Morphogenesis of Planktotrophic Veligers of Naticidean Gastropods

by

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Abstract

Phytoplanktotrophic larval development of the carnivorous marine snails *Polinices lewisii* and a related but unidentified genus of *Natica* was observed and described. Both genera are in the family Naticidae of the prosobranch gastropods. The veliger larvae were provided with phytoplankton and lived under laboratory conditions for over 100 days, during which they developed a protoconch II and 4-lobed velum. Only the veligers of *Natica sp.* settled and metamorphosed.

Specimens at different stages of development were prepared for histological examination to complement observations on live larvae. Characteristics of the growing shell were observed using scanning electron microscopy. Histological serial sections from three developmental stages assisted description of the changes of the mantle cavity and associated organs, muscular, digestive, circulatory, excretory, nervous and sensory systems. Study of the ontogeny of these larvae revealed that extensive development must occur before settlement and metamorphosis. Many structures are previously undescribed for pre-metamorphic naticids such as preliminary development of boring organ, proboscis and esophageal gland in the foregut of the digestive system. These descriptions may assist with identification of *P. lewisii* in plankton samples and provide further morphological information to aid in understanding how the rudiments of the benthic structures develop without encumbering larval swimming and feeding.

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Introduction

Descriptive studies on the life history of a marine organism, while initiated by curiosity, have value for a number of reasons. Knowledge of the larval, juvenile, as well as adult form is essential in building a correct understanding of the ecological context of an organism, including patterns of recruitment, ecological associations, allocations of resources and responses to bioturbation. Examination of the embryogenesis and morphogenesis of larval organs affords comparisons to similar stages in other organisms, thereby providing insights into evolutionary diversification (Davidson *et al.*, 1995; Raff and Kaufman, 1983). Studies of morphogenesis can also help identify homologous structures among organisms, which can assist in the building of phylogenetic hypotheses. When embryological development expresses morphological anomalies or unexpected structural changes, precipitating environmental factors may be identified. These may contribute to an understanding of the impact of historical meteorological events or present day ecological influences.

Polinices lewisii (Gould) is one of six naticid species recognized on the shorelines of southern Vancouver Island (see Appendix). The snail is indigenous to intertidal waters of the northeastern Pacific ranging from Alaska to California (Marincovich, 1977). The shell of this moon snail is globose with a large aperture and distinct umbilical opening. The operculum is proteinacous (Bernard, 1967). Several other species of moon snail, belonging to the genus *Natica*, have been reported for subtidal waters off the coast of Vancouver Island (Kozloff, 1974). The features of this genus are similar to those of *P.*

lewisii, but the shell is imperforate and generally smaller while the operculum is calcareous (Marincovich, 1977). Moon snails are usually found buried in fine marine sand and mud where they feed by drilling through the shell of bivalves (Kozloff, 1987).

This study was undertaken to elucidate and describe the larval development of the moon snail *P. lewisii*. The description is supplemented by developmental information about a related but unidentified species of *Natica,* to improve the understanding of metamorphosis and settlement of these animals. Information from this study provides insight into the life history of moon snails and into present interpretations of caenogastropod larval morphogenesis. Although information is available on the ecology of the adult stage of *P. lewisii*, and on its embryological development (Bernard, 1967; Siemens, 1981), there is no detailed information about the period between hatching until metamorphosis. My investigation has uncovered a misunderstanding about the life history pattern for this species.

Literature Review

Marine invertebrates can be categorized by their developmental patterns (Thorson, 1950; Chia, 1974; Bonar, 1978; McEdward and Janies, 1993). The patterns are used to define the life history of marine invertebrates that undergo dramatic changes during development (Strathmann, 1986). Marine gastropods that normally crawl on the bottom are described as having either a pelagic or benthic developmental pattern. The presence of a pelagic larval stage is usually associated with the ability of the snail to disperse and invade new habitats. However a pelagic developmental pattern also means that the larval body must undergo extensive reorganization both before and after settlement to form the benthic adult.

The extent of growth and morphological development that occurs during the pelagic stage is defined by the manner in which the free-living stage derives its energy. Planktotrophy implies that the energy required by the larva is derived from feeding on phytoplankton and a planktotrophic larva tends to live in the plankton for a long period after hatching (Bonar, 1978). Alternatively the energy may be supplied as nutrients invested in the egg. These lecithotrophic larvae, if they are pelagic, are usually capable of settling on the bottom shortly after hatching (Chia, 1974).

Pelagic gastropod larvae rely on ciliary structures for moving through the water and for capturing food (Hyman, 1967). The ciliated structure is called the velum, and the associated pelagic life stage is the veliger. Some of the features that are present in veligers are unique to the veliger stage and are often reduced as the larva develops into an adult snail. Consequently, the morphological development of the uniquely larval organs and prospective adult structures in the pelagic veliger requires consideration.

Developmental studies on planktotrophic larvae of caenogastropods

Fretter and Graham (1962) and Moor (1983) summarized the available literature on gastropod larval morphogenesis. Features of interest in the present study are the shell, velum, foot, mantle cavity with associated organs, muscular system, foregut region of the digestive tract, the nervous, circulatory and excretory systems. This description of the cellular differentiation of these structures is limited to caenogastropods having planktotrophic larvae.

Shell

Until recently, investigations of the larval shells of caenogastropods were based mainly on larval stages retrieved from the plankton. Descriptions focused on the size and sculpture of the shell or lack of sculpture as a means of identifying the larval species and interpreting the developmental pattern. Thorson (1950) and Amio (1955) presented studies on larval shells of gastropods, emphasizing identification based on the configuration of shell whorls and, to some extent, its sculpturing. These are features within the range of light microscopy. Robertson (1974), using scanning electron microscopy, distinguished two components of the pre-metamorphic shell. Protoconch I is the shell secreted prior to hatching, whereas protoconch II is the shell secreted during the pelagic larval stage. The post-metamorphic shell is called the teleoconch. Transitions between protoconch I and II and between the protoconch and teleoconch are often marked by changes in shell shape and sculpturing.

Thorson (1950) recognized that the shape of the pre-metamorphic shell, which is usually visible at the apex of the adult shell, is an indicator of the life history pattern of the snail. Species with long-lived, planktotrophic larvae have a small protoconch I and a protoconch II with multiple whorls. Species with short-lived, lecithotrophic larvae or direct development have a large, bulbous protoconch I and no protoconch II. This fact is of considerable interest to paleontologists because it allows correlations between species longevity and life history pattern, as recorded in the fossil record (Jablonski and Lutz, 1981).

Velum

A pair of symmetrical ciliated lobes on the anterior region of caenogastropod larval stages is called the velum. The margin of the velum in planktotrophic larvae is bi-layered with pre-oral and post-oral ciliary bands situated on the peripheral edge. The outer pre-oral band is the most apparent of the ciliated bands. This long compound ciliary band is believed to provide the major locomotory force of the velum (Fretter, 1967). The post-oral band is composed of relatively short cilia, consisting of a row of four or five cells. It helps to retain food particles in the food groove as well as reject and clear non-food particles (Fretter and Montgomery, 1968). Non-feeding, lecithotrophic veligers do not have the post-oral ciliary band. The velum of planktotrophic veligers with a long pelagic life often acquires additional lobes during larval development (Fretter and Graham, 1962).

The absorption or loss of the velar lobes signifies the end of pelagic larval life (Moor, 1983).

Foot

The foot of caenogastropod veligers eventually consists of propodial and metapodial regions, but only the metapodium is present at hatching (D'Asaro, 1965). In a newly hatched caenogastropod veliger, an oversized thin membranous operculum is often found on the dorsal surface of the foot (Bernard, 1967; D'Asaro, 1965, 1966, 1969). Hypertrophy and proliferation of the pedal cells enlarge the foot and operculum during pelagic development. The extent and rate of development of the foot varies between species.

Muscular system

The retractor muscle is the largest muscle in caenogastropod larvae and eventually forms the columellar muscle in adult animals. It is present at hatching in pelagic veligers, where it is called the larval retractor muscle. Fretter (1967, 1972) described the insertions of distal branches of the larval retractor in several caenogastropod larvae. Branches extend to the mentum, a protuberance on the lower lip of the veliger, and to the velum and foot. Contraction of the larval retractor muscle pulls the velum and foot into the larval shell.

Muscle cells underlie the epidermis throughout the body of pelagic veligers. These cells contract the hemocoel for movement of hemolymph and for localized movements of the foot, head, and mantle (Fretter, 1972; D'Asaro, 1965).

Mantle cavity

The mantle is a thin epithelium covering the visceral mass of the snail. A mantle, or pallial, cavity is formed by an infolding of the mantle in the dorso-anterior region of the developing snail. The peripheral edge of the mantle fold is the area of shell secretion (Hyman, 1967). The mantle cavity contains the gill filaments, osphradium, anus, and hypobranchial gland.

In caenogastropods, a single gill plate forms on the left side of the mantle from a thickened band of epithelium (D'Asaro, 1965). Later gill filaments evaginate off the gill plate, each retaining a connection with the underlying blood sinuses (Hyman, 1967).

The hypobranchial gland in the emergent veliger of *Strombus gigas* is a collection of secretory cells at the entrance to the mantle cavity (D'Asaro, 1965). The gland is gradually shifted to the posterior region of the mantle cavity (Fretter and Graham, 1962).

D'Asaro's (1969) studies on *Bursa corrugata* and *Distorsio clathrata* showed that the osphradium rudiment forms on the dorsal surface of the mantle cavity. It can be distinguished by its row of cells with long cilia and remains closely associated with the osphradial ganglion. In adults, the osphradium lies at the left-side of the entrance to the mantle cavity to sense water properties (Fretter and Graham, 1994).

Digestive system

The digestive system of the planktotrophic veliger of *Crepidula fornicata* has been described and illustrated by Fretter and Montgomery (1968), Fretter (1972) and Werner (1955). The foregut of the digestive system is formed by the larval mouth, located at the ventral aspect of the velum, and esophagus. Uniformly ciliated cells line the foregut of pelagic veligers at the time of hatching (Moor, 1983). Fretter (1972) noted that the radula and associated musculature of *Nassarius* develop from an invagination of the prospective ventral wall of the buccal cavity. Yet the development of the proboscis and other post-metamorphic changes of the foregut have not been described for naticid gastropods.

Reid and Friesen (1980) described an epithelial constriction at the junction of the foregut with the midgut in adult naticids. This narrowing may prevent dense mucus secretions and food particles in the stomach from passing into the esophagus. Fretter and Montgomery (1968) observed a ciliary valve in this position in caenogastropod veligers that apparently has a similar function.

In planktotrophic larvae, the stomach wall is complex. At its ventral end, immediately inside the ciliary valve, is an area lined by long cilia called the vestibule. The epithelium on the lateral walls of the ventral stomach forms the gastric shield. Within the dorsal area of the stomach the epithelium is uniformly and densely ciliated to form the style sac. Occasionally a mucus rod, or protostyle, is observed lying within this sac (Fretter and Montgomery, 1968). In adult carnivorous snails, the stomach is lined with columnar epithelia underlain by muscle cells (Reid and Friesen, 1980). The gastric shield is absent although a style sac is present (Graham, 1949).

Opening into the vestibule of the stomach are the ducts of the sac-like digestive glands. In pelagic veligers these digestive glands are designated right and left, unlike the convoluted and divided structure seen in adult caenogastropods. Most of the cells are phagocytic and have been shown to contain vacuoles (Fretter and Graham, 1962). Several other cell types have been described, including muscle cells, that may contract the glands, and ciliated cells with large vacuoles (D'Asaro, 1965).

The tubular ciliated intestine leaves the dorsal region of the stomach, curves gradually toward the right side and then empties into the mantle cavity (Fretter and Graham, 1994). Fretter (1972) explained that the degree of flexion of the intestine changes as the mantle cavity enlarges and deepens.

Nervous system and sensory structures

D'Asaro (1965) showed that the cerebral and pedal ganglia are present at hatching in *Strombus gigas*. Paired cerebral ganglia proliferate from shallow invaginations of cephalic plates early in development and are connected to each other by a commissure. Pedal ganglia differentiate within the base of the foot and eventually produce two sets of nerves that extend towards the propodial and metapodial regions of the foot. The pedal ganglia are interconnected by a pedal commissure.

The pleural, buccal, esophageal and visceral ganglia differentiate after the cerebral and pedal ganglia (Raven, 1958; D'Asaro, 1966). All these ganglia become linked by various connectives formed by secondary outgrowths of each ganglion. Buccal ganglia differentiate from the wall of the foregut near the radular sac (Raven, 1958). Paired pleural ganglia may arise immediately behind the velum (Raven, 1958) or proliferate from the pedal ectoderm, as do the pedal ganglia (Moor, 1983). Apparently, pleural ganglia come to lie near the cerebral ganglia in neoteanioglossan gastropods (Fretter and Graham, 1962).

Esophageal ganglia arise from the floor of the mantle cavity (Raven, 1958). The right, or supraesophageal ganglion, is located in a position above the esophagus, whereas the left, or subesophageal ganglion is located beneath the esophagus (Raven, 1958). This condition is known as streptoneury (Fretter and Graham, 1962). The osphradial ganglion is connected to the supraesophageal ganglion and is on the left side of the mantle cavity. According to Raven (1958), the unpaired visceral ganglion differentiates from mantle ectoderm lining the roof of the mantle cavity near the heart. Fretter and Graham (1962) describe the visceral ganglion as bilobed in adult caenogastropods.

Optic vesicles, or eyespots, differentiate lateral to the cerebral ganglia and are visible at hatching in veligers of *Thais haemastoma floridana* (D'Asaro, 1966). Tentacles extend from the cephalic plates (Raven, 1958) and contain nerve tracts extending to the cerebral ganglia. Tentacles are first apparent near the eyespots in pelagic caenogastropod veligers either before or shortly after hatching.

D'Asaro (1965, 1969) stated that the statocysts early in embryogenesis develop from invaginations ventral to the pedal ganglia. Statocysts of pelagic veligers are apparent during intracapsular development and are used throughout the life of the snail for equilibrium and orientation.

The apical organ, found between the cerebral ganglia in close association with the cerebral commissure, is present in pelagic veligers (Fretter, 1972). It projects into the center of the velum, where D'Asaro (1969) distinguished short cilia covering the surface of the velar disc. He believed it served some sensory function because it connects to the cerebral ganglia through apical nerves. Moor (1983) concurred by summarizing that the coordination of the velum, retraction of the foot and operculum is controlled by the cerebral ganglia in pelagic larvae.

Excretory system

Paired larval kidneys, present in prosobranch veligers with intracapsular development, are organs with conspicuous cells containing vacuoles and granules (Moor, 1983). They are found on either side of the head close to the junction with the velar lobes. Recently these organs have been considered protonephridia (Ruthensteiner and Schaefer, 1991). According to Raven (1958), these transitory structures are absorbed shortly after hatching and the adult kidney, lying close to the pericardial sac, is used for larval and later for adult excretion.

Circulatory system

Caenogastropod veligers may have both a larval heart and an adult heart but the larval heart differentiates before the adult heart. Werner (1955) stated that the larval heart lies at the surface of the neck region in many veligers. He described the larval heart as a thin layer of squamous epithelium underlain by muscle fibres. Apparently it functions to maintain a flow of blood through the velum or water circulation in the mantle cavity. According to Fretter and Graham (1962), the larval heart is present until settlement and metamorphosis, after which the adult heart is used exclusively. The adult heart differentiates in the dorso-posterior region of the veliger and is composed of an auricle and ventricle that are enclosed in a pericardial sac (Hyman, 1967). It pumps blood from the arteries, that connect to the ctenidial sinuses, into the aorta. From there the aortic artery delivers blood to the visceral and cephalopedal sinuses.

Study Organism

Life History of Naticid Snails

Naticid snails are carnivorous gastropods that burrow or plough through soft marine substrates. Two groups can be distinguished based on their life history patterns (Thorson,. 1946; Giglioli, 1955; Amio, 1963). A benthic or direct developing group, which includes the snails *Natica clausa, Amauropsis purpurea* and other species, retains their embryos within the egg capsules until the crawling stage. In contrast, pelagic or indirect developing naticid snails, such as *Natica gualtieriana* and *Neverita didyma*, undergo embryonic development within the egg capsule but they eventually hatch as swimming larvae that complete pre-metamorphic growth and development while in the plankton. These veliger larvae pursue a planktonic life for a period that is species specific, but which is also dependent upon food quality and temperature, before they settle and metamorphose on an appropriate substrate (Fretter, 1969).

Hertling (1932) and Thorson (1935) initiated research on the biology of naticids by examining both adult animals and their embryos. These and other studies established the basis of our understanding of naticid development. For example, Thorson (1935) undertook a general ecological and developmental survey of *Natica groenlandia*, *N. clausa* and *N. islandica*. Hertling (1932) examined, in a cursory fashion, the embryological development of *Natica putchella*. Giglioli (1955) classified the egg masses and developmental pattern of several naticids. Amio (1955) documented the development to hatching of *Sinum papilla, Neverita reininana, Neverita didyma, Natica maculosa, Natica adamsiana* and *Natica janthostomoides*. Fioroni (1966) described a veliger of *Polinices (Natica) catena*. Thiriot-Quievreux (1974) captured a veliger of *Natica alderi* in the plankton and described its external characteristics and anatomy. She completed an extensive description of the internal anatomy, through serial sections of a pre-metamorphic stage. Berg (1976) studied the development of carnivorous behavior in *Natica gualtieriana* from veligers captured from the plankton.

Although a description of the sequential morphological changes occurring during the larval stage of naticids is wanting, economic and natural history concerns continue to stimulate research on naticid snails (Melville, 1930; Bernard, 1967; Carriker, 1981). Since naticids are predatory on commercial bivalve species, several researchers examined the effect of moon snail predation on bivalve populations (Stinson and Medcof, 1946; Bernard, 1967; Peitso *et al.* 1993).

The present study documents the morphogenesis of the indirect developing naticids *Polinices lewisii* and an unidentified species of the genus *Natica*. Preliminary accounts of development in the former species are provided by Bernard (1967) and Siemens (1981), who briefly examined the embryonic stages and hatching larvae. The egg diameter of *P. lewisii* is reported to be 150 to 250 μm (Bernard, 1967; Giglioli, 1955), which is approximately half the size of eggs produced by direct developing naticids. Descriptions of the structure and histochemistry of these veligers complement studies completed on the adult animal (see Bernard and Bagshaw, 1969; Reid and Friesen, 1980; Reid and Gustafson, 1988).

Reproduction of naticid snails

Naticids are dioecious and mating involves deposition of sperm and prostatic secretions into the bursa copulatrix on the right side of the female mantle cavity (Fretter and Graham, 1962). In each spawn mass, a female naticid lays from 50 to 10000 eggs, that are fertilized as they pass from the ovary through the oviduct. In the albumen gland, eggs are embedded in albumen and individually encapsulated by an inner capsular membrane, or vitelline membrane, as is typical of gastropod eggs (Raven, 1958). An outer thicker capsular wall or chorion membrane (Giglioli, 1955) is then secreted by the capsule gland. Finally, egg capsules are embedded in a gelatinous material that forms the bulk of the egg mass. As the eggs are deposited, sand particles are incorporated into the gelatinous material giving the egg mass a rubbery granular texture.

