)	
12	H. cyanocaudata	Heller & Thompson, 1983	H & T, 1983	coral rubble, 1.5 m	
13	H. cyanomarginata	Heller & Thompson, 1983	H & T, 1983	coral rubble, 1.5 m	
14	H. cymbalum	Quoy & Gaimard, 1833	Kay, 1979	intertidal, rocky pools	
15	H. decora	Brazier, 1878	Brazier, 1878	11 fa, mud	
			Pilsbry, 1893	11-20 fms, sandy mud	
16	H. elegans	Gray, 1825	Humfrey, 1975	20 , sand & mud	common
			Marcus, 1956	mud, below low tide	
			Thompson, 1977	in gravel	with spawn in July
17	H. fusca	A. Adams, ?	A. Adams, 1855	sandy mud, low water	
			Pilsbry, 1893	25 fms (shell)	
18	H. gracilis	Sowerby, 1897	Kil&Rip, 1982	high rock pools, mud	on Zostera, Enteromorpha
			MacNae, 1962	sandy-mud	
19	H. grisea	Smith, 1875	Pilbry, 1893	48 fms (shell)	
20	H. hydatis	Linne, 1758 (66?)	?, 1889	estuary, mud substrata	swimming ?
			Berrill, 1931		lecithotrophic development
			Fbs&Hny,1853	in [illegible]ria zone	
			Grell, 1960		describes cleavage
			Thopmson, 1981	on subtidal & low tidal Ulva	with spawn in August
			Th&Brown,1976	muddy sand, lower shore	diet- herbiv.,sm.bivalves
21	H. labrea	Olsson, 1928	Olsson, 1928	in Turritella beds	eocene fossil

#	SPECIES	AUTHOR	REFERENCE	HABITAT	NOTES
22	H. linda	Marcus & Burch, 1965	M & B, 1965	sand lagoon, at 2 m	
23	H. maugeansis	Burn, 1966	Burn, 1974	on Zostera, shingle, algae	[illegible] prey of Aglaja
24	H. musetta	Marcus & Burch, 1965	M & B, 1965	tide flats	
25	H. natalensis	Krauss, 1848	MacNae, 1962	sandy mud	[illegible]
26	H. navicula	Da Costa, 1778	Edlinger, 1982	sand substratum	[illegible] change
			Th&Brown,1976	littoral on Zostera	
27	H. nigropunctata	Pease, 1868	Pease, 1868	shallow water,on seaweed	
28	H. papyrus	Salis, 1793	Brazier, 1878	sand, 30 fms (shell)	
29	H. petersi	Martens, 1879	MacNae, 1962	on eelgrass & mud	colour adaptation w substrate
30	H. postangulata	Clark & Woodford,1927	C & W, 1927		mid-Eocene fossil
31	H. simillima	Pease, 1868	Eliot, 1906	intertidal, on seaweed	
32	H. solaria	Olsson, 1928	Olsson, 1928		eocene fossil
33	H. solitaria	Say, 1822	Abbott & Dance	intertidal grass	common
34	H. strigosa	A. Adams, 1862	Pilsbry, 1893	25 fms (shell)	
35	H. subcylindrica	Sowerby, 1897	MacNae, 1962	sandy-mud	
36	H. tenera	A. Adams, 1850	Burn, 1966	on Zostera & Chaetamorpha	epiphytic grazer, intertidal
			Mac & Gab,1962	sandy-mud	common
37	H. tomaculum	Pilsbry, 1920	Pilsbry, 1917	6-8 fms (shell)	
38	H. vesicula	Gould, 1855	Abbott, 1954	littoral, bay	common
			Mor.etal,1980	mud flats & sandy bays	seasonally common
			Richards, 1923		cites Leonard- spawn
			Sm[illegible]arl.,1975	sloughs, lagoons, mudflats	on Enteromorpha,Polysiphonia
39	H. virescens	Sowerby, 1833	Abbott, 1954	littoral, open coast	common
			Bradshaw, 1895	intertidal, rocky reef	rare
			MacG&MacG,1949		white ribbon like egg mass
			M & M, 1967	intertidal	abundant in spring
			Mor.etal, 1980	upper intertidal rocky pools	seasonally common
			Richards, 1921	tidal flat	spawn mass, development
			Richards, 1923		development, brief
			Sm&Carl.,1975	high tidepools, rocky areas	open coast
40	H. virescens rosacea	Spicer, 1933	Spicer, 1933	mudflat	uniform size at June coll.
41	H. vitrea	A. Adams, 1850	Brazier, 1878	inside reef, on mud	
42	H. zelandiae	Gray, 1825	Powell, 1979	tidal mudflats, on Zostera	herbivorous, common
			Rudman, 1971	mud flats & coraline rocky	herbivorous, move by ciliary
				Zostera, Corallina	action, mucous tubes

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CHAPTER 3

DESCRIPTION OF A NEW SPECIES OF *HAMINOEA*, *HAMINOEA CALLIDEGENITA* (OPISTHOBRANCHIA: CEPHALASPIDEA).

INTRODUCTION :

A population of *Haminoea* was discovered in Spencer's Spit, Lopez Island, Washington, by the late Professor R.L. Fernald of the University of Washington, Seattle. Subsequently, a second population was found at Rock Point, Samish Bay, Washington. These *Haminoea* were considered unusual in that they differed developmentally from *H. vesicula* Gould 1855, a superficially similar species common in the Pacific Northeast.

Animals from these 2 populations were examined and compared both morphologically and developmentally with individuals known to be *Haminoea vesicula* in an attempt to distinguish the two species. It appeared that not only were the Spencer's Spit and Rock Point populations distinct from *H. vesicula*, but a review of the literature also indicated that they represented a new species.

Haminoea callidegenita n. sp. were found on muddy substrata in intertidal and shallowly subtidal zones, as is typical of the genus. In the Spencer's Spit population, animals and egg masses were found in dense mats of the alga *Chaetamorpha linum*. In the Rock Point population, they were found on beds of the grass *Phyllospadix scouleri*. They differ from *H. vesicula* in being slightly more reddish-brown in colour, having a deeply bifurcate cephalic shield, and a thicker, more ovate shell. The morphologies of the penis complex, Hancock's organ, and radula are also diagnostic characters.

In this chapter, I describe this new species, *Haminoea callidegenita*, and present criteria for distinguishing among 3 species

In this chapter, I describe this new species, *Haminoea callidegenita*, and present criteria for distinguishing among 3 species of *Haminoea* presently known from the Pacific Northeast coast: *H. vesicula* Gould 1855, *H. virescens* Sowerby 1833, and *H. callidegenita*, n.sp..

MATERIALS AND METHODS:

Specimens of *Haminoea callidegenita* n. sp. were collected from 2 locations; Spencer's Spit, Lopez Island, Washington (48° 33' N, 122° 51' W) throughout the period from November 1984 to October 1986, and the Rock Point Oyster Company, Samish Bay, Washington (48° 36' N, 122° 28' W) in October 1986.

Animals were kept at Bamfield Marine Station, Bamfield, British Columbia, in aquaria with continuously flowing seawater at ambient temperature (with an annual range from 6 ° to 14 ° C). Adults were supplied with *Chaetamorpha linum* and *Ulva* sp. as food. Egg masses were collected and maintained in Pyrex beakers containing bag-filtered (1 μm) seawater. Larvae and juveniles were cultured in Pyrex dishes without antibiotics, and after metamorphosis, were provided with *Chaetamorpha* and *Ulva* as food. Light microscopic observations and measurements were made using a calibrated ocular micrometer on a Reichert compound microscope, and on a Wild M5 dissecting microscope.

Total body length of adults and juveniles was measured while animals were actively crawling. Sketches and additional measurements were made with a camera lucida. Both fresh (7% MgCl anaesthetized) and fixed (10 % phosphate buffered formalin)

specimens of *H. callidegenita* were used unless otherwise indicated. Each structure was examined in a minimum of 10 specimens for both populations. For the radulae, the number of uncini per row of teeth was determined at the widest point. Radulae of the formalin-fixed specimens were prepared for examination by scanning electron microscopy by removing the investing tissue layers with 6 % sodium hypochlorite, followed by rinsing with distilled water. Gizzard plates were removed from fresh specimens, rinsed in seawater with a 15 s sonication, and fixed in 2.5 % glutaraldehyde in seawater, followed by a secondary fixation in 2 % osmium tetraoxide. The plates were then dehydrated in ethanol, rinsed in amyl acetate overnight, and critical point dried. Specimens of radulae and gizzard plates were examined at the University of Alberta on a stereoscan 100.

A morphological comparison was made between specimens of *H. vesicula* Gould 1855, *H. virescens* Sowerby 1833, and *H. callidegenita*, n.sp.. *H. vesicula* were collected from Grappler and Bamfield Inlets, Bamfield, British Columbia, from False and Fisherman's Bays, in the San Juan Islands, and from the Rock Point Oyster Company, Samish Bay, Washington. *H. virescens* were borrowed from the Santa Barbara Museum of Natural History, Santa Barbara, California (wet specimens, No. B3212, collected at Goleta, Coal Oil Point, California), and from the San Diego Society of Natural History, San Diego, California (shells, No. 29020, collected from Laguna Beach, California; No. 29021, San Pedro, California; No. 2667; Ocean Beach, California; and No. 18880, San Diego, California). Observations of these 2 species were made as outlined for *H. callidegenita* on both fresh and fixed specimens of *H. vesicula*, and fixed only (10 % formalin with hexamene) for *H.*

virescens.

RESULTS AND DISCUSSION:

DESCRIPTION OF THE GENUS:

Class: Gastropoda

Subclass: Opisthobranchia

Order: Cephalaspidea

Family: Haminoeidae Pilsbry, 1895 (Cernohorsky, 1985)

Genus: *Haminoea* Leach, 1818 (*in* Gray, 1847)

DIAGNOSIS:

Body oblong, with a broad, depressed head, bilobed posteriorly. Eyes sessile in the middle of the head. Foot subquadrate, with 2 large swimming lobes [parapodia] which nearly cover the shell. Shell convolute, thin , horny, transversely grooved, and destitute of spire (from Adams, 1855). Shell convulute, ovate, thin, generally horny, with spire concealed; inner lip very thin, with columella curved; outer lip elevated above the spire (from Reeve, 1868).

TYPE SPECIES : *Bulla hydatis* Linnaeus 1758

DESCRIPTION OF A NEW SPECIES, *HAMINOEA CALLIDEGENITA*.

DIAGNOSIS :

Ground colour ranging from grey- brown to light brown, tinged with reddish gold, and sprinkled with dark brown pigment spots. Cephalic shield deeply bifurcate posteriorly. Parapodial lobes covering the anterior third of the shell, but not meeting dorsally. Shell pale reddish white in colour, and measuring 13.8 x 10.3 mm (in a 28 mm specimen). Apex depressed and imperforate, with insertion of the apertural lip on the left. Hancock's organ not lamellated, but

consisting of a long, narrow, convoluted band. Penis unarmed, and with a unilobular, slightly pear-shaped prostate. Radular formula n.1.1.1.n (n from 12 to 21); rachidian tooth tricuspid, and first laterals distally notched.

ETYMOLOGY:

This species was given the name *callidegenita* (from the Latin *callidus*, meaning clever or cunning, and *genare*, meaning to give birth), which translates as one who gives birth in a versatile and elegant manner. This name referred to the pattern of development exhibited by this species: from each egg mass, some individuals hatched as veligers and some as juveniles, and thus exploited both dispersive and benthic larval strategies. This development pattern is unusual, and was considered as a suitable basis for the species name.

TYPE MATERIAL:

Type specimens will be deposited at the following museums. *Holotype*: British Columbia Provincial Museum, collected at Spencer's Spit, Lopez Island, Washington (48 ^{o} 33 ' N, 122 ^{o} 51 ' W), by G. Gibson, October 11, 1986, at a depth of 0.25 m, from a silty substratum dominated by the green alga *Chaetamorpha linum*, live body length 28 mm (17 mm fixed), fixed in 10% phosphate buffered formalin and transferred to 70% ethanol. *Paratypes*: University of Alberta Museum, live body length 26 mm, same date and locality of collection as holotype, 10% phosphate buffered formalin fixation. California Academy of Sciences, Invertebrate Zoology, live body length 26 mm, same date and locality of collection as the holotype, 10% phosphate buffered formalin fixation. Additional paratypes (both wet specimens and shells) will be deposited with each of the above specimens.

DESCRIPTION:

a) External Features:

Ground colour, variable between individuals, ranges from grey-brown to light brown and is tinged with reddish-gold. Numerous dark brown pigment spots, of different sizes and configurations, are distributed over the animal, especially but not exclusively, on the dorsal surface. Pigment is concentrated along the edges of the parapodial lobes, the posterior pallial lobe, and in a V-shape on the head, the [illegible] the cleft of the posterior lobes of the cephalic shield (Fig.6). Orange spots are scatter[illegible]out, as are distinct white spots which are also concentrated along the margins of the parapodial lobes, the posterior pallial lobes, and the lobes of the cephalic shield. The transparent shell reveals a similar pigment distribution in the underlying mantle tissue. Growth lines in the shell are clearly visible. The eyespots are covered by a thin layer of lightly pigmented tissue. The overall effect of this pigmentation pattern is a reddish, or greyish brown colouration that is darker dorsally and along the margins of the various lobes. Specimens collected at Rock Point are slightly more reddish than those collected at Spencer's Spit, but otherwise the pigmentation patterns are identical. Colour adaptation, reported in *H. havicula* by Edlinger (1982) was not observed.

The body shape is bullaeform, as is typical of the genus. The parapodial lobes are reflexed over the anterior third of the shell and do not meet dorsally. The anterior foot is flared and flattened in the region parallel to the eyes. The anterior cephalic shield is laterally extended into 2 small,flexible protrusions which are highly variable as the animal crawls about. Posteriorly it is deeply cleft into 2 defined

lobes which project over the anterior part of the shell. The posterior pallial lobe is partially reflected up over the posterior edge of the shell; the rest of the pallial lobe is flattened.

The ovate shell (Fig.7; also, Chapter 2, Fig. 1) is white, with a pale reddish tinge, externally and internally. Colour intensity is variable between individuals but not correlated with size, as reported by Marcus (1957) in *H. elegans*. In a 28 mm specimen, the shell was 13.8mm x 10.3mm in size, giving a L:W ratio of 1.4:1, with width measured at the widest point just posterior to the middle of the shell. Variation in the length:width ratio among similar and over a range of shell sizes is shown in Chapter 2, Fig. 2. The apex is rounded, depressed, and imperforate. The outer lip rises sharply from the left side of the apex and is rounded slightly above the apex. The columella is concave, and the reflected callous variable in breadth but consistently thick between individuals. The callous is broadest on the body whorl, then narrows to encircle the apical depression. The callous is usually white, but may have a slight creamy or reddish tinge in some specimens. The umbilicus is not depressed. Growth lines are distinct and uniform along the length of the shell. Fine, regular, wavy, spiral striae were visible with a magnification of 6 x. Shells were always composed of 1.5 whorls, regardless of size, and supportive of Marcus' (1957) theory that in this genus the central portion is dissolved as the periphery grows.

Hancock's organ (Fig. 7) ias not divided into distinct lamellae, as has been described in other species of *Haminoea*, (Fig. 7; also, Chapter 2, Table 4), but is slightly folded, resembling that of *H. cymbalum* and *H. zelandiae* (Rudman, 1971). This species differs in that Hancock's

organ is formed by a long, narrow (3.4 mm x 0.15 mm), slightly convoluted band, surrounded by an oval-shaped, non-inflated area of lightly pigmented tissue.

b) Internal Anatomy :

Sizes listed for the following characteristics were measured in a 28 mm specimen, unless otherwise indicated.

The chitinous jaws are of the same configuration as those in other species that have been examined (Fig. 7; also, Chapter 2, Table 4). They are 0.9 mm x 0.6 mm in size, and are covered by a cross-hatched pattern.

The radula was 1.7 mm x 1.2 mm (measured at the widest point). The formula in this specimen was 19.1.1.1.19, n counted at the widest portion of the radula. The number of laterals (n) varies among specimens, ranging from 12 in a 14 mm animal to 21 in a 26 mm animal. The median tooth is tricuspid, the first lateral has a 15μm medial notch, and the uncini are all similar in shape and decrease in size from medial to distal. A slight variation in the size and shape of the rachidian tooth was observed among individuals from both study populations (Chapter 2, Fig. 4).

The 3 gizzard plates (Fig. 7) were 1.6 mm x 1.1 mm, with 12 medial ridges, and show the gross morphology considered typical of the genus (Marcus and Marcus, 1967). The presence of long, pointed papillae on the medial surface of these ridges was noted (Chapter 2, Fig. 5). Size and ridge number are variable between specimens, but not correlated with specimen size.

The morphology of the penis complex has also been demonstrated as a diagnostic character (Marcus and Marcus,1967;

Rudman, 1971; Thompson,1977). *Haminoea callidegenita* has an unarmed penis (Fig. 7), without cuticularized spines such as described in *H. elegans* (Marcus, 1956). The penis sheath was 1.9 mm long, and was connected via a 2.9 mm coiled duct to a unilobular, slightly pear-shaped, 1.6 mm long prostate.

The digestive, reproductive, nervous, and circulatory systems are as descibed in *Haminoea zelandiae* (Rudman, 1971).

HABITAT, RANGE AND NATURAL HISTORY:

Haminoea callidegenita have been observed at two sites, Spencer's Spit, Lopez Island (48° 33' N, 122° 51' W) and the Rock Point Oyster Company, Samish Bay (48° 36' N, 122° 28' W), both in Washington State, U.S.A.. A search was done throughout the San Juan Islands in July and August 1986, but no additional populations were found. Possibly other populations exist along at least the Washington coast, but have not been recognized by others because of this species' external similarity to the common *Haminoea vesicula*.

The lagoon at Spencer's Spit consists of a long, straight sand spit extending perpendicularly from the shore. Marshes are present along the north side, forming a shallow lagoon that is kept from becoming totally isolated by a narrow (~1.5 m wide) channel to the ocean. Depth fluctuates slightly with tidal cycle, but the lagoon was rarely deeper than 1 m at it's deepest point. The substratum is silty mud. Two types of algae dominated the lagoon, *Chaetomorpha linum* and *Ulva* sp., both of which form dense mats.

Haminoea callidegenita were observed crawling on any solid substrata present, including the sediment, branches, and *Ulva*, but most frequently were found within or underneath the floating mats of

Chaetamorpha. Animals were collected in November 1984, January, February, and June through November 1985, and April through October 1986. Although an extensive population was observed during the 1984-85 winter, no animals were found in the 1985-86 winter. Body size of animals collected, ranged from 1 to 33 mm, variable with time of year, but with a wide range present at each time of collection (eg., from 7 to 20 mm in February 1985, and from 3 to 29 mm in July of the same year). Abundant spawn at a variety of developmental stages, were observed on branches, on *Ulva*, and most frequently on *Chaetamorpha*. Egg masses were found throughout the year, with the highest densities from May to October. *H. vesicula*, frequently observed outside the lagoon in a *Phyllospadix* bed at the tip of the spit, were also found inside the lagoon (October 8, 1986, and April 17, 1987). Adults plus eggs were observed on both occasions.

Specimens of *Haminoea callidegenita* were collected at Rock Point on October 8, 1986 and April 16, 1987. Body length of crawling animals ranged from 3 to 29 mm. Rock Point was a wide, gently curving bay, with a mixed sand and mud substrate. *Haminoea callidegenita* were found in the slight depressions formed by drainage channels, with a mud substratum and containing beds of *Phyllospadix scouleri*. *Haminoea vesicula* adults were also present. Animals were collected at low tide, as they crawled on the substratum as well as over the *P. scouleri*. Abundent spawn of both species were present on the eelgrass.

Haminoea callidegenita fed by grazing diatoms and detritus seemingly from any available surface, including *Chaetamorpha, Ulva, Phyllospadix*, and glass walls of aquaria. Examination of the stomach

contents and fecal pellets revealed sand particles, organic detritus, several species of diatoms, either fragmented or most often entire, and clumps of *Ulva* cells. Cells identifiable as *Chaetamorpha* were not observed, neither were adults observed actually rasping off and ingesting particles of the *Chaetamorpha* filaments. Small clumps of cells that appeared to be epidermal cells of *Phyllospadix* were found in the fecal pellets of animals collected at Rock Point. However, the cells were unpigmented, unlike expelled *Ulva* cells, suggesting that they were dead before being accidently grazed up by radulae not sufficiently equipped to break up the fibrous eelgrass blades.

Animals were generally aggregated, whether in the field or in culture. They secreted a mucous tube when crawling, and "trailing" of other individuals along these tubes was commonly observed. When severely agitated, they secreted a grey milky substance, the presence of which initiated a similar response in other individuals.

Egg masses were ovate, typically 15 x 4 x 4 mm in size, and up to a maximum observed size of 33 x 6 x 6 mm. They contained an average of 21 eggs/ mm ^{3} (n= 10 egg masses), for a total of 300 to 700 eggs per mass. Eggs were individually encapsulated and arranged in a continuous string which spiraled through the outer layers of the mass. Uncleaved eggs were 320μm in diameter and bright orange-yellow in colour. Spawning appeared to be gregarious, as embryos within masses of spawn collected in the field were often of similar developmental stage. In the laboratory, spawning was often synchronous throughout a tank. Oviposition usually occurred at dawn, but individuals often were observed in the process of laying throughout the day and as late as 11 PM.

Development was synchronous within the mass, and hatching occurred 30 to 34 d after spawning (15 ^{o} C). Siblings from one mass hatched either as lecithotrophic veligers, or as juveniles, with a greater proportion of veligers early in the hatching period (3 to 12 d duration), and decreasing as the hatching proceded. Metamorphosis of veligers could occur spontaneously, but appeared to be enhanced by the presence of *Chaetamorpha*. Juveniles began feeding 3 to 4 d post-metamorphosis, often on the diatoms that had by then overgrown the egg mass jelly, and later fed on *Chaetamorpha linum* and *Ulva* sp., the adult food sources.

MORPHOLOGICAL COMPARISON WITH OTHER PACIFIC NORTHEAST SPECIES OF *HAMINOEA*:

In addition to *Haminoea callidegenita* n. sp. there are 2 other species of *Haminoea* commonly found in the Pacific Northeast: *H. vesicula* Gould 1855, and *H. virescens* Sowerby 1833.

Haminoea vesicula is an intertidal species, found on mud flats and sandy bays from Alaska to the Gulf of California (Morris, *et al.*, 1980), usually in association with *Zostera* or *Phyllospadix* beds. Animals were found up to 42 mm in length and had a brown base colour with black, dark brown, and cream pigmentation. The posterior cephalic shield is unilobular and the epipodial lobes cover the anterior third of the shell. The radular formula is n.1.1.1.n, with 30 uncini in a 36 mm specimen. The rachidian tooth is tricuspid, and the first lateral is serrated distally (Chapter 2, Fig. 4). Hancock's organ has 7 pairs of lamellae and the prostate is bilobed. Shells are globose-ovate in shape (Oldroyd, 1924; Fig. 8; also, Chapter 2, Fig. 1), and pale greenish yellow in colour. The vertex is depressed and imperforate,

and the columella very concave with a narrow, thin callous. Close, fine spiral striae covered the entire shell (Pilsbry, 1893; Abbott, 1954). Details of the anatomy (Hancock's organ, gizzard plate, jaws, and the penis complex) have been illustrated in Fig. 8, and summarized in Table 8. *H. olgae* Dall 1919 has been considered as a synonomous species (Pilsbry, 1893).

Haminoea virescens is found in upper intertidal pools along rocky shorelines from Alaska to Panama (Morris, *et al.*, 1980); additional collections have been from San Pedro (Pleistocene) and the Caloosahatchie beds in Florida (Pliocene; Oldroyd, 1927). Adults are generally a few millimeters larger than those of *H. vesicula*, and are dark brown with yellow pigment granules (Abbott, 1954). Shells are globose-ovate in shape, and strongly truncated posteriorly. They were reported to be greenish-yellow (Pilsbry, 1893), but the shells I have seen, dry specimens without the animal, have been whitish with a heavy, brown periostracum. The apex is impressed and perforate, and the columella deeply arcuate with a narrow callous (Pilsbry, 1893). The radula and penis complex have been illustrated by Marcus (1961). The radula formula is 1.n.1, with up to 64 uncini per half row (Marcus, 1961). The rachidian tooth has short, sharp cusps, and all the laterals are smooth (Chapter 2, Fig. 4). Hancock's organ has 18 leaflets on either side, and the penis complex contained both prostate and "muscle sac" (Marcus, 1961; this paper). Details of the anatomy (as for *H. vesicula*) have been illustrated in Fig. 9 and summarized in Table 6. Species considered synonomous are : *H. cymbiformis* Carpenter 1853 (Morris, *et. al.*, 1980; type considered incomplete and unidentifiable by Pilsbry, 1893); *H. dalli* Bartsch (Pilsbry, 1933); possibly *H. strongi*

Baker and Hanna 1927 (considered synonymous by Abbott,1954, but not by Grant, *in* Pilsbry, 1933, reasons not specified); not *H. olgae* Dall 1919 as has been suggested by Abbott, 1954 (Pilsbry, 1893; also confirmed by details included in Dall's description).

CONCLUSION:

Haminoea callidegenita, n. sp., have been found in Spencer's Spit, Lopez Island, and Rock Point, Samish Bay, both in Washington State. They were found in intertidal, muddy habitats, and appear to feed by grazing epiphytes and particles from the surface of *Chaetamorpha linum* and *Phyllospadix scouleri*. They are slightly smaller and more reddish-brown than the sympatric *H. vesicula*. Diagnostic morphological features are: deeply bifurcate cephalic shield, broad head, unilobular prostate, unarmed penis, tubular Hancock's organ, and gizzard plates with pointed papillae on the ridges. Their development is unusual in that some of the lecithotrophic hatchlings emerge as veligers and some as juveniles.

Figure 6. Photograph of an adult *Haminoea callidegenita*, n. sp. collected from Spencer's Spit, Lopez Island, Washington (body length is 26 mm).

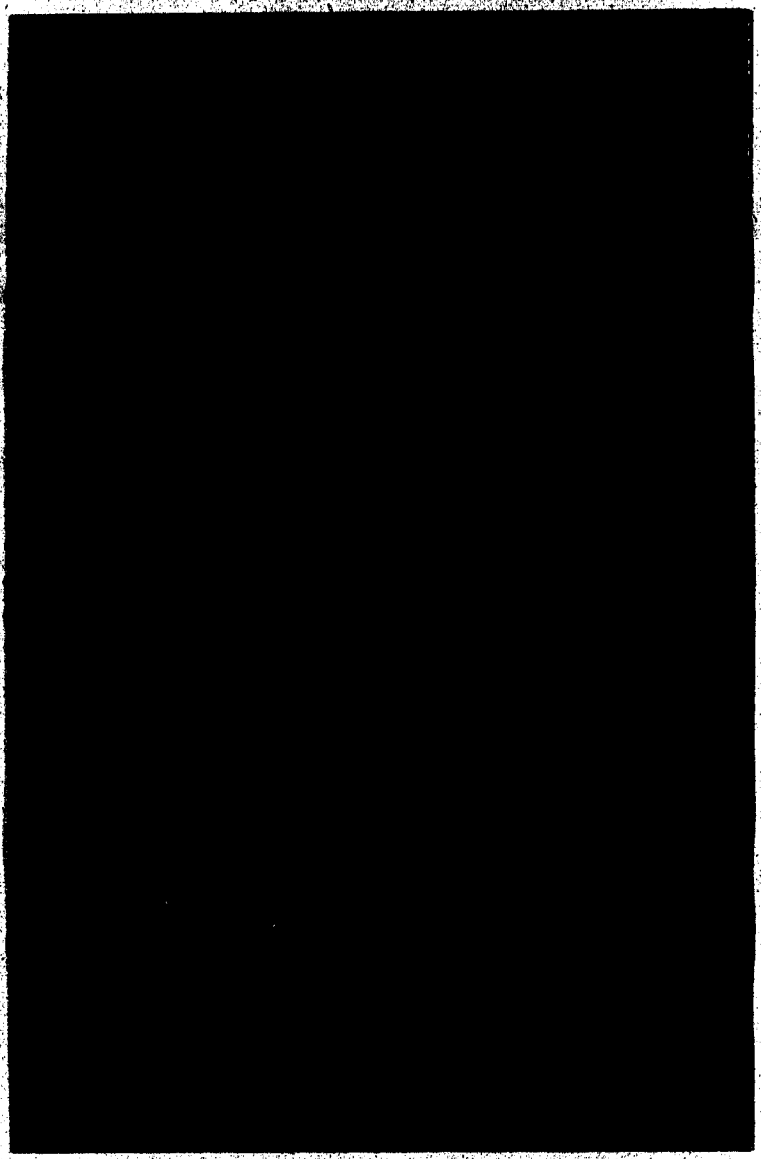

Figure 7. Diagnostic morphological features of *Haminoea callidegenita*, n. sp..

Legend:
A. penis and prostate complex. Scale bar= 1mm.
B. Hancock's organ. Scale bar= 1 mm.
C. gizzard plates. Scale bar= 1 mm.
D. jaws. Scale bar= 0.5 mm.
E. shell. Scale bar= 5 mm.
F. shell vertex. Scale bar= 3 mm.

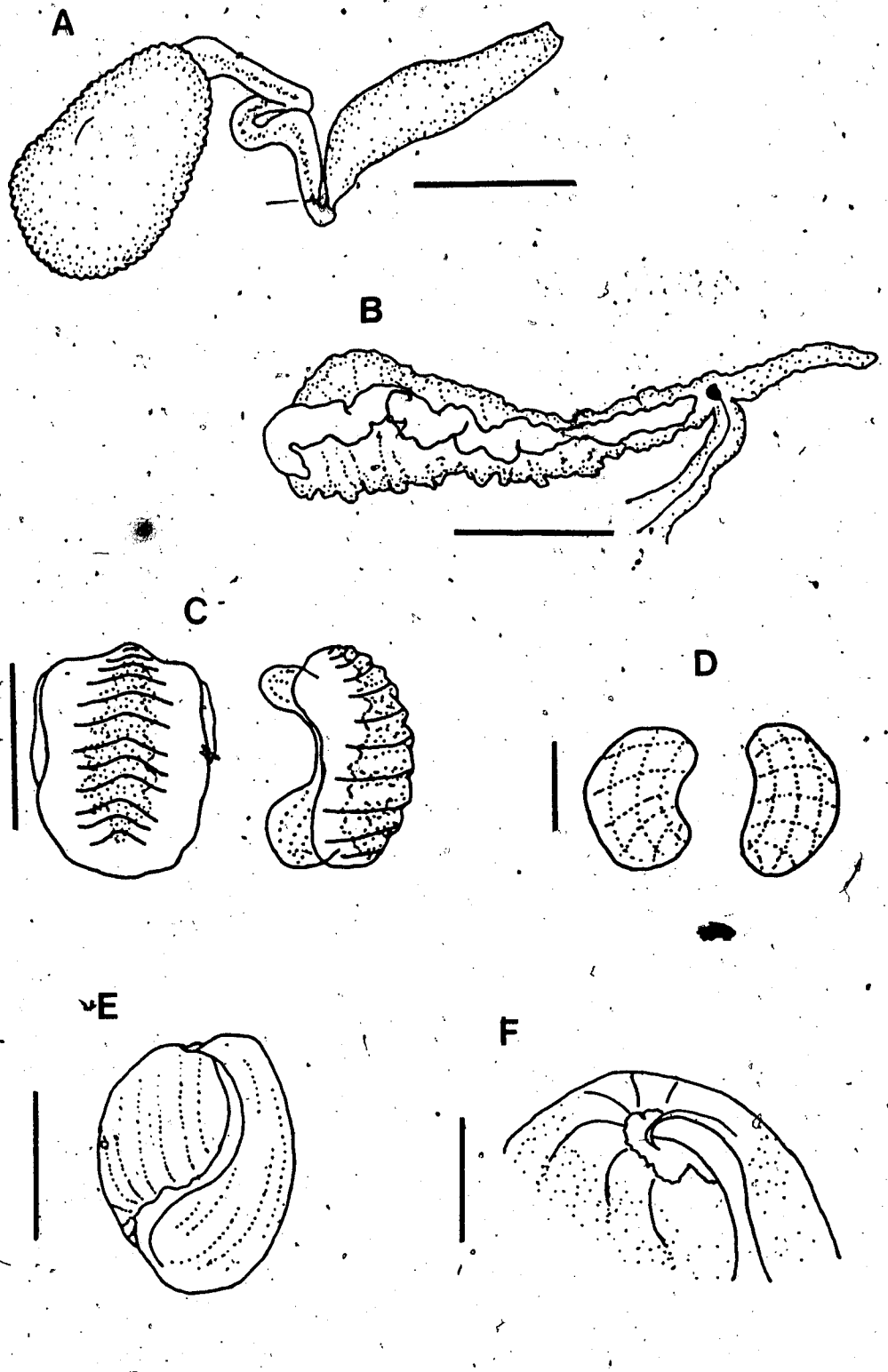
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Figure 8. Sone diagnostic morphological features of *Haminoea vesicula* Gould.

Legend:

A. penis and prostate complex. Scale bar= 1 mm.
B. Hancock's organ. Scale bar= 1 mm.
C. gizzard plates. Scale bar= 0.5 mm.
D. jaws. Scale bar= 0.5 mm.
E. shell. Scale bar= 5 mm.
F. shell vertex. Scale bar= 3 mm.

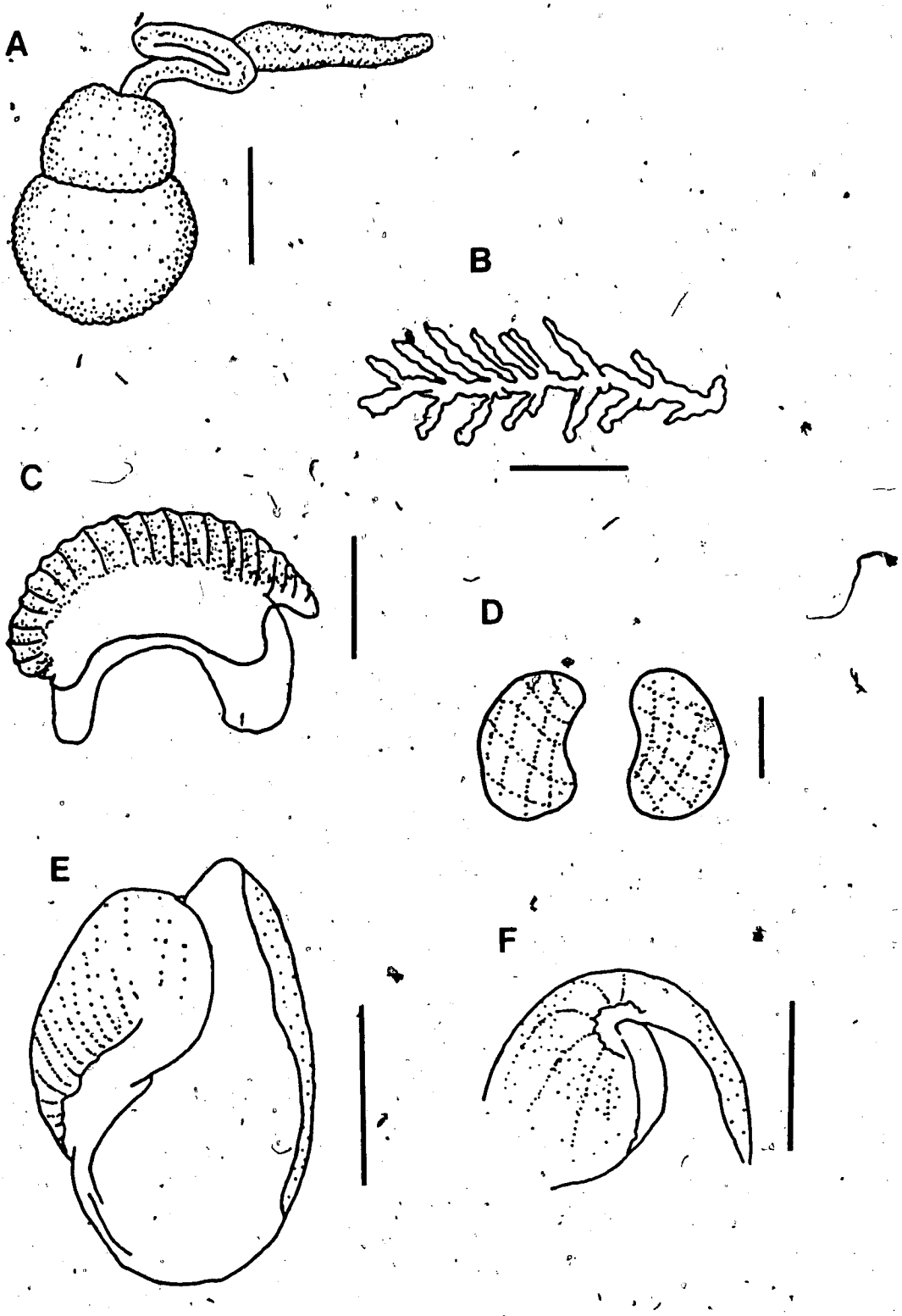
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Figure 9. Some diagnostic morphological features of *Haminoea virescens* Sowerby.

Legend:
A. penis and prostate complex. Scale bar= 1 mm.
B. Hancock's organ. Scale bar= 0.5 mm.
C. gizzard plate. Scale bar= 1 mm.
D. jaw. Scale bar= 1 mm.
E. shell. Scale bar= 5 mm.
F. shell vertex. Scale bar= 3mm.

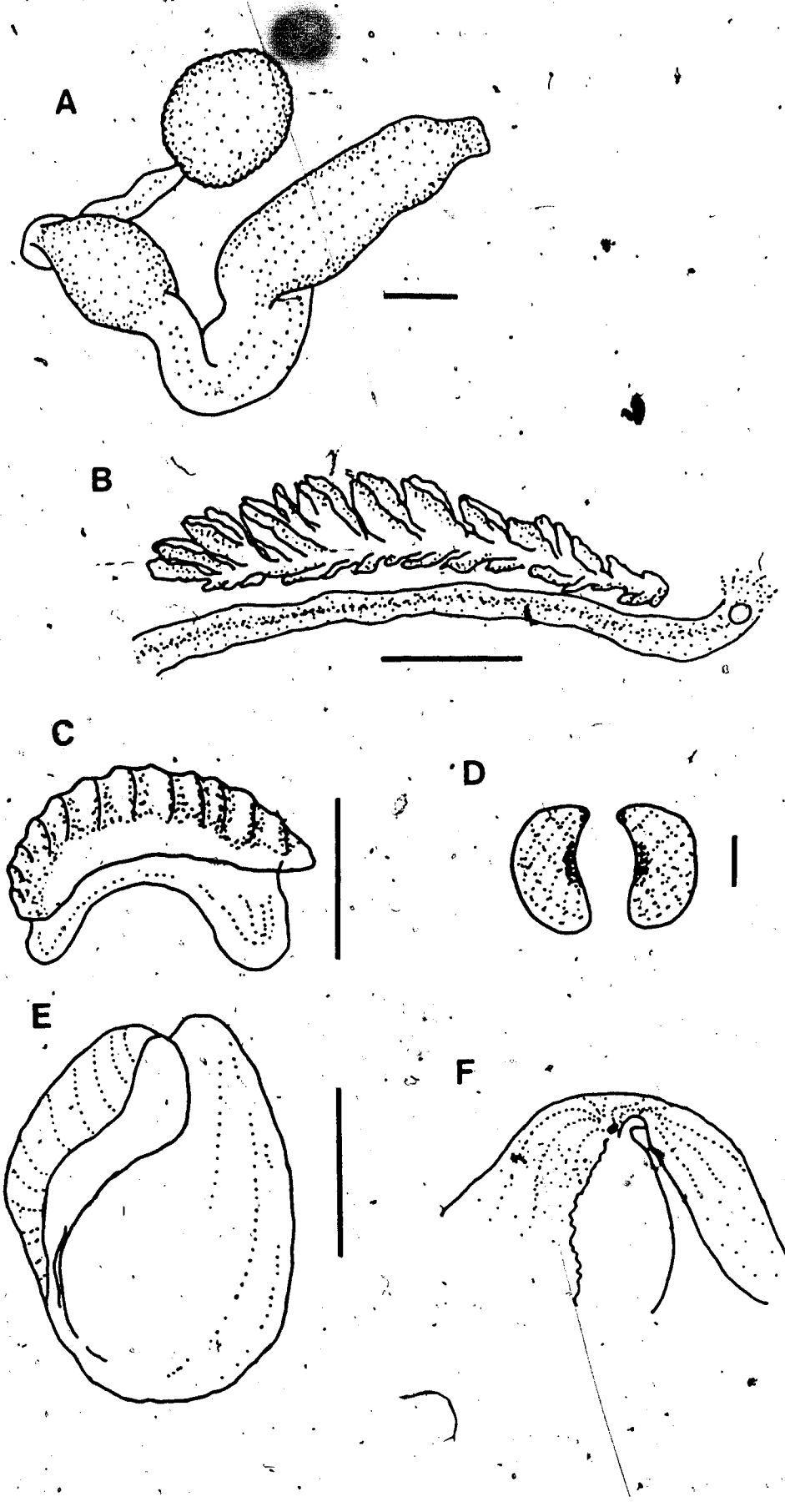
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Table 6. A summary of the diagnostic features of three species of *Haminoea* found in the Pacific Northeast: *H. callidegenita* n. sp., *H. vesicula* Gould, and *H. virescens* Sowerby.

SPECIES	HAMINOEA CALLIDEGENITA	HAMINOEA VESICULA	HAMINOEA VIRESCENS
MAXIMUM SIZE (mm)	to 33	to 42	slightly > 42
BASE COLOUR	reddish brown	brown	dark brown
MAJOR AUXILIARY PIGMENT	white and orange	black	brown and yellow
SHELL - SHAPE	ovate	globose-ovate	globose-ovate, truncated
- COLOUR	reddish-white	greenish-yellow	greenish-yellow
- VERTEX	depressed, imperforate	depressed, imperforate	impressed, perforate
CEPHALIC SHIELD	bifurcate	unilobular	unilobular
HANCOCK'S ORGAN	tubular	7 pairs of lamellae	18 pairs of lamellae
DENTITION OF FIRST LATERAL TOOTH	1 medial notch	serrated distally	smooth
PROSTATE	unilobular	bilobed	unilobular, with muscle sac
GIZZARD PLATE PAPILLAE	pointed, restricted to ridges	rounded, restricted to ridges	triangular, on ridges and troughs

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CHAPTER 4

THE DEVELOPMENT OF *HAMINOEA CALLIDEGENITA*, N.SP., WITH EMPHASIS ON HATCHING.

INTRODUCTION :

Opisthobranch molluscs are hermaphroditic, with most taxa exhibiting mutual copulation, and cephalaspideans, including *Haminoea*, showing unilateral copulation (Beeman, 1977). Fertilization is internal (Morton,1979). As spawning occurs, fertilized eggs are enclosed either individually or in groups by membranous capsules which are then linked together to form strings within a gelatinous mass (Purchon, 1977). The shape of the egg mass, the arrangement of the eggs, the number of eggs per capsule, and the mode of attachment to the substrate are species specific (Hurst, 1967; Eyster, 1980; Boucher, 1983). The development of a number of opisthobranch species has been examined (Thompson, 1958, 1967; Smith, 1967; Chia, 1971; Rao, 1971; Bridges, 1975; Switzer-Dunlap and Hadfield, 1977; Chia and Koss, 1978; Clark, *et al.*,1979; Williams, 1980).

Comprehensive descriptions of *Haminoea* development have been made in 3 species: *H. solitaria* Say (Smallwood, 1904 a and b; Harrigan and Alkon, 1984), *Bulla* (=*Haminoea*) *hydatis* Linne (Berrill, 1931), and *Haloa* (=*Haminoea*) *japonica* Pilsbry (Usuki, 1966). *H. solitaria* has planktotrophic larvae which hatch 7- 10 d after oviposition (18 - 20 ^{o}C). After a 20 d pelagic period, metamorphosis can be induced by a primary film inducer. The spherical egg masses are attached to the substratum by a 1 - 2 cm gelatinous stalk (Harrigon and Alkon, 1984). *H. hydatis* produces C- shaped egg masses containing approximately 70 eggs, each 100μm in diameter (Thompson, 1981). Berrill (1931) records 2 eggs/ capsule in *H. hydatis* ; other *Haminoea* species are

reported to have only 1 egg/ capsule. *H. hydatis* hatch in 2 or 3 weeks (temperature unspecified) as lecithotrophic veligers, some settling immediately, others remaining planktonic for a few days (Berrill, 1931). *H. japonica* produce cylindrical egg masses, each containing approximately 600 eggs that are 240 µm in diameter which hatch as lecithotrophic veligers after 24 - 28 d (13 - 16 °C). Metamorphosis occurs 3 - 7 d after hatching (Usuki, 1966).

The objective of this chapter is to describe the development of *H. callidegenita* with special reference to the developmental stage at hatching. The effect of enhancing substrata on metamorphosis and aspects of the juvenile biology are noted.

MATERIALS AND METHODS :

A. Description of the Collection Site:

Adults and egg masses of *Haminoea callidegenita* were collected from Spencer's Spit, Lopez Island, Washington at monthly intervals from June 1985 to October 1986, with one additional collection in April 1987. Spencer's Spit is a shallow (<1 m) lagoon with a silty substrate and limited access to open water. The water level in this lagoon is only slightly influenced by tidal fluctuations and variations in physical conditions, such as temperature, salinity, and oxygen tension, are probably extreme. The inland side of the lagoon is filled with mats of *Chaetamorpha linum* and *Ulva* sp., both of which provide grazing surfaces for adults and juveniles.

B. Culture of Animals:

Cultures were maintained at Bamfield Marine Station, Bamfield, British Columbia, unless otherwise stated. Adults were maintained in glass aquaria with a continual flow of seawater at ambient temperatures which ranged from 9 to 12 °C, and were supplied with

Chaetamorpha linum and *Ulva* sp. as food. Egg masses were collected immediately after spawning and maintained in pyrex or glass dishes at ambient seawater conditions, 14 - 15 °, or 20 - 23 °C. Culture water was replaced daily with bag filtered (1μm) seawater. Observations made of egg masses that were spawned in the lab were checked against masses collected in Spencer's Spit. Newly hatched veligers and juveniles were removed daily, and cultured as outlined for egg masses; with the addition of *C. linum* and *Ulva* sp. as food. Flakes of cetyl alcohol were added to reduce the surface tension, thus decreasing the rate at which larval shells became trapped at the surface (Hurst, 1967). Cultures of larvae and / or juveniles were cleaned every second day. When juveniles reached approximately 3 mm in length (measured while actively crawling) they were transfered to partially submersed 500 mL Tripour beakers with vents of 542μm Nitex mesh to provide a gentle but continual flow of seawater and at temperatures of 12 to 15 °C.

Light microscopic observations and measurements of embryonic, larval, and early juvenile stages were made using a calibrated ocular micrometer on a Reichert compound microscope. Photomicrographs were taken using a Wild Photoautomat MPS 45 camera on a Wild compound microscope.

C. Determination of Developmental Stage at Hatching:

Hatching ratios were determined by counting the number of veligers and juveniles that emerged from the egg masses each day. Cleavage stages were cultured under the following experimental conditions: 1) intact egg masses cultured at 3 temperature regimes (9 - 12°, 14 - 15 °, and 20- 23 °C); 2) egg masses sliced into 2 mm thick segments and maintained at 14 -15 °C; and 3) encapsulated embryos completely separated from the egg mass, with all remnants

of the mass jelly removed, and maintained at 14 - 15 °C. Entire masses and slices of masses were cultured at individually in 100mL jars. Separated embryos were maintained at densities of 50 - 60 per dish. All dishes contained 40 mL of seawater. The third group was subdivided into 3 sets: a) embryos only; b) embryos plus *Chaetamorpha linum* (2 mg blotted wet weight / 40 mL SW, or 0.05 mg/ mL); and c) embryos with pieces of egg mass jelly in sea water (14 mg blotted wet weight / 40 mL SW, or 0.35 mg/ mL), but not in direct contact with the embryos. Egg mass jelly was replaced if necessary, but this was usually not required. In a few cultures, the jelly was replaced once, late in the culture period. All cultures were checked and cleaned every second day and maintained under the specified conditions until hatching was completed (32 - 38 d after oviposition). At the onset of hatching, each culture was examined daily, the new hatchlings removed, and veligers and juveniles counted. The first series of cultures (whole masses, sliced masses, and separated encapsulated embryos) was maintained at Bamfield Marine Station, Bamfield, British Columbia from May to July 1986, and repeated at the University of Alberta, Edmonton, Alberta, in October and November 1986. The second series (encapsulated embryos under a variety of conditions) was maintained at the University of Alberta, in October and November 1986, and repeated in April and May 1987. Ten replicates were maintained for each experimental condition, unless otherwise specified. Statistical analyses were carried out as outlined in Sokal and Rohlf (1981).

D. Metamorphosis:

Metamorphic inducers were examined by providing veligers with one of several substrata on the day of hatching. The culture dishes (10 x 50 mm plastic petri dishes) were treated with chlorox (5% sodium

hypochlorate) for 2 h, then triply rinsed and soaked in distilled water. Several substrata were examined: 1) bag filtered (1μm) seawater only (control conditions); 2) filtered seawater plus *Chaetamorpha linum* ; 3) filtered seawater plus *Ulva* sp.; 4) filtered seawater plus sediment; and 5) filtered seawater plus pieces of egg mass jelly. Cultures contained 5 veligers per dish. Sample sizes were variable between conditions (Table 7), and ranged from 35 to 75. Observations were made at 12 h intervals until metamorphosis had occurred or the veliger died (up to a maximum period of 20 d). Culture dishes were rinsed and the water replaced daily. Dishes were not treated with chlorox after the onset of the experiment. All dishes were maintained at temperatures between 20 - 23 ^{o}C. Substrata were collected from the adult habitat (Spencer's Spit lagoon, Lopez Island, Washington).

E. Determination of Veliger and Juvenile Growth:

The growth rates of veligers and juveniles were measured under laboratory conditions at temperatures of 12-15 ^{o}C. Veliger growth was determined by measuring the length and width of the shells with a calibrated ocular micrometer on a Reichert compound microscope. Shell dimensions (excluding the velum) were used rather than total larval length because of difficulties in consistently obtaining the same extension of the velum. Juveniles were measured by total body length while actively crawling. Small juveniles (less than 2 mm)were measured with a calibrated ocular micrometer in a Wild M5 microscope, and large juveniles with a Canlab ruler either with the aid of a Wild M5 microscope, or by eye.

RESULTS :

A. Oviposition:

Under laboratory conditions, oviposition by *Haminoea*

callidegenita took place most frequently between 0500 and 0900 h, although adults were often observed laying masses during later daylight hours and less frequently late in the evening (2300 h). It took approximately 20 min for a 15 mm egg mass to be produced. Occasionally, adults were observed to produce 2 smaller egg masses sequentially, even if not visibly disturbed. Adults did not show any substrate preference for oviposition and deposited egg masses on any available solid substratum. This was also observed in the field, where spawn were frequently attached to *Chaetamorpha linum*, *Ulva* sp., and submersed branches. Egg masses, often all at the same stage of development, were usually found in aggregates under both laboratory and field conditions.

Haminoea callidegenita egg masses were characteristic of Hurst's (1967) type D opisthobranch egg mass. The masses were attached to the substrate along the length of one side. They were slightly curved in shape, a result of the adult turning slightly towards the mass during oviposition. Egg mass shape was variable with size: small masses (10 x 4 x 4 mm) were almost ovate, and larger masses (up to 32 x 5 x 5 mm in size) were cylindrical. A typical mass produced by a 26 mm long adult was 15 x 4 x 4 mm (Fig. 10a).

Eggs were individually encapsulated and arranged in a continuous string. This string spiraled through the periphery of the egg mass (at a depth of approximately 1.5 mm, although this was variable; Fig. 10b) leaving the center portion of the jelly free of embryos. Egg masses contained an average of 21 eggs/ mm^3 egg mass (n= 10 egg masses), for a total of 200 to 700 eggs per mass. Density of eggs was variable within a single mass, as well as between masses.

B. Development:

The eggs were a bright orange- yellow. Uncleaved eggs

measured 230 x 210μm, and were encased in a 410 x 330μm capsule (Fig. 11a). Development was synchronous within the mass. The major developmental features have been summarized in Table 6. The rate of development increased with the temperature of the culture conditions (Table 6); those mentioned here are of embryos cultured at 15 °C.

Each egg underwent 2 mitotic divisions and subsequently cleaved in a spiral pattern. The first cleavage occurred 24 h after spawning (Fig. 11b). The 2 daughter cells were initially widely separate, although connected, and then pulled together before the second cleavage (46 h; Fig. 11c). The second cleavage produced 4 cells which rounded together until they were difficult to distinguish. The first 2 cleavages were holoblastic and almost equal. The third cleavage (51 h) produced the first quartets of micromeres and macromeres, and subsequent cleavages (Fig. 11d) produced a blastula by day 6 (Fig. 11e). Gastrulation was completed by day 8 (Fig. 11f).

The cephalopedal rudiment was visible on day 10. Cilia appeared by day 12, accompanied by the appearence of the posterior shell gland (Fig. 11g). The embryos began to rotate irregularly within the capsules. The foot and velar rudiments became distinct by day 13 (Fig. 11h). The shell was also more visible at this time, as it slightly constricts the posterior quarter of the yolk mass. Rotation of the veligers was more regular. By day 14, the velum was bilobed, ciliary beating was metachronic, and by day 15, the veligers could arrest beating of the cilia for short periods. By day 16, the operculum was present, and the shell had grown anteriorly to the base of the cephalopedal complex and had separated slightly from the developing digestive glands (Fig. 11i). As the shell developed over the next 3 days, it grew through a 90 ° curvature to the left and rounded above the veliger through 1 1/4 coils. The body whorl protruded slightly to

the left as the shell and mantle moved anteriorly. Further growth of the shell mainly involves deepening of the whorls until after metamorphosis.

By day 16, the veligers were able to reverse the direction of the ciliary beat, accompanied by a corresponding change in direction of rotation within the capsule. The rate of rotation was slower, as the veligers became rounder and filled more of the capsule. On day 18, the statocysts were visible and the 2 digestive glands were rounder although they were still yolky. Eyes were visible on day 20, and on day 22, the esophagus was visible and the intestine was beginning to coalesce (Fig. 12a).

Slight flexions of the velar lobes were also observed on day 22, indicative of contractions of the developing larval retractor muscle. Complete retraction was observed on day 25. If disturbed, as with bright light or sudden movements of the culture dish, the veligers would rapidly retract, and remain in their shells for a few seconds to several minutes. They would then slowly extend their velum and begin rotating again. The propodium developed over the period from 21 to 25 days.

By day 25, the stomach and 2 digestive glands were distinct. The heart developed during this period and contractions were visible by day 29. The anus was also evident by day 29 at the post- torsional position on the anterior right side of the larva, posterior to the head. Capsular albumen was not visible at any time during the encapsulated period.