Giglioli (1955) described the formation of the egg masses, or collars, by naticids. The collar-like shape of the egg masses is thought to result from interstitial pressure compressing the egg mass on the body of the female as the eggs are laid. Therefore, the size of the collar corresponds to the size of the adult, although the arrangement of egg capsules in the collars seems to vary between species (Giglioli, 1955; Amio, 1955). Egg masses of *P. lewisii* are circular with smooth apical and basal margins (Bernard, 1967; Giglioli, 1955). The egg capsules are scattered irregularly between the sand layers and are not visible externally. The egg masses for the unidentified species of the genus *Natica* are not recognized in the literature.

Under laboratory conditions, embryonic development of *P. lewisii* is usually complete in 55 days at 10 to 12°C (Siemens, 1981). Cleavage follows the typical holoblastic, spiral pattern and is determinate. Initial cell divisions produce a stereoblastula that gastrulates apparently by invagination or epiboly (Siemens, 1981; Raven, 1958). Differentiation of the apical band cells into ciliated cells and the formation of the stomadeaum and lumen of the gut produces a trochophore larval stage (Raven, 1958). Further development produces the foot, shell and velum, permitting the newly formed veliger larvae to move within the egg capsules (Hertling, 1932; Thorson, 1946).

After formation of the veliger larval stage during embryonic development, hatching occurs at approximately 10 or 40 days, according to Bernard (1967) and Siemens (1981), respectively. However, this difference may merely reflect subjective differences in what constitutes the veliger larva stage. Emergent larvae have an oval bi-lobed velum, shell, operculum on the foot, eyespots and statocysts. Embryogenesis for *Natica* sp. is likely similar.

Taxonomic Preview

Polinices lewisii (Gould, 1847) and *Natica* sp. belong to the family Naticidae and subfamilies Polinicinae and Naticinae, respectively. Both species are resident to the eastern Pacific Ocean. They are grouped in the prosobranch gastropod superfamily Naticoidea, which occur in all seas, at a broad range of depths, as well as in Cenozoic sediments worldwide (Marincovich, 1977). Within this superfamily are the families Ampullinidae and Naticidae (Ponder and Warén, 1988) (Table 1). The family Naticidae are burrowing snails with globose shells and a drilling apparatus that facilitates their predatory behavior. Otherwise these snails exhibit a generalized neotaenioglossan organization (Fretter and Graham, 1994; Ponder and Warén, 1988).

Table 1. The taxonomic placement of the moon snails.
After Ponder and Warén (1988) and Marincovich (1977).

Class Gastropoda
Subclass Prosobranchia
Superorder Caenogastropoda
Order Neotaenioglossa
Suborder Discopoda
Superfamily Naticoidea
Family Ampullinidae
Subfamily Ampullospiranae
Family Naticidae
Subfamily Naticinae
Subfamily Polinicinae
Subfamily Sigaretinae
Subfamily Tylostominae
Order Neogastropoda

Marincovich (1977) critically reviewed the systematics and classification of the extant naticids of the eastern Pacific. His analysis clears up some of the confusion experienced by researchers who try to identify species of naticids. To compare organisms on a phylogenetic basis, taxonomic competence is as important as complete anatomical descriptions. Appendix 1 provides a review of naticid systematics to clarify the species present in the Vancouver Island region of the northeastern Pacific.

Purpose

Development of *P. lewisii* was chosen as a research topic to contribute information on morphogenesis of caenogastropods. This caenogastropod seemed an opportune choice as adults and egg masses are conspicuous on soft-bottom tidal flats of Vancouver Island throughout the spring and summer. Furthermore, there is a misunderstanding in the published literature regarding the developmental pattern of this species. Giglioli (1955) maintained, based on preserved samples of egg masses, that small lecithotrophic embryos of *P. lewisii* became planktotrophic, pelagic veligers. Bernard (1967) contested this statement and predicted a short-lived, non-feeding larval stage for *P. lewisii*. No veligers were found in water or sediment samples yet 2-3 mm juveniles were located in the benthos during an extensive survey by Bernard (1967). However, Bernard (1967) was unable to account for the absence of sizes between these 2-3 mm juveniles and the much smaller shell size of hatching veligers. As neither Bernard (1967) nor Giglioli (1955) reared the snail in the laboratory the controversy remained unresolved.

The pelagic development of the unknown species of the genus *Natica* provided additional information on the morphogenesis of naticid snails. The egg mass, collected through serendipitous circumstances, was a naticid egg collar, but no adults were nearby to permit identification of the species. The larvae were reared as a peripheral project to the main study on *Polinices lewisii*, however only the unknown species of the genus Natica was successfully reared through metamorphosis. The taxonomic assignment to genus *Natica* was based on the presence of a calcified operculum in laboratory reared juveniles, a characteristic of the genus.

I have studied the morphogenesis of the carnivorous marine snails *Polinices lewisii* and *Natica* sp. This report resolves the controversy about the development of *P. lewisii,* and gives information about the planktotrophic larval development of *P. lewisii* and an unidentified species of the genus *Natica*, based on histological sections of sequential developmental stages.

Methods

Collection and Maintenance of Egg Masses

Egg masses of *P. lewisii* were collected from the intertidal and subtidal flats of Patricia Bay, Saanich Inlet and of Trevor Channel, Barkley Sound on Vancouver Island. Egg masses of *Natica* sp. were collected from the subtidal area bordering the San Josa Islets in Barkley Sound. Whole egg masses, known as collars, were transported to the laboratory in containers filled with seawater. A small section of each egg mass was examined to estimate the stage of intracapsular development.

At Bamfield, egg collars were maintained in the flow-through sea water system of the Marine Station. At the University of Victoria, egg collars were kept in flasks of standing sea water at 11°C and aerated continuously. Sea water for maintaining egg masses and larvae at the University was collected by hand from Ten Mile Point, a coastal promontory off Cadboro Bay, Vancouver Island, that is subjected to strong tidal currents. The egg masses were observed daily for the hatched veligers.

Larval Cultures

Four cultures of naticid veligers were attempted during this study; these were initiated in February, May, July and November of 1995. Only the February reared veligers of *Natica* sp. survived until metamorphosis in June. (This genus was identified by the calcarous operculum produced by the juvenile.) The three later cultures were *Polinices lewisii*, as confirmed by collection of adults near egg masses. The May culture was inadvertently spilt during a laboratory clean up at the Bamfield Marine Station after 40 days. The July and November cultures became unhealthy at 130 days and 65 days, respectively.

After veligers emerged from the egg mass, they were collected on a 64 μm Nitex screen and pipetted into flasks containing 500 mL of sea water at densities of 50 to 100 larvae per flask. Larval cultures were maintained at 11°C. During the 4 month pelagic period, the seawater was changed every second day using a sieve constructed from a small plastic cup with the bottom replaced with 64 μm mesh *Nitex* cloth. The sieve was immersed into a seawater-filled finger bowl and the larval culture gently poured into the sieve. Freshly filtered seawater (0.8 μm filter) was poured over the larvae on the bottom of the sieve to wash out the old culture water and debris surrounding the larvae. The overflow of seawater was trapped in a larger container and discarded. The veligers were transferred by pipette, using a dissecting microscope, into clean 500 mL flasks containing the pre-filtered seawater. Sixty mg L^{-1} streptomycin sulfate and 50 mg L^{-1} penicillin G (Sigma Chemical Company) were added once a week to the cultures.

Larvae were fed unicellular phytoplankton in concentrations of 5-10 x 10^5 cells mL^{-1}. The algal cell density was determined by a haemocytometer and the appropriate volume of algal suspension added directly to the cultures. Phytoplankton used in this study, *Rhodamonas* sp., *Pavlova lutheri,* and *Isochrysis galbana*, were cultured as follows to provide a continuous supply of food for the veliger cultures.

Two species of golden brown algae, *Pavlova lutheri* and *Isochrysis galbana* (Carolina Biological Supply), were cultured separately in 500 mL flasks containing 0.45 μm Millipore filtered seawater and 10-12 mL Carolina Alga-gro® Concentrate. The cultures were maintained at 20-23°C with constant aeration and fluorescent illumination. When ambient temperature and light conditions were low, the flasks were placed in Styrofoam containers, which helped to maintain temperatures suitable for rapid growth. The red algae *Rhodamonas* sp. was also cultured using similar solutions but this species was grown under room illumination and without continuous aeration.

Metamorphosis of *Natica* sp. larvae was stimulated by sediment taken from the habitat of adult snails. The juveniles were maintained in the laboratory for 3 months during which time they consumed small (<1mm) bivalves by drilling through the shell. Using a dissecting microscope, the bivalves, *Tapes japonica* and *Tresus nuttalli,* were collected from the top 3 cm of sandy-mud from the lower intertidal zone of Patricia Bay, Saanich Inlet. Bivalve collections occurred from late July until September of 1995. Attempts to stimulate metamorphosis of veligers of *P. lewisii* began from the time of larval emergence from the egg capsule. The veligers were exposed to sediment from the adult habitat for 2 day periods and observed.

Photography and Size Measurement

Measurements of the eggs, embryos, and veligers were made with an ocular micrometer placed on the objective eyepiece of a Wild dissecting microscope, and a Leitz compound microscope. Photographs of live larvae and juveniles were taken with a 35 mm camera mounted on the compound microscope. Larvae were narcotized with a solution of high magnesium and low calcium (artificial) sea water (225 mM NaCL, 5 mM KCl, 102 mM $MgCl_2 \cdot 6H_2O$, 1 mM $CaCl_2 \cdot 2H_2O$ dissolved in 1 L distilled H_2O) to prevent larval retraction into the shell during observation. Larvae were pipetted onto a depression slide or conventional microscope slide with a few drops of seawater. Plasticine supported coverslips were placed over the larvae, thus preventing the shells from becoming crushed while taking measurements and photographs. Shell length was measured through the apex of the shell (Jablonski and Lutz, 1981).

Scanning Electron Microscopy (SEM)

To complement the observations on live larvae and juveniles, the sculpture and shape of the growing shell were examined using SEM. The protoconchs I and II of *P. lewisii*, the teleoconch of *Natica* sp., and bivalve shells drilled by laboratory-reared *Natica* sp. were photographed.

Shells of the larvae at different developmental stages were cleaned using a dilute bleach solution. Appropriate specimens were placed into labeled 20 mL glass vials and ¾ of the seawater was aspirated from the vial. A 2:1 solution of seawater and bleach (12 % sodium hypochlorite) was added to the ¾ level. The solution was changed twice in one hour or until the shells looked clean. The shells were rinsed in Millipore® filtered seawater then distilled water to remove the bleach solution. Residual lipid-rich organic material was removed by rinsing the shells in 100% methanol, then transferring them to a 1:1 solution of chloroform and methanol. This solution was changed twice over a half hour period. The shells were rinsed three times with 100% methanol to remove the water and any bubbles that may have formed inside the shells, then three times each in 100% methanol, distilled water, 70% and 100% acetone. Cleaned shells were stored in acetone in the refrigerator until processed for photography.

For SEM preparation, the shells were dried on lens tissue paper over several layers of filter paper. To prevent loss of shells, the paper layers were taped together. The shells were mounted onto SEM metal stubs using small dabs of nail polish, which had been allowed to harden slightly. Specimens were coated with gold and examined using a Jeol JSM-35 scanning electron microscope. Specimens were viewed at an accelerating voltage of 15 Kv with a working distance of 15 mm and photographed on VP 120 Kodak Verichrome pan film.

Fixation and Histological Sections

As extensive relaxation of veligers provided better clarity of anatomical details in histological sections, veligers were anaesthetized before fixation using an ice-cold solution of high magnesium and low calcium seawater. Larvae were pipetted into an ice-cooled 10 mL vial marked at 0.25, 0.5 and 0.75 levels. Excess natural seawater was removed to the 0.25 level. Fifteen drops of artificial seawater were added to the vials at 3 minute intervals until the volume reached the 0.75 level. The procedure was repeated until the larvae remain relaxed, taking approximately 1 to 24 hours depending upon the size and age of the specimens. Once the larvae were relaxed and ciliary movement slowed, a few drops of a saturated solution of chlorotone in seawater were added.

Specimens were initially fixed in 2.5% glutaraldehyde solution in 0.2 M Millonig's phosphate buffer at pH 7.6 and 0.14 M NaCl. The larvae were placed in the fixative solution for 4 hours at room temperature. Following primary fixation the specimens were decalcified in a 1:1 mixture of 10% ethylenediaminotetraacetic acid (EDTA) and glutaraldehyde solution. A freshly made solution of 10% EDTA acts rapidly to remove the calcium ions from the thin larval shell. Decalcification took approximately 2-24 hours depending on the age of the veliger.

Following decalcification, specimens were rinsed three times at 10 minutes each with 2.5% $NaHCO_3$ (pH 7.2) and post-fixed in a 1: 1 mixture of 4% osmium tetroxide and 2.5% $NaHCO_3$ for one hour. Specimens were dehydrated in a graded series of ethanol (percentage of ethanol 30, 50, 70, 90, 95) for 10 minutes at each wash. They were rinsed three times in 100% ethanol and three times in propylene oxide. Specimens were infiltrated with a 1:1 mixture of Epon epoxy and propylene oxide for 8 hours, followed by a further 8 hours in Epon epoxy alone. Specimens were pipetted into polymerizing dishes, centered and placed in a 60 °C oven for 48 hours.

Serial sections of 1 micrometer thickness were cut with glass knives using an ultramicrotome, and stained with 1% methylene blue and 1% azure blue in 1% sodium borax (Richardson *et al.*, 1960). Sections were analyzed and photographed using a Ziess ultraphotomicroscope and TMAX 100 film.

Histochemical survey

The digestive tract of a 110 day veliger of *P. lewisii* was examined for esterase, mucoproteins and phosphatases using established histochemical methods. The specimen was anaesthetized in the same manner as those prepared for epon embedding but fixed using a process that preserves enzymatic activity.

The specimen was preserved in 4% paraformaldehyde buffered with Millonigs's phosphate buffer at 4°C for 2 hours. Following fixation, the specimen was dehydrated in an ethanol series (30, 50, 70, 90) and embedded in JB4 (glycol methacrylate). A moldform that attached directly to the microtome stub was used. The specimen was stored at 4°C during infiltration and polymerization. The block face was trimmed to a mesa (arrow) shape just before sectioning (Burns and Bretschneider, 1981).

Sections were cut at a thickness of 4 μm using glass knives, then placed on a slide with a drop of water and allowed to air dry at 4°C. Histological examination was aided by counter staining with the combinations of Celestine blue, Haematoxylin and Ponceau stains (a combination similar to Haematoxylin-Eosin) or Fast Green stain. Sections were photographed and examined using a Leitz compound microscope.

Histochemical staining techniques used a substrate that combined a diazonium salt in a buffered medium (0.1 M maleic acid and 0.1 M Tris) mixed to the appropriate pH (Pearse, 1961). As the resolution of each enzyme required different chemicals for incubation media, each procedure is outlined below (see Humanson, 1979, for further information).

Esterase

Esterase catalyses the hydrolysis of ester linkages between carboxylic acids and some alcohols or phenols. The products of the reaction stain blue-black with this protocol. Counterstaining was with Celestine blue, which colored nuclei blue; haematoxylin that stained acidic structures purplish-blue; and Ponceau that stained general cell structures reddish-pink.

The incubation medium contained 25 mg α-naphthyl acetate dissolved in 0.625 mL acetone with 50 mL Millonigs's phosphate buffer. The solution was shaken until most of the initial cloudiness disappeared, then 125-250 mg Fast Garnet GBG diazonium salt dye was added and shaken again. The slides were immersed in the medium using Coplin jars.

The slides were incubated for 15 minutes and washed in running water for 2 minutes. Background tissue was stained with Celestine blue for 2 minutes, washed for 2 minutes, soaked in haematoxylin for 3 minutes, bleached for 3 minutes, washed for 3 minutes and stained with Ponceau for 2 minutes. Final wash was in running water for 3 minutes. Slides were dried on a hot plate before immersing in toluene for a minimum of 3 minutes. Coverslips and mounting medium were placed over sections immediately after removal from toluene.

Alkaline phosphatase

Alkaline phosphatase enzymes break down phospholipids in food particles. The activity of the enzyme stained a brown-black using the azo-dye method. The slides were incubated in the sodium α-naphthyl phosphate solution, (25-50 mg Na α-naphthyl phosphate dissolved in 50 mL 0.1 M Tris buffer (pH 10), followed by the addition of 50 mg of Fast Violet B, and stirred well), for 2 hours at ambient temperature, washed in running water 3 minutes and counterstained as described in the esterase section.

The 0.1 M Tris buffer (pH 10) contained 3.025 g Tris (hydroxylethyl amino-ethene) with 2.9 g maleic acid dissolved in 250 mL distilled water to which 650 mL of 0.1 M NaOH was added and made up to 1L with 120 mL distilled water.

Acid phosphatase

Demonstration of acid phosphatase activity in lysosomes of tissues was aided by an incubation medium with sodium α-naphthyl phosphate and Fast Garnet GBG salt. Enzymatic activity stained brown-black. The slides were incubated at 37°C for 3 hours, washed for 2 minutes and counterstained as described in the esterase section.

The incubation medium contained 2 mg Na α-naphthyl phosphate in 50 mL 0.1 M Tris maleic acid buffer with 3 mg Fast Garnet GBC salt (0.3025g Tris, 0.29g maleic acid added to 25 mL distilled water pH adjusted to 5 with NaOH; volume made up to 100 mL.)

Periodic Acid Schiff (PAS)

The presence of mucoproteins and insoluble carbohydrates was demonstrated with the PAS reaction (Pearse, 1961). A positive PAS reaction stained mucoproteins deep purplish red and glycoproteins a paler red-pink. Periodic acid (HIO_4) oxidizes hydroxyl groups on adjacent carbon atoms or adjacent hydroxyl and amino groups to produce aldehydes. Schiff reagent, fuchsin-sulfurous acid, forms an additional product with aldehydes to produce a magenta-colored reaction product. The amount of color developed by the reaction is dependent on the amount of reactive insoluble carbohydrate present (Putt, 1972). General cell structures were stained green.

Reagents were mixed in small quantities. The Periodic acid reagent consisted of 0.6 gm Periodic acid in 100 mL distilled water with 2 drops of concentrated hydronitrate HNO_3. Schiff's reagent contained 2.5 gm basic fuchsin in 85 mL warm water. The solution was shaken to dissolve 1.9 gm potassium metabisulphate ($K_2S_2O_5$), then 15 mL 1N hydrochloric acid was added. The reagent was shaken for 2 hours and stored frozen until needed. The bleaching solution contained 0.5g (NO_2SO_3) in 100 mL distilled water with 5 drops 1N hydrochloric acid.

The sections were incubated for 5 minutes in Periodic acid reagent and washed for 5 minutes in running water. Slides were immersed in Schiff's reagent for 2-15 minute periods at room temperature and washed for 2 minutes in running water. They were then bleached for 2 minutes and washed for 5 minutes. Background tissue was stained with Fast Green FCF for 5 minutes, washed for 5 minutes and cleared in toluene before mounting.