Hatching generally occurred over a period of several days (3 to 7d duration), beginning approximately 32 d after oviposition. Some individuals hatched as veligers (Fig. 12c), but the majority metamorphosed within the egg capsule (Fig. 12d) and hatched as

juveniles. That is, the cilia were cast off, the velar lobes resorbed, the head narrowed, and the eyes pulled closer together. Within a few days of hatching, the foot began to elongate posteriorly, and the shell had shifted toward the adult position, so that the center of the aperture became positioned slightly to the right of the head. A few days before hatching, the jelly mass began to soften and deteriorate and was colonized by ciliates and nematodes, as is characteristic for opisthobranch egg masses (Davis, 1967). Hatching of both veligers and juveniles occured in the same way. The embryonic capsule softened and split as the larva probed the lining with its foot, allowing the individual to escape. This process took approximately 1 1/2 to 2 min after the onset of the softening of the capsule. After the larva had emerged from the capsule it slowly crawled out of the jelly mass.

Extracapsular metamorphosis occurred as described for metamorphosis within the egg capsule. Newly metamorphosed juveniles, with most of the velum resorbed, had narrower heads than the veligers (Fig. 12e), and the foot was flattened to extend both anteriorly to project slightly in front of the head and posteriorly to the edge of the aperture. As the foot grew posteriorly, the operculum was lost (approximately 3-4 d after metamorphosis). The velar lobes were gradually resorbed, except for a slight extension on the posterior part of the head which developed into the cephalic lobe buds (Fig. 12f).

Juveniles began feeding within 2 to 3 days of metamorphosis, as indicated by the digestive glands becoming brown. The buccal mass, radula, salivary glands, gizzard, and gizzard plates were visible and functioning 5 d after metamorphosis. Feeding setae, as found in *H. hydatis* by Berrill (1931), were not observed. Shell growth was broader on the left side of the juvenile and projected posteriorly along the right side of the aperture. Thus, its overall shape changed from

the veliger coil to a longer shell with an elongate aperture. Growth of the foot followed the flaring of the aperture and, approximately 10 d after metamorphosis, the posterior pallial complex began to project beyond the body whorl of the shell (Fig. 12f).

C. Determination of Hatching Stage:

From each egg mass of *Haminoea callidegenita* , individuals hatched as either pelagic veligers (Fig. 12c) or benthic juveniles (Fig. 12e). There was considerable variation in the veliger to juvenile hatching ratio between egg masses cultured under identical conditions (Fig. 13; Table 8).

The percentage of total hatchlings that emerged as veligers varied from 9.02 % to 71.57 %, although most masses fell within the 30 to 50 % range. The egg mass with the smallest veliger component (9%; mass # 5 in Fig. 13) was a medium sized mass (approximately 400 hatchlings) and hatching occurred over a long period (10d; Table 8). The relatively lengthy hatching period could account for the large juvenile component. The mass with the largest veliger component (70%; mass # 7 in Fig. 13) was a large mass (approximately 600 hatchlings) and hatching occurred over a short period (3 d). Only one other mass had a 3 d hatching period (mass # 6 in Fig. 13); approximately 40 % of the hatchlings emerged as veligers from this mass. Mass # 6 was also very small (150 hatchlings).

From one egg mass, hatchlings emerged over several days (from 3 to 11 d in the masses illustrated in Fig. 13), and the relative proportions of veligers and juveniles changed throughout this period. A comparison of the percentage of daily hatchlings that emerged as veligers or as juveniles (Fig. 14 a and b) showed that the proportion of veligers decreased and the proportion of juveniles increased with time. This is to be expected as juveniles represent a later stage of

development. The estimation of the juvenile component is probably slightly high, as observations were made every 24 h and veligers have been observed to metamorphose within this time interval.

There was a few days variation in the onset of hatching between masses. This variability was reflected in Fig. 15a, where the percent daily hatchlings that emerged as veligers was compared against a time interval including the encapsulated period (i.e., day 1 represented the date of oviposition). Despite scatter caused by temporal differences in the onset of hatching, the same distribution of the developmental stages (i.e., veliger or juvenile) at hatching was visible in the individual masses, as if compared with day 1 representing the first day of hatching (Fig. 15b). Because of the variable nature of the onset of hatching, in this section Day 1 is assigned to the first day of hatching per egg mass.

Given the variability observed in this system, attempts were made to manipulate the veliger to juvenile hatching ratio by altering two environmental factors: temperature and the availability of oxygen. Data are presented as plots of mean +- standard error (Fig. 16, 17, and 18).

Entire egg masses were maintained at 9 ^{o} (n= 10), 15 ^{o} (n=9), and 21 ^{o}C (n=10). The masses raised at 9 ^{o}C (ambient seawater temperature during the experimental period from May to June, 1986) showed a high incidence of abnormal development and mortality; therefore, these data were disregarded during further analyses. A comparison of the percent daily hatchlings that emerged as veligers (the veliger component) between the 15 and 21 ^{o}C cultures revealed that there was a slight decrease in the number of veligers released per day with an increase in temperature (i.e., an increase in the relative proportion of juveniles), but there was also sufficient variation to

encompass the difference between these 2 conditions (Fig. 16). The rate of decrease in the number of veligers released was comparable between the 2 conditions.

It has been suggested that in opisthobranch egg masses, the jelly affects oxygen diffusion so that O_2 tension is lower in the center of an egg mass than at the periphery, thus slowing the rate of development in the central embryos (Strathmann, 1987, *pers. comm.*) although this has yet to be demonstrated. Oxygen tension was considered a potentially influential factor in the development of *Haminoea callidegenita* which produce thick egg masses (a mean size of 15 x 4 x 4 mm). The effects of oxygen concentration were indirectly examined in the following set of experiments.

H. callidegenita egg masses were subdivided into 3 groups: 1) entire egg masses; 2) masses cut transversely into 2 mm thick slices to examine the possible effects of decreasing the distance necessary for oxygen diffusion; and 3) encapsulated embryos that were separated from the jelly layers altogether to examine the possible effects of completely removing the diffusion barrier produced by the jelly mass. Encapsulated embryos could be raised successfully without the additional invested jelly layers. There was a success rate of 100 % hatching of seemingly normal veligers and juveniles, which proceded to metamorphose (in the case of the veligers) and grow at the expected rate, under laboratory conditions (0.02 mm/d, as in Fig. 20).

Veligers from entire and sliced egg masses showed approximately the same hatching rate (Fig. 17). Approximately 60 % of the hatchlings released at the onset of hatching (Day 1) were veligers. The veliger component decreased to approximately 5 % of the hatchlings by day 7, and to 0 % by the end of the hatching period. However, embryos that were separated from the jelly mass showed

approximately 70 % hatchlings released as veligers and this rate remained relatively consistent throughout the hatching period, but decreased to 60 % on the last day of hatching (day 9).

In a second set of experiments, embryos were again isolated and introduced to a variety of conditions, all at 15 ^{o}C. The conditions were as follows: 1) embryos only (control conditions); 2) embryos in dishes containing *Chaetamorpha linum*, the adult food source; 3) embryos in dishes containing pieces of egg mass jelly; and 4) embryos in dishes that were continually being gently aerated.

The embryos in subset 4 (those continually aerated) showed an unusually high proportion of abnormal development and mortality, and therefore were excluded from further analyses and comparisons. Data from the remaining 3 subsets are presented in Fig. 18.

Isolated embryos showed hatching ratios comparable to those of the previous experiments: 90 % of the hatchlings were veligers on day 1, decreasing to 75 % on the last day of hatching (day 5). Embryos cultured in water containing *Chaetamorpha* showed similar results (73 % released as veligers on day 1 and 85 % on the last day, day 4). However, embryos cultured in water containing pieces of egg mass jelly followed the same pattern as depicted by hatchlings released from entire egg masses: 72 % hatched as veligers on day 1, decreasing to 0 % on day 6 , the last day of the hatching period.

D. Induction of Metamorphosis:

Although metamorphosis can occur within the egg capsule, it was examined in individuals hatched as veligers to see if the rate of metamorphosis could be enhanced by substrata collected from the adult habitat. Four substrata were tested, all of which were frequently observed in association with small juveniles in the field: *Chaetamorpha*, *Ulva*, (both grazed by the adults and juveniles in

feeding), silt, and egg mass jelly. These data were compared to the rate of metamorphosis of embryos maintained in filtered seawater only (control conditions). Metamorphosis occurred in all of these conditions (Fig. 19). The presence of *Chaetamorpha*, *Ulva*, and egg mass jelly enhanced the rate of metamorphosis such that it took 9 d for every veliger to have successfully metamorphosed rather than 20 d in the control conditions. Cultures containing silt as a possible substratum showed a rate of metamorphosis comparable to that of the controls. Cultures containing water only, or with silt had higher mortalities (5.0 % and 5.7 % respectively) than did the cultures containing *Chaetamorpha* (2.9 %), *Ulva* (0%), or egg mass pieces (0%; Table 9).

E. Post-Embryonic Growth:

Veliger growth (measured as shell growth) did not occur even in those individuals that remained pelagic for a 2 week period. Yolk reserves were gradually depleted, but otherwise, the veligers appeared unchanged.

Growth of juveniles was recorded over a 260 d period. Juveniles grew at an overall rate of 0.02 mm/d (Fig. 20). The initial growth rate was 0.04 mm/d. Growth rate slowed after 100 days, accompanied by an increase in mortality. The smallest animals observed producing egg masses were 13 mm in length, giving an estimated age at maturity of 580 d, based on laboratory observations.

DISCUSSION:

Haminoea callidegenita, n. sp., produces cylindrical egg masses which contain eggs that are 230μm in diameter. From each egg mass, lecithotrophic hatchlings were released, either as veligers or as juveniles. Most of the hatchlings that emerged early in the hatching

period were veligers, and most of the later hatchlings were juveniles, as would be expected as juveniles represent a later stage of development.

There was a certain amount of variability in the percent of total hatchlings that emerged as veligers among masses cultured simultaneously under identical conditions. Although mass size and the duration of the hatching period probably affected the hatching ratio of a particular egg mass, it seemed that there was a greater variance than could be accounted for by only these two components (Fig. 13).

Attempts were made to manipulate the the developmental stage at hatching. Although temperature was influential in determining the rate of development (Table 7), it did not appear to be a major factor in determining the developmental stage at hatching (Fig. 16). One interesting observation arising from the temperature experiments was that embryos cultured at 9 ^{o}C showed a high incidence of mortality and abnormal development, while embryos cultured at 15 and 21 ^{o}C developed normally. Survival at 9 ^{o}C seems possible for an intertidal species and, in particular, one known to reproduce during the winter months (a few viable egg masses were collected in Spencer's Spit in February and November 1985). Perhaps a continuous exposure to cold conditions as experienced in the laboratory was detrimental.

The experiments designed to indirectly assess the effects of oxygen tension on the hatching ratio were inconclusive. The veliger components for entire and sliced egg masses were similar throughout the hatching period (Fig. 17), indicating that O_2 diffusion was either not strongly affected by an increase in the diameter of egg mass jelly, or, if affected, was not a limiting factor in *H. callidegenita* development. Isolated embryos had a high veliger component; possibly the remaining layer of jelly in the sliced egg masses was sufficiently

thick to slowly decrease the rate of O_2 diffusion and to delay hatching (i.e., to increase the juvenile component). However, the following results suggested that if this indeed occurred, it did not play a major role in determining stage at hatching.

Most of the embryos cultured in the absence of egg mass jelly hatched as veligers. When jelly was returned to a culture chamber (although not in direct contact with the embryos), the distribution of developmental stages at hatching was similar to that observed in the whole egg masses. This suggested that either the egg mass jelly or something on the jelly influenced the developing embryos in such a way that individuals were inhibited from hatching as veligers, or were induced to metamorphose within the egg capsule. If the compound(s) influencing hatching was derived from something associated with the jelly, it was apparently specialized to the jelly as other contaminants (such as the diatoms, primary film, etc. present on *Chaetamorpha linum*) failed to produce the same effect.

It is possible that egg mass jelly functions not as passive enveloping layers, but rather plays an active role in the development of *H. callidegenita*, and in particular, in determining whether the hatching form will be a dispersive or non-dispersive stage. Perhaps the nature of the jelly is under maternal control. That is, an adult which produces a particular egg mass in some way regulates the components of the jelly layers to produce a majority, although not exclusively so, of one type of hatchling. This mechanism is supported by the observed variance between masses cultured under identical conditions.

The observed variance also suggests genetic rather than environmental control, although the two are not mutually exclusive. An adult prior to oviposition may alter the components of the

investing jelly layers in response to environmental conditions at the time of spawning. However, the long embryonic period (approximately 32 d) and the fluctuating physical attributes of the habitat suggest that a more direct interaction between the jelly and the environment may be a sounder strategy. However, the potential role of the physical environment as a influential factor has yet to be demonstrated.

There also appears to be a certain amount of heterogeneity among the larvae themselves. Within every culture, some hatchlings emerged as veligers and some as juveniles, regardless of culture conditions or egg mass characteristics, suggesting that some individuals are more sensitive than others to the potential veliger inhibiting compound. This heterogeneity on the part of the veligers, and possibly of the adults as well, presents a versatile developmental strategy, given the potential for environmental instability of the habitat (Clark, 1975; Chapter 6).

A similar hatching process has been observed in *H. hydatis* Linne (Gurrill, 1931). *H. hydatis* produces lecithotrophic veligers that hatch when competent to metamorphose. Some hatchlings settle and metamorphose immediately; whereas some remain pelagic for a few days. However, metamorphosis within the embryonic capsule was not reported. Given the similarity in the hatching process of these two congeners, it would be interesting to attempt similar manipulations of *H. hydatis* development.

Although metamorphosis did occur within the embryonic capsule, the rate of metamorphosis in individuals that hatched as veligers was enhanced by the presence of *Chaetamorpha linum*, *Ulva* sp., and egg mass jelly (Fig. 19).

One problem with the design of the metamorphosis experiments was that while chloroxed culture chambers were used at the onset of

the experiment, dishes were not re-chloroxed throughout the experiment. It is possible that the development of a primary film derived from the introduced algae or egg mass jelly was the functional inducer, rather than the introduced substrata. However, the rate of metamorphosis of veligers cultured with sediment collected from the same habitat as the algae (possibly colonized by the same or similar contaminants) was similar to that of the control conditions (1μm filtered SW only). Whether the actual metamorphic enhancer was the introduced substrata in the case of the algae, or egg mass jelly, or the associated contaminants (i.e., the epiphytes, diatoms, bacteria, ciliates, etc.) is undetermined. In the field, adults and large juveniles have been observed on the surface sediments, and the majority of individuals and egg masses are usually found within the mats of *Chaetamorpha*, or on *Ulva* blades.

The 3 substrata (*Chaetamorpha, Ulva*, and egg mass jelly) are considered as metamorphic enhancers rather than inducers because they seem to increase the rate of metamorphosis, yet the majority of veligers will settle and metamorphose when they are not present (5 % mortality). It is possible that primary film developed from the unchloroxed dishes and filtered seawater ("control" conditions) acted as an inducing substratum. However, the rate of metamorphosis was increased by specific substrata, or associated contaminants. *Chaetamorpha* and *Ulva* seem probable enhancers, as they constitute the major food source (grazing surface for picking up epiphytes and particulate matter) for juveniles and adults. Egg mass jelly also seems to provide a favorable habitat for small juveniles. Young juveniles have been observed feeding on ageing egg masses in the laboratory. Whether these juveniles were feeding on the jelly itself, or on the diatoms and ciliates which colonize the egg masses as they

begin to decay was not determined.

There was a lengthy period of veliger competency involving 3 types of metamorphosis. The first type (embryonic) occurred while individuals were still encapsulated. The factors which control which embryos will metamorphose before hatching are unknown. Possibilities include heterogeneity of the embryos themselves and maternal selection through the ooplasm, both potentially in association with the jelly investing layers either through maternal or environmental influences.

The second group involved hatched veligers who encountered a favorable (inducing) substratum, possibly one providing food suitable for a newly metamorphosed juvenile. The final type involved hatched veligers which delayed metamorphosis for an additional period (20 d), until appropriate conditions were met. If these conditions were not encountered, the majority of veligers were still capable of metamorphosis.

Juveniles that metamorphosed during any of the 3 types of metamorphosis contained sufficient (although decreasing) yolk reserves to allow several days delay in the onset of feeding. If food was available, juveniles began feeding usually within 24 h of metamorphosis. The juveniles were epiphytic and particle grazers, as were the adults. They would rasp and ingest particles from the surfaces of *Chaetamorpha linum*, *Ulva* sp., and the glass petri dish. They also rasped particles from the surfaces of sand and silt, and from the decaying organic matter present in the silt.

H. callidegenita juveniles grew at a rate of 0.02 mm/d, under laboratory conditions. The growth rate slowed after approximately 100 d in culture (post- metamorphosis; Fig. 20). These data possibly reflected the nature of the culture conditions rather than

representing the true growth rate. The smallest individual observed to spawn was approximately 13 mm in total length, or approximately 580 d old at a growth rate of 0.02 mm/d. At the initial growth rate of 0.04 mm/ d, a 13 mm individual would be approximately 300 d old. Even this generous interpretation of the growth rate was too slow to account for growth in an annual species exhibiting a maximum (observed) size of 36 mm.

A more realistic growth rate may have been achieved by improving the culture conditions. Juveniles were cultured at approximately 15 ^{o}C. Warmer temperatures, and /or fluctuations in diurnal temperatures, may have produced a faster rate of growth. The diet of the juveniles in culture was probably sufficient as these animals grazed a variety of particles. *Chaetamorpha linum* and *Ulva* sp. were provided in abundance, and the culture chambers were quickly colonized by diatoms and other algae. Quantity and diversity of the food supplied appeared to be sufficient, but this was difficult to ascertain as the exact dietary requirements of the juveniles are not known.

Table 7. Summary of developmental events in *Haminoea callidegenita* n. sp. for egg masses cultured at 15° and 21°. Time is listed in hours (h) and days (d).

DEVELOPMENTAL STAGE	TIME (h, d) (n=10)	
	15	21
OVIPOSITION	0 h	0 h
FIRST CLEAVAGE	24 h	5 h
SECOND CLEAVAGE	46 h	6 h
THIRD CLEAVAGE	51 h	9 h
BLASTULA	6 d	32 h
GASTRULATION	7-8 d	36-45 h
CEPHALOPEDAL RUDIMENT VISIBLE	10 d	3 d
CILIA AND SHELL GLAND APPEAR	12 d	4 d
FOOT AND VELAR RUDIMENTS SEPARATE	13 d	4 .5 d
VELUM BILOBED	14 d	5 d
METACHRONIC BEATING	15 d	5 d
SHELL COILED 1 1/4 TURNS	16 d	5 d
OPERCULUM VISIBLE	16 d	5 d
STATOCYSTS AND DISTINCT DIGESTIVE GLANDS	18 d	6 d
EYES VISIBLE	20 d	6 d
ESOPHAGUS AND INTESTINE VISIBLE	22 d	6 d
VELAR FLEXION	22 d	7 d
COMPLETE RETRACTION	25 d	8 d
HATCHING	32 - 38 d	9 - 15 d

Figure 10. Photomicrographs of *Haminoea callidegenita* n. sp. egg mass.

A. Scale bar= 2 mm.
B. Scale bar= 0.5 mm.

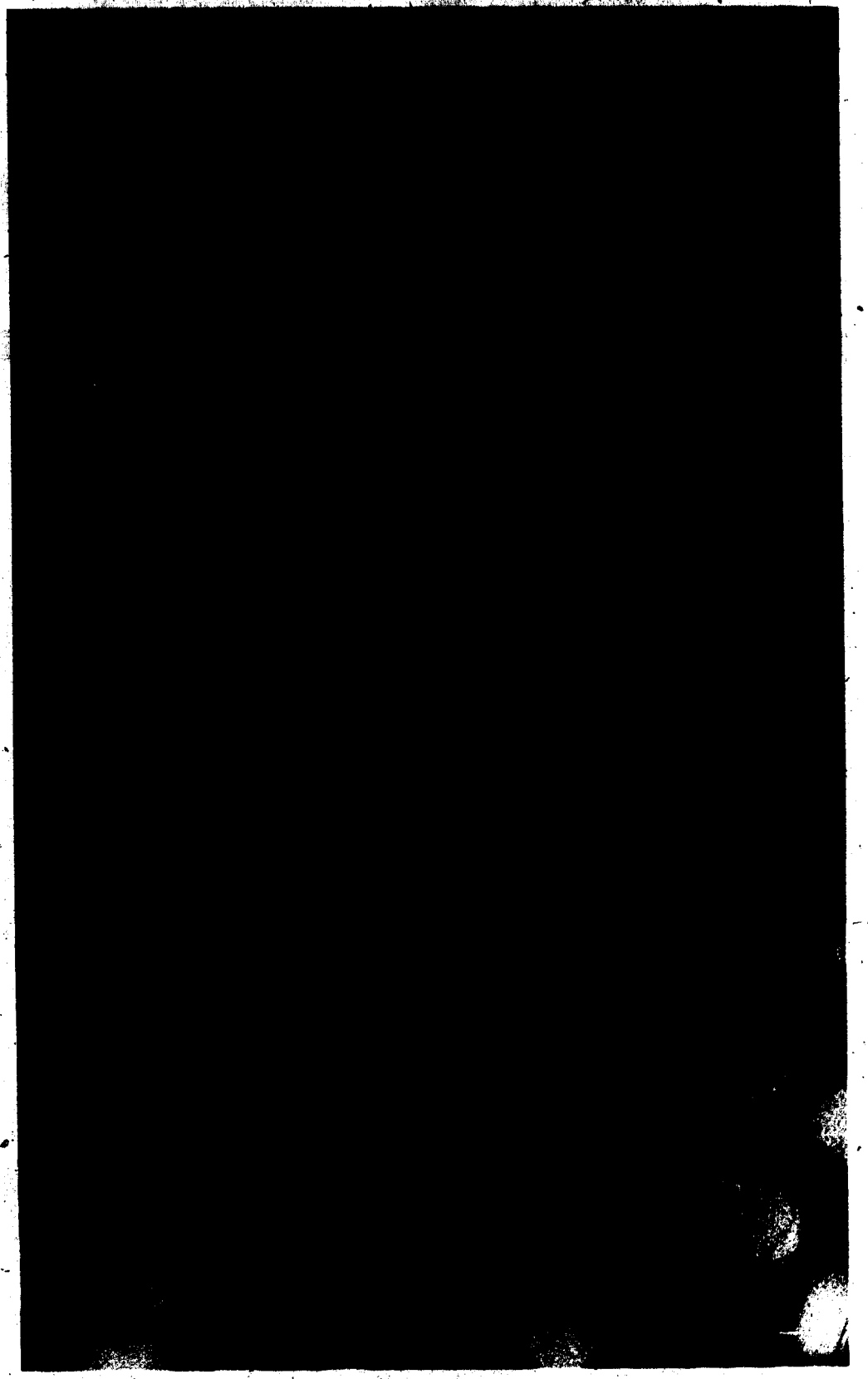


Figure 11. Photomicrographs of the early developmental stages of *Haminoea callidegenita*. Numbers listed in brackets below are the age of the larvae in hours and days from cultures maintained at 15° C.

Legend:
A. 1 cell stage (0 h). Scale bar= 270μm.
B. 2 cell stage (24 h). Scale bar= 150μm.
C. 4 cell stage (46 h). Scale bar= 270μm.
D. 8 cell stage (51 h). Scale bar= 150μm.
E. blastula (6 d). Scale bar= 80μm.
F. gastrula (8 d). Scale bar= 100μm.
G. early veliger (10 d). Scale bar= 50μm.
H. early veliger (10 d). Scale bar= 100μm.
I. early veliger (16 d). Scale bar= 90μm.

b - blastopore.
f - foot.
fr - pedal rudiment.
sh - shell.
v - velum.
vr - velar rudiment.
y - yolk.

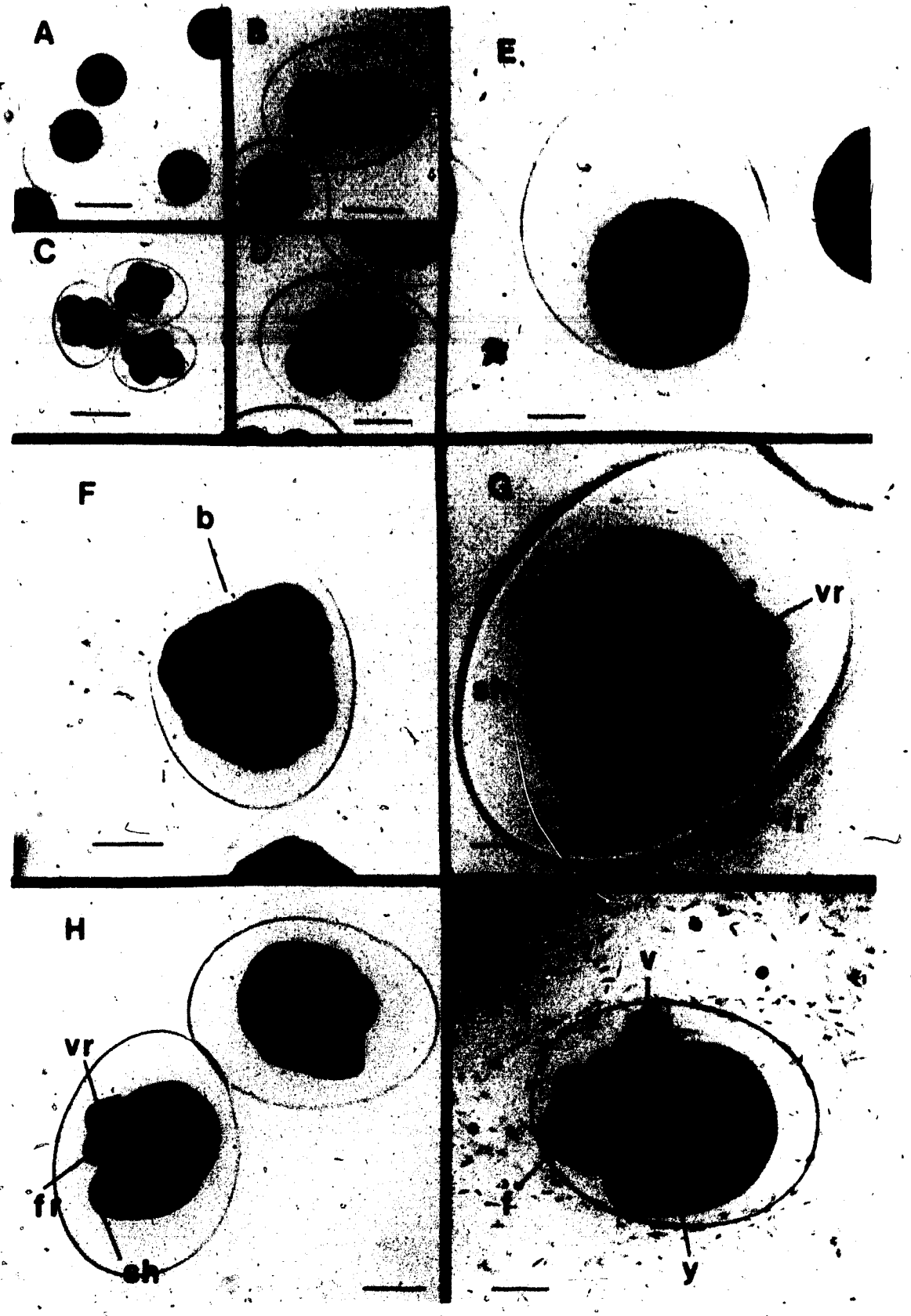

A
B
C
E
F
b
vr
H
vr
fl
eh
v
y

Figure 12. Photomicrographs of the development of *Haminoea callidegenita* veligers and juveniles. The numbers listed in brackets below are the age of the veligers and juveniles (in days; animals were maintained at 15° C).

Legend:
A. unhatched veliger (22 d). Scale bar= 100μm.
B. unhatched veliger (28 d). Scale bar= 100μm.
C. hatched veliger (1 d hatched). Scale bar= 100μm.
D. unhatched juvenile (33 d). Scale bar= 100μm.
E. juvenile (3 d hatched). Scale bar= 164μm.
F. juvenile (12 d hatched). Scale bar= 300μm.

bw - body whorl of shell.
clb - cephalic lobe bud.
dgl - digestive gland.
e - eye.
f - foot.
gz - gizzard.
i - intestine.
lr - larval retractor muscle.
m - metapodium.
mp - mantle pigment.
o - operculum.
p - propodium.
rsv - resorbing velum.
sgl - salivary gland.
sh - shell.

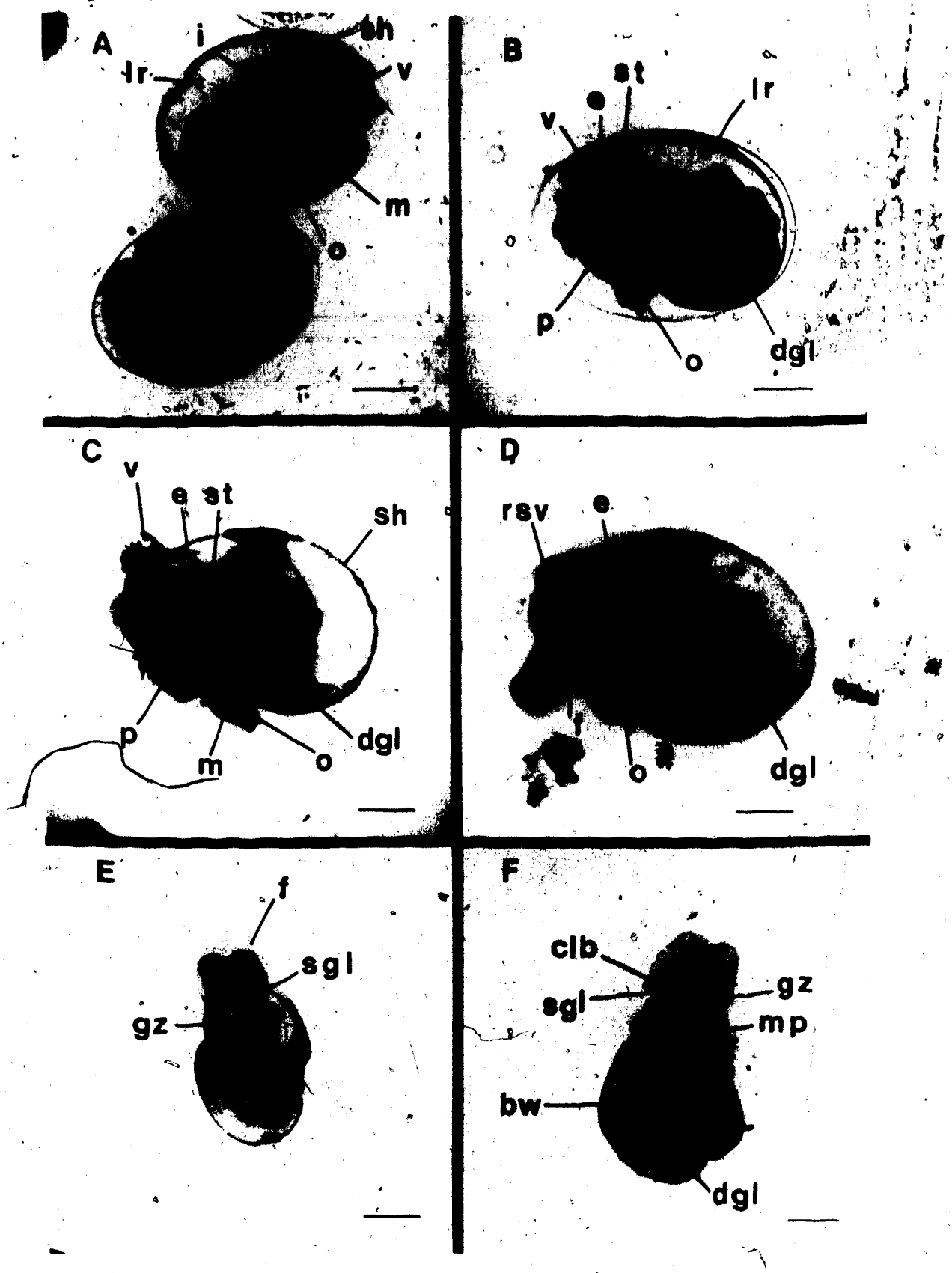
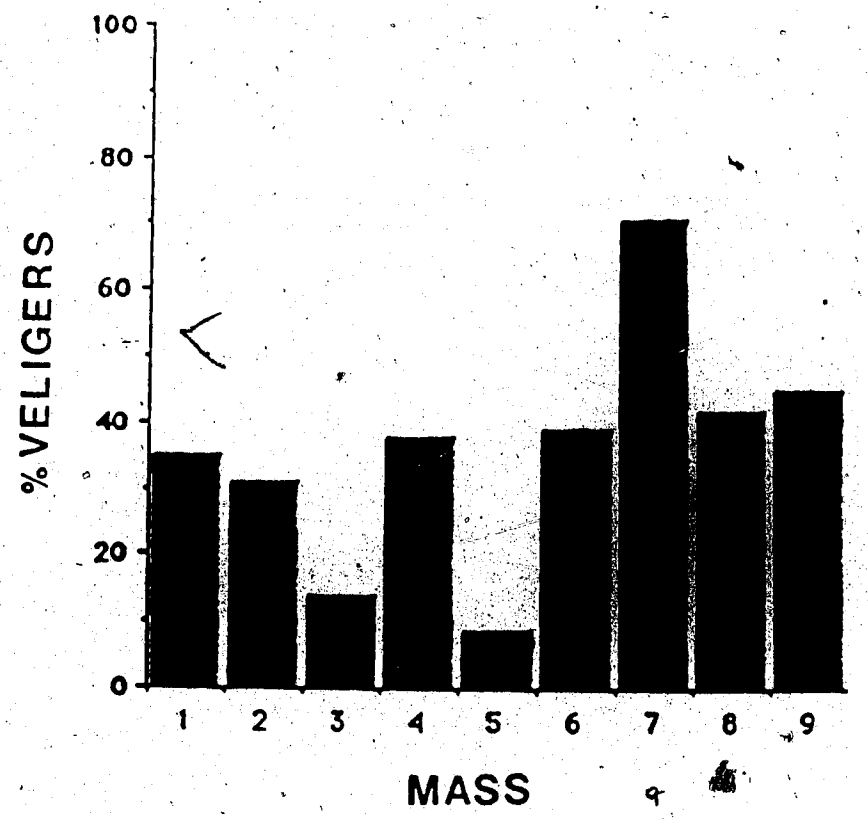

A
i
sh
lr
v
m
o
B
st
lr
v
p
o
dgl
C
v
e
st
sh
p
m
o
dgl
D
rsv
e
o
dgl
E
f
sgl
gz
F
clb
gz
sgl
mp
bw
dgl

Figure 13. Hatching in *Haminoea callidegenita* egg masses: values plotted are the percent of total hatchlings per mass that emerged as veligers (n = 9 egg masses, maintained at 15 ^{o} C).

Table 8. Hatching in *Haminoea callidegenita* : values listed are the total number of hatchlings released from each egg mass and the duration (in days) of the hatching period (n = 9 egg masses, maintained at15 ^{o} C).



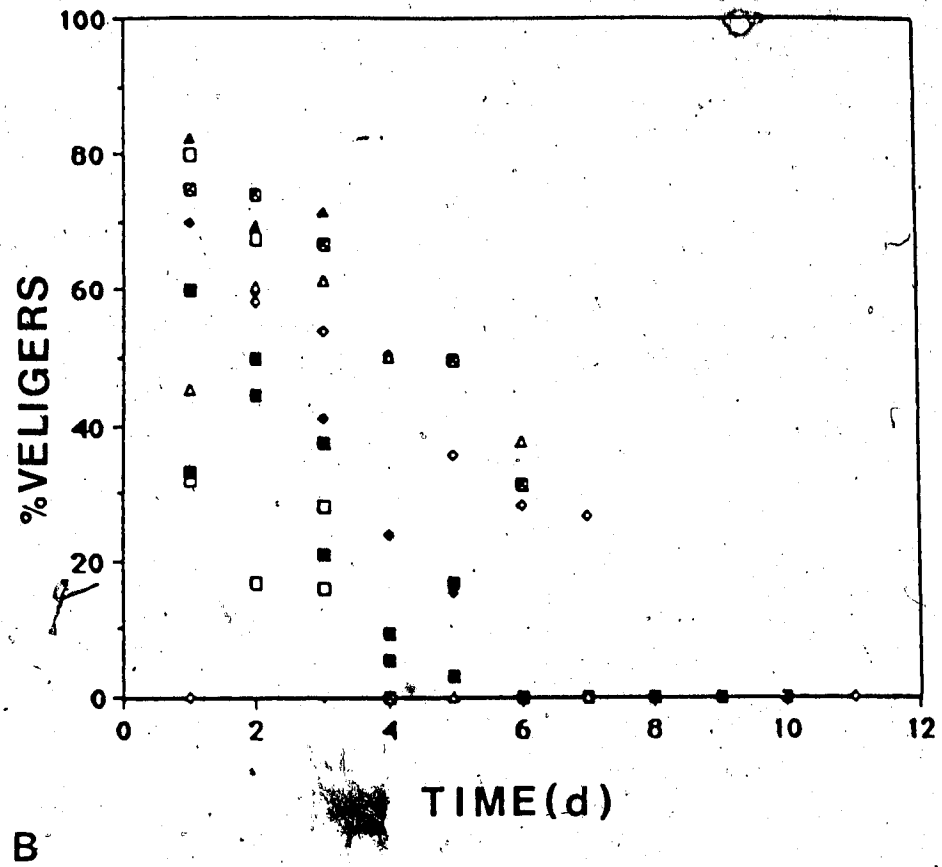
MASS #	1	2	3	4	5	6	7	8	9
TOTAL # HATCHLINGS	426	446	222	545	388	155	591	426	343
HATCHING PERIOD (d)	6	8	9	11	10	3	3	7	6

Figure 14. The distribution of developmental stages at hatching examined throughout the hatching period (d) in *Haminoea callidegenita* n.sp. Values plotted are the percent of daily hatchlings that emerged as veligers (A) or as juveniles (B). n = 9 egg masses, all maintained at15^{o} C).

Legend:

	Mass #
□	1
◆	2
■	3
	4
◇	5
■	6
□	7
▲	8
▲	9

A


100
80
60
40
20
0
%VELIGERS
0
2
4
6
8
10
12
TIME(d)

B

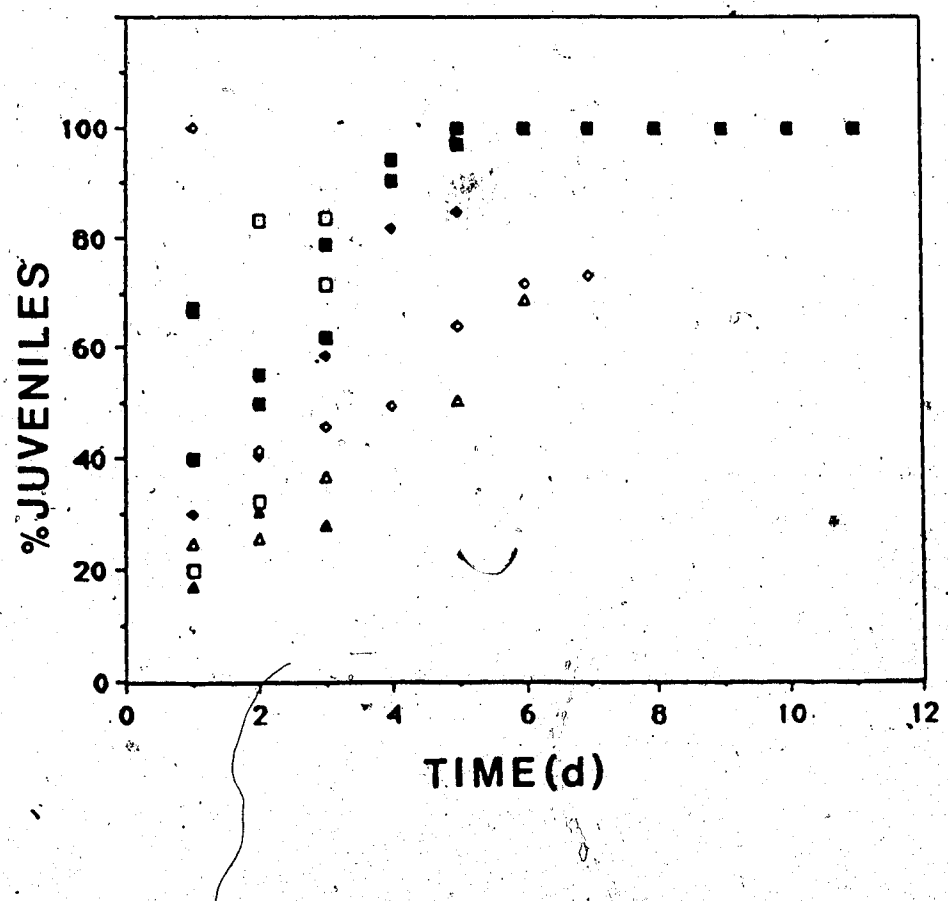
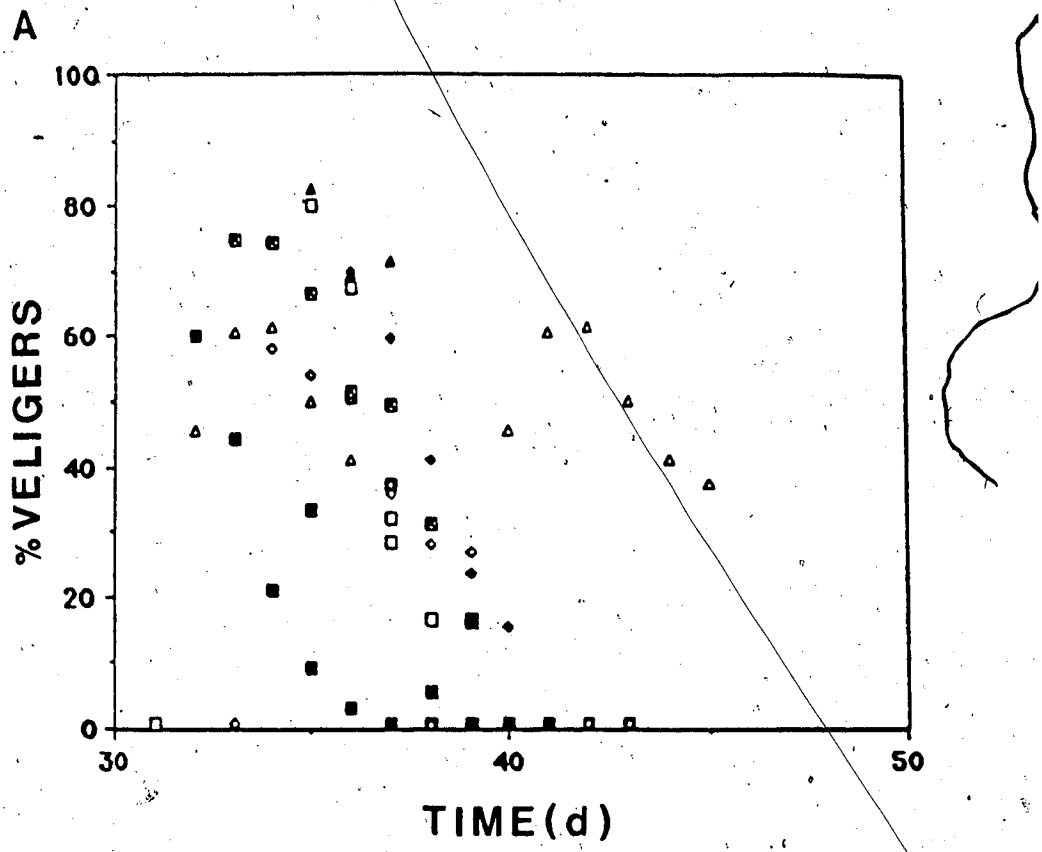

100
80
60
40
20
0
%JUVENILES
0
2
4
6
8
10
12
TIME(d)

Figure 15. The distribution of developmental stages at hatching in *Haminoea callidegnita* n. sp.. Values plotted are the percent of daily hatchlings that were released as veligers. (A) encorporates the entire developmental period (i.e., day 1=the date of oviposition for individual egg masses, although only dates involving the hatching period are shown (d31 to d45). (B) depicts the hatching period only (i.e., day1=the first day of hatching for individual egg masses regardless of date of oviposition), expressed for the same time interval as plot (A), n=9 egg masses, all maintained at 15° C.

Legend:

Mass #

1
2
3
4
5
6
7
8
9


A
100
80
60
40
20
0
%VELIGERS
30
40
50
TIME(d)

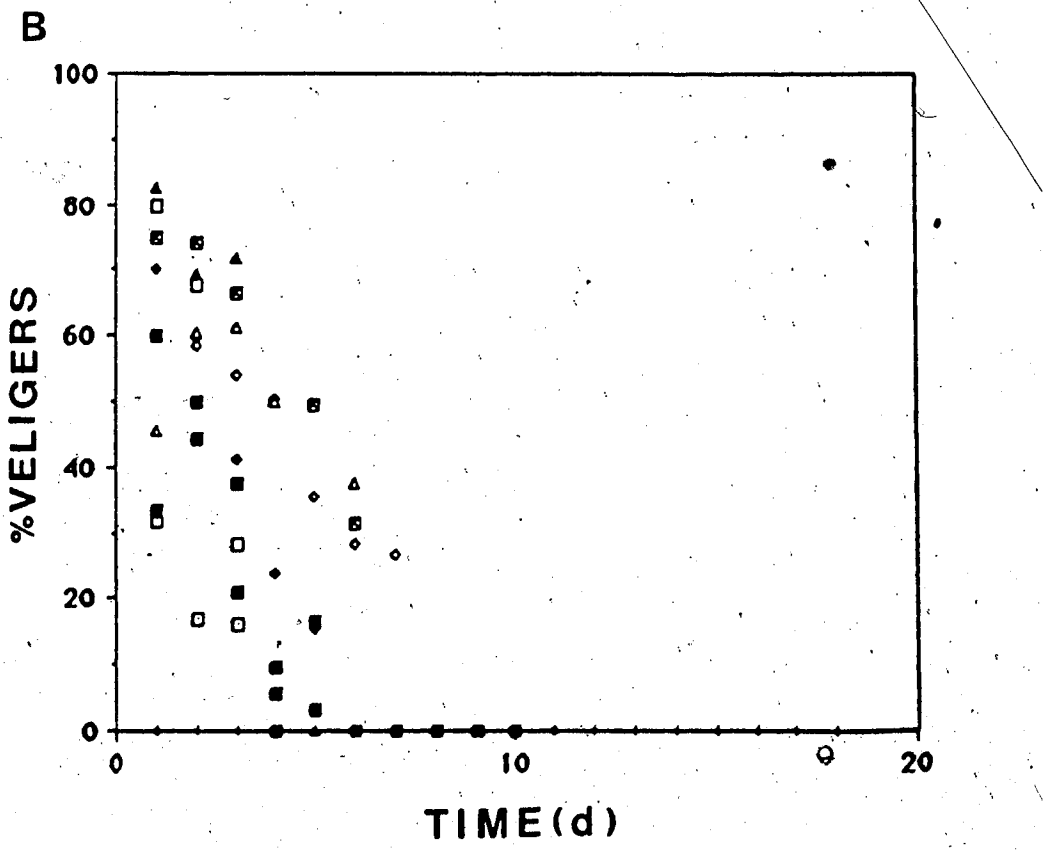

B
100
80
60
40
20
0
%VELIGERS
0
10
20
TIME(d)

Figure 16. The effects of temperature on the developmental stage at hatching in *Haminoea callidegenita* . Values plotted are the means with standard error bars for the percent of daily hatchlings that were released as veligers. Egg masses were cultured at 15^{o} (A, n= 9 egg masses) and at 21^{o}C (B, n=10 egg masses).

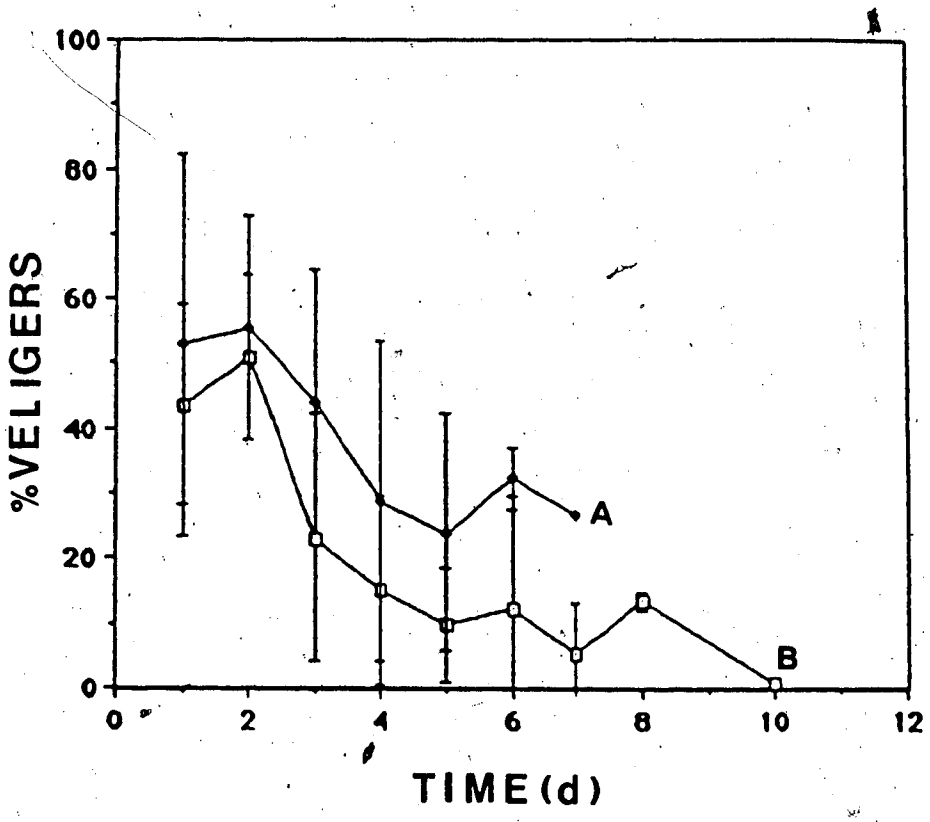

100
80
60
40
20
0
%VELIGERS
0
2
4
6
8
10
12
TIME(d)
A
B

Figure 17. The effects of removing egg mass jelly on the developmental stage at hatching in *Haminoea callidegenita* . Values plotted are the means with sdtandard error bars for the percent of daily hatchlings that emerged as veligers from three groups of egg masses: A (solid squares)- embryos separated from the egg mass jelly (n=10)entire egg masses (n=9), sliced egg masses (n=10), B (solid diamonds)- egg masses sliced into 2 mm thick segments, and C (open boxes) entire egg masses. Embryos in all three treatments were cultured at 15^{0} C.

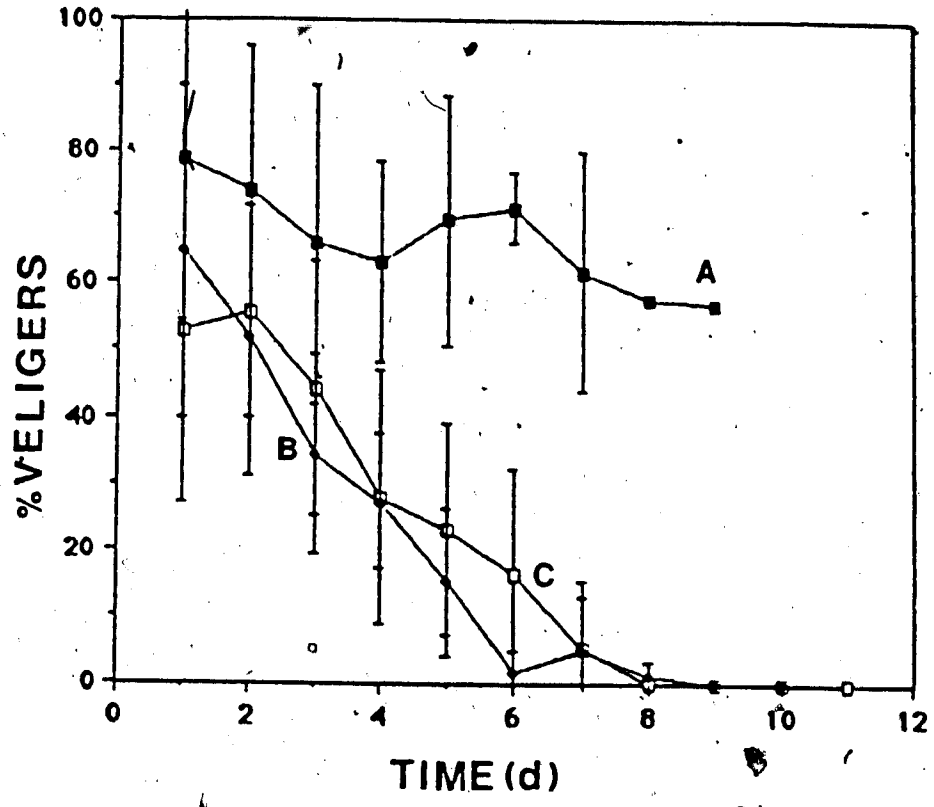

100
80
60
40
20
0
%VELIGERS
0
2
4
6
8
10
12
TIME (d)
A
B
C

Figure 18. The effects of raising separated *H. callidegenita* embryos under three culture conditions: A (open boxes) in seawater only (n=10), B (solid squares) in seawater plus *Chaetamorpha linum*, and C (solid diamonds) in seawater plus egg mass jelly. Values plotted are the means with standard error bars for the percent of daily hatchlings that emerged as veligers in cultures maintained at 15^{0} C.