Results

External Development

Hatching veligers of *Polinices lewisii* and *Natica* sp. undergo an obligatory period of pelagic planktotrophic development before they are capable of metamorphosis into a crawling, carnivorous juvenile (Figure 1). I describe progressive changes in the external appearance of these snails during three developmental stages. These are the veliger at the time of hatching from the egg capsule, the pelagic, post-hatching veliger, and the crawling juvenile (Table 2). Age is an unreliable indicator of the rate of differentiation during the post hatching larval stage. Developmental events often required a variable period even among sibling larvae within the same culture. In my study, most veligers of *Natica sp.* reached metamorphic competence at 107 days, while veligers of *P. lewisii,* raised in a similar fashion, did not settle or metamorphose at 130 days after hatching.

Egg masses

The two naticid species examined lay collar-shaped egg masses. As indicated in Table 2, the egg mass of *P. lewisii* is large and protected by fine sediment, whereas, the egg mass of *Natica* sp. is smaller and incorporates bits of shell and coarse sediment. The egg capsules of both species are not visible externally and are irregularly distributed amongst the sand grains within the egg mass (Figure 2A). Embryological development of *Natica* sp. is presumably similar to that of *P. lewisii*, but this could not be confirmed as the collar collected during this study contained late-stage embryos only. No nurse eggs were present; all eggs in collars of both species developed into veliger larvae and each capsule held only one egg (Figure 2A inset).

Figure 1. Schematic representation of the life history strategy of *Polinices lewisii* and *Natica* sp.

The sketches show the changes in velum structure and pigmentation. Sketches are not drawn to scale.

A. Lateral view of adult snail and collar shaped egg mass on ocean bottom.

B. Apical view of emergent veliger in the water.

C. Apical view of post-hatching veliger at approximately 25 days. The velar lobes elongate and develop pigmented spots on each tip.

D. Apical view of post-hatching veliger at approximately 40 days. The lengthened velar lobes eventually divide to form 4 lobes, each tipped with a pigmented spot.

E. Lateral view of crawling juvenile.

Explanation of lettering

e = eye
f = foot
o = operculum
s = shell
t = tentacle
v = velum

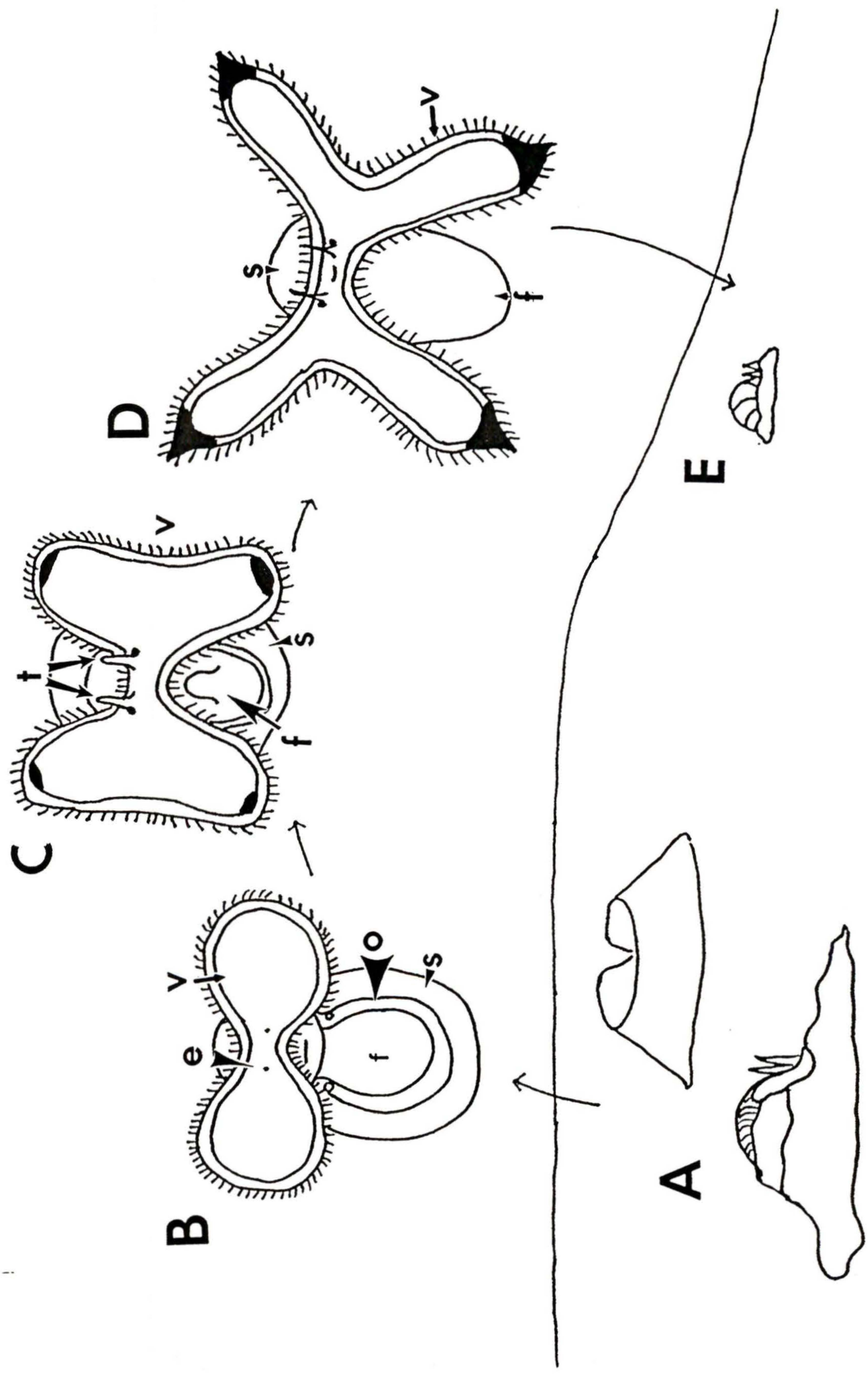
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Table 2. Comparison of the external morphological characteristics of naticid snails reared from southern Vancouver Island during 1995.
The number of days indicates the approximate time required by the larvae to reach each stage of development.

Polinices lewisii	*Natica* sp.
egg mass	
Smooth circular collar-shaped egg mass composed of fine sediment; random distribution of egg capsules. Collar dimensions (N = 10): apical diameter 78 mm, basal diameter 163 mm, height 77 mm.	Smooth circular collar-shaped egg mass composed of shell pieces and coarse sediment; random distribution of egg capsules. Collar dimensions (N = 1): apical diameter 40 mm, basal diameter 100 mm, height 50 mm.
emergent veliger (Day 0)	
Velum with two lobes and no pigmentation, eyespots apparent, symmetrical foot with oversized operculum, gut outline visible, shell sculptured with puncta, shell length 164-220 µm.	Features similar to *P. lewisii* except no sculpturing on protoconch I, shell length 200 µm.
post-hatching veliger (0-107 days from emergence from egg capsule)	
Cephalic tentacles appear, gut becomes pigmented, propodium develops, velum becomes four lobed with pigmentation on the tips of each lobe, protoconch II sculptured with spiral growth lines, shell length at mid-pelagic life ~545µm.	Features similar to *P. lewisii* including spiral growth lines sculpturing protoconch II, shell length at mid-pelagic life ~600µm.
crawling (settled and metamorphosed) juvenile (107 days from emergence from egg capsule)	
no data available	Further development of the propodium, darkly stained protoconch I with spiral sculpturing of teleoconch indistinguishable from protoconch II, >2½ whorls, shell length ~1350 µm.

Larvae at emergence from the egg capsules

The hatching stage veligers of *P. lewisii* and *Natica* sp. are structurally alike. At emergence from the egg capsule, both species have a pair of velar lobes, a small foot, paired eyespots and a transparent embryonic shell called the protoconch I (Figure 2B). The newly emerged veligers swim actively in the water.

For *P. lewisii*, the velar lobes extend 35-50 μm beyond the shell aperture and show no pigmentation. The foot is wide, flat and is slightly shorter than the operculum (Figures 2B and 2C). The mouth is dorsal to the ciliated foot. Eye pigmentation, present above this region, has a hemi-spherical shape. The statocysts, retractor muscle, and contours of the gut are visible through the transparent protoconch (Figure 2C). The features of emergent veligers of *Natica* sp. are similar to those of *P. lewisii*.

Post-hatching veliger

Within ten days of planktonic life, the post-hatching veliger develops tentacles near the eyespots (Figure 3A). After about 30 days, the velum enlarges, with each lobe changing in shape from oval to oblong, and two patches of pigmented cells appear on each velar lobe (Figure 1C). The foot enlarges greatly, acquires pigmentation and becomes regionally differentiated into a propodium and metapodium (Figures 3B and 3C). The foot may function as a tactile organ, as the post-hatching veliger was observed extending its foot, as if to feel its way in the water. During the pelagic period, each velar lobe bifurcates to produce 2 pairs of velar lobes that is also called a 4-lobed velum (Figure 1D). The pigmented cells are clustered at the apex of each lobe (Figures 1D and 3C).

Figure 2. Encapsulated veligers at one week prior to hatching and emergent veliger stages of *P. lewisii*.

Scale bars = 50 μm.

A. Encapsulated veligers (indicated by stars) are interspersed among sand grains that appear as dark irregular masses. Each egg capsule contains one embryo in various orientations.

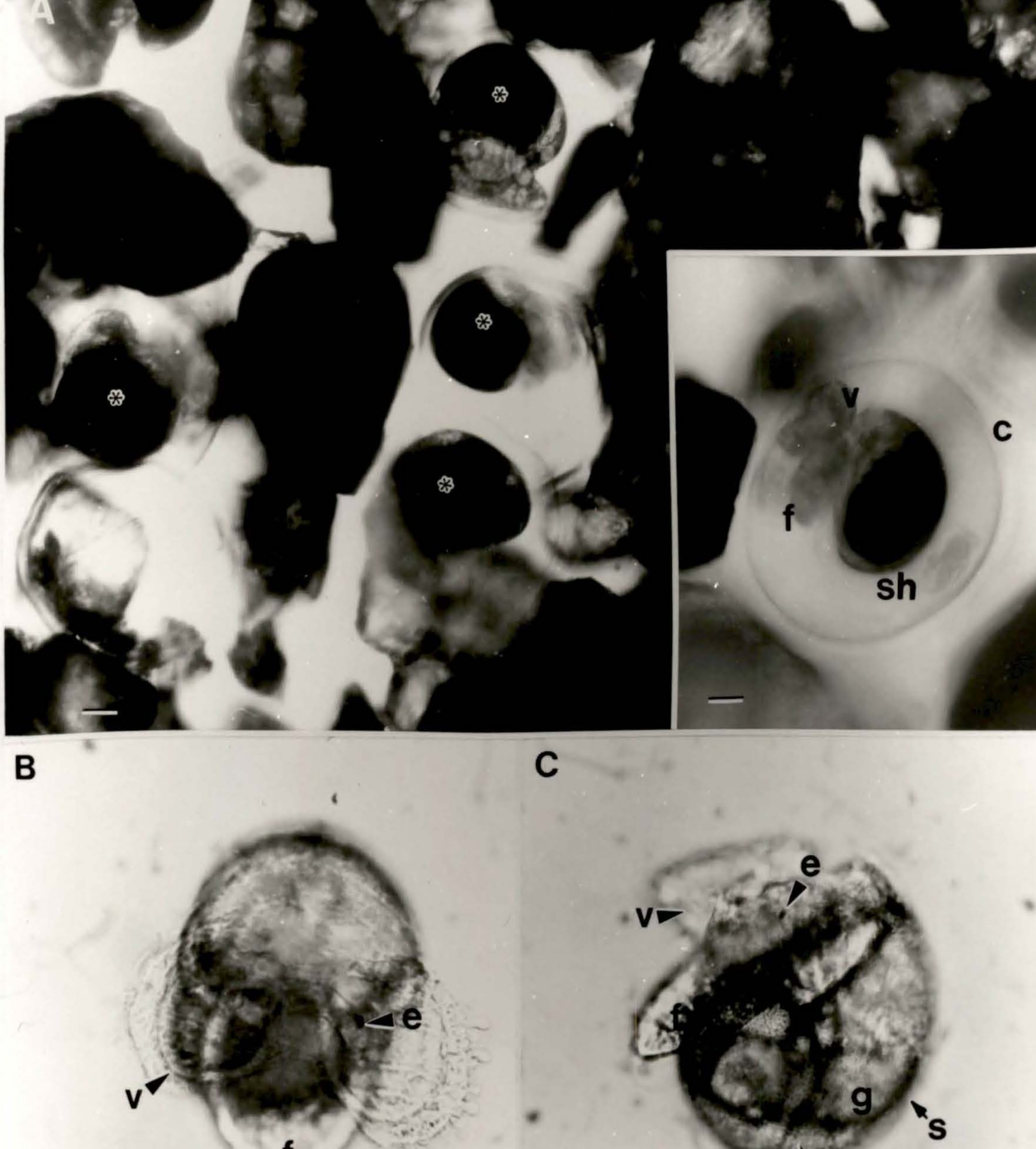
Inset. Enlargement of lateral view of encapsulated veliger. The outlines of the chorion membrane, shell, velum, and foot of the veliger are visible.

B. Apical view of emergent veliger showing the eyespots, velum, shell, and foot.

C. Oblique left lateral view of emergent veliger showing the eyespots, velum, foot, retractor muscle and outline of the gut.

<u>Explanation of lettering</u>

c = chorion membrane
e = eyespot
f = foot
g = gut
rm = retractor muscle
s = shell
* = veliger
v = velum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The post-hatching veligers of both *P. lewisii* and *Natica* sp. begin to consume phytoplankton within 6 days of hatching. These veligers swim actively in the rearing vessels, although they tend to remain close to the bottom for significant periods of time. This may be a resting period, as the velum is retracted, perhaps indicating that the veligers are satiated with food. Once the 4-lobed velum forms, the veligers do not move as actively as they did during early pelagic life.

Crawling juvenile

Both naticid species remained in the veliger phase for over 100 days, indicating a long obligatory planktonic period. Onset of the post-metamorphic, or juvenile, stage occurs when veligers settle onto the foot and lose the velum. Settlement and metamorphosis occurred for the veligers of *Natica* sp., but I was unable to rear veligers of *P. lewisii* to the stage of metamorphic competence.

The veligers of *Natica* sp. settled and lost their velum in response to sediments obtained from the egg mass collection site. Initially, the velum was withdrawn into the shell as the larvae attempted to burrow into the sediment. The gradual loss of the velum occurred over 3 days although I could not determine if the velum was cast-off, eaten, or absorbed. The crawling juvenile has a foot differentiated into an elaborate propodium with an anterior flap (Figure 3D), and a broad metapodium with lateral extensions.

The crawling juveniles were maintained in the laboratory for 3 months, during which time they grew to about 1.35 mm. They consumed several prey items by drilling holes through the shells. Prey included ostrocods and small juvenile bivalves. Initially the bored holes were round openings (Figure 4A). The boreholes became less round and countersunk with beveled edges as the snails matured (Figure 4B and 4C), perhaps indicating changes in drilling abilities and behavior. The juveniles also left several prey items incompletely drilled.

Figure 3. Post-hatching stage veligers of *P. lewisii* and crawling juvenile of *Natica* sp.

A. Frontal view of living veliger of *P. lewisii*. Notice tentacles (indicated by dots) protruding above the velar lobes and statocysts within base of foot. 35 days. Scale bar = 20 μm.

B. Right lateral view of living veliger of *P. lewisii* photographed from video screen showing metapodium and enlarged propodium. 30 days. Scale bar = 40 μm.

C. Left lateral view of veliger of *P. lewisii*. A pigmented tip of one (indicated by star) of the 4 velar lobes is visible. The foot and the digestive tract also contain dark pigments. Whole mount. Fixed in buffered paraformaldehyde. No stain. Mounted in JB4. 110 days. Scale bar = 80 μm.

D. Dorsal view of crawling juvenile of *Natica* sp. The flap of the propodium extends along the anterior rim of the shell. Some debris is on the shell. 137 days. Scale bar = 50 μm.

<u>Explanation of lettering</u>

c = mantle cavity
fl = flap of propodium
g = gut
i = intestine
m = metapodium
M = mouth

o = operculum
p = propodium
st = statocysts
s = shell
t = tentacles
v = velum

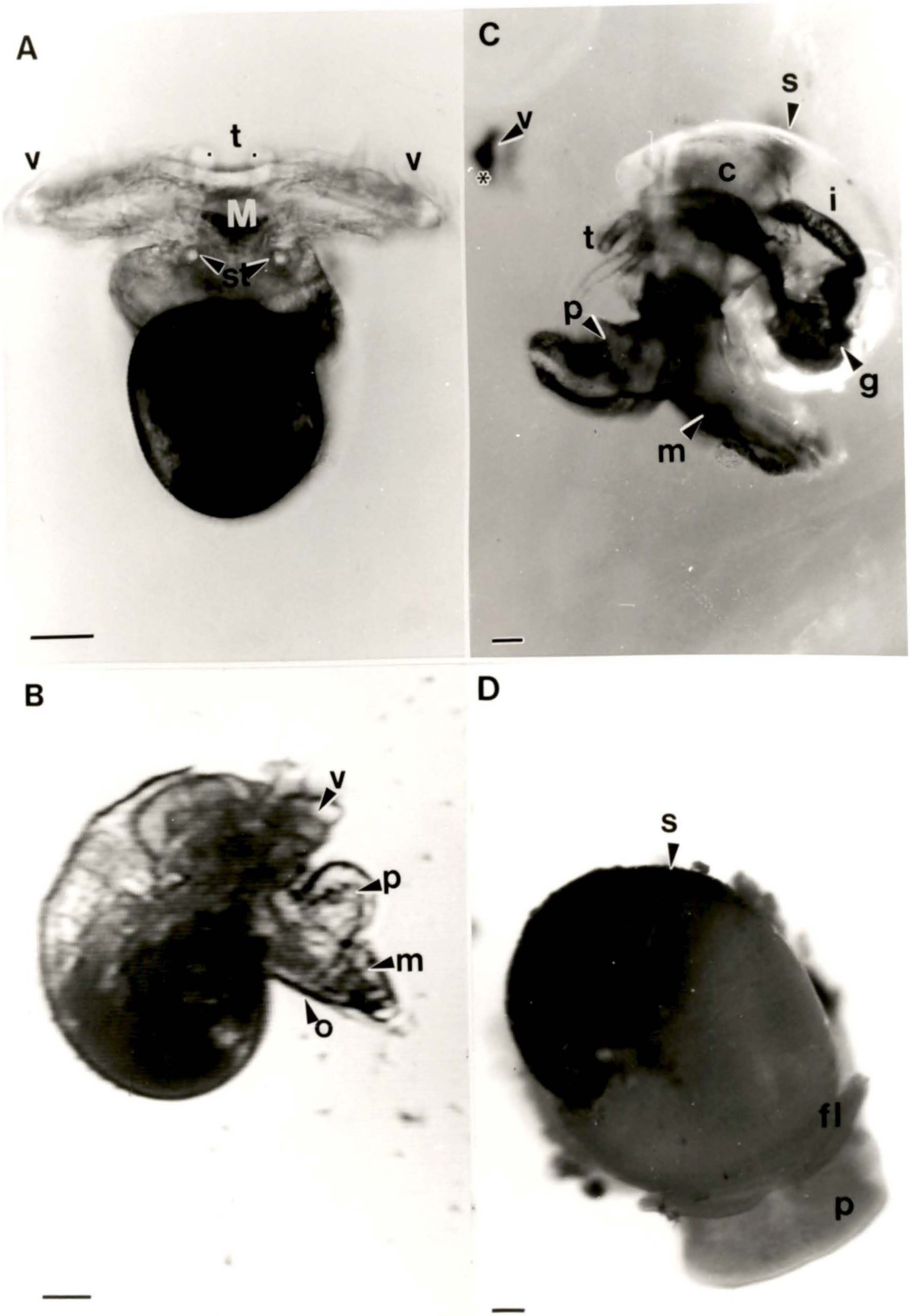
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Figure 4. Boreholes drilled by juveniles of *Natica* sp. that were reared in the laboratory. Scale bars = 100 μm.