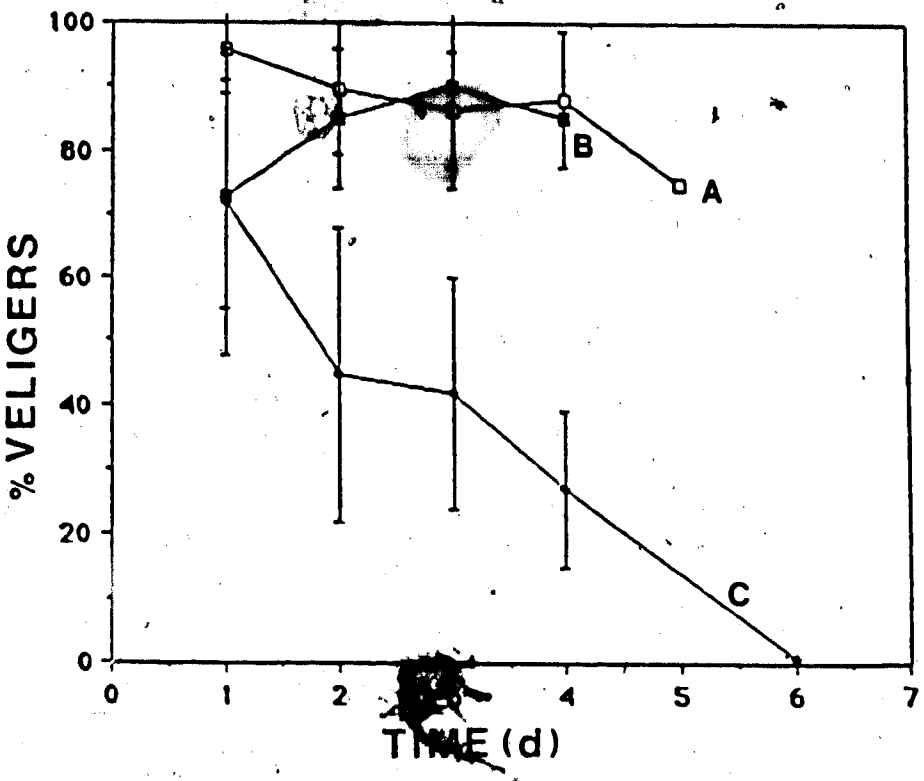

100
80
60
40
20
0
% VELIGERS
0
1
2
4
5
6
7
TIME (d)
A
B
C

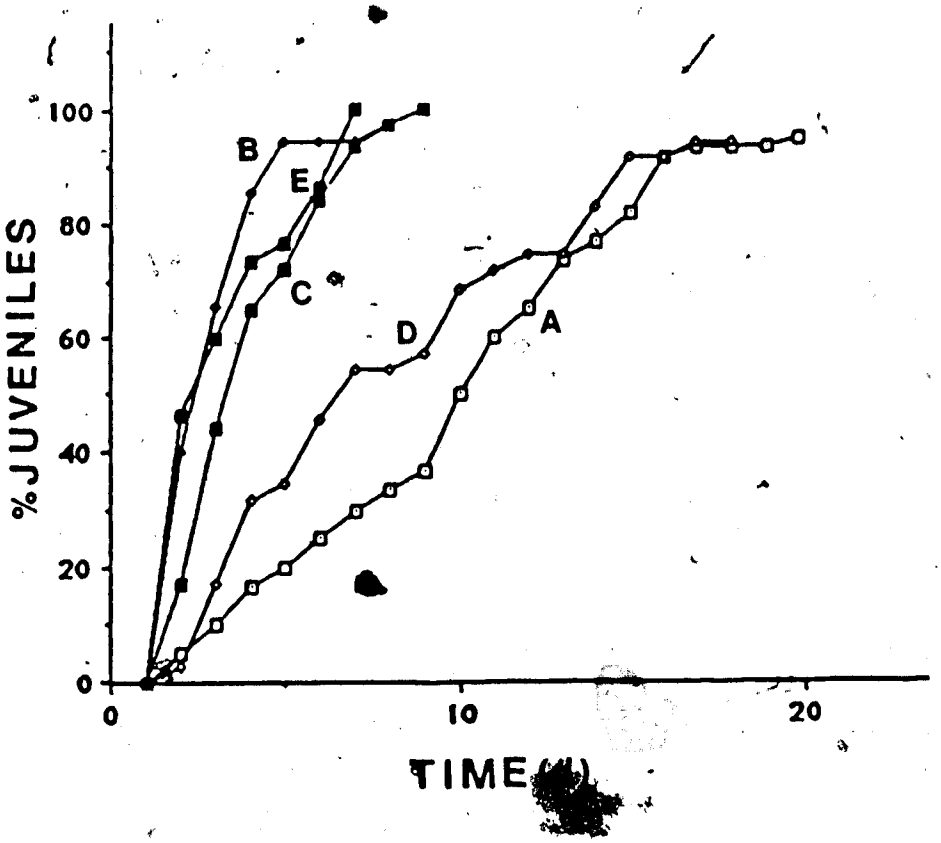
Figure 19. Metamorphosis of *Haminoea callidegenita* , expressed as the number of individuals that had successfully completed metamorphosis by the indicated day, as a percent of the original number of veligers per substratum.

Legend:

Substrata:

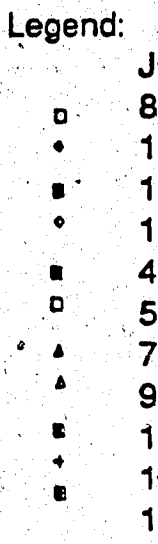
A seawater only
B *Chaetamorpha linum*
C *Ulva* sp.
D sediment
E egg mass jelly

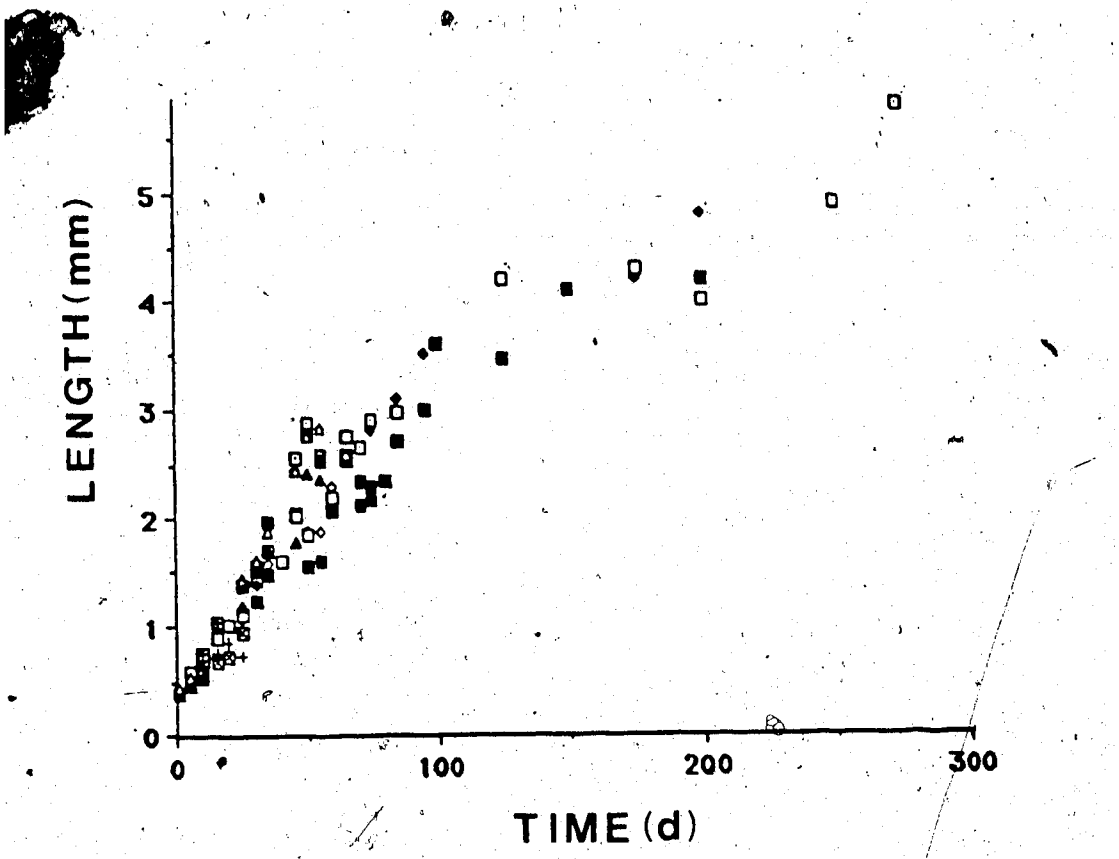
Table 9. Metamorphosis of *H. callidegenita* : values listed are sample size and percent mortality for each of five substrata used in enhancing metamorphosis.



CONDITION	n	% MORTALITY
sea water	60	5
Chaetamorpha linum	35	2.9
Ulva sp.	35	0
sediment	35	5.7
egg mass jelly	75	0

Figure 20. Growth of *Haminoea callidegenita* juveniles from the time of metamorphosis (day 1; n=11juveniles, all maintained at 21°C).




LENGTH(mm)
0
1
2
3
4
5
0
100
200
300
TIME (d)

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CHAPTER 5

THE DEVELOPMENT OF *HAMINOEA VESICULA* GOULD (OPISTHOBRANCHIA: CEPHALASPIDEA).

INTRODUCTION :

Haminoea vesicula Gould 1855 follows the pattern of development characteristic of other planktotrophic opisthobranchs (Thompson, 1967; Chia, 1971; Harris, 1975; Chia and Koss, 1978), and in particular is similar to the planktotrophic *Haminoea solitaria* Say 1822 (Smallwood, 1904 a and b; Harrigon and Alkon, 1984). The early embryological stages of *H. vesicula* were described by Leonard (1918), who concentrated mainly on spindle formation and early cell lineage. However, the later embryology and larval development of *H. vesicula* have not been described, despite the fact that populations of adult *H. vesicula* are common in muddy bays along the Northeast Pacific coast. In addition, the observed high fecundity of this species (Chapter 6) suggests that the veligers potentially constitute a large proportion of the planktonic community, at least within the adult-inhabited bays.

The objective of this chapter is to present a brief, descriptive account of the embryology, larval, and juvenile development of *Haminoea vesicula* . In Chapter 6, the description will be continued in a comparison with *H. callidegenita* , n.sp., a sympatric species with lecithotrophic larvae.

MATERIALS AND METHODS:

A. Collection and Culture of Animals:

Adults and egg masses of *Haminoea vesicula* were collected from Grappler and Bamfield Inlets, Barkley Sound, British Columbia throughout the period from May 1985 to July 1986. Cultures were

maintained at Bamfield Marine Station, Bamfield, British Columbia.

Adults were maintained in glass aquaria with a continual flow of seawater at ambient conditions (rangeing from 9 to 14 ^{o}C), and supplied with *Zostera marina* and *Ulva* sp. for food, both collected from the adult habitat. Egg masses were collected immediately following oviposition and maintained in glass or Pyrex dishes at ambient seawater temperature (9 to 12 ^{o}C). Culture water was replaced daily with bag-filtered (1μm) seawater. The development of embryos produced in the laboratory were compared to those in egg masses collected from either Bamfield or Grappler Inlets.

Flakes of cetyl alcohol were added to each culture one day before hatching to prevent the hydrophobic veliger shells from being entrapped in the surface tension (Hurst, 1967). Newly hatched veligers were removed daily and cultured using the technique of Kempf and Willows (1977), with the exception that antibiotics were generally not used. Veligers were maintained at concentrations of 0.8 to 1.0 larvae/ mL. Several unicellular algae were supplied as food (at concentrations of 10^{5} cells/ mL), including *Dunaliella* sp., *Tetraselmis* sp., *Thallassosira* sp., and *Cyclotella cryptica*). However, because of improvement in larval growth and survival, equal proportions of *Isochrysis galbana* (Tahitian strain) and *Pavlova lutheri* were used most frequently. All veliger cultures were cleaned and fed every second day. Veliger growth rates were determined every second day by measuring the shell (length x width) of 10 individuals in each of 10 cultures, with a calibrated ocular micrometer in a Reichert microscope.

B. Metamorphosis:

Several techniques were employed in attempts to isolate metamorphic inducers. *H. ves* were considered

competent to metamorphose when they exhibited a well developed propodium, maximum shell size (240 x 180μm), and changes in swimming behavior including prolonged periods of swimming near the bottom of the culture vessel. These veligers were placed, either individually or in groups of up to 100 larvae, in culture chambers containing one or a combination of potentially inducing substrata, all of which were freshly collected from the adult habitat. Substrata used were: adult *H. vesicula* , *Zostera marina* , *Ulva* sp., surface sediment, and cultured primary film. Cultures were maintained at the 9 to 12^{o}, 14 to 15^{o}, or 19 to 23^{o} C , and were either observed and cleaned daily, or were left undisturbed for variable periods of stagnancy (2 to 5 d). Cultures were maintained until metamorphosis had occurred, or until all the veligers had died.

C. Determination of Juvenile Growth:

Juveniles were obtained either through metamorphosis induced in the laboratory or by field collections in the autumn. Juveniles were cultured at 14-15 ^{o}C, in 60 x 15 mm Pyrex dishes. Juveniles greater than 2 mm in length were transferred to chambers with a gentle, continous flow of seawater. These chambers consisted of 500 mL Tripour beakers with the bottom replaced with 542μm Nitex mesh and were partially submersed in a seawater table. Juveniles were supplied with *Zostera marina* , *Ulva* sp., and primary film for food. Cultures were cleaned daily (in the case of the Pyrex dishes) or weekly (Tripour beakers), and the food was replaced as required. Growth measurements (total body length) were taken when the animals were actively crawling, either with a calibrated ocular micrometer in a Wild M-5 dissecting microscope, or for the larger juveniles with a Canlab ruler.

RESULTS :

A. Oviposition:

Oviposition of *Haminoea vesicula* under laboratory conditions took place most frequently in the morning, although adults were observed laying eggs throughout the day and during the evening. Under both laboratory and field conditions, egg masses were attached along one edge to any solid substratum.

H. vesicula egg masses were ribbon-like in shape (Fig. 21a), and typically 36 x 5 x 1 mm in size, as produced by a 42 mm long adult. The egg masses were of opisthobranch Type A (Hurst,1967), and were often attached to the substratum in a "C" shape. eggs were individually encapsulated, and arranged in a continuous string which wound back and forth through the mass in parallel, closely-aligned rows (Fig. 21b). There was an average of 180 eggs/ mm mass (linear), for a total of 10 000 to 300 000 eggs / mass.

B. Development of Encapsulated Embryos and Larvae:

The eggs were yellow in colour, and measured 90 µm in diameter (Fig. 22a). Development was synchronous within an egg mass (Chaffee and Strathmann, 1984). The major developmental events are summarized in Table 10. The rate of development increased with an increase in temperature (Table 10); times mentioned here are of individuals cultured at 15 ^{o}C.

Each egg underwent 2 holoblastic divisions, and subsequently cleaved in a spiral fashion (Fig. 22b to e) and produced a blastula approximately 24 h after oviposition (Fig. 22f). Gastrulation by invagination occurred 26 to 35 h after oviposition (Fig. 22g). Trochophores developed within 3 d (Fig. 22h), each producing a pedal ridge which separated into pedal and velar rudiments at 4 d (Fig. 22i).

The velum was bilobed (Fig. 22j) and the cilia were capable of metachronic beating at 6 d. The shell gland appeared at 4.5 d, and the shell grew anteriorly over a 2 d period to form Thompson's (1976) type 1 larval shell, comprised of 0.75 whorls arranged in a planar spiral (Fig. 22k). The statocysts, operculum, and pedal cilia also appeared at this time. As the larval shell and underlying mantle became more clearly defined, the digestive organs coalesced, and a distinctive bright red larval kidney appeared (at 8 d; Fig. 22k and l). The larval retractor muscles became functional at this time, and the veligers were capable of complete retraction if jarred or exposed to a sudden, bright light.

Hatching occured approximately 9-16 d after oviposition. The gelatinous matrix of the egg mass softened and was colonized by ciliate protozoans and nematodes. The hatching process differed from that observed in *H. callidegenita* veligers (Chapter 4), but was similar to that of *H. antillarum* (Davis, 1967). The egg capsules along the margins of the mass softened, and the veligers broke through by rapid back and forth motions against the capsule walls. The edges of the egg mass disintegrated, gradually proceeding inward, until finally the innermost veligers hatched and escaped. Newly hatched veligers had a shell length of 120μm.

C. Growth of Hatched Veligers:

Ingested particles were noted in the stomachs of veligers 1-2 d post hatching (Fig. 23a). Veligers remained pelagic for 30 to 35 d (Fig. 23a to d). During the pelagic period they increased in shell length at a rate of 1.63μm/ d (Fig. 24). Veligers were active swimmers and remained at the top of the culture dish throughout most of the pelagic period. There was a high mortality of veligers at 9 to 12 d and again at 18 to 24 d (Fig. 25). Veligers which survived these periods grew to

an approximate shell length of 180μm, showed a well developed propodium (Fig. 23c and d), and underwent behavioral changes such as swimming near the bottom of the culture dish. Competent veligers were placed in dishes with a variety of substrata in attempts to induce metamorphosis.

D. Metamorphosis:

Inducing metamorphosis in *H. vesicula* proved difficult. The actual inducer(s) remains unknown, but metamorphosis occurred in a few veligers maintained under the following conditions. Competent veligers were placed in 500 mL Pyrex beakers containing one of or various combinations of: 5 d growth of primary film, *Zostera marina*, *Ulva* sp., and adult *H. vesicula*. *Isochrysis galbana* and *Pavlova lutheri* were provided for food. Cultures were left undisturbed at ambient seawater temperatures for 3 to 4 d, then searched for remaining veligers or juveniles. Experiments involving one, or a combination of 2 or 3 of the above substrata were unsuccessful. Metamorphosis occurred only when all the substrata were present.

E. Growth of Juveniles:

All juveniles that metamorphosed in the laboratory had initiated feeding and growth by the first observation (up to 4 d post-metamorphosis; Fig. 23e). Subsequent growth was similar to that of *H. callidegenita* (Fig. 23f, and Chapter 4). Under laboratory conditions, juveniles grew at a rate of 0.04 mm/d (Fig. 25).

DISCUSSION:

Haminoea vesicula produced planktotrophic larvae which hatched after a period of 9 to 12 d. The veligers grew continuously throughout the pelagic period at a rate of approximately 1.63μm/d. The general pattern of development was typical of that of

planktotrophic opisthobranchs (Thompson, 1967, 1976), and in particular, was similar to *H. solitaria* Say (Harrigan and Alkon, 1984).

H. vesicula veligers differed from the lecithotrophic *H. callidegenita* veligers (Chapter 4) morphologically and behaviorally. Morphologically, *H. vesicula* veligers were smaller, contained less yolk, had a greater differentiation of the digestive system, and had a prominent, red larval kidney. Behaviorally, *H. vesicula* were much stronger swimmers, and generally remained high in the water column of each culture dish until metamorphic competency was reached. When competent, *H. vesicula* veligers dropped to the bottom of the culture chamber, whereas *H. callidegenita* veligers remained at the bottom throughout the pelagic period. These characteristics are typical of long-term planktotrophic opisthobranch veligers, and of lecithotrophic veligers that are competent at the time of hatching (Thompson, 1967).

Experiments involving the induction of metamorphosis of *H. vesicula* veligers were inconclusive. The substrata that actually induce metamorphosis remain undetermined, although metamorphosis did occur if veligers were provided with a combination of substrata from the adult habitat. It is unknown whether a combination of a few or even all of the substrata were involved in inducing metamorphosis, or whether they provided the veligers with a component (possibly nutritional) that enhances veliger survival until metamorphosis takes place. However, it appears that competent *H. vesicula* veligers will not settle and metamorphose when exposed to primary film only, as occurred in *H. solitaria* (Harrigan and Alkon, 1984).

Data obtained in the induction of metamorphosis in *H. vesicula* also suggested that in this species, metamorphosis requires a period during which the competent larvae are undisturbed (possibly involving stagnant conditions). Adult *H. vesicula* were found in quiet bays only,

often in enclosed, stagnant areas. Numerous populations of *H. vesicula* were found in both Barkley Sound and The San Juan Islands, suggesting that in the field, inducing substrata are commonly encountered. Also, while the laboratory cultured *H. vesicula* veligers appeared healthy, it is possible that they were lacking a nutritional component required either for the survival of a lengthy pelagic period or for metamorphosis. This was supported by the observed variation in larval growth and mortality.

H. vesicula juveniles were morphologically similar to those of *H. callidegenita* , although initially smaller. Juvenile growth was also similar between the two species, although *H. vesicula* grew slightly more rapidly.

Table 10. Summary of developmental events for *Hamtnoea vesicula* embryos cultured at 15° and 21°C. Times are listed in hours (h) and days (d).

DEVELOPMENTAL STAGE	TIME (h,d)	
	15	21
OVIPOSITION	0 h	0 h
FIRST CLEAVAGE	10 h	4 h
SECOND CLEAVAGE	13 h	5 h
BLASTULA	23 h	15 h
GASTRULATION	26-35 h	21-27 h
PROTOTROCH	3 d	31 h
CEPHALOPEDAL RUDIMENT VISIBLE	4 d	36 h
SHELL GLAND APPEARS	4.5 d	47 h
VELUM BILOBED	5.5 d	2 d
METACHRONIC BEATING OF CILIA	6 d	2.5 d
STATOCYSTS APPEAR	7 d	2.5 d
STOMACH VISIBLE	8 d	3 d
LARVAL KIDNEY APPEARS	8.5 d	3 d
COMPLETE RETRACTION	8.5 d	4 d
HATCHING	9-16 d	5-11 d

Figure 21. Photomicrographs of *Haminoea vesicula* egg mass.

A. Scale bar= 1 mm.
B. Scale bar= 300μm.

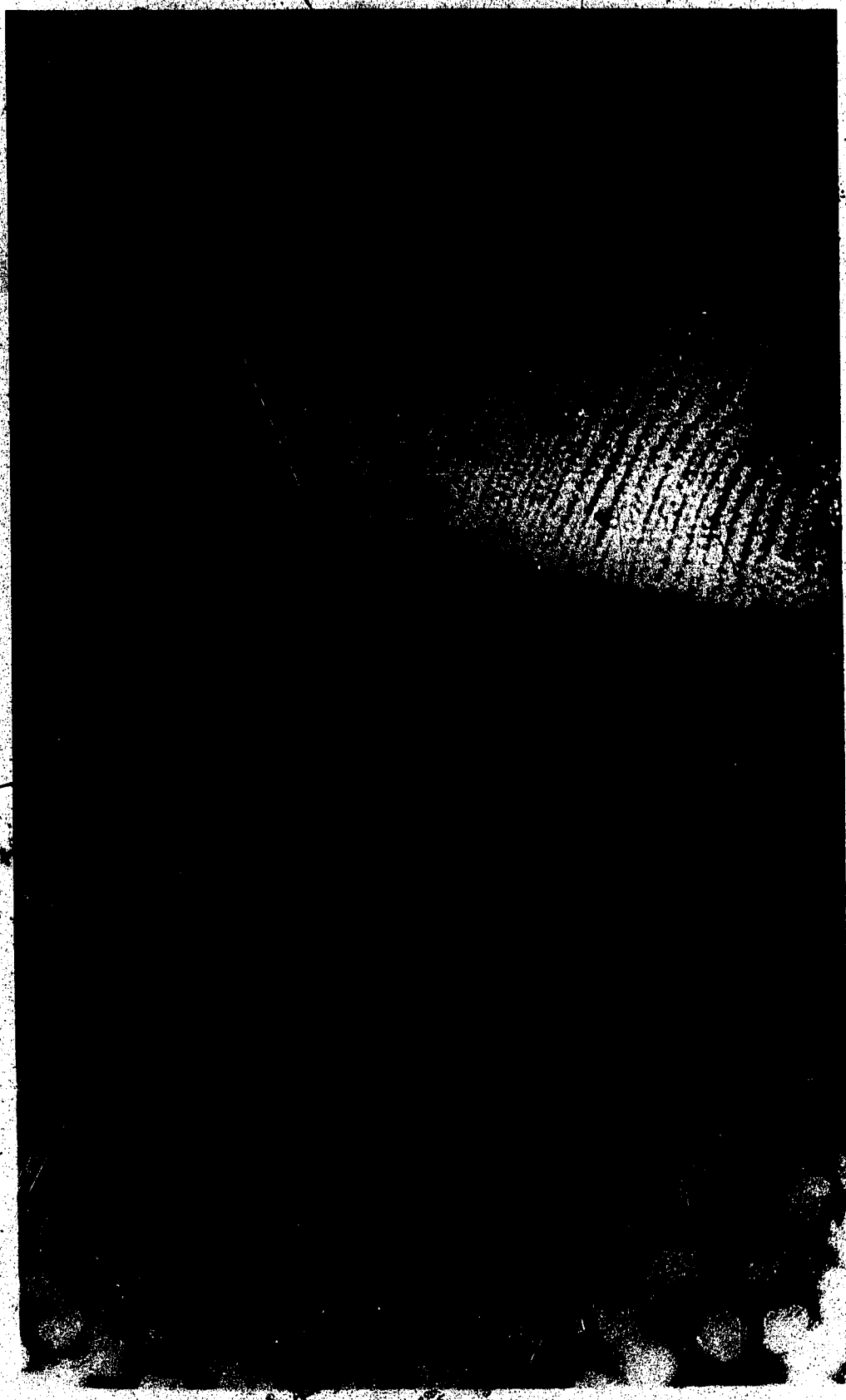


Figure 22. Photomicrographs of the early developmental stages of *Haminoea vesicula*. Numbers listed in the brackets below are the ages of the embryos in hours (h) and days (d).

Legend:
A. 1 cell (0 h). Scale bar= 100μm.
B. 2 cell (10 h). Scale bar= 100μm.
C. 4 cell (13 h). Scale bar= 100μm.
D. 8 cell (15 h). Scale bar= 100μm.
E. 32 cell (18 h). Scale bar= 100μm.
F. blastula (23 h). Scale bar= 100μm.
G. gastrula (34 h). Scale bar= 100μm.
H. trochophore (3 d). Scale bar= 50μm.
I. later trochophore (4.5 d). Scale bar= 20μm.
J. early veliger (7 d). Scale bar= 20μm.
K. veliger (8 d). Scale bar= 40μm.
L. veliger (9 d). Scale bar= 50μm.

b - blastopore
c - cilia
f - foot
i - intestine
lk - larval kidney
lr - larval retractor muscle
ma - macromere
mi - micromere
o - operculum
s - stomach
v - velum
vr - velar rudiment