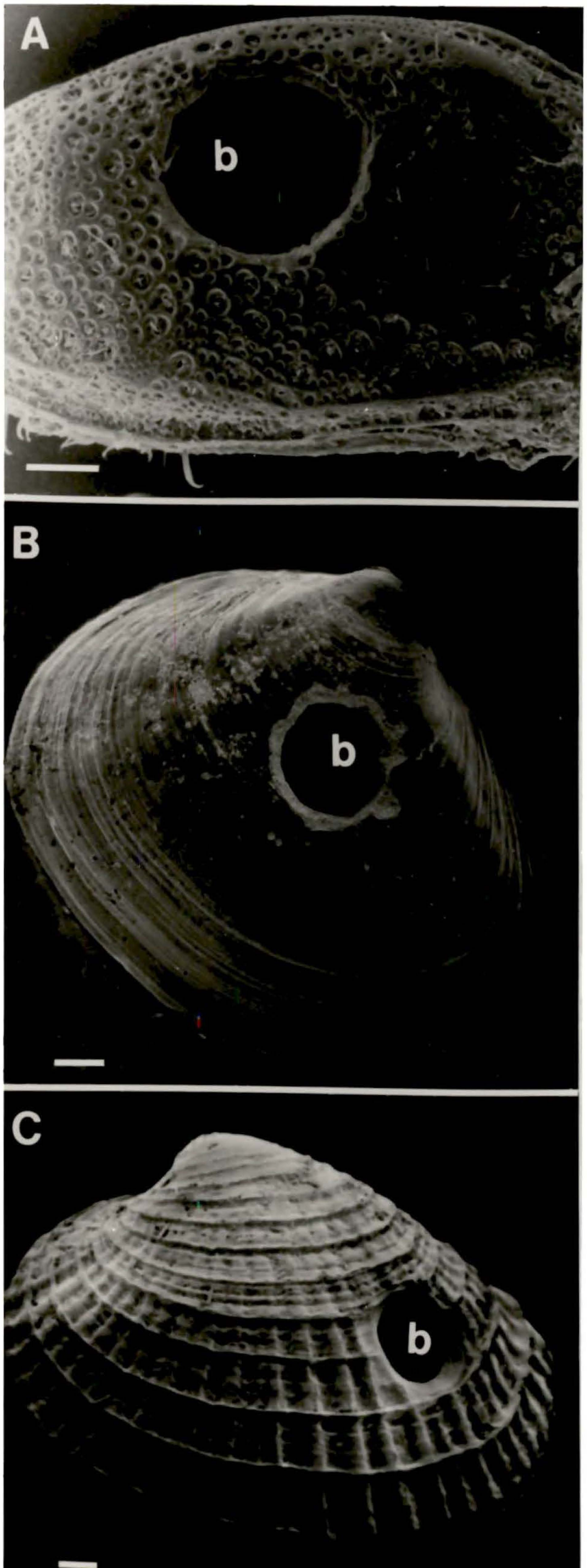
A. Circular borehole on the external surface of an ostrocod shell.

B. Slightly beveled borehole on the shell of the bivalve *Tresus nuttalli.*

C. Beveled and countersunk borehole on the valve of the bivalve *Tapes japonica*.

Explanation of lettering

b = borehole


A
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b
C
b

Growth of the Shell

For *P. lewisii*, the embryonic shell at hatching is 164-220 μm in length, forming ¾ to 1 whorl (Figure 5A). The protoconch I is sculptured with puncta (Figures 5A and 5B). Emergent veligers of *Natica* sp. have a smooth, transparent protoconch I with a length of about 200 μm and a single whorl.

As the veligers of both species increase in size, the protoconch II enlarges by accretion of the shell material around the aperture (Figure 5C). Successive increments of added shell appear as striations running parallel to the apertural rim. After 21 days, the veligers have a protoconch with 1¼ coils but no umbilicus formation. The growing protoconch II of both naticids shows a dextral orthostrophic spiral and formation of the umbilicus (Figures 5D and 6A to F). When veligers of *Natica* sp. were competent to metamorphose, they had a shell with nearly 2½ coils and a 1 mm diameter.

The post-metamorphic shell, or teleoconch, of *Natica* sp. grows in a dextral orthostrophic shape and is sculptured with concentric growth lines (Figure 6D and 6E). The teleoconch has a partially closed umbilicus (Figure 6F). No differences were observed in the growth pattern between the protoconch II and the teleoconch of *Natica* sp.

Figure 5. Shape and microsculpture of protoconch I and II of *P. lewisii* larvae. SEM.

A. Left lateral view of protoconch I with puncta sculpturing. Emergent veliger. Scale bar = 25 μm.

B. Ventral view of protoconch I showing aperture and puncta sculpturing. Emergent veliger. Scale bar = 25 μm.

C. Right lateral view of protoconch II showing accretion of shell material as striated growth lines parallel to the aperture rim. 21 days. Scale bar = 40 μm.

D. Oblique ventral view of protoconch II demonstrating dextral orthostropic growth and formation of the umbilicus. 38 days. Scale bar = 100 μm.

Explanation of lettering

a = aperture
sp = puncta sculpturing
u = umbilicus
1 = protoconch I
2 = protoconch II

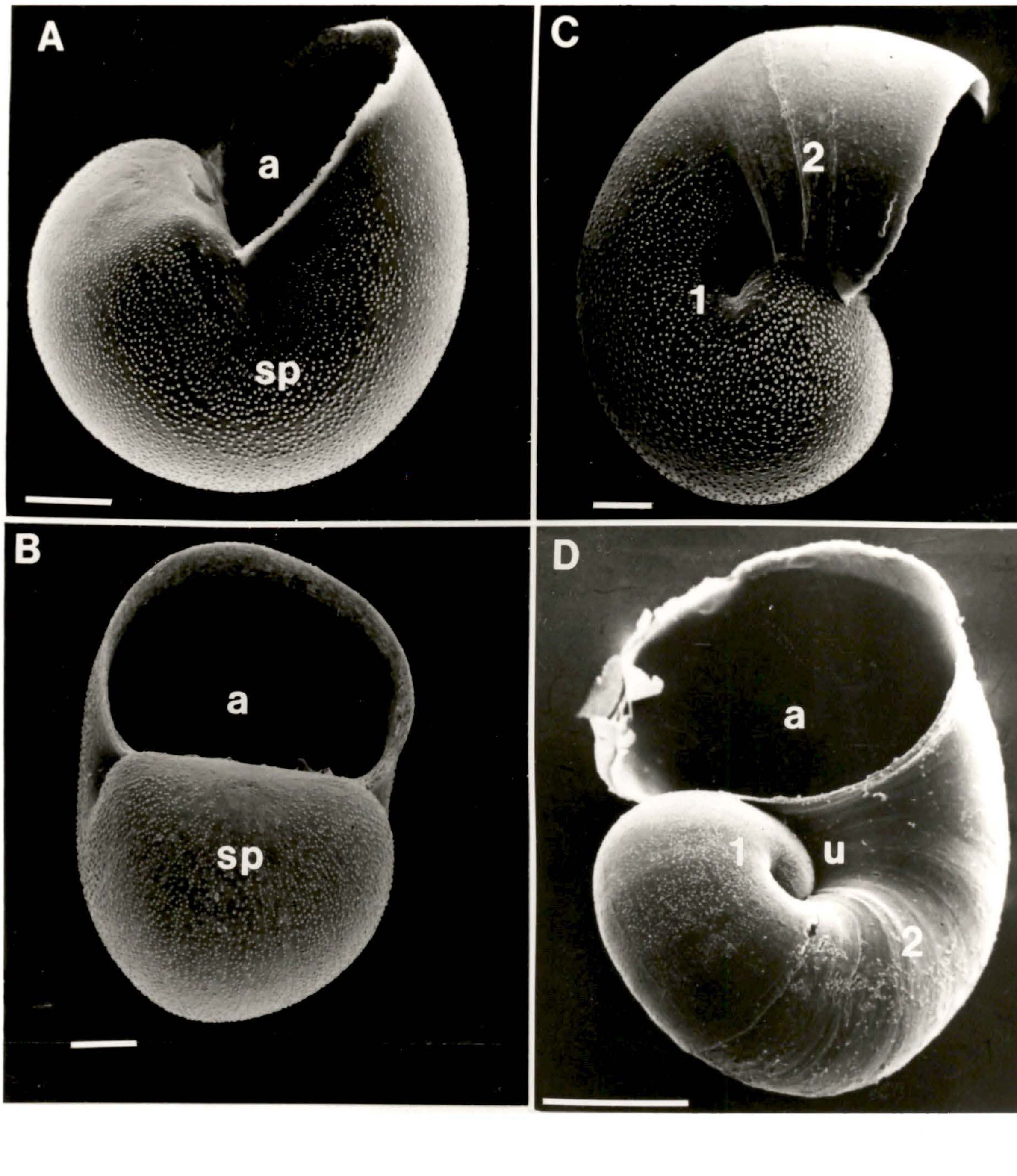
A
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Figure 6. Form and microscuplture of shells from veligers of *P. lewisii* and the teleoconch of crawling juvenile of *Natica* sp.

SEM. Scale bars = 100 μm.

A. Dorsal view of dextral orthostrophic protoconch II of *P. lewisii*. 90 days.

B. Right lateral view of protoconch II of *P. lewisii* showing striated growth lines. 90 days.

C. Ventral view of open umbilicus on the protoconch II of *P. lewisii*. 90 days.

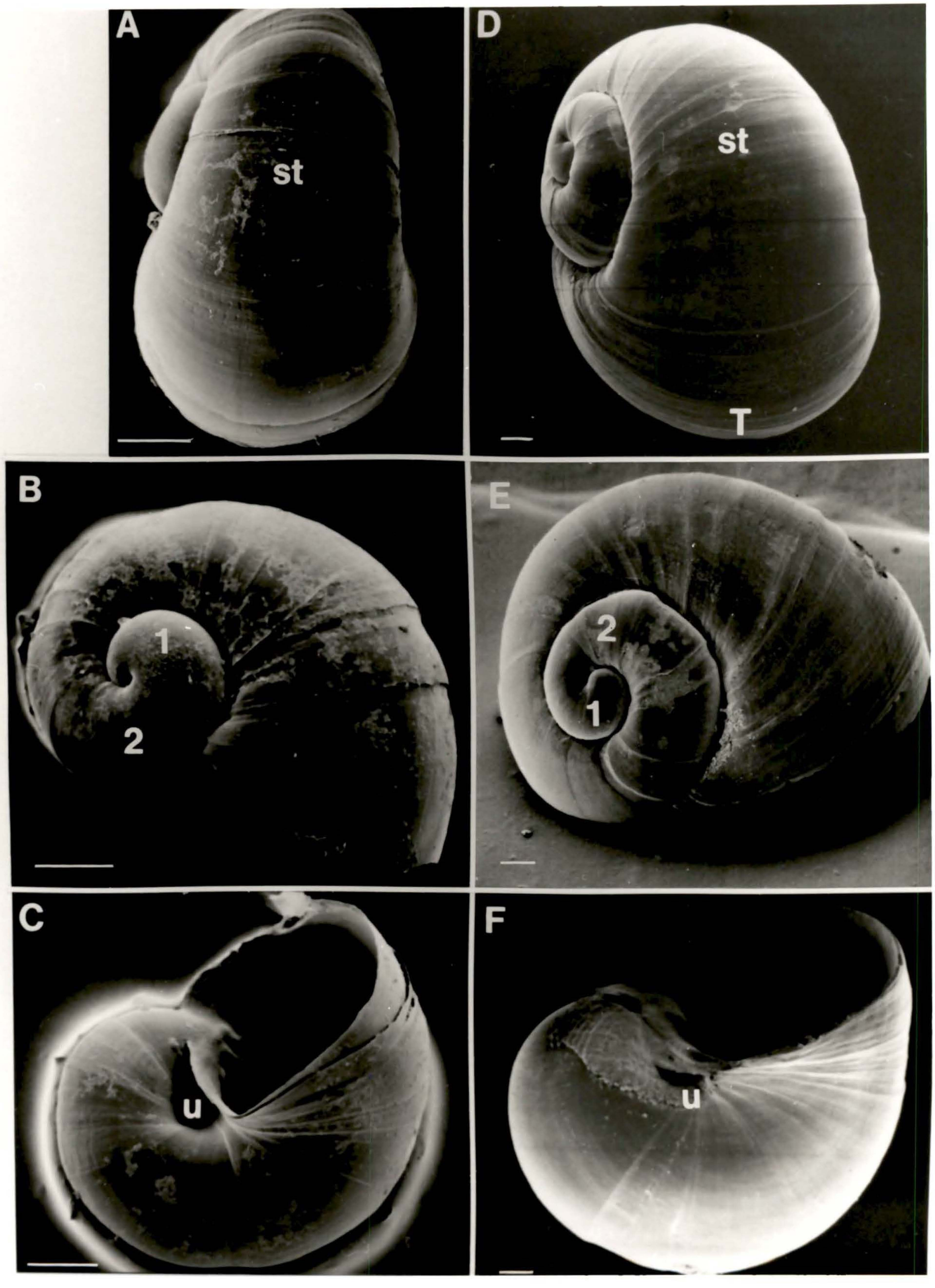
D. Dorsal view of dextral orthostrophic shell of *Natica* sp. 137 days.

E. Right lateral view of shell of *Natica* sp. showing striated growth lines. 137 days.

F. Ventral view of shell of *Natica* sp. demonstrating a slit-shaped umbilicus. 137 days.

Explanation of lettering

st = striated growth lines
T = teleoconch
u = umbilicus
1 = Protoconch I
2 = protoconch II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Internal Morphogenesis

Internal developmental changes during the larval stage were studied by examining histological sections of *P. lewisii* veligers that were fixed at successive time intervals after hatching. Sections of pre- and post- metamorphic stages of *Natica* sp. were examined to document structural changes accompanying metamorphosis. Serial sections were cut in both cross sectional and longitudinal orientations to provide a 3-dimensional view of the anatomical position of the structures within the veliger (Figures 7 and 8). The progressive development of the following structures is described: velum, foot, mantle cavity and associated organs, muscular, digestive, nervous, sensory, excretory and circulatory systems.

Velum

Upper, pre-oral and lower, post-oral bands of large ciliated cells extend along the periphery of each lobe giving the margin of the velar lobes a bi-lobed appearance in cross-sectional profile (Figure 9A). Each cell of the pre-oral band has many, long cilia on the apical surface and contains clear vacuoles. On the ventral surface of the velum, the post-oral band cells have fewer, shorter cilia. Between the two bands, a V-shaped trough forms the food groove (Figure 9A). As the velum elongates and divides into 4 velar lobes, it retains the bilobed, ciliated periphery.

Figure 7. Series of longitudinal sections of *P. lewisii.*

These longitudinal serial sections showing the internal anatomy as viewed from left to right. The lines on these photographs correspond to the planes of section shown in Figure 8A to D. Veliger of *P. lewisii*. 15 days. Epon. One micrometer. Richardson's stain. Scale bars = 30 μm.

A. Left side of veliger passing through the operculum, foot, left statocyst, left digestive gland, retractor muscle, esophagus, intestine, osphradium, mantle cavity and cerebral commissure.

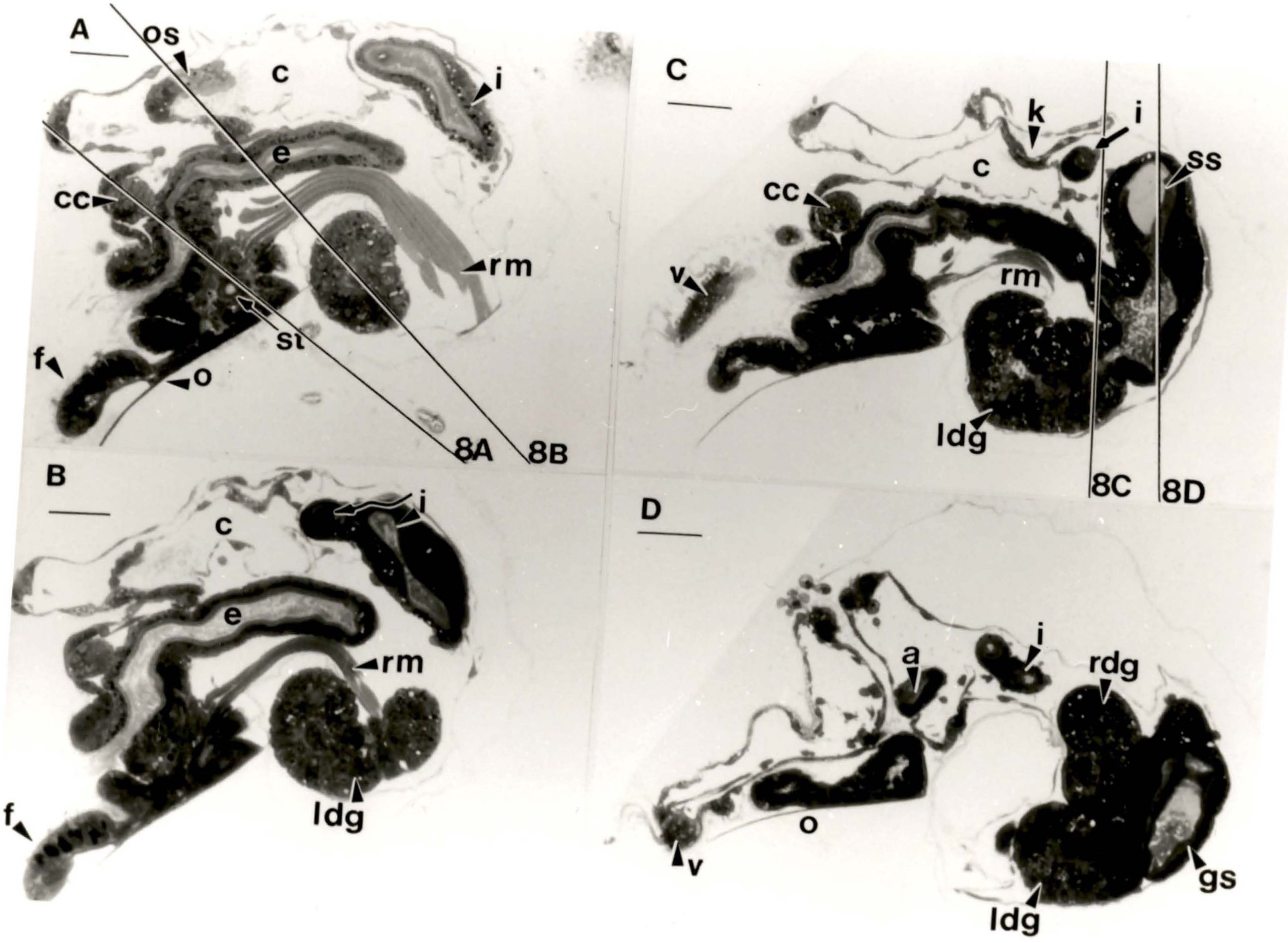
B. Median sagittal section of a veliger passing through the operculum, foot, left digestive gland, retractor muscle, esophagus, intestine, osphradium and mantle cavity.

C. Right side of veliger passing through the operculum, left digestive gland, retractor muscle, esophagus, intestine, style sac region of the stomach and mantle cavity.

D. Far right side of the veliger passing through the operculum, foot, velar lobe, anus, intestine, gastric shield of the stomach and right digestive gland.

Explanation of lettering

a = anus
c = mantle cavity
cc = cerebral commissure
ldg = digestive gland
e = esophagus
f = foot
gs = gastric shield
i = intestine
k = kidney
o = operculum
os = osphradium
rdg = right digestive gland
rm = retractor muscle
ss = style sac
st = statocyst
v = velum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gs

Figure 8. Series of cross sections of *P. lewisii.*

This series of cross sections was cut from anterior to posterior regions. The lines of section shown in Figure 7 correspond to these photographs. Emergent veliger of *P. lewisii*. Epon. One micrometer. Richardson's stain.

A. Anterior region of the veliger sectioned through the operculum, velum, statocysts, esophagus, cerebral commissure, mantle cavity and mantle epithelia. Scale bar = 10 µm.

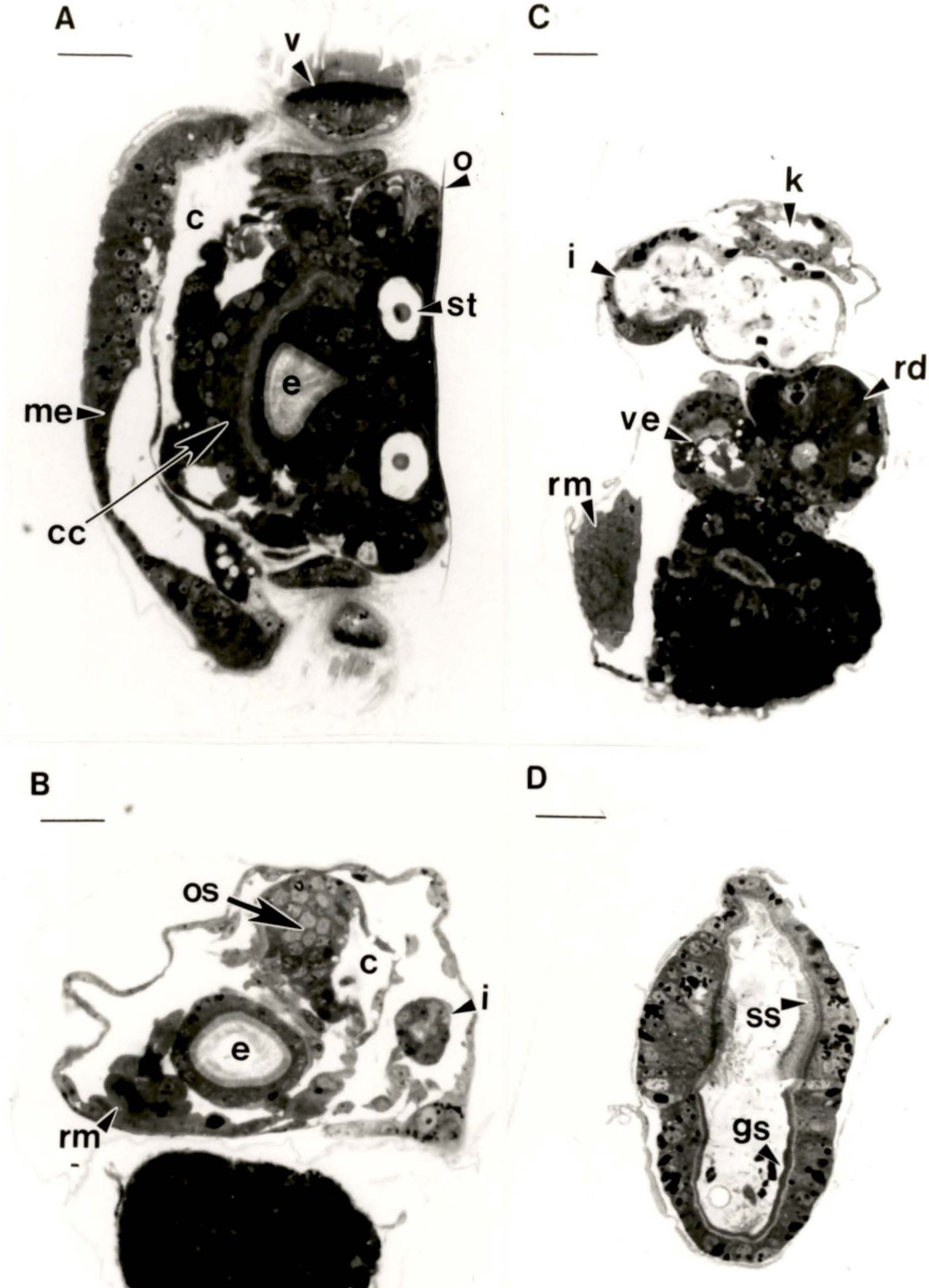
B. Mid-anterior region of the veliger sectioned through the left digestive gland, esophagus, osphradium and associated ganglion, intestine, mantle cavity and retractor muscle. Scale bar = 20 µm.

C. Mid-posterior of the veliger sectioned through the right digestive gland, valve of the esophagus, intestine, secondary kidney and retractor muscle. Scale bar = 20 µm.

D. Posterior region of the passing through the gastric shield and style sac regions of the stomach. Scale bar = 20 µm.

Explanation of lettering

c = mantle cavity
cc = cerebral commissure
ldg = left digestive gland
e = esophagus
gs = gastric shield
i = intestine
k = kidney
me = mantle epithelium
o = operculum
os = osphradium
rdg = right digestive gland
rm = retractor muscle
ss = style sac
st = statocysts
v = velum
ve = valve of esophagus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The rest of the velar epithelium is formed by squamous cells that are underlain by muscle cells (Figure 9A). In emergent veligers, the muscle cells from conspicuous tracts that extend above and beneath the esophagus and connect with the larval retractor muscle. As the velar lobes divide to form the 4 lobe velum, the muscle tracts serving them separate to maintain dorsal and ventral muscular control for each lobe.

Foot

Ultimately, the foot of naticid veligers consists of both an anterior propodium and a posterior metapodium. The hatching stage veligers of *P. lewisii* and *Natica* sp. possess only the metapodial rudiment (Figures 2B and 2C). At this stage the metapodium is a small symmetrical structure with an oval operculum attached to its dorsal surface. The edges of the operculum extend well beyond the foot (Figure 9B). The epidermis of the metapodium consists mainly of non-ciliated, cuboidal epithelial cells, but a tract of ciliated cells extends down the midline of the foot. Intrinsic muscle cells underlie the pedal epithelium.

Two clusters of epidermal glandular cells are present on the metapodial rudiment of hatching larvae. A cluster of multicellular glandular cells, containing purple staining granulated material as stained with Richardson's stain, opens into the midline of the foot (Figure 9B). A single pair of purple staining glandular cells are located on each side of the base of the foot (Figure 9B).

Figure 9. Development of the velum and foot.

A. Transverse section demonstrating velar muscle tract leading to the tips of the velar lobe. This muscle (arrow) extends to the retractor muscle that lies along the esophagus. Veliger of *P. lewisii*. 10 day. Epon. One micrometer. Richardson's stain. Scale bar = 25 µm

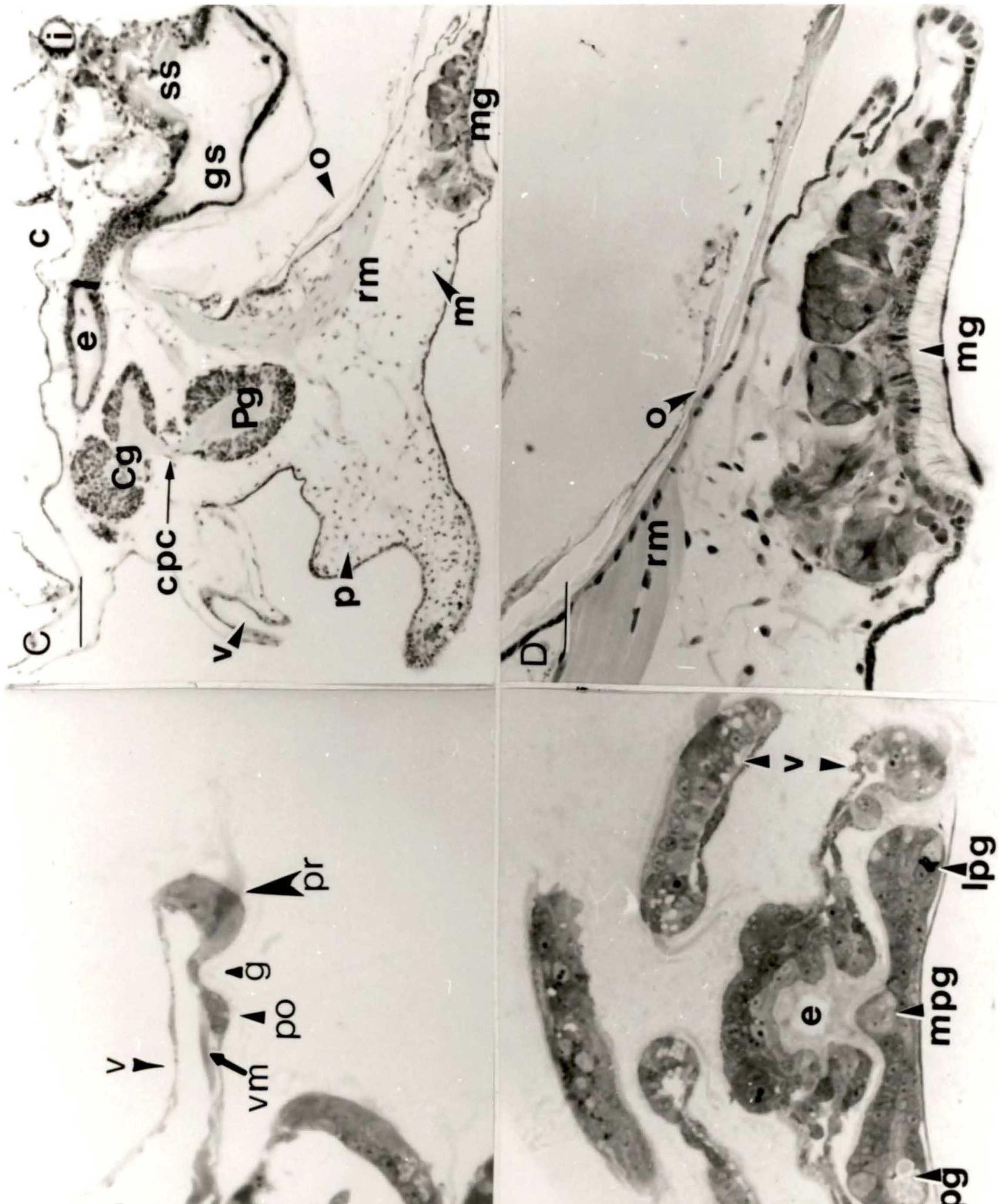
B. Frontal section showing midline and lateral unicellular glandular cells in the foot. Emergent veliger of *P. lewisii*. Epon. One micrometer. Richardson's stain. Scale bar = 20 µm

C. Longitudinal section of the foot showing regional differentiation and the cerebro-pedal connective. Veliger of *P. lewisii*. 110 day. JB4. Four micrometers. Histochemical staining for esterase. Scale bar = 40 µm

D. Enlargement of the multicellular glandular cells within the metapodium (enlarged from Figure C) of the veliger of *P. lewisii*. Ciliated epithelial cells line the ventral surface of the metapodium. The retractor muscle is attached to the cells underlying the operculum. 110 day. JB4. Four micrometers. Histochemical staining for esterase. Scale bar = 10 µm

<u>Explanation of lettering</u>

c = mantle cavity
cpc = cerebro-pedal connective
Cg = cerebral ganglion
e = esophagus
g = groove
gs = gastric shield
i = intestine
lpg = lateral pedal gland
m = metapodium
mg = metapodium gland
mpg = midpedal gland
o = operculum
p = propodium
Pg = pedal ganglion
po = post-oral band of ciliated cells
pr = pre-oral band of ciliated cells
rm = retractor muscle
ss = style sac
v = velum
vm = velar muscle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In post-hatching veligers, the metapodium enlarges to cover the operculum through proliferation of the pedal epithelial and glandular cells. The increase in foot epithelium also produces the propodial rudiment (Figure 3C), a ciliated protuberance at the anterior end of the foot. Additional glandular cells differentiate within both the propodial and metapodial regions of the foot (Figure 9D). The ducts of these open onto the sole of the foot. During the post-hatching larval stage, intrinsic pedal musculature becomes an elaborate, interconnected network throughout the pedal hemocoel (Figure 9D).

Muscular system

Muscle systems present in the emergent veliger of *P. lewisii* are the larval retractor muscle and subepidermal intrinsic muscles.

In the emergent veliger, the larval retractor muscle is slender, but it undergoes extensive growth during pelagic development. The origin of the retractor muscle is on the epithelium lining the inner wall of the shell to the left of the mid-sagittal plane (Figures 7A, 10A and 10B). The muscle tract extends forward along the left side of the esophagus then splits into three branches. Two branches insert on the epithelia of the paired velar lobes and the third extends into the foot and head region.

In the post-hatching veliger, the pedal tract of the retractor muscle enlarges dramatically. Fibers of this tract insert on the epithelium underlying the operculum (Figure 10C). Figure 10D shows a portion of the massive pedal tract of a pre-metamorphic veliger of *Natica* sp. The tract is intimately associated with the esophagus before entering the foot. In addition, the attachment plaque of the retractor muscle migrates anteriorly along the left wall of the shell during larval development. This migration, together with the orthostrophic coiling of the growing protoconch II, places the origin of the retractor muscle on the columella, or central coiling axis, of the shell (Figure 10C).

Intrinsic muscle fibers from an extensive network within the foot, the velar lobes and the mantle. The intrinsic musculature is connected to distal fibers of the larval retractor muscle.

Figure 10. Development of the muscular system of *P. lewisii.*

A. Cross section showing the insertion of the retractor muscle on the epithelium lining the shell and a more distal region of the muscle as its fibers spread around the esophagus. Cilia on the cells of the osphradium extend into the mantle cavity. The osphradial ganglion lies immediately behind the osphradium. Veliger of *P. lewisii.* 10 days. Epon. One micrometer. Richardson's stain. Scale bar = 25 μm

B. Cross section showing the trunk of the retractor muscle and its origin on the left wall of the shell. Veliger of *P. lewisii.* 10 days. Epon. One micrometer. Richardson's stain. Scale bar = 25 μm

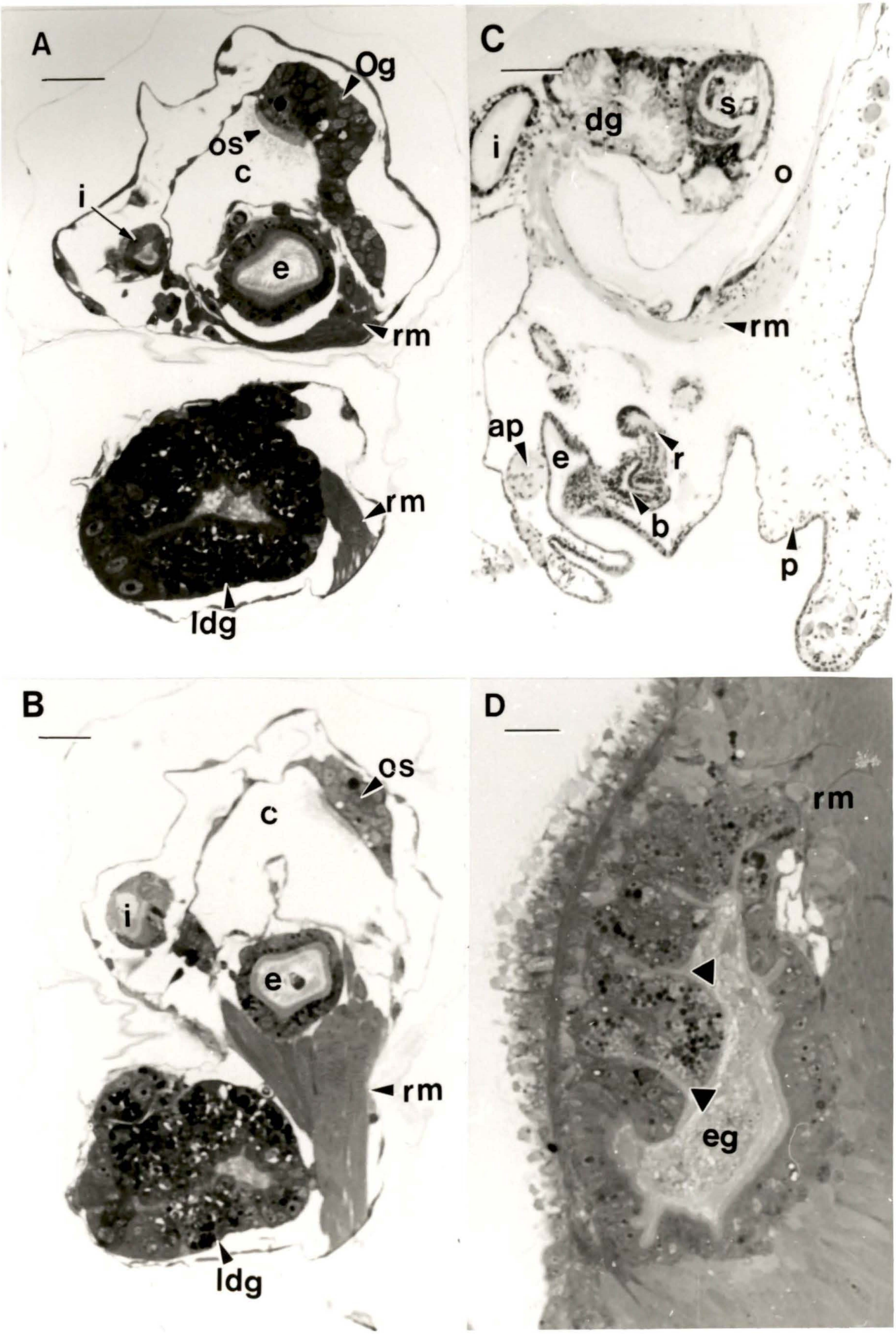
C. Longitudinal section showing retractor muscle extending from the operculum to its basal attachment on the columella of the shell. Intrinsic muscle fibers underlie the epidermis of the foot. Veliger of *P. lewisii.* 110 days. JB4. Four micrometers. Histochemical staining for esterase. Scale bar = 40 μm

D. Enlargement of a frontal section showing the extensive development of the retractor muscle around the esophagus. Arrowheads indicate folds of the esophageal gland. Veliger of *Natica* sp. 107 days. Epon. One micrometer. Richardson's stain. Scale bar = 20 μm

<u>Explanation of lettering</u>

ap = apical organ
b = buccal apparatus
c = mantle cavity
dg = digestive gland
e = esophagus
eg = esophageal gland and esophagus
i = intestine
ldg = left digestive gland

o = operculum
os = osphradium
Og = osphradial ganglion
p = propodium
r = radula
rm = retractor muscle
s = stomach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Mantle cavity

In emergent veligers of *P. lewisii* and *Natica* sp., the mantle cavity is wide and shallow, although it is deeper on the right side than the left (Figure 8B). However, during post-hatching development the mantle cavity enlarges dramatically. Eventually, the post-hatching larva demonstrates a mantle cavity that resembles that of the adult containing the osphradium, ctenidium and hypobranchial gland.