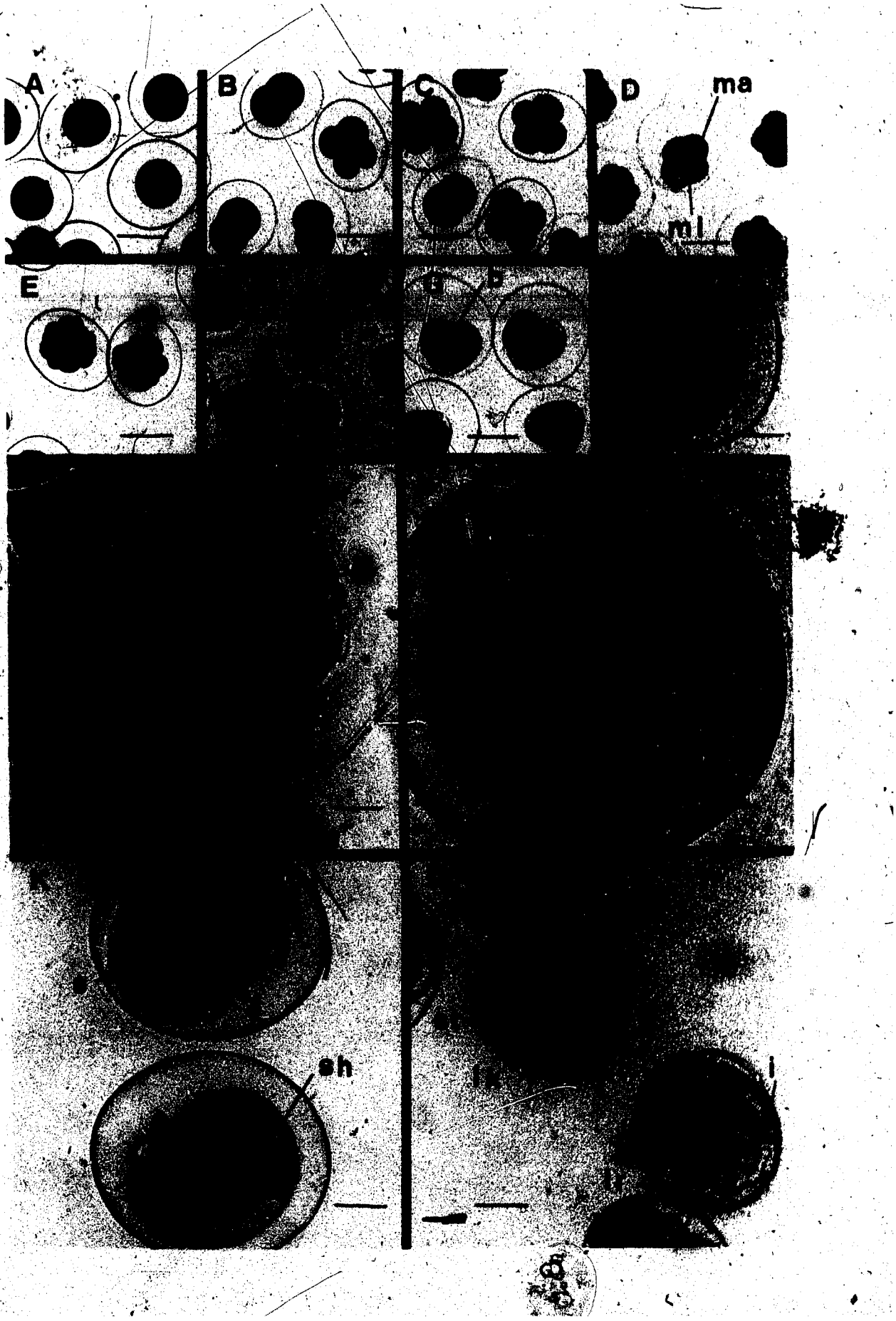
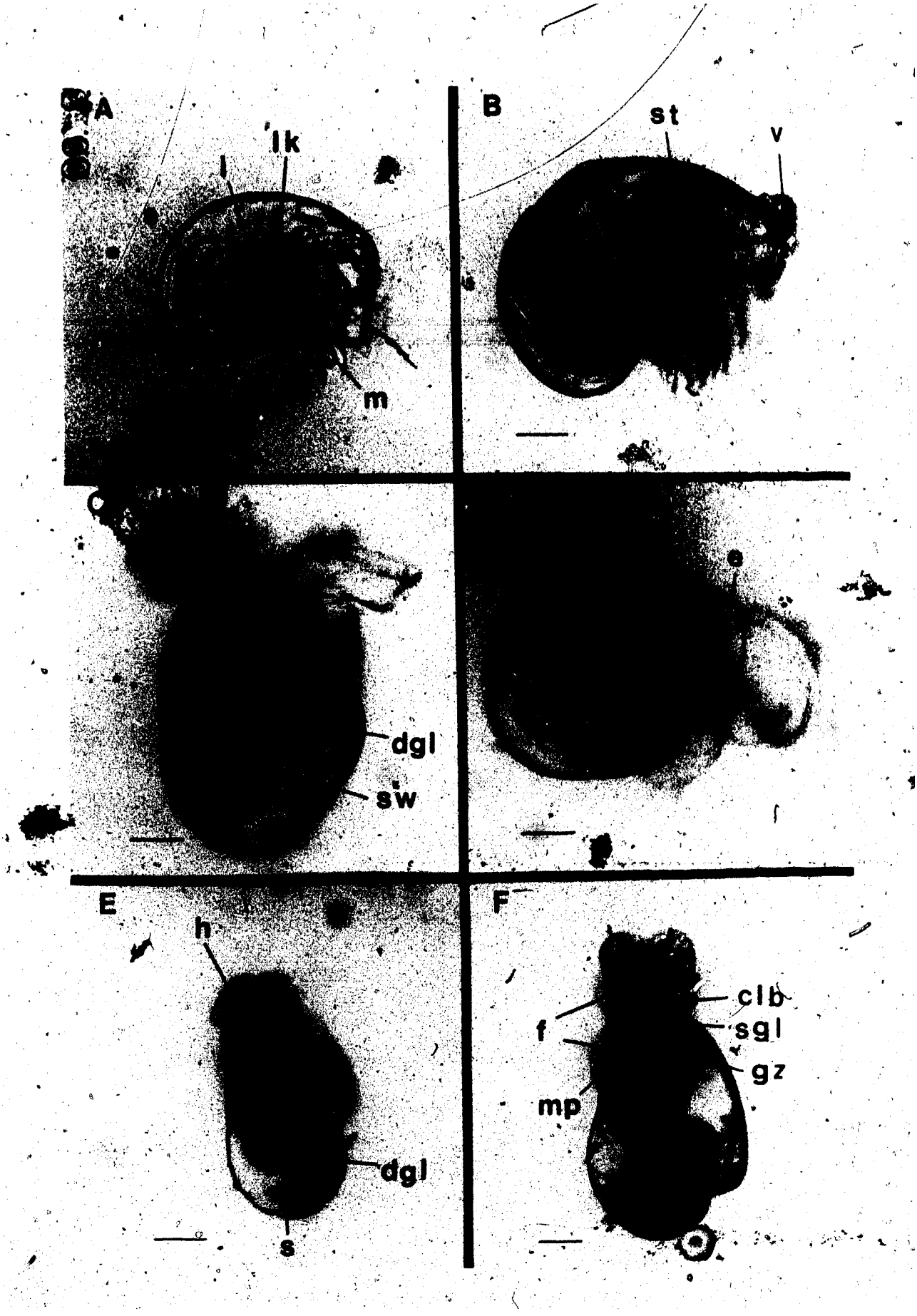

A
B
C
D
ma
ml
E
sh
l

Figure 23. Photomicrographs of *Haminoea vesicula* hatched veligers and juveniles. Numbers listed in the brackets below are days since hatching occurred. Times listed for the juveniles are approximations as the exact date of metamorphosis is not known.

Legend:
A. veliger (1 d hatched). Scale bar= 40μm.
B. veliger (9 d). Scale bar= 35μm.
C. competent veliger (31 d). Scale bar= 25μm.
D. competent veliger (31 d). Scale bar= 25μm.
E. juvenile (38 d hatched , 4 ? dmetamorphosed). Scale bar= 20μm.
F. juvenile (48 d hatched, 12 ?d metamorphosed). Scale bar= 20μm.

dgl - digestive gland
e - eye
f - foot
gz - gizzard
h - head
i - intestine
lk - larval kidney
m - metapodium
mp - mantle pigment
o - operculum
s - stomach
sgl - salivary gland
st - statocyst
sw - shell whorl
v - velum


A
lk
l
m
B
st
v
dgl
sw
E
h
dgl
s
F
clb
sgl
gz
f
mp

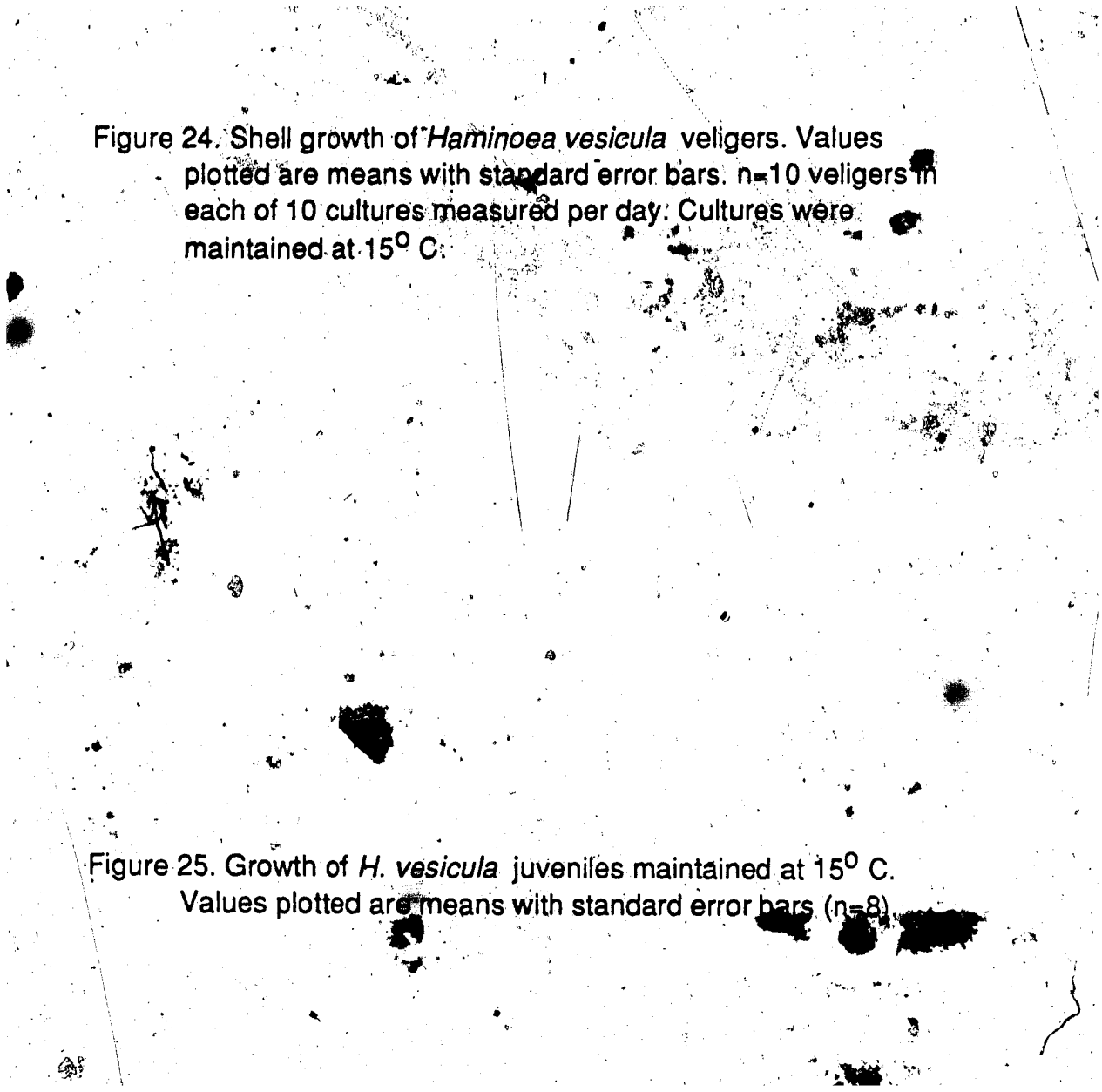
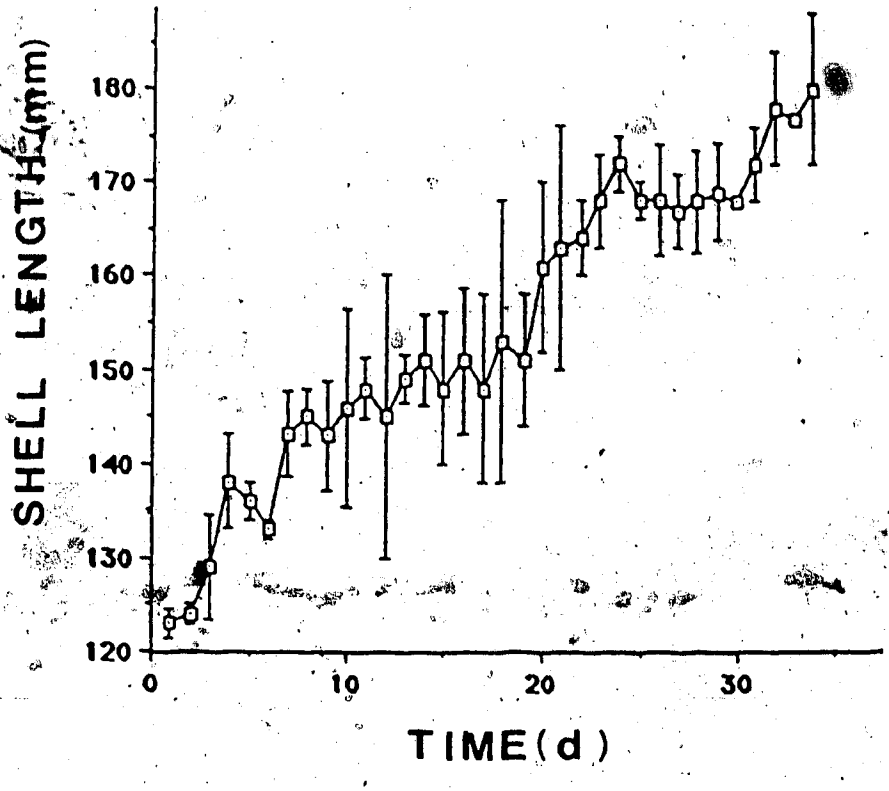


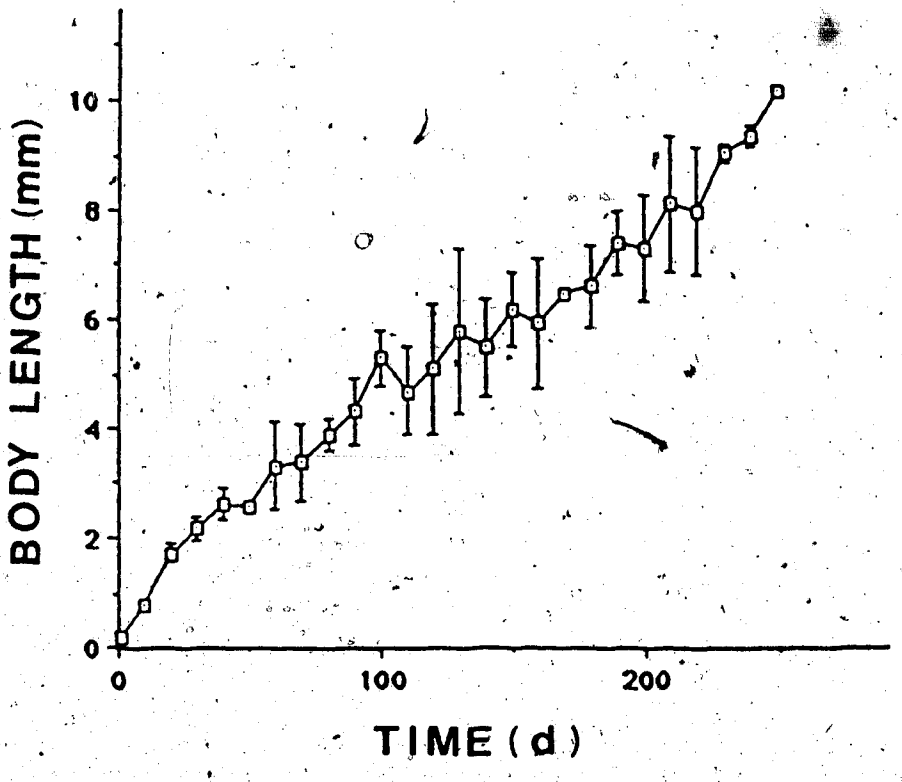
Figure 24. Shell growth of *Haminoea vesicula* veligers. Values plotted are means with standard error bars. n=10 veligers in each of 10 cultures measured per day. Cultures were maintained at 15° C.

Figure 25. Growth of *H. vesicula* juveniles maintained at 15° C. Values plotted are means with standard error bars (n=8).

24


SHELL LENGTH (mm)
180
170
160
150
140
130
120
0
10
20
30
TIME(d)

25


BODY LENGTH (mm)
10
8
6
4
2
0
0
100
200
TIME (d)

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CHAPTER 6

A COMPARISON OF FECUNDITY, EGG ORGANIC CONTENT, AND POPULATION SIZE FREQUENCY IN TWO SPECIES OF *HAMINOEA* (OPISTHOBRANCHIA: CEPHALASPIDEA).

INTRODUCTION :

Thorson's (1946, 1950) observations on reproduction in benthic marine invertebrates initiated much interest in reproductive and larval strategies. Thorson categorized marine invertebrate larvae into 3 groups: planktotrophic (pelagic and feeding), and lecithotrophic (non-feeding), either pelagic or benthic (direct developers and brooders). It is believed that planktotrophy gave rise to the other 2 categories (Chia, 1974; Strathmann, 1985) , and the forces instrumental in selecting development type have been the source of much discussion (Mileikovsky, 1971; Vance, 1973 a and b; Chia, 1971; Menge [redacted] Crisp, 1976; Clark and Goetzfried, 1978; Caswell, 1983; Strathmann, 1985). Direct examination of these development types involves assessments of reproductive energetics (Browne and Hunter, 1978; Clark and Goetzfried, 1978; Todd, 1979; Hughes and Roberts, 1980; Perron, 1981, 1982; McEdward and Coulter, 1985), ecological factors such as trophic and climatic stability (Clark, 1975; Menge, 1975; Clark and Goetzfried, 1979), interactions between species (Menge, 1975), and life history information on the species considered (Chia, 1971; Clark, 1975; Clark and Goetzfried, 1979; Todd, 1979; Perron, 1982; Rex and Waren, 1982), in attempts to categorize developmental strategies and the factors selecting for them.

Haminoea callidegenita , n. sp., and *H. vesicula* Gould coexist in morphologically and behaviorally similar. Despite these similarities,

they have different patterns of larval development: *H. vesicula* is planktotrophic, and *H. callidegenita* is lecithotrophic with partial pelagic and partial benthic larval development.

In this chapter, I shall compare the fecundities, energetic content of the eggs, features of the life cycles, and annual population characteristics of these 2 species. These types of data are not yet available for other cephalaspidean species, although similar work has been done in part for nudibranchiate opisthobranchs (Chia, 1971; Clark, 1975; Clark and Goetzfried, 1979; Todd, 1979).

MATERIALS AND METHODS :

A. Culture of Animals :

Adults of both *Haminoea callidegenita* and *H. vesicula* were maintained at Bamfield Marine Station, Bamfield, British Columbia from May to July, 1986. Adults were placed in aquaria with a slow, continuous flow of seawater at ambient temperatures (9 - 14 ^{o}C), and supplied with an excess of food (*Zostera marina* in the case of *H. vesicula* ; *Chaetamorpha linum* for *H. callidegenita*, and *Ulva* sp. for both species).

Egg masses were removed from the aquaria daily and maintained in Pyrex beakers containing bag-filtered (1 μm) seawater at ambient temperatures. Culture water was changed daily, and flakes of cetyl alcohol were added 1 d before the onset of hatching to prevent the hydrophobic larval shells from being caught in the surface tension (Hurst, 1967). Embryos were measured daily with a calibrated ocular micrometer on a Reichert research microscope. Egg size was calculated as spherical volume, using the [illegible] for each

species ($V=4/3\pi(d/2)^3$).

Larvae were collected daily upon hatching. The planktotrophic *H. vesicula* veligers were cultured using the technique of Kempf and Willows (1977), with the exception that antibiotics were generally not used. Veligers were maintained at concentrations of 0.8-1.0 larvae/ mL. *Isochrysis galbana* and *Pavlova lutheri*, at concentrations of 10^5 cells/ mL, were supplied as food. Maintenance of the lecithotrophic *H. callidegenita* veligers paralleled that of *H. vesicula*, with the exception that unicellular algae were not supplied as food. All cultures were cleaned , and in the case of *H. vesicula*, fed, every second day.

Veliger growth was determined by measuring the length of 10 individuals in each of 10 cultures with an ocular micrometer every second day. After hatching, shell growth was measured rather than total length of the larvae because of the difficulty in insuring complete extension of the velum under anaesthetic. Care was taken to ensure consistent orientation of the veligers before measurements were made. Relative larval growth was estimated between *H. vesicula* and *H. callidegenita* as an increase in shell length from uncleaved egg diameters. These data are presented as a means of comparing relative size changes between these species, rather than as an absolute measure of growth, for which volumetric estimates or energetic content would be more appropriate (McEdward, 1984).

Metamorphosis was induced as described (for *H. callidegenita* in Chapter 4, and for *H. vesicula* Chapter 5). Small juveniles were measured with an ocular micrometer on a Wild M-5 microscope; large juveniles and adults were measured with a Canlab ruler. All juveniles

and adults were measured while actively crawling.

B. Analysis of Egg Organic Content :

Three subsamples were analyzed per egg mass (n = 3 egg masses in the case of *H. callidegenita*, and n = 6 egg masses for *H. vesicula)*. For *H. callidegenita*, 125 eggs were counted per subsample, and in the case of *H. vesicula*, 6000 eggs were required for each subsample. Egg density / mm egg mass was determined, and the length of egg mass containing 6000 eggs was estimated and removed. The investing jelly layers in both species were removed by heating each sample in 42 % H_3PO_4 for 15 min, at 100 to 110 ^oC, then triply rinsing the eggs in isotonic (3 %) Na_2SO_4, and decanting the excess fluid. Eggs were surrounded by embryonic capsules and capsular fluid. Extraembryonic capsular albumen was not visible in either *Haminoea* species and its presence was not examined separately.

Total organic content of the eggs was determined by a modification of the analysis of particulate lipid by wet oxidation, involving spectrophotometric measurements of dichromate reduction (Parsons, *et al.*, 1984, as modified by McEdward and Coulter, 1984). After removal of the jelly layers, eggs were incubated in 70% H_3PO_4 to remove residual chloride (at 110^o C for 15 min), then oxidized in potassium dichromate (0.484%) in concentrated sulfuric acid (at 110^o C for 15 min). The amount of organic carbon oxidized (expressed as the reduction in dichromate concentration) was compared spectrophotometrically (440 nm, 1 cm path length) with a known glucose standard (0 to 300 μg C). Organic carbon was reported as the weight of glucose (μg) yeilding equivalent reduction in dichromate concentration. Organic carbon was converted to joules based on

constants (1 μg C = 3.90 x 10^{-2} J) given by Parson *et al.* (1984).

C. Fecundity :

Paired adults of both *H. callidegenita* (13 pairs) and *H. vesicula* (15 pairs) were observed daily for 15 d. Adults were maintained in 500 mL Tripour beakers, with the bottoms replaced with 542 μm Nitex mesh, in order that the beakers could be partially submersed to allow for a continual flow of seawater. Food was supplied as outlined in Part A. The adults ranged in size from 21 to 28 mm in the case of *H. callidegenita*, and 34 to 42 mm for *H. vesicula*. Egg masses were collected daily, and egg number per mass estimated by determining the number of eggs / mm mass in 3 sections of each mass, and by using the mean to calculate the total number of eggs.

D. Population Size Frequency :

D.1. *Haminoea callidegenita*:

Animals were collected at monthly intervals from Spencer's Spit, Lopez Island, Washington, during the period from July 1985 to August 1986, with additional collections in November 1984, February 1985, October 1986, and April 1987. Distribution of animals and fragility of the habitat made it difficult to sample a pre-determined area of Spencer's Spit lagoon. Animals were sampled by removing a mat of *Chaetamorpha linum* from the lagoon, and searching through the mat until 50 individuals were found. Animals were measured while actively crawling.

D.2. *Haminoea vesicula* :

Animals were collected from Grappler Inlet, Bamfield, British Columbia, at monthly intervals from May 1985 to August 1986, with one additional collection in February 1985. Adults were sampled by

carefully searching the *Zostera marina*, algae, and surface sediments along a low-intertidal transect. Again, animal distribution and the delicate nature of the habitat made it difficult to sample a pre-determined length of transect; therefore, searching was continued until 50 animals were found.

Small *H. vesicula* juveniles were collected by sampling 0.25 m^2 areas of surface sediment. In the lab, these samples were sieved, and examined under a Wild M-5 microscope. Surface sediments were sampled monthly from August 1985 to January 1986, and again in May and June 1986. Adults and juveniles were measured while actively crawling.

RESULTS:

A. Development and Growth of Embryos and Larvae:

Haminoea callidegenita, n. sp., have lecithotrophic larvae with large, yolky eggs (230μm in diameter; Table 11). The period of encapsulation lasted between 31 - 36 d (15 ^{o}C), during which the embryos grew at a rate of 4.30μm/ d (measured as an increase in length), to hatch as 360μm long veligers or juveniles. The planktonic period ranged from 0 to 20 d, depending on the developmental stage at hatching and whether a substratum suitable for enhancing metamorphosis was present (Chapter 4). Veliger growth did not occur during the pelagic period. Metamorphosis occurred 31-51 d after oviposition, depending on the length of the planktonic period. At metamorphosis, individuals are approximately 360μm long (linear shell length), having increased in size by 56.52 % during the pre-metamorphic period (growth restricted to the period of

encapsulation).

Haminoea vesicula, with planktotrophic larvae (Table 11) produced eggs that were 90μm in diameter. During the embryonic period (9-12 d, at 15 °C), the embryos grew at a rate of 4.78μm/d to hatch as 133μm long veligers (shell length). There was a relatively long planktonic period (30-34 d; Chapter 5), during which the planktotrophic veligers grew at a rate of 1.68μm/d to reach competency at approximately 173μm in size (shell length). From oviposition to metamorphosis, individuals increased in length by approximately 100% (approximately half each in the encapsulated and free swimming periods).

Although the relative duration of the encapsulated and pelagic phases were different in these 2 species, length of the pre-metamorphic period was comparable between *H. vesicula* and some individuals of *H. callidegenita* (Table 11), depending on when the *H. callidegenita* individuals metamorphosed (Chapter 4). Growth rates during the pre-metamorphic period differed between these 2 species. The increase in length of the non-feeding *H. callidegenita* was only about half that shown by the feeding *H. vesicula*, in terms of the percent increase in length from the diameter of uncleaved egg (Table 11).

B. Energetics and Fecundity:

H. callidegenita produced eggs containing approximately 1.39μg C (5.4×10^{-2} joules/ egg, including egg capsule and intracapsular fluid), with an energetic density of 2.88×10^{-3} μg C/μm^3 egg. There were approximately 400 eggs/mass (Table 12). Measured over a 15 d period in the lab, individuals produced a mean of 0.064 egg masses/ d,

for a mean egg production of 27.36 eggs/d, and an investment of 38.03 µg C in eggs/ individual per d (Table 13).

H. vesicula produced eggs containing approximately 0.025 µg C (1.0×10^{-3} joules/ egg, including the egg capsule and intracapsular fluid) with an energetic density of 0.14×10^{-3} µg C/µm^3 egg. There was a mean value of 73 020 eggs/mass (Table 12). In the lab (over a 15 d period), individuals produced a mean of 0.08 egg masses/ d, for an egg production rate of 4663.80 eggs/d (120.79 µg C invested in eggs/ individual per d; Table 13).

These estimations of the energetic content of the eggs are similar to those obtained by Todd (1979) on *Onchidoris bilamelata* (which produced eggs of 90 µm diameter, each containing 2.10×10^{-9} cal/ egg or, 3.31×10^{-3} joules/ egg) and *Adalaria proxima* (with 180 µm eggs, each containing 5.38×10^{-9} cal/ egg or, 6.69×10^{-2} joules/ egg).

Although the energetic content per egg was much higher in *H. callidegenita*, relative fecundity differed so that overall investment in eggs was greater in *H. vesicula*. Laboratory estimates of fecundity per month indicate that parental investment in eggs in *H. callidegenita* was lower than that of *H. vesicula*, both in terms of egg number (0.5 % of the number of eggs produced by *H. vesicula*), and in terms of energy (31 %). This estimate of parental investment does not take into account energy involved in gametogenesis, maintenance of the reproductive organs, and energy contained in the egg mass jelly (probably much higher in *H. callidegenita* which produces thick, cylindrical egg masses than in *H. vesicula* with ribbon-like egg masses).

C. Reproductive Season:

In Spencer's Spit Lagoon, viable *H. callidegenita* egg masses have been observed in all months, excluding December and January (Fig. 26).

In Grappler Inlet, *H. vesicula* egg masses have been observed from May (1985, 1986) to September (1985; Fig. 27).

The length of individual reproductive periods in both species is unknown. However, individuals maintained in isolation in the laboratory have continued to produce viable egg masses for up to 17 weeks in the case of *H. callidegenita* , and up to 16 weeks in the case of *H. vesicula*.

D. Population Size Frequency:

1. *H. callidegenita* :

The size structure of the *H. callidegenita* population at Spencer's Spit, Lopez, Washington was examined over a 1 year period (from July 1985 to August 1986, with additional collections in November 1984, February 1985, October 1986 and April 1987; Fig. 26). As the size structure differed between 1985 and 1986, the data for these 2 years are described separately.

Throughout 1985, each monthly sample revealed a wide range in sizes (January, 9.26 +- 11.12 mm; July, 15.96 +- 7.08; October, 8.80 +- 4.03 mm; values listed are mean +- standard error), suggesting continuous recruitment throughout the year.

From December 1985 to March 1986, no animals were found. In April 1986, both animals and egg masses were observed. The population size structure indicated one cohort growing throughout the summer (sizes of 18.38 +- 2.93 mm in April, to 20.72 +- 2.96 in June),

with newly-settled individuals first appearing in July, approximately 3 months after the first egg masses were observed in that year (2 cohorts visible, with sizes of 6.13 +- 2.58 mm, and 20.11 +- 3.28 mm). A 3 month lapse between initial spawning and first observed recruitment was predictable, assuming 1 month between oviposition and hatching, and 2 months to grow to 2-3 mm in length (calculated as a growth rate of 0.042 mm/ d, as compared to a rate of 0.03 mm/ d as observed in lab). These 2 cohorts were still apparent in October 1986, but additional recruitment was indicated by a continuum of sizes.