Osphradium

In emergent veligers, the osphradium is located close to the dorsal midline (Figure 8B). The epithelium of the osphradium is composed of columnar cells with long cilia on their apical surface. The basal surfaces of these cells connect with the osphradial ganglion (Figure 10A).

In post-hatching veligers, the cells of the osphradium proliferate but the structure remains close to the anterior region of the mantle (Figure 7A). While the cells projecting into the mantle cavity remain lined with cilia, underlying cells multiply and the inner region eventually consists of numerous cuboidal cells (Figure 11A). The osphradium develops progressive enfolding as it meets with the gill (Figure 11B).

Figure 11. Development of the mantle cavity organs: gill, osphradium and hypobranchial gland.

A. Transverse section demonstrating the osphradium and ctenidium on roof of mantle cavity. Veliger of *Natica* sp. 107 days. Epon. One micrometer. Richardson's stain. Scale bar = 20 µm.

B. Transverse section showing the folding of the osphradium as it merges with the gill filaments. The hypobranchial gland is formed by cells with a translucent appearance. The blood sinuses lie inside the gill filaments. Veliger of *Natica* sp. 107 days. Epon. One micrometer. Richardson's stain. Scale bar = 20 µm.

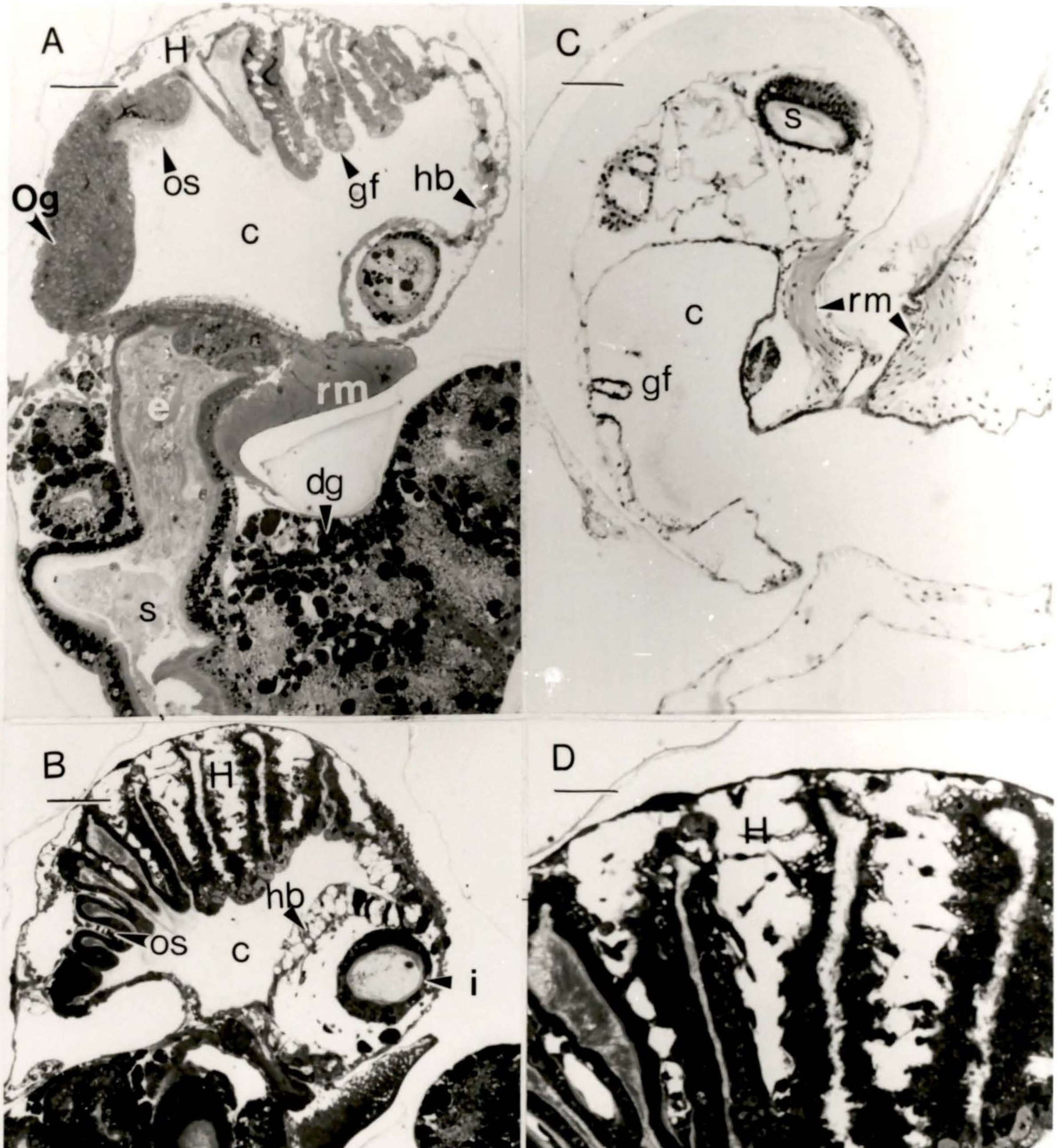
C. Longitudinal section showing outgrowth of a gill filament on roof of mantle cavity. Veliger of *P. lewisii.* 110 days. JB4. 4 micrometers. Histochemical stains for esterase. Scale bar = 40 µm.

D. Enlargement of the gill filaments. The arrowhead points to the mucus cells on the tip of the gill filaments. The arrow indicates the hypobranchial gland situated dorsal to the intestine. Veliger of *Natica* sp. 107 days. Epon. One micrometer. Richardson's stain. Scale bar = 10 µm.

Explanation of lettering

c = mantle cavity
dg = digestive gland
e = esophagus
gf = gill filament
hb = hypobranchial gland
H = hemocoel

i = intestine
os = osphradium
Og = osphradial ganglion
rm = retractor muscle
s = stomach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Gill

Eventually naticid larvae develop a single gill to oxygenate their blood. In emergent veligers, gas exchange probably occurs by diffusion across the velar epithelium.

The gill develops from an epithelial thickening near the osphradium late in post hatching veligers. These epithelial lobes differentiate and evaginate into longitudinal folds composed of cuboidal cells (Figure 11C). In the pre-metamorphic veliger of *Natica* sp., the lobes, or gill filaments, are located on the left side of the mantle cavity, to the right of the osphradium and extend over to the right side. The epithelium of the gill becomes ciliated and pseudocolumnar and it encloses the blood sinuses of the mantle skirt. Glandular cells containing large granulated vacuoles differentiate on the tips of the gill leaflets (Figure 11D).

Hypobranchial gland

The hypobranchial gland differentiates from an epidermal thickening within the posterior region of the mantle cavity during late larval development. The cells acquire a translucent appearance as they fill with secretory product. In the pre-metamorphic veliger of *Natica* sp., the hypobranchial gland lies near the anal opening (Figure 11B).

Digestive system

The series of sections in Figure 7 and the sketch in Figure 12A show the basic design of the gut of planktotrophic veliger larvae. The gut has three components. The foregut extends posterior from the mouth to the esophageal-stomach junction. The midgut is composed of a stomach and left and right digestive glands, located ventral and dorsal to the stomach and hindgut. The esophagus and digestive glands open into the ventral portion of the stomach. The hindgut, or intestine, leaves the dorsal border of the stomach, curves to the right and extends anteriorly to open into the right side of the mantle cavity. In naticid gastropods, these 3 divisions undergo different degrees of elaboration during planktotrophic development (Figure 12B).

Foregut

In emergent veligers, scattered yolk particles are present in the tissues of the gut. At this early stage, the wall of the esophagus is formed by ciliated cells and occasional unicellular gland cells, or mucocytes (Figure 13A). The mucocytes are columnar cells with slightly granular cytoplasmic components and prominent nuclei at the basal end. The rudiment of the buccal apparatus is represented by a slight thickening of the ventral wall of the anterior esophagus.

Post-hatching veligers retain a ciliated esophagus (Figure 13B) with mucocytes. A positive PAS reaction indicates that glycoproteins line the length of the esophageal tract. These glycoproteins are likely the product of the mucocytes.

Figure 12. Sketch of the developmental changes of the digestive tract.

The foregut is composed of the mouth, esophagus and esophagus gland. The midgut is formed by the stomach and digestive glands. The hindgut consists of the intestine and anus.

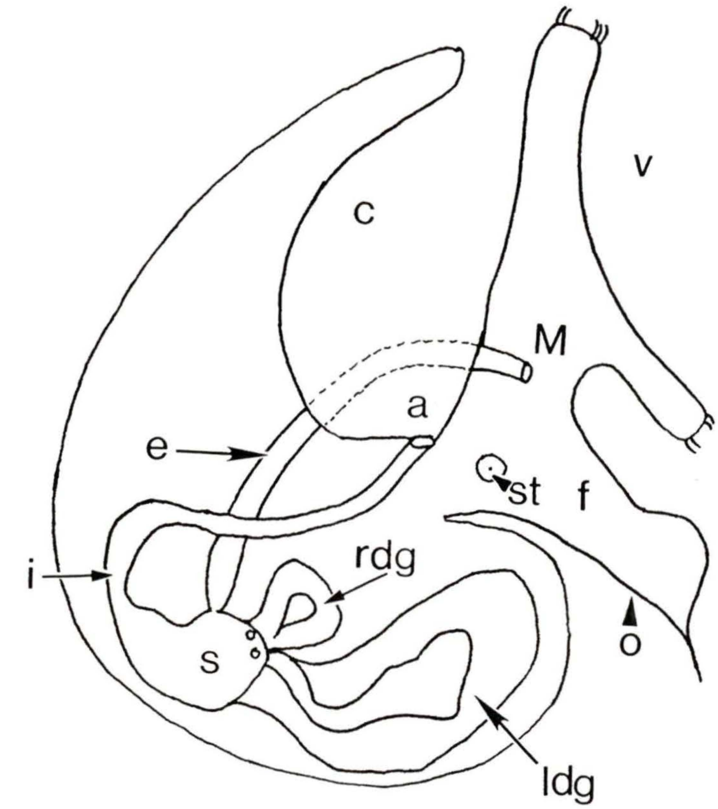
A. Sketch of digestive system in an emergent veliger based on emergent veliger of *P. lewisii*.

B. Sketch of digestive system in a pre-metamorphic veliger based on post-hatching veligers of *P. lewisii* and *Natica* sp.

Explanation of lettering

a = anus
b = buccal apparatus
Bo = boring organ
c = mantle cavity
e = esophagus
eg = esophageal gland
f = foot
i = intestine
ldg = left digestive gland
M = mouth
o = operculum
r = radula
rdg = right digestive gland
s = stomach
st = statocyst
v = velum

A



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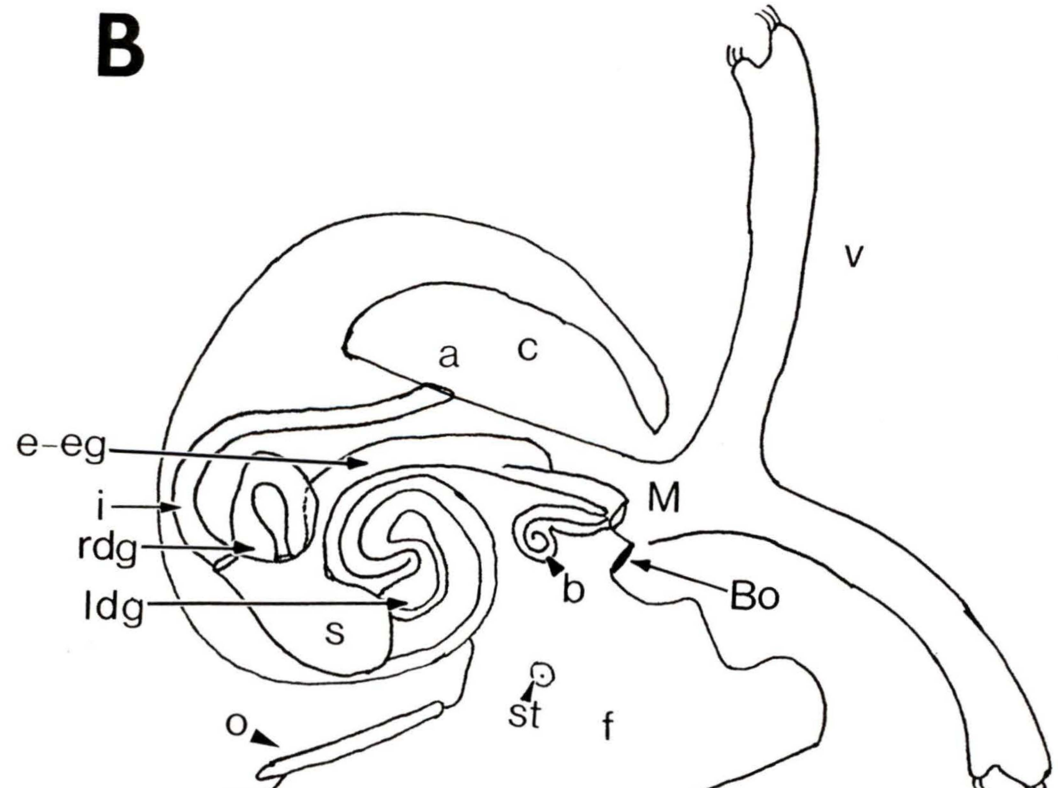

Figure 13. Development of esophagus, radula and proboscis rudiment.

A. Frontal section showing the buccal cavity and esophagus. Emergent veliger of *P. lewisii*. Epon. One micrometer. Richardson's stain. Scale bar = 25 µm.

B. Oblique transverse section showing the buccal cavity and esophagus lined by ciliated cells and unicellular gland cells. The cerebral commissure lies above the esophagus while the statocyst lies between the pedal and pleural ganglia. Veliger of *P. lewisii.* 41 days. Epon. One micrometer. Richardson's stain. Scale bar = 50 µm.

C. Longitudinal section showing the formation of the radula and proboscis rudiment beneath the buccal cavity of the foregut. Veliger of *P. lewisii.* 110 days. JB4. 4 micrometers. Histochemical stains for esterase. Scale bar = 30 µm.

D. Frontal section showing the protrusion of the radula membrane into the lumen of the future proboscis. The paired tentacles extend above the head. Veliger of *Natica* sp. 107 days. Epon. One micrometer. Richardson's stain. Scale bar = 10 µm.

Explanation of lettering

ap = apical organ
c = mantle cavity
cc = cerebral commissure
e = esophagus
f = foot
o = operculum
Pg = pedal ganglion
Plg = pleural ganglion
Pr = proboscis rudiment
r = radula
rm = retractor muscle
st = statocyst
t = tentacle
v = velum

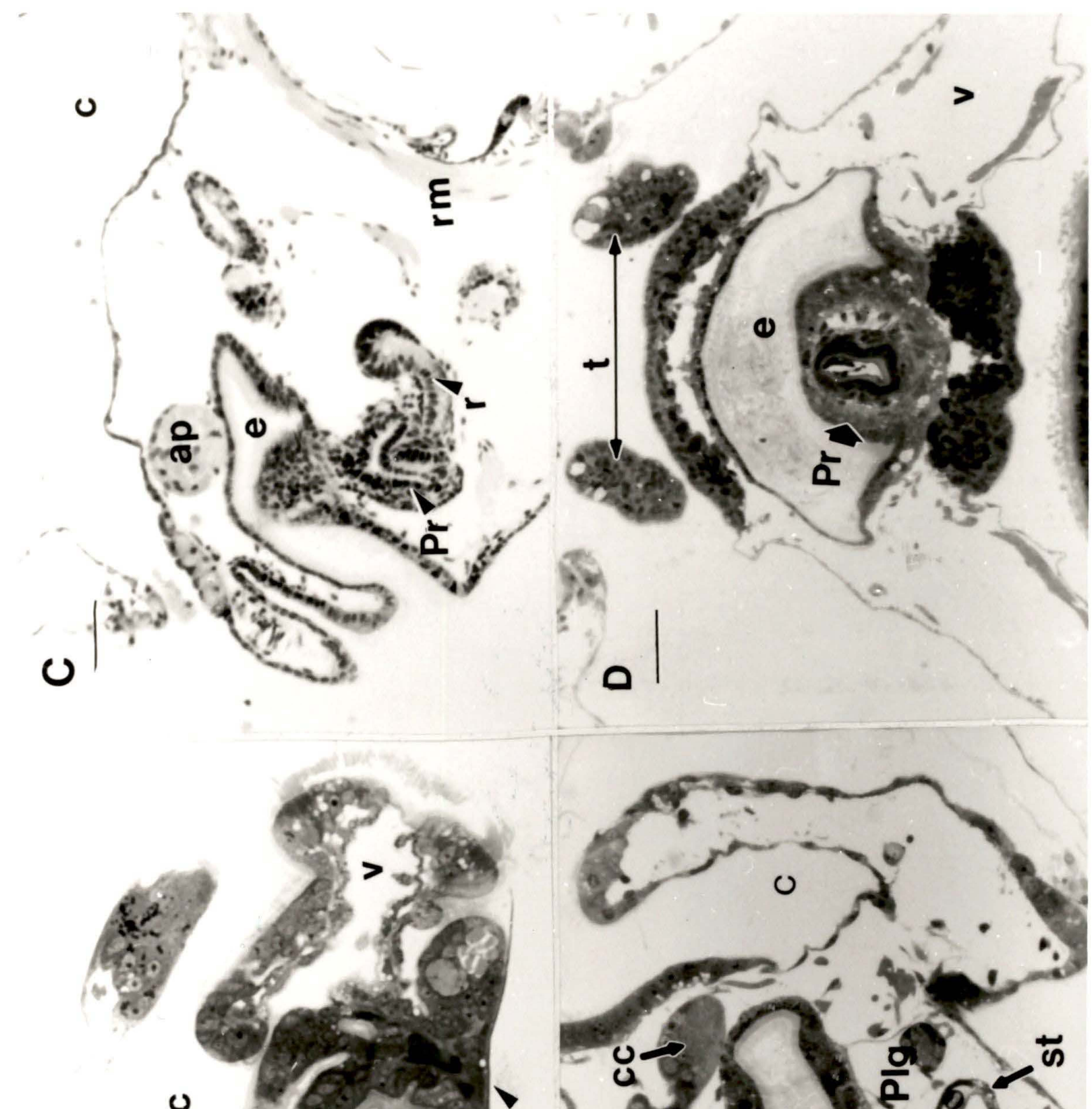
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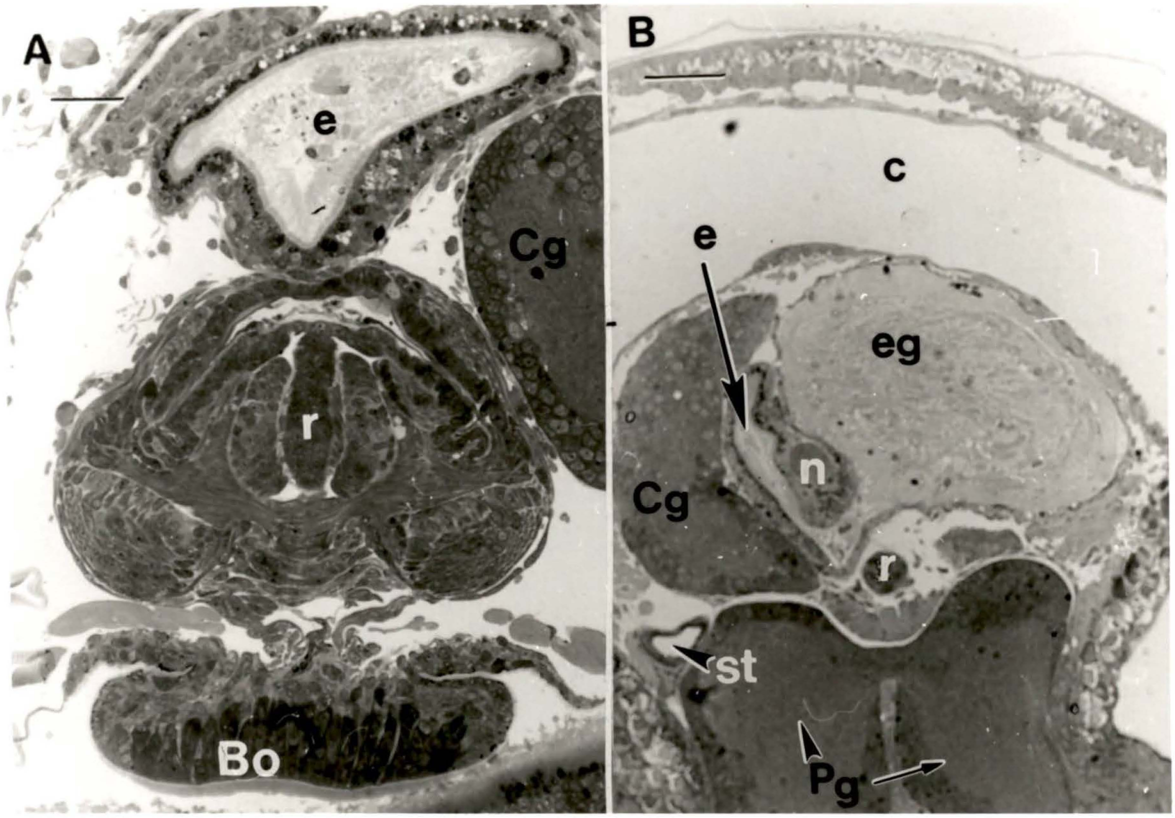
Figure 14. Development of the foregut (continued).

A. Frontal section showing the morphology and differentiation of the radula and buccal musculature. The rudiment of the accessory boring organ protrudes below the radular apparatus. Veliger of *Natica* sp. 107 days. Epon. One micrometer. Richardson's stain. Scale bar = 10 µm.

B. Frontal section showing the undifferentiated lumen on the esophageal gland and the connection with the esophagus. The supraoesophageal-visceral connective (n) lies within a groove between the esophageal gland and esophagus. Veliger of *Natica* sp. 107 days. Epon. One micrometer. Richardson's stain. Scale bar = 10 µm.

Explanation of lettering

Bo = boring organ
c = mantle cavity
Cg = cerebral ganglia
e = esophagus
eg = esophageal gland
n = nerve tract
Pg = pedal ganglia
r = radula
st = statocyst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Radular apparatus

In post-hatching veligers, the prospective radular sac invaginates from the ventral wall of the esophagus (Figure 13C). The radular rudiment acquires a high degree of complexity by the end of the larval stage. In pre-metamorphic veligers the radular begins to protrude into the proboscis rudiment (Figure 13D) and it includes an odontophore, radular teeth and a complex musculature (Figure 14A). The radular apparatus lies immediately anterior to the cerebral-pleural-buccal ganglia complex.

Proboscis

The acremboic proboscis of the adult naticid is not evident in emergent veligers of *P. lewisii* and *Natica sp.*. In post-hatching veligers, the future proboscis differentiates beneath the floor of the larval esophagus (Figures 13C and 13D). The radular ribbon runs into the lumen of the proboscis rudiment, but this lumen does not have a distal opening before metamorphosis. The lumen of the proboscis rudiment, in pre-metamorphic larvae, is lined with cuboidal epithelium surrounded by muscle fibers.

Accessory boring organ

The accessory boring organ ultimately lies below the proboscis opening in naticid snails. This structure begins to differentiate late in larval morphogenesis as a circular protrusion of pseudocolumnar cells located ventral to the oral opening in the pre-metamorphic veligers of *Natica* sp. (Figure 14A).

Esophageal gland

The esophageal gland differentiates late in larval morphogenesis. In emergent veligers, the dorsal surface of the esophageal tube has a slight thickening, which is the presumptive rudiment of the esophageal gland. The thickening remains unmodified in the post-hatching veliger until shortly before metamorphosis. The 110-day veliger of *P. lewisii* revealed no differentiation of the esophageal gland thickening, through either cellular morphogenesis or histochemical staining (Figure 13C).

In the pre-metamorphic veliger of *Natica* sp., a thin epithelium of the esophageal gland forms an elongated pouch off the right lateral surface of the esophagus (Figure 14B). The esophageal gland merges with the esophagus as both extend toward the stomach (Figure 10D).

Midgut

The larval stomach lies in the posterior region of the veliger larvae of *P. lewisii* (Figures 7C and 7D) and *Natica* sp. At its antero-ventral extremity it receives the esophagus and the ducts of the left and right digestive glands (Figure 15A). During most of larval life, a distinctive ciliary valve structure is located at the junction of the esophagus and stomach (Figure 15B).

From the time of hatching and throughout planktonic development, the stomach consists of ventral and dorsal chambers each having distinctive histological characteristics. The anterior portion of the ventral stomach consists of densely ciliated cells and constitutes a collection area or vestibule. Ducts from the digestive glands and

Figure 15. Development of midgut and hindgut.

A. Frontal section showing the darkly stained cells of the left and right digestive glands and the extension of the intestine toward the right side of the body. The adult kidney lies dorsal to the intestine. Veliger of *P. lewisii.* 6 days. Epon. One micrometer. Richardson's stain. Scale bar = 20 μm.

B. Frontal section showing the ciliary valve at the junction between the esophagus and the stomach. The intestine lies on the left side of the body. Veliger of *P. lewisii.* 10 days. Epon. One micrometer. Richardson's stain. Scale bar = 30 μm.

C. Transverse section indicating the vestibule where the ducts exit the digestive glands and enter the stomach. Veliger of *P. lewisii.* 41 days. Epon. One micrometer. Richardson's stain. Scale bar = 50 μm.

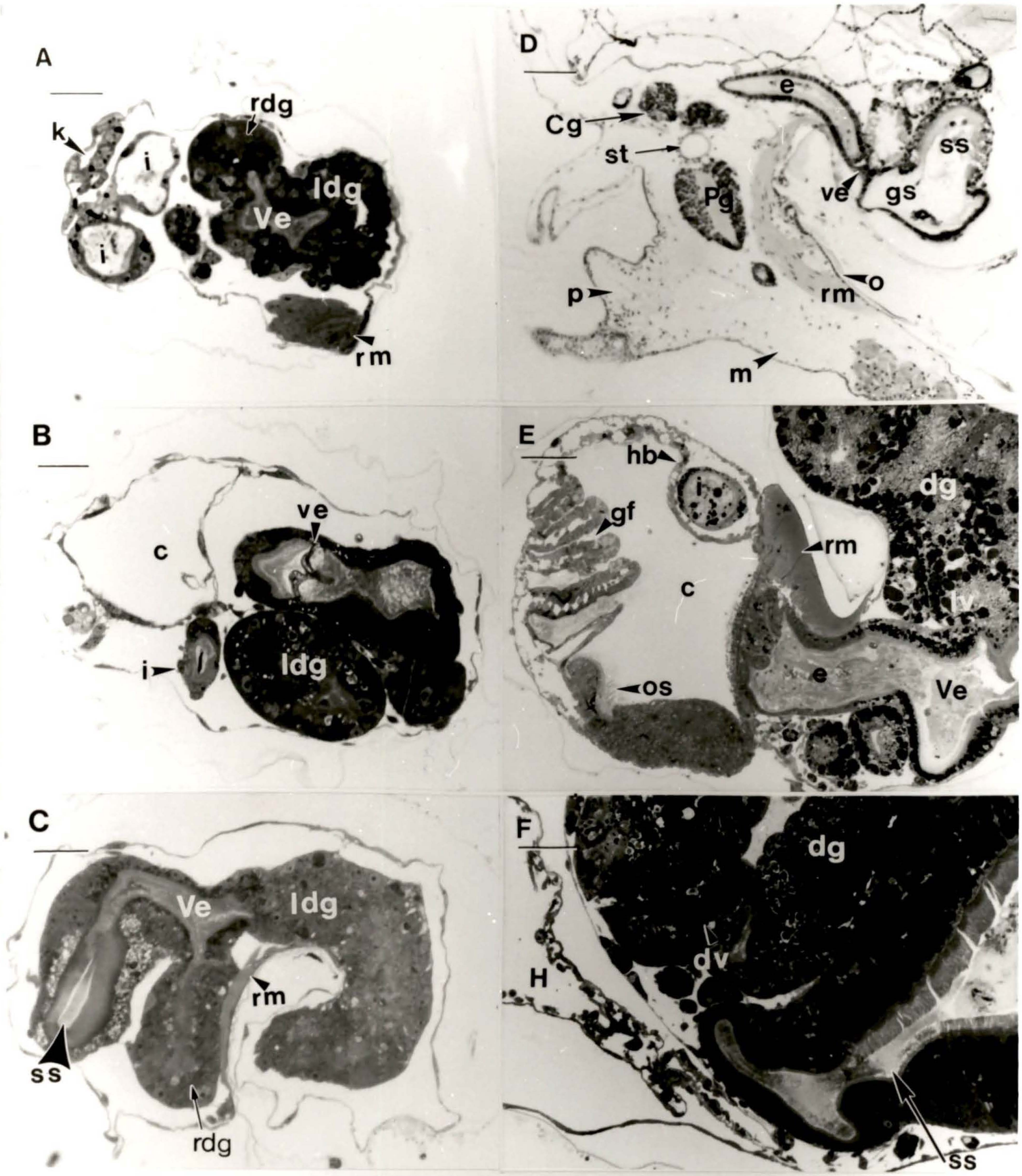
D. Longitudinal section showing the connection of the esophagus with the gastric shield and style sac of the stomach. The cell bodies in the cortex and the nerve tracts in the medulla of the pedal ganglia are visible below the statocyst. Veliger of *P. lewisii.* 110 days. JB4. Four micrometers. Histochemical stains for phosphatase and esterase. Scale bar = 40 μm.

E. Frontal section showing the junction of the esophagus with the stomach and cells of the digestive glands. The osphradium and the gill filaments project into the mantle cavity. Veliger of *Natica* sp. 107 days. Epon. One micrometer. Richardson's stain. Scale bar = 20 μm.

F. Enlargement of frontal section showing the ciliated style sac of the stomach and the lipids stored in the cells lining the stomach. Veliger of *Natica* sp. 107 days. Epon. One micrometer. Richardson's stain. Scale bar = 2 μm.

<u>Explanation of lettering</u>

c = mantle cavity
Cg = cerebral ganglia
dg = digestive gland
dv = densely staining vesicles
e = esophagus
gf = gill filaments
gs = gastric shield
hb = hypobranchial gland
H = hemocoel
i = intestine
k = kidney
ldg = left digestive gland
lv = lipid vesicles
m = metapodium
p = propodium
o = operculum
os = osphradium
Pg = pedal ganglia
Plg = pleural ganglia
rdg = right digestive gland
rm = retractor muscle
ss = style sac
st = statocyst
ve = valve in esophagus
Ve = vestibule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esophagus empty their contents into the vestibule (Figures 15A and 15C). Epithelium in this region is cuboidal with large vacuoles filled with lipid or yolk granules in hatching veligers.

The remainder of the ventral stomach is lined by the gastric shield (Figures 7D, 8D and 15D). The gastric shield of the 110 day veliger of *P. lewisii* showed sparse alkaline phosphatase activity. Esterase enzyme, which has been found in the gastric shield region of adult *P. lewisii* (Reid and Friesen, 1980), was not detected in these larvae, although mucoproteins are present as indicated by a positive PAS reaction.

The dorsal area of the stomach, also known as the style sac, is lined by epithelium composed of densely ciliated cells (Figures 7C, 8D and 15D).

Emergent veligers have a small right digestive gland and large left digestive gland that are connected to the vestibule of the ventral stomach. At hatching these small sac-like structures contain cuboidal cells that are dense with lipid and yolk reserves (Figure 15A).

In post-hatching veligers both digestive glands are composed of very large, sparsely ciliated digestive cells (Figure 15E). The digestive cells contain phagosomes and large spherical lipid inclusions (Figure 15F). The cells of the digestive glands stained negative for the histochemical tests of alkaline and acid phosphase, esterase and PAS reactions.

The ciliary valve of the esophagus-stomach junction is no longer present in pre-metamorphic veligers of *Natica* sp. (Figure 15E).

Hindgut

The intestine exits the style sac region of the stomach as a tube formed by ciliated cuboidal epithelium (Figure 15A). This tube curves broadly to the right and then runs anteriorly to open into the mantle cavity.

In post-hatching veligers, the intestine enlarges slightly before the anal opening, forming a rectal region. The esterase enzyme is extracellular and interspersed around the cilia of the intestine. No glands are associated with the anal region.

Nervous system and sensory structures

Paired statocysts are present within the base of the foot of hatching veligers (Figure 7A and 16A). These gravity receptors are visible before the larvae hatch. Paired eyespots are also present at hatching (Figure 2B). Each eye is located next to the ipsilateral cerebral ganglion and consists of a collection of cells with darkly stained granules arranged in a hemi-spherical shape around a lens.

Tentacles begin to develop during early post-hatching development as cylindrical outgrowths of epithelium lying dorsal to the cerebral ganglia (Figure 16B). Development of the osphradium within the mantle cavity has been described previously.

The emergent veligers of *P. lewisii* and *Natica* sp. have cerebral ganglia located on the lateral region of the distal esophagus (Figure 16C). These ganglia are connected by a cerebral commissure that extends over the anterior region of the esophagus (Figures 7A, 16A and 16C). Rudiments of the pedal ganglia can also be distinguished within the base of the foot of hatching veligers.

Figure 16. Development of the nervous system and sensory structures.

A. Enlargement of a frontal section showing the paired statocysts containing statoliths above the operculum. Emergent veliger of *P. lewisii*. Epon. One micrometer. Richardson's stain. Scale bar = 10 µm.

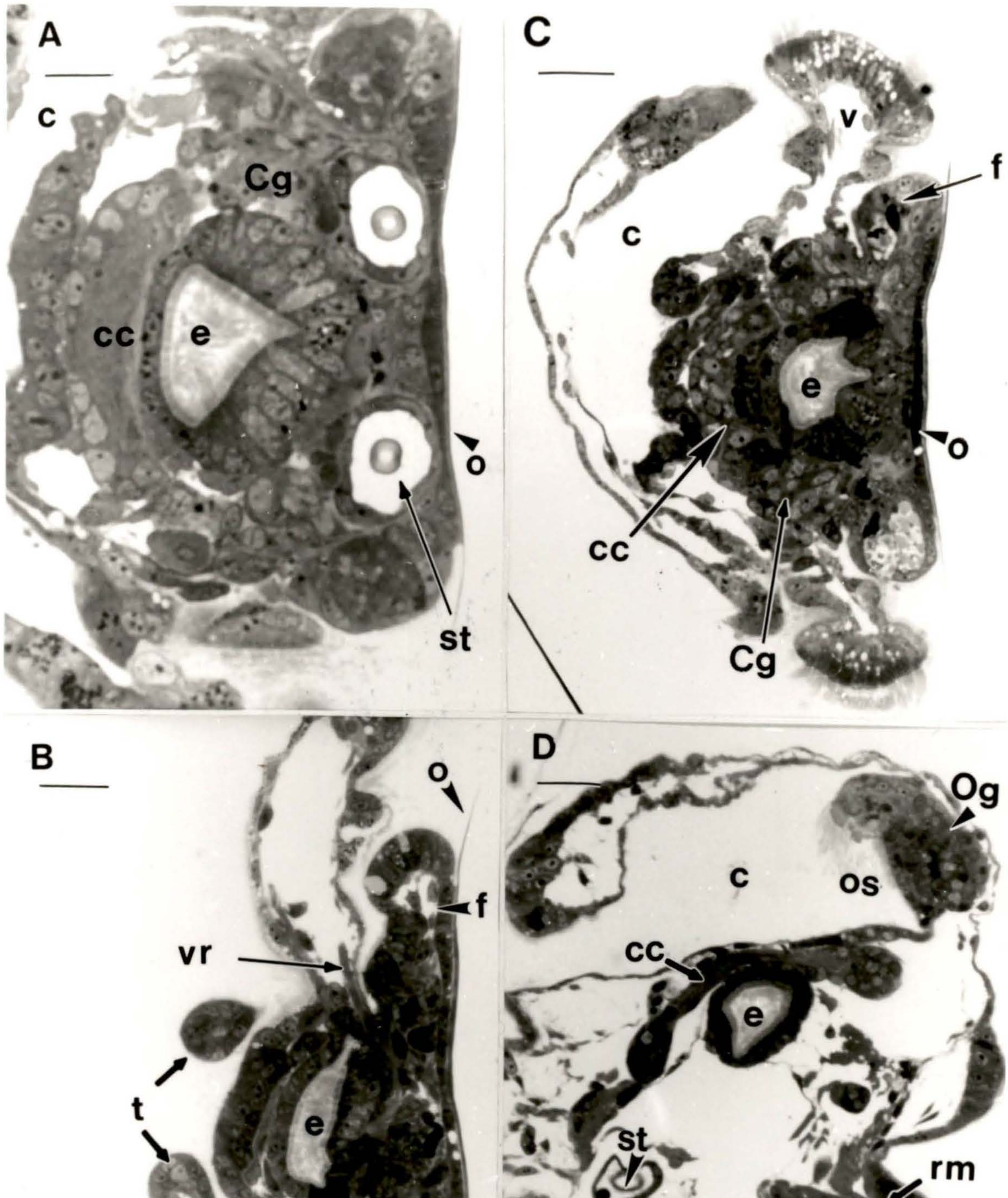
B. Oblique frontal section showing paired tentacles situated above the mouth opening on the anterior region. Veliger of *P. lewisii.* 10 days. Epon. One micrometer. Richardson's stain. Scale bar = 30 µm.