Only one collection was made in 1987 (April, mean size of 9.19 +- 5.78 mm), suggesting a size structure similar to that observed throughout most of 1985.

These data suggest a possible annual cycle of the *H. callidegenita* population found in Spencer's Spit. Within the population, both egg production and larval recruitment occurred throughout the year. Juveniles matured at various times of the year, depending on when settlement occurred. The overwintering population consisted of juveniles and reproductively active adults (1985), or of juveniles only (1986). Why the structure of the Spencer's Spit population was variable between 1985 and 1986 was not determined, but possibly the unusually cold temperatures and high snowfall in December 1986 produced sufficiently unfavorable conditions in Spencer's Spit lagoon to cause a high mortality.

2. *H. vesicula* :

The size structure of a *H. vesicula* population in Grappler Inlet, Bamfield, British Columbia, was examined over a 1 1/2 year period (from May 1985 to August 1986, with one additional collection in

February 1985; Fig. 27). Data for both 1985 and 1986 suggested the same pattern.

The size structure indicated one cohort which grew throughout the year. Surface sediment sampling first indicated the presence of small juveniles (one individual was collected that was 1.5 mm in length) in September; other individuals collected at this time were 36 +- 2.45 mm long. These data suggest that recruitment in this population occurred from mid-summer to early fall, based on the following observations: onset of oviposition in the field in May, an approximate 50 d period before metamorphosis, and an approximate 40 d growth as juveniles before reaching the observed 1-2 mm body length (calculated as a growth rate of 0.05 mm/d and supported by a growth rate of 0.048 mm/ d observed in the laboratory). These juveniles increased both in size and abundance throughout the fall (although size increases would influence observations on abundance since the larger juveniles were easier to find). The length of the smallest juveniles collected in November 1985, indicates settlement in early October, following the same calculations. In December 1985, individuals were 3.08 +- 0.47 mm long, in March 1986, 10.50 +- 2.69 mm, and in June 22.83 +- 4.65 (1985) and 31.11 +- 2.66 mm (1986). The largest adult observed was 38 mm long (October 1985).

These data suggest a possible cycle that may have occurred annually in the Grappler Inlet population of *H. vesicula*. Animals began spawning in early May. First recruitment of planktotrophic veligers was in late June and July. Adults died in the fall, and same-year recruited juveniles overwintered and grew in the surface sediments, and reached maturity in the late spring (late April and early May).

Adults spawned throughout the summer and juveniles were recruited to the population from mid-summer to early fall.

E. Overwintering:

Although opisthobranchs are seasonally abundant, the annual life cycle, and in particular the overwintering stage, is not generally understood (Swennen, 1961; Thompson, 1967; Clark, 1975). Individuals of both *H. vesicula* and *H. callidegenita* were present in [redacted] habitat all year. *H. vesicula* overwintered as juveniles, which lived and grew in [redacted] sediments. The overwintering stage of *H. callidegenita* consisted of egg masses, juveniles and adults found in both the surface sediments and in *Chaetamorpha linum* mats. However, the stages found differed in the collections for the 2 years.

DISCUSSION :

Descriptions of opisthobranch life cycles have included only those of nudibranchs and sacoglossans (Thompson, 1958, 1962, 1967; Swennen, 1961; Clark, 1975). Most species of these two orders are specialized feeders, and their life cycles are closely linked to those of their prey species (Thompson, 1976; Clark, 1975; Todd, 1979). Clark (1975) classified the life-cycle patterns of nudibranchs and sacoglossans into 2 ecological groups: 1) exploitist, which included species with a transient food supply, a short, subannual life-cycle, and with continuous egg production and recruitment throughout the year (r-selected); and 2) strategist, which included those species with a stable food supply, one annual reproductive season, and one, brief period of recruitment (K-selected).

Haminoea callidegenita and *H. vesicula* do not fit into either of Clark's (1975) categories. Populations of both species showed long reproductive seasons, probably involving several spawning cycles per individual per year. Their food sources were, if not stable in composition, appearently sufficient to maintain *Haminoea* populations all year.

Despite the long period of reproductive activity in both species, patterns of recruitment differed between them (as indicated by the appearence of juveniles that settled and metamorphosed 1 to 2 months prior to collection). In the case of *H. callidegenita* viable egg masses were found year round, and the composition of Spencer's Spit community did not appear to undergo drastic seasonal changes, which potentially may inhibit settlement and juvenile survival; therefore, continuous recruitment seems feasible. The size frequency of the *H. vesicula* population suggests that recruitment took place over several months, with a possibility of loss of veligers that hatched late in the reproductive season. In Grappler Inlet, seasonal changes in floral composition occurred. These changes may have influenced recruitment either through a loss of substrata suitable for inducing metamorphosis, or a reduction in the substrata involved in enhancing survival of small juveniles by providing nutrition or a protective microhabitat. Loss of veligers from one habitat does not necessarily mean that they died, as it is possible that some of these individuals may be recruited by other populations (Clark, 1975) in communities that have not yet undergone seasonal shifts in composition. Preliminary observations indicated slight temporal differences in populations of both *Haminoea vesicula* and *Zostera marina* between

Grappler and Bamfield Inlets, indicating that variable recruitment was possible. Spatial and temporal variability are common in opisthobranch populations, both in terms of size structure and in timing of the reproductive season (Thompson, 1967; Clark, 1975). The developmental stage composing the overwintering population was different between *H. callidegenita* and *H. vesicula*. However, in both species, animals were found year-round.

Haminoea vesicula and *H. callidegenita* have different patterns of larval development. *H. vesicula* have pelagic, feeding larvae, with a high fecundity, and invested slightly more energy in total egg production than did the lecithotrophic *H. callidegenita*. Higher fecundity of lower energy eggs, but an overall greater energy investment in eggs was considered characteristic of planktotrophic species (Chia, 1974 ; Mileikovsky, 1971; Strathmann, 1985; Todd, 1979), while lecithotrophic species were considered more energetically efficient (Menge, 1975; Vance, 1973), although the efficiency may be imposed on a species through ecological constraints (Menge, 1975). Comparisons of parental investment in this paper represent energy included in the eggs over a 2 week interval only. They are, therefore, underestimations of reproductive effort because they omit energy invested in egg mass jelly, capsules, gametogenesis and maintenance of reproductive organs which also require substantial portions of the energy budget (Stickle, 1973; Tinkle and Hadley, 1975; Browne and Hunter, 1978; Hughes and Roberts, 1980; Perron, 1981; Grahame, 1982; Tuomi *et al.*, 1983).

H. callidegenita eggs contained almost 100 times more organic carbon than *H. vesicula* eggs, in terms of individual eggs. Despite

differences in energy available for development (as the energy invested per egg including intracapsular fluid; extraembryonic albumen was not visible optically), and in length of the pre-hatching period, approximately the same amount of growth of encapsulated individuals of both species relative to uncleaved egg size occurred. The relative growth of encapsulated *H. vesicula* larvae was interesting, given the low energy content of the eggs. Perhaps the short period between oviposition and hatching allowed for such low energy content, in that there would be lower energy demands for maintenance, than there would be in *H. callidegenita*.

At hatching, *H. vesicula* veligers contained no visible yolk, and begin feeding immediately. Hatched *H. callidegenita* veligers had enough yolk reserves to sustain them for up to 20 d (discounting the possibility of an auxilliary supply of energy provided by the uptake of dissolved organic matter (Vance, 1973a; de Burgh and Burke, 1983), and visibly depleting yolk reserves were observed during the pelagic period. Possibly, the higher energy content of the *H. callidegenita* eggs acted as a reserve in case the veligers encountered unfavorable environmental conditions, and were forced to delay metamorphosis. However, most *H. callidegenita* individuals hatched as juveniles and begin feeding 2-3 d post-hatching (Chapter 4). Further postponement of the onset of feeding in the juveniles seemed unlikely as a frequently encountered situation, because of the abundance of potential food sources in Spencer's Spit throughout the year. This suggests that either another factor was involved in determining the energetic requirements of the *H. callidegenita* egg, or that some of the yolk reserve was potentially superfluous in the majority of

individuals. Observations on the relative yolk depletion in the veligers of *H. vesicula* and *H. callidegenita* were based on visible morphological changes, rather than direct measurements of energy content.

The evolution of larval strategies in benthic marine invertebrates has been the subject of much interest since Thorson's (1946, 1950) classification of developmental types. Opisthobranchs typically have a "mixed" larval strategy (following Mileikovsky's, 1971, re-organization of Thorson's classification), involving an initial period of benthic development (within an egg mass) and followed by a pelagic phase (either as feeding or non-feeding veligers) and which is vestigial in some species (Thompson, 1958, 1967, 1976; Hadfield, 1963; Hurst, 1967; Chia, 1971; Clark, 1975; Clark and Goetzfried, 1979; Chia and Koss, 1978). The relative advantages of different larval strategies and possible selective forces acting on them were discussed by many authors (Mileikovsky, 1971; Vance, 1973 a and b; Strathmann, 1974; Menge, 1975; Clark and Goetzfried, 1978; Pechenik, 1979). It is interesting to consider a few of these factors as possibly influential in selecting the larval strategy of *H. callidegenita* and *H. vesicula* , given the observed morphological and ecological similarities between the adults of these species. However, it must be realized that the limited data available for this consideration are purely qualitative, and do not necessarily reflect causal relationships.

Dispersal has been considered as a major advantage of planktotrophy as a larval strategy (Thorson, 1946; Mileikovsky, 1971; Strathmann, 1974; Crisp, 1976; Pechenik, 1979; Clark and Goetzfried, 1978). Both *H. vesicula* and *H. callidegenita* have the potential for

dispersal, whether through pelagic veligers or through egg mass rafting. *H. vesicula* veligers are pelagic for a longer period, with possibilities of achieving a greater dispersal distance, although in itself, long range dispersal might not have a selective advantage (Palmer and Strathmann, 1981). Egg masses of both species are usually, but not exclusively, deposited on buoyant substrata (such as *Zostera* and *Ulva*), and in the case of *H. vesicula*, "rafting" egg masses have been found floating in and just at the outer limits of bays (personal observations). "Rafting" *H. callidegenita* egg masses were not observed, but this may reflect the sparsity of populations, rather than an inability for this type of dispersal). Therefore, it appears that the potential for dispersal exists for both species. A second advantage attributed to planktotrophy is an increased fecundity (Chia, 1971; Mileikovsky, 1971; Palmer and Strathmann, 1981; Strathmann, 1985), which is undoubtly much higher in *H. vesicula* than in *H. callidegenita*. A major advantage of a longer benthic phase, as evident in *H. callidegenita*, has been suggested as being an increased period of protection of vulnerable larval stages (Pechenik, 1979; Menge, 1975).

Two factors considered as selective forces on opisthobranch life cycles are trophic and climatic stability (Thompson, 1964; Clark, 1975). While potential food sources change in composition seasonally, food was available to populations of both *Haminoea* species throughout the year. Climate, and other physical environmental factors, such as local topography, are not stable in intertidal, muddy bays which are subject to wide fluctuations in temperature and salinity.

Other forces potentially influential on the determination of life

history strategies are planktonic mortality rate (Vance, 1973 a and b; Menge, 1975), and interactions between species (Menge, 1975; Pechenik, 1979). The effect of planktonic mortality on *H. callidegenita* and *H. vesicula* cannot be assessed, although the lengthy pelagic period of *H. vesicula* may increase the risk of predation (Pechenik, 1979; Vance, 1973a; Strathmann, 1985). Two interspecific interactions will be briefly considered: competition for food, and predation. The most likely major competitors in these habitats are other *Haminoea*. Examination of stomach and fecal pellet contents indicate that similar epiphytes and particles are ingested by the adults of both species. However, the abundance of food in the habitats observed suggests that food is not a limiting factor. The effects of predation were not assessed. Observations on 2 known predators indicate the palatability of *Haminoea* species (*Navanax* , also a cephalaspidean opisthobranch, *in* Morris *et al.*, 1980, and flounders, *in* Burn, 1966). However, populations of both species are dense throughout most of the year, and in the case of *H. vesicula*, widespread. While these features might make them attractive as prey these data also suggest that predation probably is not occuring to the extent where it would be limiting to either population.

Therefore, it seems possible that in *H. vesicula* and *H. callidegenita*, a number of factors may have contributed to the selection of a particular larval strategy, with physical environmental factors potentially playing a major role. *H. vesicula* have retained planktotrophy , probably not because of advantages derived from long range dispersal but because the climatic and physical instability associated with this habitat have selected for increased fecundity.

Lecithotrophy, an energetically "efficient" strategy has been selected for in *H. callidegenita* through exploitation of a stable food source. One feature of lecithotrophy is that the larger eggs will have a slower development, a longer encapsulated phase, and therefore, a longer period of veliger protection. The unpredictable physical aspects of the habitat provide enough instability to encourage the retention of some pelagic veligers per egg mass, with the ability to either settle and metamorphose immediately or after a variable pelagic period, as soon as a favorable substratum is encountered.

Table 11. Summary of life history characteristics of *Haminoea callidegenita* n.sp. and *H. vesicula* Gould.

SPECIES		H. CALLIDEGENITA	H. VESICULA
LARVAL TYPE		lecithotrophic	planktotrophic
SIZE OVA (µm)		230	90
EMBRYONIC PERIOD			
	DURATION (d, 15°)	31-36	9-12
	SIZE AT HATCHING (µm)	360 +- 16	133 +- 17
	INCREASE IN LENGTH	130 +- 7	43 +- 8
	GROWTH RATE (µm/d)	4.3	4.78
	GROWTH (% egg size)	56.52	47.78
PELAGIC PERIOD			
	DURATION (d, 15°)	0-20	30-34 (?)
	SIZE AT METAMORPHOSIS (µm)	360 +- 15	170 (?)
	INCREASE IN LENGTH (µm)	none	50 +- 6
	GROWTH RATE (µm/ d)	0	1.68
	GROWTH (% hatching size)	0	37.59
	GROWTH (% egg size)	56.52	103.33
JUVENILES			
	GROWTH RATE (mm/d)	0.033 +- 0.018	0.048+- 0.012
	SIZE AT MATURITY	13	15

Table 12. Estimates of fecundity in *Haminoea callidegenita* and *H. vesicula*, based on egg and egg mass production over a 15d period.

SPECIES		H. CALLIDEGENITA	H. VESICULA
TIME (d)		15	15
ADULTS	# PAIRS	13	15
	SIZE RANGE (mm)	21-28	34-42
EGG MASSES	TOTAL # EM	25	37
	# EM/ IND x 15d	0.96 +- 0.59	1.27 +- 0.36
	# EM / IND x d	0.066 + 0.04	0.08 + 0.029
EGGS	TOTAL # EGGS	9066	2 098 755
	# EGGS/ MASS	401.47 + 229.80	73020.23 + 122649.71
	# EGGS/ IND x 15d	348.69	69958.8
	# EGGS/ IND x d	27.36 + 28.04	4663.80 + 3398.94

Table 13. The reproductive energetics of *Haminoea callidegenita* and *H. vesicula* , including both egg number and energetic content.

SPECIES	H. CALLIDEGENITA	H. VESICULA
MAXIMUM ADULT SIZE (mm)	36	44
SIZE OVA- diameter (µm)	230+-7	90+-3
- volume (µm 3)	6.37×10^{6}	0.38×10^{6}
ENERGETIC CONTENT		
joules/ egg	5.4×10^{-2}	1.0×10^{-3}
µg C - per egg	1.39 +- 0.19	0.0259 +- 0.0047
- perµm3 egg	2.18×10^{-7}	0.66×10^{-7}
# EGGS/ MASS	401.47 +-229.80	73020.23+-122649.71
# EM / IND x d	0.064 +- 0.048	0.08 +- 0.041
# EM / IND x month	1.92 +- 1.29	2.42 +- 0.95
# EGGS/ IND x d	27.36+- 46.71	4663.8+- 4231.34
# EGGS/ IND x month	821 +- 618	139914 +- 140145
µg C/ EGGS x d	38.03 +- 58.32	120.79 +- 3253.26
µg C/ EGGS x month	1140.9 +- 1324.7	3623.7 +- 64294.9

Figure 26. Population size frequency of *Haminoea callidegenita* at Spencer's Spit, Lopez Island, Washington. Animals were measured during the period from July 1985 to August 1986, with additional data from November 1984, February 1985, October 1986, and April 1987.

Legend:
NC - not collected
NF - none found
e - egg masses observed

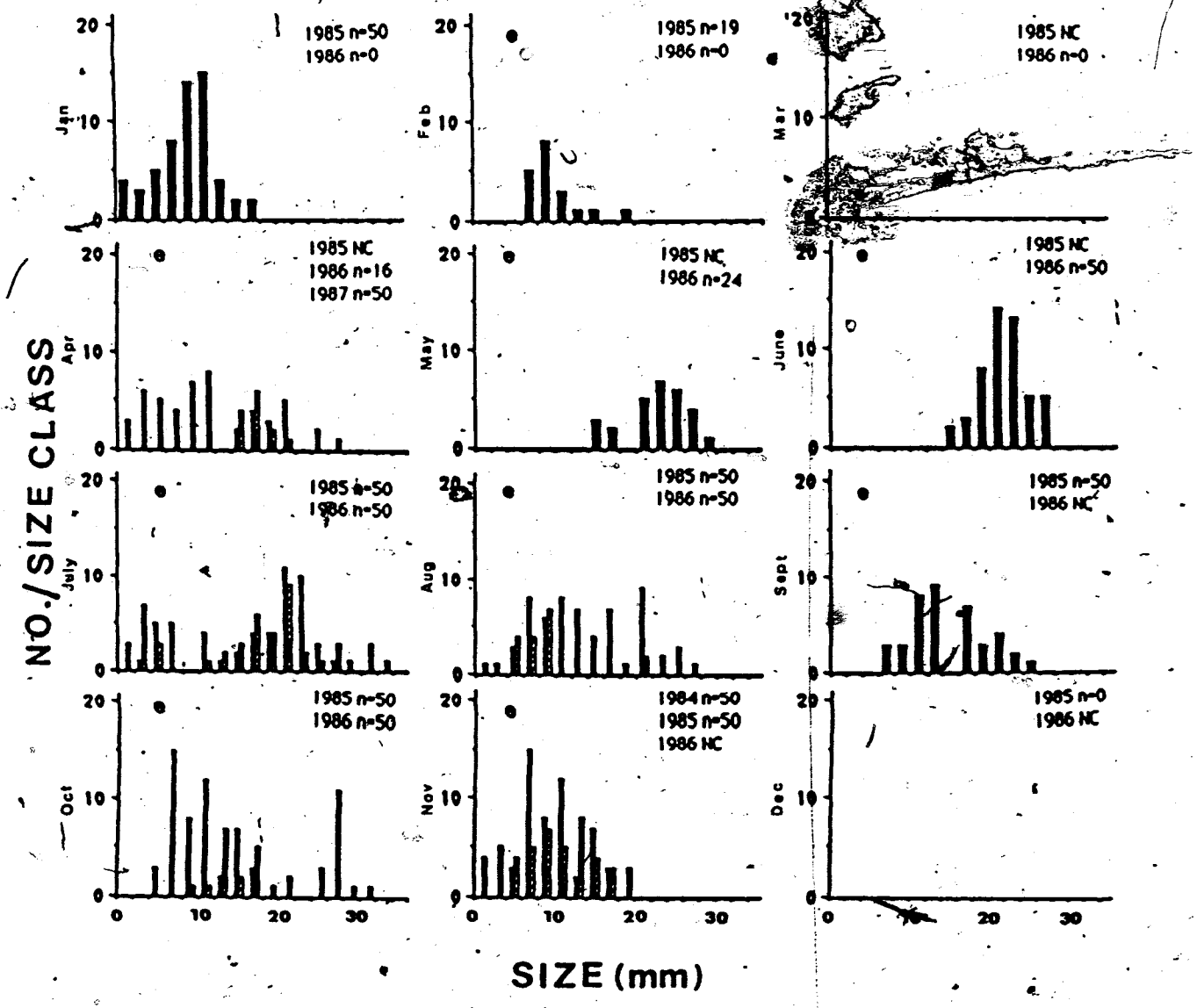
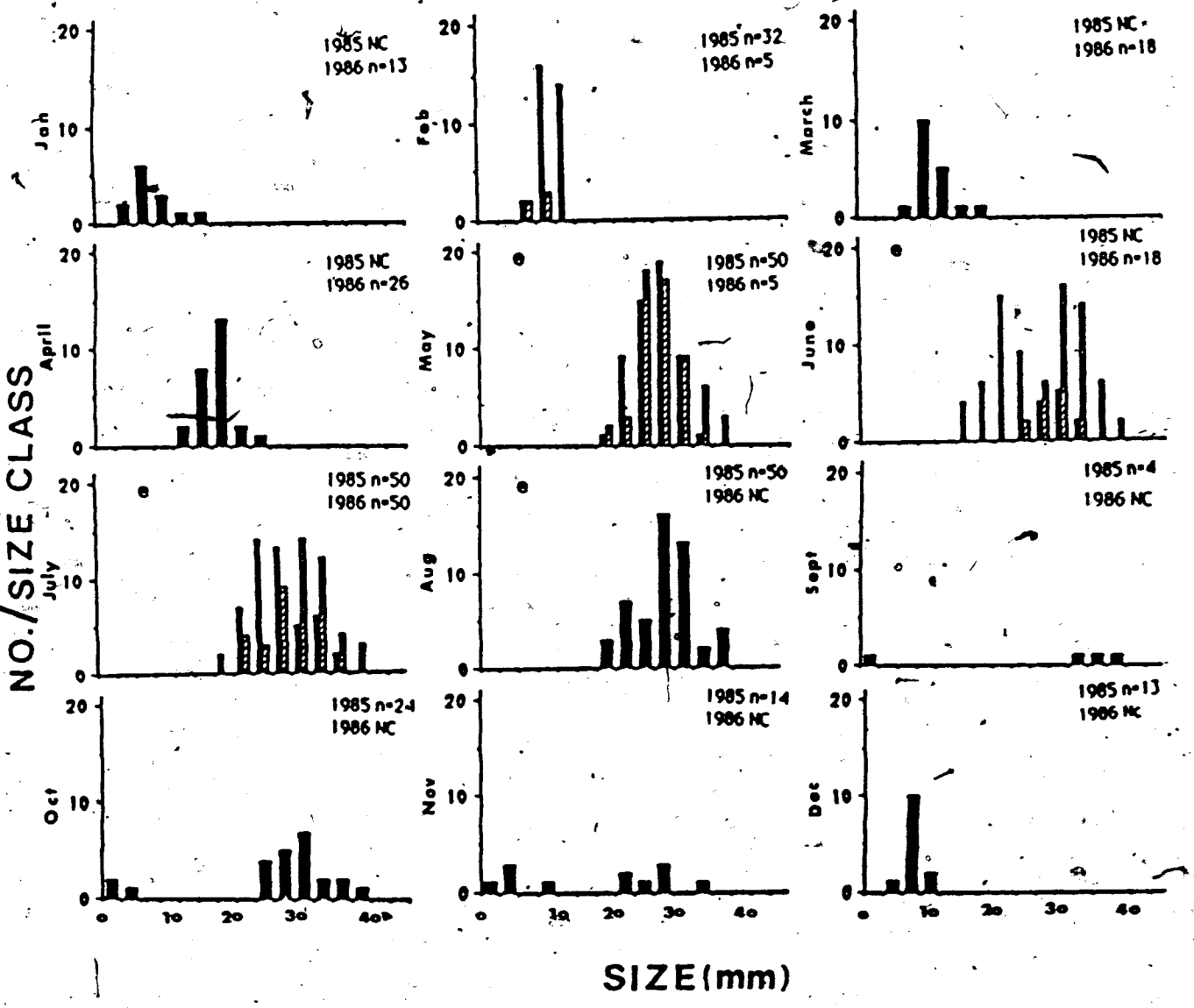

NO./SIZE CLASS
SIZE (mm)
Jan
1985 n=50
1986 n=0
Feb
1985 n=19
1986 n=0
Mar
1985 NC
1986 n=0
Apr
1985 NC
1986 n=16
1987 n=50
May
1985 NC
1986 n=24
June
1985 NC
1986 n=50
July
1985 n=50
1986 n=50
Aug
1985 n=50
1986 n=50
Sept
1985 n=50
1986 NC
Oct
1985 n=50
1986 n=50
Nov
1984 n=50
1985 n=50
1986 NC
Dec
1985 n=0
1986 NC

Figure 27. Population size frequency of *Haminoea vesicula* at Grappler Inlet, Barkley Sound, British Columbia. Animals were measured during the period of May 1985 to August 1986, with additional data from February 1985.

Legend:
NC - not collected
NF - none found
e - egg masses observed


NO./SIZE CLASS
SIZE(mm)
Jan
1985 NC
1986 n=13
Feb
1985 n=32
1986 n=5
March
1985 NC
1986 n=18
April
1985 NC
1986 n=26
May
1985 n=50
1986 n=5
June
1985 NC
1986 n=18
July
1985 n=50
1986 n=50
Aug
1985 n=50
1986 NC
Sept
1985 n=4
1986 NC
Oct
1985 n=24
1986 NC
Nov
1985 n=14
1986 NC
Dec
1985 n=13
1986 NC

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CHAPTER 7

CONCLUSIONS.

The 2 major objectives of this thesis were: 1) to examine taxonomic problems and diagnostic features in the genus *Haminoea* , and to use these features in the description of a new species, *H. callidegenita* ; and, 2) to examine the development of *H. callidegenita* n.sp., and of *H. vesicula* Gould, which exhibit different modes of larval development.

The major diagnostic features used in *Haminoea* taxonomy were reviewed. Characteristics suggested as being useful diagnostically are: external morphology (such as pigmentation, and bifurcation of the cephalic shield), Hancock's organ, the penis complex, and details of the surface of the gizzard plates. Other characters, such as radular dentition, are potentially useful; but must be thoroughly examined before being used in confidence because of the possibility of intraspecific variation. While shell morphology can be useful, such as in identification of specimens collected from one geographic region, difficulties in determining reliable diagnostic features suggest that shell structure is not sufficient as the basis for descriptions of new species. Shells alone should not form the basis for subdivision of the genus.

The genus *Haminoea* is potentially large, and has been established for approximately 170 years. However, the taxonomy of these animals has become problematic because of changes in the perception of the relative importance of shell morphology as a useful diagnostic tool by malacologists (Clark, 1973, 1978; Lindberg, 1985, 1986; Kemp and Bertness, 1984) coupled with the limited knowledge

of *Haminoea* morphology and general biology. In descriptions of both new and established species, it is recommended that descriptions of the structures mentioned above be provided, and also that information on features such as habitat exploitation and reproductive biology be included. Consideration of such features may lead to the subdivision of the genus.

The second objective of this thesis was to examine the development of 2 species of *Haminoea* with different larval types. The developmental patterns of both *H. vesicula* and *H. callidegenita* are typical of opisthobranchs in general. The one major exception is the role of egg mass jelly in determining stage of hatching in *H. callidegenita* , either in a veliger inhibiting or an intracapsular metamorphosis enhancing capacity. It would be interesting to continue this research along 2 lines. First, if the influential compound(s) could be extracted from the egg mass jelly, how would it (they) effect the development of other species of *Haminoea* and other opisthobranchs? It would be interesting to study the influence on species with 1 known larval type (such as *Adalaria proxima* , *in* Thompson, 1958, *Rostanga pulchra* , *in* Chia and Koss, 1978, and *Phestilla sibogae* , *in* Switzer-Dunlap and Hadfield, 1977), or with strategies that are variable temporally (such as *Elysia cauze* , *in* Clark, *et al.*, 1979), or spatially (*Tenellia pallida* , *in* Eyster, 1979, and *Elysia chlorotica* , *in* West, *et al.*, 1984). Second, the ecological and evolutionary implications are also interesting, especially in consideration of the differences between individual egg masses. Was the observed variation an artifact, a random event, or is the composition of the egg mass jelly influenced by genetic or

environmental factors?

In a brief comparison of reproductive energetics in *H. callidegenita* and *H. vesicula*, it was found that *H. callidegenita* eggs contain more organic carbon than do *H. vesicula* eggs with comparable energetic densities. *H. vesicula* have a higher fecundity, with an overall greater investment in eggs than does *H. callidegenita*. Although these data do not take into account energy invested in the egg masses themselves, they follow a general trend evident in other benthic marine invertebrates among planktotrophic and lecithotrophic species (Chia, 1974; Todd, 1979; Strathman, 1985).

Examination of population size structure and the length of the reproductive season indicates that neither of the *Haminoea* species studied follows the life cycle patterns considered characteristic of nudibranchiate opisthobranchs (exploitist and strategist; Clark, 1975), but have a long term approach, possibly based on a stable food supply. Individuals were also found to overwinter in the same habitat occupied by actively reproducing adults in the summer. This has not been shown previously in nudibranchiate species (Clark, 1975; Thompson, 1967; Todd, 1979).

As is the nature of any type of research, a few additional avenues of interest have appeared. One of the more interesting is, given the morphological, ecological, and behavioral similarities between adult *H. callidegenita* and *H. vesicula*, what factors have selected for the observed divergent larval strategies ? Trophic and climatic stability have been suggested as the major selective forces determining development type in opisthobranchs (Clark, 1975). If so, it would seem

possible that climatic and environmental instability may have selected for retention of a pelagic phase in *H. vesicula*, and to a lesser extent in *H. callidegenita*, while trophic stability may select for lecithotrophy and an increased proportion of benthic development in *H. callidegenita*. Although the adults of both *Haminoea* species are ecologically similar, the differences in development provide divergent niches for the larvae which may be important in terms of larval competition in bays if the rate of loss of larvae from the habitat was low, given the high fecundity in these two species.

A second observation which needs further consideration is the morphology of the gizzard plates, and their role in feeding. These observations would be useful in *Haminoea* research, to an understanding of both *Haminoea* biology and its roles as an abundant member of muddy, intertidal communities are not well understood.

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Appendix 1. Summary of references on *Haminoea* species.

SPECIES	AUTHOR	REFERENCE	DESCRIPTION										
			TYPE	LOCALE	ADULT	SHELL	FIG.	REFS	SYN.	RANGE	DEV	NATHIST	OTHER
H. adamsii	Dunker, 1861	Kay, 1979							•				
		Kobelt, 1896							•				ref-crocata
H. aequistriata	Smith, 1872	Cook, 1886							•				
		Pilsbry, 1893				•			•				
		Smith, 1872	?			•				•			
H. alfredensis	Bartsch, 1915	Bartsch, 1915	•	•		•	•			•			
		Kil.&Rip.,1982				•	•		•	•		•	list name
		MacNae, 1962			•	•	•	•		•		•	anatomy
H. ambigua	A. Adams,?	Adams&Adams,1858											
		A. Adams, 1855				•	•			•			
		Kobelt, 1896				•	•	•		•			
		Pilsbry, 1893				•	•	•		•			
		Reeve, 1868				•	•	•					
H. angelensis	Baker&Hanna, 1927	Baker&Hanna,1927	•	•		•	•			•			
H. angustata	A. Adams, 1850	Kobelt, 1896				•	•	•		•			
		Pilbry, 1893				•	•	•		•			
		Reeve, 1868				•	•			•			
		Smith, 1872						•		•			
		Tryon, 1868											cites Reeve
H. antillarum	d'Orbigny, 1841	Abbott, 1954				•				•			
		Humfrey, 1975				•	•			•		•	
		Kobelt, 1896				•	•	•	•	•			
		Marcus&Marcus,'67				•	•	•	•	•			anatomy
		Marcus, 1976						•		•			
		Marcus, 1977						•		•			
		Olmsted,1917			•								locamotion
		Pilsbry, 1893				•	•	•	•	•			
		Rudman, 1971 b			•								anatomy
		Thompson, 1977			•	•	•		•			•	anatomy
H. ant. guadalupensis	Sowerby, 1853	Marcus&Marcus,'67											list name
		Pilsbry, 1893				•	•			•			
H. aperta	Pease, 1868	Marcus&Burch,1965				•							
		Pease, 1868	•			•	•			•			
		Pilsbry, 1893				•	•	•		•			
		Pilsbry, 1917											list name
		Kobelt, 1896				•	•	•		•			
H. aperta oahensis	Pilsbry, 1917	Pilsbry, 1917	•	•		•	•			•			
		Pilsbry, 1920				•					•		section Halea
H. artencensis	Addicott, 1966	Addicott, 1966	•			•							
H. binotata	Pilsbry, 1895	Marcus&Burch,1965			•	•		•					
H. bin. japonica	Pilsbry, 1895	Marcus&Burch, 1965				•		•					
H. brevis	Q & G, 1832	Adams&Adams,1858											list name

SPECIES	AUTHOR	REFERENCE	DESCRIPTION										
			TYPE	LOCALE	ADULT	SHELL	FIG	REPS	SYN	RANGE	DEV	NATHIST	OTHER
		A. Adams, 1855				•	•	•					
		Burn, 1966			•					•		•	
		Burn, 1974							•			•	now Liloa
		Kobelt, 1896				•	•	•	•	•			
		Mac&Gab.,1962			•	•	•			•		•	
		Pilsbry, 1893			•	•	•	•	•	•			gizzard plts
		Pilsbry, 1920											section Liloa
		Reeve, 1868				•	•	•		•			
H. brevissima	A. Adams, 1862												
H. cairnsiana	Melvill&Standen,1895	M & S, 1895	•			•	•						
		Pilsbry, 1917											lists name
		Pilsbry, 1920											sec.Liloa
H. calliosa	Preston, 1908	Marcus&Burch,1965				•		•					
H. canalis	Dall, 1912	Dall, 1912	•	•		•							
H. castanea	A. Adams, 1850	Adams&Adams,1858											list name
		A. Adams, 1855				•	•			•		•	
		Kobelt, 1896				•	•	•		•			
		Pilsbry, 1893				•	•			•			
		Reeve, 1868				•	•	•					
H. cerina	Menke, 1853	Adams&Adams, 1858											list name
		Kobelt, 1896											ref. name
		Pilsbry, 1893							•				
H. constricta	A. Adams, 1850	Adams&Adams, 1858											list name
		A. Adams, 1855				•	•	•		•		•	
		Kobelt, 1896				•	•	•		•			
		Pilsbry, 1893				•	•	•		•			
		Reeve, 1868					•						
		Smith, 1872						•					cites Reeve
		Tryon, 1868											
H. cornea	Lamarck, 1822	Lemche, 1948						•	•				
		Kobelt, 1896											ref. name
		Pilsbry, 1893							:	:			
H. corticata	Beck. 1842	Pilsbry, 1893				•							
H. crocata	Pease, 1860	Annandale,1924			•	•							
		Kay, 1965	•		•	•		•					
		Kay, 1979			•	•						•	
		Kobelt, 1896				•	•	•	•	•			
		Marcus&Burch,1965						•					
		Nagarajan, 1970											chromosome #
		Ostergaard, 1950									•		spawn
		Pilsbry, 1893			•	•	•	•	•	•			
		Pilsbry, 1917								•			

SPECIES	AUTHOR	REFERENCE	DESCRIPTION										
			TYPE	LOCALE	ADULT	SHELL	FIG.	REFS	SYN.	RANGE	DEV	NATHIST	OTHER
		Pilsbry, 1920				•	•	•	•				sec.Haloa
		Reeve, 1868				•	•	•					
		Rudman, 1971			•							•	anatomy
		Smith, 1872						•		•			
H. curta	A. Adams, 1850	Adams&Adams,1858				•							list name
		A. Adams, 1855				•	•						
		Cooke, 1896							•				
		Kay, 1979				•			•			•	
		Kobelt, 1896				•	•	•		•			
		Pilsbry, 1893				•	•	•	•	•			
		Pilsbry, 1917											cites name
		Pilsbry, 1920				•	•	•					
		Thiele, 1925											subg.Liloa
H. curta tornaculum	Pilsbry, 1917	Pilsbry, 1917	•			•	•					•	
H. cuticulifera	Smith, 1872	Kobelt, 1896				•	•	•		•			
		Mac & Gab,1962							•				
		Pilsbry, 1893				•	•	•		•			
		Pilsbry, 1917											cites name
		Pilsbry, 1920											sec.Liloa
H. cuvieri	Leach, 1852	Smith, 1872	•			•				•			
		Lemche, 1948						•	•				
		Kobelt, 1896											ref. name
		Pilsbry, 1893							•				
H. cyanocaudata	Heller&Thpsn, 1983,	H & T, 1983	•	•	•	•				•		•	rad, prostate
H. cyanomarginata	Heller&Thpsn, 1983	H & T, 1983	•	•	•	•				•		•	
H. cymbalum	Quoy&Gaimard, 1833	Adams&Adams,1858											list name
		A.Adams, 1855				•	•	•		•			
		Kay, 1979				•			•	•		•	
		Kobelt, 1896				•	•	•		•			
		Pease, 1868											cites native
		Pilsbry, 1893				•	•	•		•			
		Reeve, 1868				•	•	•		•			
		Rudman, 1971			•								anatomy
H. cymbiformis	Carpenter, 1853	Baker&Hanna,1927											lists name
		Morris etal,1980							•				
		Pilsbry, 1893				•		•		•			
		Pilsbry, 1933							•	•			
H. dalli	Bartsch?	Pilsbry, 1933											name only
H. decora	Brazier, 1878	Brazier, 4878	•			•						•	
		Pilsbry, 1893				•				•			
		Ponder, 1972											
		Pilsbry, 1893							•				

SPECIES	AUTHOR	REFERENCE	DESCRIPTION										
			TYPE	LOCALE	ADULT	SHELL	FIG.	REFS	SYN.	RANGE	DEV	NATHIST	OTHER
H. diaphana	Coutherier, 1849	Adams&Adams,1873											ref. name
		Kobelt, 1896							•				
		Pilsbry, 1893											ref. name
H. dilatata	Leach, 1847	Fischer, 1879					•		•				
		Lemche, 1948						•	•				
		Pilsbry, 1893							•				
H. elegans	Gray, 1825	Abbott, 1954				•				•			
		A. Adams, 1855				•	•	•		•			
		Adams&Adams,1858								-			ref. name
		Humfrey, 1975				•				•		•	
		Kobelt, 1896						•	•				
		Lemche, 1948						•	•				
		Marcus, 1956			•								anatomy
		Marcus, 1957				•	•			•			anatomy
		Marcus, 1970				•		•		•			
		Marcus, 1977						•		•			
		Mar&Mar, 1963						•	•	•			
		Mar&Mar, 1967				•	•	•	•	•			anatomy
		Pilsbry, 1893				•	•	•	•	•			
		Reeve, 1868				•	•	•					
		Thompson,1977			•	•	•			•		•	
H. exarata	Philippi, 1849	Adams&Adams,1873											ref. name
		Kobelt, 1896				•	•	•	•	•			
		Pilsbry, 1893				•	•	•	•	•			
H. ferruginea	Chemnitz, ?	Kobelt, 1896											ref. name
		Reeve, 1868				•	•	•					
		Pilsbry, 1893							•				
		Smith, 1872							•				
H. flavescens	A. Adams,?	A. Adams, 1862				•	•						
		Adams&Adams,1872											ref. name
		Kobelt, 1896				•	•	•		•			
		Pilsbry, 1893				•	•	•					
		Reeve, 1868				•	•	•					
H. folliculus	Menke,1853	Adams&Adams,1858											ref. name
		Kobelt, 1896							•				
		Lemche,1848						•	•				
		Pilsbry, 1893							•				
H. fulgida	A. Adams, 1862	A.Adams, 1862				•				•			
		Pilsbry, 1893				•				•			
H. fusca	A.Adams, ?	A.Adams, 1855				•	•			•			
		Adams&Adams,1858											ref. name
		Kobelt, 1869				•	•	•	•	•			

SPECIES	AUTHOR	REFERENCE	DESCRIPTION										
			TYPE	LOCALE	ADULT	SHELL	FIG.	REFS	SYN.	RANGE	DEV	NATHIST	OTHER
		Pilsbry, 1893				•	•	•	•	•			
		Reeve, 1868				•	•	•					
		Smith, 1872							•				
H. galba	Pease, 1860	Kay, 1965		•	•	•		•				•	
		Kay, 1979				•			•	•			
		Kobelt, 1869				•	•	•		•			
		Mar&Burch,1965				•		•					
		Pilsbry, 1893		•	•	•	•		•	•			
		Pilsbry, 1917								•			
		Pilsbry, 1920				•			•				sec.Haloa
		Reeve,1868				•	•						
		Smith, 1872						•		•			
H. glabra	A.Adams, 1850	Abbott, 1954				•				•			
		A.Adams, 1855				•	•						
		Adams&Adams,1858											ref. name
		Kobelt, 1869				•	•			•			
		Marcus, 1977								•			
		Pilsbry, 1893				•	•	•		•	•		
		Smith, 1872						•		•			
H. gracilis	Sowerby, 1897	Bartsch, 1915								•			
		Kil&Rip, 1982				•	•		•	•		•	
		MacNae, 1962				•	•	•		•			anatomy
H. grandis	Aldrich, ?	Olsson, 1928											eocene fossil
H. grisea	Smith, 1875	Pilsbry, 1893				•		•		•			
H. guadalupensis	Sowerby, 1868?	Kobelt, 1896				•	•	•		•			
		Reeve, 1868				•	•			•			
		Tryon, 1868						•					
H. guildingi	Swainson, 1840	A.Adams, 1855				•	•	•		•			
		Adams&Adams,1858											ref. name
		Kobelt, 1896				•	•	•	•	•			
		Pilsbry, 1893							•				
		Pilsbry, 1893							•				
		Reeve, 1868				•	•	•		•			
H. hydatis	Linné, 1758	A.Adams, 1855				•	•	•		•			
		Adams&Adams,1873											ref. name
		Berrill, 1931									•	•	
		For&Hanl,?			•	•		•		•	•	•	
		Grell, 1960 ?									•		
		Kobelt, 1896				•	•	•		•	•		
		Lemche,1948			•	•		•	•				radula
		Pilsbry, 1893				•	•		•	•			6 varieties
		Pilsbry, 1920				•	•						sec.Haminoea

SPECIES	AUTHOR	REFERENCE	DESCRIPTION										
			TYPE	LOCALE	ADULT	SHELL	FIG.	REFS	SYN.	RANGE	DEV	NATHIST	OTHER
		Reeve, 1868				•	•	•	•	•			
		Thiele, 1963						•					radula
		Thompson, 1981			•	•	•				•	•	anatomy
		Th&Brown, 1976			•	•	•			•		•	
H. hydalis miocoenica	Berger, 1953	Berger, 1953				•	•	•					
H. incincta	Mighels, 1844	Adams&Adams,1858											ref. name
H. insculpta	Totten, 1835	A.Adams, 1855				•	•	•		•			
		Adams&Adams,1858											ref. name
		Kobelt, 1896							•				
		Lemche, 1948							•				
		Pilsbry, 1893							•				
		Reeve, 1868				•	•	•	•	•			
		Smith, 1872							•				
H. labrea	Olsson, 1928	Olsson, 1928	•	•		•	•					•	eocene fossil
H. linda	Marcus & Burch, 1965	Marc&Burch,1965	•		•	•	•					•	anatomy
H. lucida	A.Adams, 1862?	A.Adams,1862?	•			•						•	
		Pilsbry, 1893				•				•			
H. luticola	C.B.Adams, ?	Adams&Adams,1858											
H. malleata	Smith, 1872	Pilsbry, 1893				•		•					
		Smith, 1872	•			•							
H. maltzani	Thiele, 1925	Thiele, 1963											subg.Haminella
H. maugeansis	Burn, 1966	Burn, 1966	•							•			diet, predators
H. musetta	Marc&Burch,1965	M & B, 1965	•		•	•	•	•				•	anatomy
H. natalensis	Krauss, 1868	A. Adams, 1855				•	•	•		•			
		Adams&Adams,1858											ref. name
		Kobelt, 1896				•	•	•	•	•			
		MacNae, 1962			•		•	•					radula
		Pilsbry, 1893				•	•	•	•	•			
		Reeve, 1868				•	•			•			
		Smith, 1972							•				
		Thiele, 1963											gizzard plate
		Tryon, 1868						•					
H. navicula	DaCosta, 1778	Brace, 1977											anatomy
		Edlinger, 1982			•								colour adapta.
		Fossato, 1982			•								pollutants
		Fret&Graham,1976			•								
		Kobelt, 1896				•	•	•	•	•			
		Lemche, 1948			•	•		•	•				radula
		Pilsbry, 1893				•	•		•	•			7 varieties
		Thompson, 1976				•							anatomy
		Thompson, 1981											prostate
		Th.&Brown, 1976				•				•		•	anatomy

SPECIES	AUTHOR	REFERENCE	DESCRIPTION										
			TYPE	LOCALE	ADULT	SHELL	FIG.	REFS	SYN.	RANGE	DEV	NATHIST	OTHER
		Yonge&Thomp,1976											anatomy
H. nigropunctata	Pease, 1868	Kobelt, 1896				•	•	•		•			
		Marc&Burch,1965			•			•					
		Pease, 1868			•	•	•			•			
		Pilsbry, 1893				•	•	•		•			
H. novi-eboraci	Sowerby, 1868	Lemche, 1948							•				
		Pilsbry, 1893							•				
		Reeve, 1868				•	•			•			
		Smith, 1872						•	•				
		Tryon, 1868						•	•				
H. obesa	Sowerby, 1868	Kobelt, 1896							•				
		Pilsbry, 1893											
		Reeve, 1868				•	•	•			•		
		Smith, 1872							•				
H. olgae	Dall, 1919	Dall, 1920		•		•							
		Oldroyd, 1924				•				•			
H. olopana	Pilsbry, 1920	Pilsbry, 1920				•	•			•			
H. orbignyana	Ferrussac, 1820	Fisher, 1879							•				
		Lemche, 1948						•	•				
		Pilsbry, 1893				•		•	•	•			
H. oryza	Totten, 1835	A. Adams, 1855				•	•	•		•			
		Adams&Adams,1858											cites name
		Reeve, 1868				•	•			•			
		Smith, 1872						•					
		Tryon, 1868						•			•		
H. ovalis	Pease, 1868	Guangyu, 1975?											as Haloa
		Kay, 1979			•					•			
		Kobelt, 1896				•	•	•		•			
		Marc&Burch,1965			•			•					
		Pease, 1868			•	•	•			•			
		Pilsbry, 1893				•	•	•		•			
H. ovoidea	Quoy & Gaimard, 1833	A. Adams, 1855				•	•			•			as Atys
		Kobelt, 1896				•	•	•	•	•			
		Pilsbry, 1893				•	•	•	•	•			
H. papyrus	Salis, 1793	A. Adams, 1855				•	•			•			
		Adams&Adams,1855											cites name
		Brazier, 1878								•		•	
		Kobelt, 1896				•	•	•		•			
		Pilsbry, 1893				•	•	•		•			
		Pilsbry, 1920											sec. Lloa
		Reeve, 1868				•	•	•		•			
H. paralleta	Gould, 1848	Adams&Adams,1873											cites name

SPECIES	AUTHOR	REFERENCE	DESCRIPTION										
			TYPE	LOCALE	ADULT	SHELL	FIG.	REFS	SYN.	RANGE	DEV	NATHIST	OTHER
H. pemphis	Philippi, 1847	A. Adams, 1873				•	•	•		•			
		Adams&Adams,1858											cites name
		Kobelt, 1896				•	•	•	•	•			
		Pilsbry, 1893				•	•	•	•	•			
		Smith, 1872											cites name
H. pemphix	Philippi, 1847	Pilsbry, 1893							•				
		Reeve, 1868				•	•	•		•			
		Smith, 1872							•				
H. perforata	Philippi, 1847	Pilsbry, 1893				•		•	•	•			
H. perplexa	Smith, 1872	Pilsbry, 1893				•		•					
		Smith, 1872	•			•							
H. perrieri	Morlet, 1889	Morlet, 1889				•	•			•			
H. peruviana	d'Orbigny, 1837	Kobelt, 1896				•	•	•	•				
		Pilsbry, 1893				•	•	•		•			
		Smith, 1872							•				
H. petersi	von Martens, 1879	MacNae, 1962			•	•	•	•			•		anatomy
		Pilsbry, 1893				•		•		•			
H. petiti	d'Orbigny, 1842	Kobelt, 1896				•	•	•		•			
		Marcus, 1976						•		•			
		Marcus, 1977						•		•			
		Pilsbry, 1893				•	•	•	•	•			
H. postangulata	Clark&Woodford,1927	C & W, 1927				•							mid-eocene
H. pusilla	Pease, 1860	Kay, 1965		•		•		•		•			
		Pilsbry, 1893	ø			•		•					
		Pilsbry, 1917								•			
H. pygmoea	A. Adams, 1862	A. Adams, 1862?								•			
H. rotunda	A.Adams, 1850	Pilsbry, 1893							•				
		Reeve, 1868				•	•	•					
		Smith, 1872							•				
H. rotundata	A. Adams, 1850	A. Adams, 1855				•	•						
		A. Adams, 1862								•			
		Adams&Adams,1858											cites name
		Hamatani, 1961								•			cites name
		Kobelt, 1896				•	•	•		•			
		Mar&Burch, 1965				•		•					radula
		Pilsbry, 1893				•	•	•					
H. rugosa	Smith, 1872	Pilsbry, 1893				•		•		•			
		Smith, 1872	•			•				•			
H. sandwichensis	Sowerby, 1868	Kobelt, 1896				•	•	•		•			
		Pilsbry, 1893				•	•	•		•			
		Pilsbry, 1917								•			
		Pilsbry, 1920				•							sec. Haloa

SPECIES	AUTHOR	REFERENCE	DESCRIPTION										
			TYPE	LOCALE	ADULT	SHELL	FIG.	REFS	SYN.	RANGE	DEV	NATHIST	OTHER
		Reeve, 1868				•	•	•		•			
		Tryon, 1868											cites name
H. savignyana	Gray, 1825	Pilsbry, 1893				•		•		•			
H. serica	Smith, 1872	Pilsbry, 1893				•		•					
		Smith, 1872				•							
H. similima	Pease, 1868	Couturier,1907				•				•			
		Eliot, 1906			•	•						•	anatomy
		Kobelt, 1896				•	•	•		•			
		Marc&Burch,1965						•					
		Pease, 1868	•			•	•			•			
		Pilsbry, 1893			•	•	•	•		•			
H. sinensis	A. Adams, 1850	A.Adams, 1855				•	•	•					
H. solaria	Olsson, 1928	Olsson, 1928	•			•	•					•	eocene fossil
H. solitaria	Say, 1822	Abbott, 1954				•				•			
		Abb&Dance, 1982				•	•			•		•	
		Gosner, 1893				•							
		Kobelt, 1896				•	•	•					
		Lemche, 1948			•	•		•	•				radula
		Pilsbry, 1893				•	•	•	•	•			
		Rudman, 1971			•			•					anatomy
		Smith, 1872							•				
H. strigosa	A. Adams, 1862	A.Adams, 1862	•			•				•			
		Pilsbry, 1893				•							
H. strongi	Baker & Hanna, 1927	Baker & Hanna, 1927	•	•		•	•			•			
		Morris et al, 1980						•	•				
		Pilsbry, 1933							•				
H. subcylindrica	Sowerby, 1897	Bartsch, 1915								•			
		MacNae, 1962				•	•	•		•			
H. subpellucida	H. Adams, 1869	Adams, 1869				•	•			•			
		Lemche, 1948						•	•				
		Pilsbry, 1893							•				
H. succinea	Conrad, 1846	Abbott, 1954				•				•			
		A. Adams, 1855				•	•	•		•			
		A. Adams, 1862								•			
		Adams & Adams, 1858											cites name
		Kobelt, 1896				•			•				
		Marcus, 1977											?
		Marcus & Marcus, 1963						•	•				
		Pilsbry, 1893				•	•	•	•	•			
		Reeve, 1868				•	•	•		•			
H. succinea solidior	Vanatta, 1901	Vanatta, 1901	•	•		•	•			•			
H. tenella	A. Adams, 1850	A. Adams, 1855				•	•						

SPECIES	AUTHOR	REFERENCE	DESCRIPTION										
			TYPE	LOCALE	ADULT	SHELL	FIG.	REFS	SYN.	RANGE	DEV	NATHIST	OTHER
		Adams & Adams, 1858											cites name
		Pilsbry, 1893							•				
		Reeve, 1868				•	•	•					
		Smith, 1872											cites name
H. tenera	A. Adams, 1850	A. Adams, 1855				•	•						
		Adams & Adams, 1858											cites name
		Burn, 1966			•	•				•		•	
		Cooke, 1886							•	•			
		Kobelt, 1896				•	•	•		•			
		MacPherson & Gabriel,1962			•	•	•		•	•		•	
		Melvill & Standen, 1895								•			
		Pilsbry, 1893				•	•	•	•	•			
		Reeve, 1868				•	•	•					
H. tomaculum	Pilsbry, 1920	Pilsbry, 1920	•			•							sec Liola
H. ventripotens	Cossman, 1913	Cossman, 1913				•	•			•			
H. vesicula	Gould, 1855	Abbott, 1954				•	•			•		•	
		Baker & Hanna, 1927											sim. spp.
		Kobelt, 1896				•	•	•		•			Hydatina
		Morris,et al., 1980				•	•	•		•	•		
		Oldroyd, 1924				•				•			
		Pilsbry, 1893				•	•	•					1 variety
		Reeve, 1868				•	•	•					
		Richard, 1923									•		
		Smith & Carlton, 1975				•		•				•	
H. virescens	Sowerby, 1833	Abbott, 1954				•			•	•		•	
		A. Adams, 1855				•	•	•		•		•	
		Adams & Adams, 1858											cites name
		Baker & Hanna, 1927											name, sim.spp.
		Bradshaw, 1895			•	•						•	
		Kobelt, 1896				•	•			•			
		MacGinitie & MacGinitie,1949									•		
		Marcus, 1961			•	•	•			•	•		
		Marcus & Marcus, 1967			•	•	•			•			
		Morris, et al., 1980						•	•				
		Pilsbry, 1893				•	•	•		•			
		Pilsbry, 1933							•	•			
		Reeve, 1868				•	•	•		•			
		Richards, 1921									•		
		Richards, 1923									•		
		Smith & Carlton, 1975				•	•			•		•	
		Tomlin, 1933				•				•			
H. virescens rosecea	Spicer, 1933	Marcus & Marcus, 1967				•		•					

SPECIES	AUTHOR	REFERENCE	DESCRIPTION										
			TYPE	LOCALE	ADULT	SHELL	FIG.	REFS	SYN.	RANGE	DBV	NATHIST	OTHER
		Spicer, 1833	•	•							•		describes colony
H. vitrea	A. Adams, 1850	A. Adams, 1855				•	•			•			
		Adams & Adams, 1858					•						cites name
		Brazier, 1878											?
		Cooke, 1886							•				
		Kobelt, 1896				•	•	•		•			
		Marcus & Burch, 1965				•		•					
		Pilsbry, 1893				•	•	•		•			
		Reeve, 1868				•	•	•		•			
H. wallisii	Gray, 1825	Burn, 1978					•			•			
		Pilsbry, 1893				•				•			
		Thiele, 1963											?
H. zanzibarica	Vanatta, 1901	Vanatta, 1901	•	•		•	•			•			
H. zelandiae	Gray, 1843	Kobelt, 1896				•	•	•	•	•			
		Pilsbry, 1893				•	•	•	•	•			
		Powell, 1979				•	•	•				•	
		Rudman, 1971 a			•								anatomy
		Rudman, 1971 b			•								anatomy
		Smith, 1872											sim. spp.
		Thompson, 1976			•						•		alimentary canal

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