C. Oblique frontal section showing the cerebral ganglia on both sides of the esophagus connected by the cerebral commissure. Emergent veliger of *P. lewisii*. Epon. One micrometer. Richardson's stain. Scale bar = 20 µm.

D. Transverse section showing differentiation of the cortex and medulla of the pedal ganglia and connectives to the medial regions of the foot. The osphradial ganglion lies in the dorsal region of the mantle cavity. The cerebral commissure extends over the esophagus. Veliger of *P. lewisii.* 41 days. Epon. One micrometer. Richardson's stain. Scale bar = 50 µm.

Explanation of lettering

c = mantle cavity
cc = cerebral commissure
Cg = cerebral ganglia
e = esophagus
f = foot
o = operculum
Og = osphradial ganglia
os = osphradium
Pg = pedal ganglia
rm = retractor muscle
st = statocyst
t = tentacles
v = velum
vr = velar retractor muscle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The nervous system develops progressively during post-hatching development and eventually resembles that of the adult. The cerebral and pedal ganglia become differentiated into an outer cortex, composed of nerve bodies, and an inner medulla, composed of nerve fibers (Figures 16D and 17A). The number of nerve cells within both pairs of ganglia increase and the ganglia gradually increase in size during the larval stage. The pedal ganglia eventually become the largest ganglia within the larval body. Each pedal ganglion is located on the ventro-lateral face of the respective statocyst (Figure 17B) and has a long connective to the ipsilateral cerebral ganglion (Figure 16D). Accessory ganglionic clusters appear along the nerve tracts extending from the pedal ganglia into the propodium and metapodium (Figure 17B).

In post-hatching veligers, another pair of ganglia, the pleurals, develops dorsal to the statocysts and postero-dorsal to the cerebrals (Figures 17A and 17B). As these ganglia enlarge they also become organized into medullary and cortical regions and eventually fuse with the cerebrals (Figures 17B and 17C).

The buccal ganglia differentiate as the radular sac rudiment begins to evaginate from the wall of the esophagus. These ganglia lie on either side of the radular sac rudiment (Figure 17D) and the buccal commissure extends between the esophagus and the radular sac diverticulum.

As illustrated in Figure 18, the supra- and sub- esophageal ganglia develop posterior to the aggregation of the cerebral and pleural ganglia. The supra-esophageal ganglion connects to the osphradial ganglion. The connections from each of the esophageal ganglia to the respective pleural ganglia are distinguishable dorsal and ventral to the esophagus.

The visceral ganglia are reported to be bilobed in the adult condition, but this is not clear the in veligers. In pre-metamorphic veligers of *Natica* sp., the visceral ganglion is located near the posterior region of the mantle cavity. Connectives extend to the visceral ganglion from the supra-esophageal (Figure 14D) and the sub-esophageal ganglia.

Figure 17. Development of the nervous and sensory system (continued).

A. Longitudinal section illustrating the apical organ, pleural and pedal ganglia. Veliger of *P. lewisii*. 110 days. JB4. Four micrometers. Histochemical staining for alkaline phosphatase. Scale bar = 40 µm.

B. Longitudinal section illustrating fusion of the cerebral and pleural ganglia. The cortex of the buccal ganglia is visible anterior to the pedals. The accessory pedal ganglia demonstrate their connectives to the pedal ganglia. Veliger of *P. lewisii*. 110 days. JB4. Four micrometers. Histochemical staining for esterase. Scale bar = 40 µm.

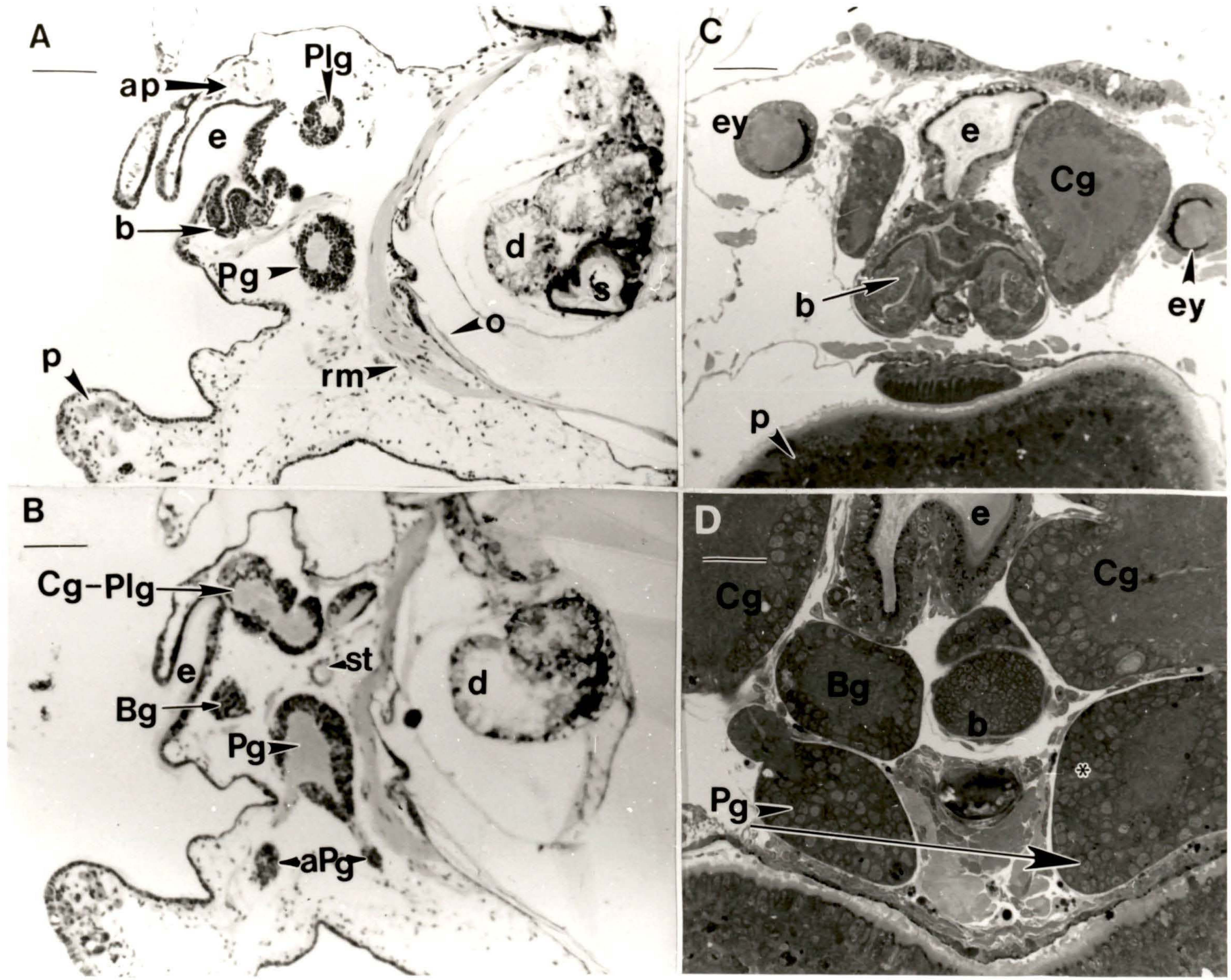
C. Oblique frontal section showing the eyespots and the close association of the cerebral (fused with pleural) and pedal ganglia. Veliger of *Natica* sp. 107 days. Epon. One micrometer. Richardson's stain. Scale bar = 20 µm.

D. Enlargement of an oblique frontal section showing the close association of the cerebral (fused with pleural), buccal and pedal ganglia. The cortex (*) and medulla of one of the pedal ganglion can be distinguished. Veliger of *Natica* sp. 107 days. Epon. One micrometer. Richardson's stain. Scale bar = 10 µm.

<u>Explanation of lettering</u>

ap = apical organ
aPg = accessory pedal ganglia
b = buccal apparatus
Bg = buccal ganglia
Bo = boring organ
Cg = cerebral ganglia
e = esophagus
ey = eye
d = digestive gland

p = propodium
Pg = pedal ganglia
Plg = pleural ganglia
o = operculum
r = radula
rm = retractor muscle
s = stomach
st = statocysts
v = velum
* = cortex of pedal ganglion


A
ap
Plg
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o
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d
aPg
C
ey
e
Cg
b
ey
p
D
e
Cg
Cg
Bg
b
*
Pg

Figure 18. Schematic representation of the developmental changes of the nervous system.

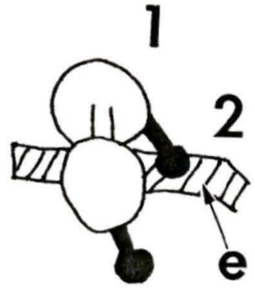
A. Left lateral view of the circumoesophageal ganglia in an emergent veliger of *P. lewisii*. Osphradial ganglia not shown.

B. Dorsal perspective of the nervous system of a pre-metamorphic veliger of *Natica* sp.

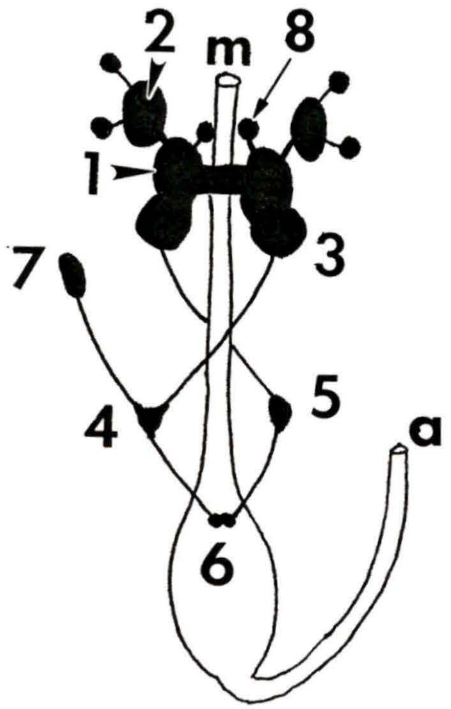
Explanation of lettering

a = anus
e = esophagus
m = mouth
1 = paired cerebral ganglia connected by commissure
2 = paired pedal ganglia with connective to cerebrals
3 = paired pleural ganglia fused with cerebrals
4 = supraoesophageal ganglion with connectives to osphradial, pleural and visceral ganglia
5 = suboesophageal ganglion with connectives to pleural and visceral
6 = visceral ganglion
7 = osphradial ganglion
8 = paired buccal ganglia with connective to cerebrals

A



B



Excretory system

Both the paired larval kidneys and the secondary or adult kidney are present in emergent naticid veligers. The larval kidneys are paired aggregations of cells with vacuolated cytoplasm located on either side of the esophagus. After 6 days these cells become filled with dark granules and are not seen in older veligers.

The secondary or adult kidney is an epithelial sac composed of cells containing intracellular vacuoles and pigmented inclusions (Figures 19A and 19B). It is located close to the adult heart, near the dorso-posterior region of the veligers (Figure 19C and 19D). The adult kidney drains into the right side of the mantle cavity through the nephridiopore (Figure 19A and 19D). A ciliated renopericardial duct runs between the secondary kidney and the pericardium (Figure 19D).

Circulatory system

The larval heart was observed beating in emergent veligers of *P. lewisii*. In one micrometer sections, it can be recognized as the thin, muscularized epithelium that lines the floor of the mantle cavity (Figure 19B).

Shortly thereafter, pulsating tissue of the adult heart was seen in the posterior-dorsal region of the body. The adult heart is surrounded by squamous epithelium of the pericardium (Figure 19C and 19D). In post-hatching veligers, the heart primoridum differentiates into an auricle and ventricle (Figure 19D). The aorta and branches can be distinguished from the body wall epithelium as they extend from the ventricle to supply blood to the visceral mass and the cephalopodium.

Figure 19. Development of excretory and circulatory systems.

A. Frontal section of showing secondary kidney with nephridiopore (arrowhead). Veliger of *P. lewisii*. 10 days. Epon. One micrometer. Richardson's stain. Scale bar = 35 μm.

B. Longitudinal section of showing cells of the kidney rudiment developing in the dorsal region of the hemocoel and epithelium of larval heart (clear arrowheads). Veliger of *P. lewisii.* 15 days. Epon. One micrometer. Richardson's stain. Scale bar = 30 μm.

C. Enlargement of transverse section to illustrate the structure of the adult heart and kidney with the intestine and mantle cavity. Veliger of *P. lewisii.* 41 days. Epon. One micrometer. Richardson's stain. Scale bar = 30 μm.

D. Oblique transverse section showing the differentiated heart and kidney cells. The renal aperture (arrowhead) opens into the mantle cavity from the kidney. The renopericardial duct (arrow) runs from the pericardium into the kidney. Veliger of *Natica* sp. 107 days. Epon. One micrometer. Richardson's stain. Scale bar = 20 μm.

Explanation of lettering

c = mantle cavity
cc = cerebral commissure
e = esophagus
gs = gastric shield
h = heart
i = intestine
k = kidney
ldg = left digestive gland
lm = lumen of digestive gland
prc = pericardium
rm = retractor muscle
o = operculum
s = stomach
ss = style sac
st = statocyst
Ve = vestibule

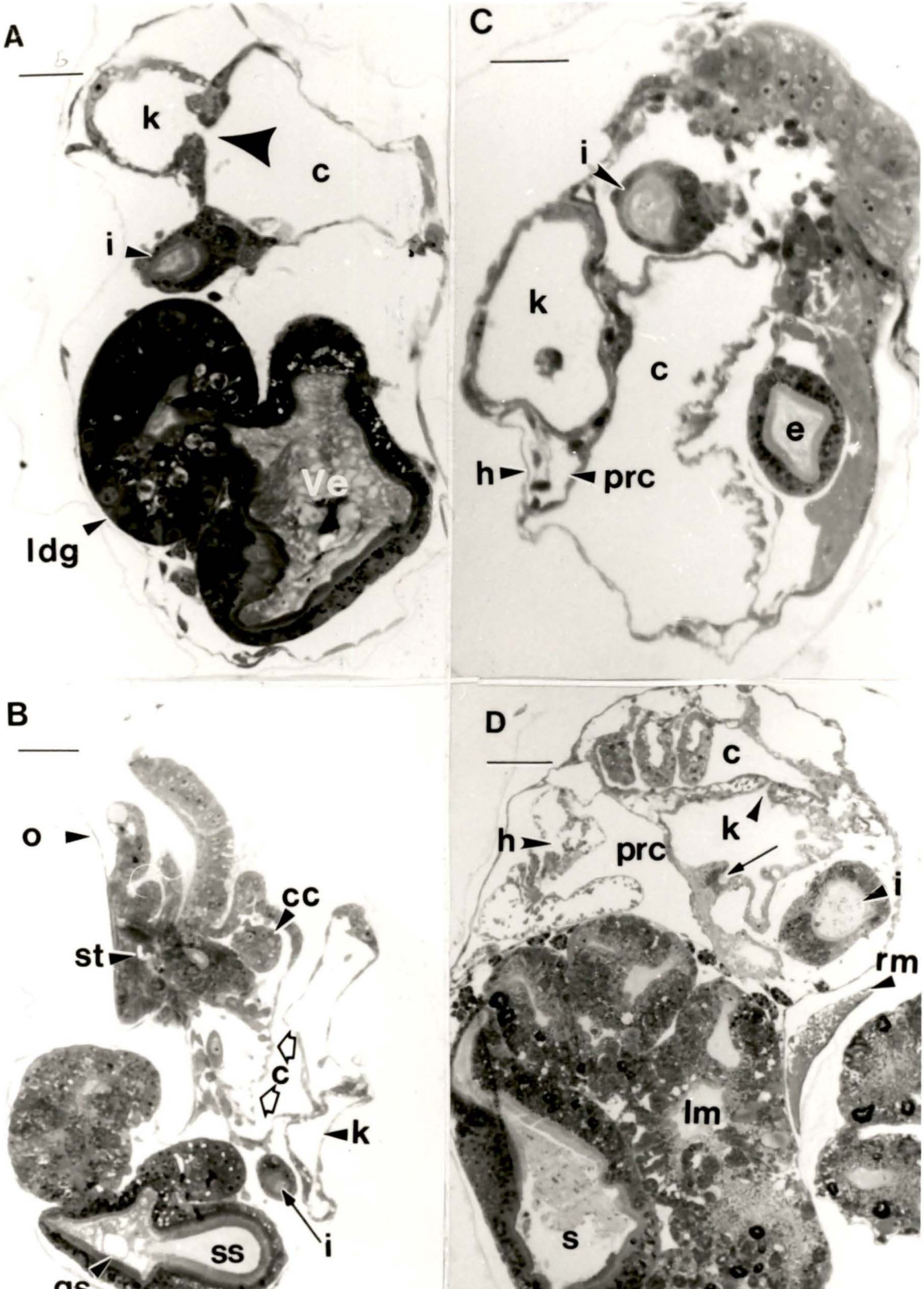

A
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Table 3. Summary of developmental changes in phytoplanktotrophic veligers of naticid gastropods.

	----------------------------*Polinices lewisii*-----		----------*Natica* sp.----------
Stage/ Feature	**Emergent Veliger**	**Post-hatching veliger**	**Crawling juvenile**
shell	protoconch I of *Polinices* is sculptured with puncta, while that of *Natica* is smooth.	striated growth lines form protoconch II	striated growth lines form teleoconch
velum	paired transparent oval lobes	paired bifurcated lobes with pigment on the apex of each lobe	absent
foot	small metapodial region	propodial rudiment forms as metapodial region enlarges	elaborate flaps and extensions on propodium and metapodium
digestive tract-foregut	ciliated mouth, ciliated esophagus	development of buccal complex and esophageal gland	differentiation of proboscis, radula apparatus and esophageal gland
digestive tract - midgut	gastric shield, style sac, left and right digestive glands	enlargement and growth of stomach and digestive glands	gastric shield in stomach lost
digestive tract-hindgut	ciliated intestine, anus	elongation and regional differentiation into rectum	elongation
circulatory	larval heart lies on ventral surface of mantle cavity	adult heart with blood vessels forms above the mantle cavity	adult heart
excretory	larval kidney cells on both sides of the head region	adult kidney forms close to pericardium	no change
respiratory	general epithelium	ctenidium develops	functional ctenidium
muscular	larval retractor muscle with branches to foot and velum	larval retractor with extensions to operculum, propodium	velar musculature lost
nervous	cerebral, pedal, osphradial	pleural, buccal, supra- and sub-esophageal, visceral	no change
sensory	eyespots, apical organ, statocysts	tentacles	apical organ lost

Discussion

Life History Pattern

Both *P. lewisii* and the unidentified species of *Natica* exhibited a long-term larval stage during which energy required for growth and morphogenesis must be derived from feeding on phytoplankton. A small foot, lacking a propodium at the time of larval hatching, a velum with pre- and post-oral ciliary bands and the eventual development of a 4-lobed or 6-lobed velum are characteristic of long-term planktotrophic larvae of many other caenogastropods (Lebour, 1936; D'Asaro, 1965, 1969; Thiriot-Quievreux, 1974; Fretter, 1969; Perron, 1980; Thiriot-Quievreux and Scheltema, 1982).

As a family, the variation seen in naticid developmental patterns tends to be correlated with the size of egg (Table 4). Planktotrophic larvae of naticids develop from eggs that are smaller than naticid eggs that develop directly into juveniles. The small egg size of the directly developing species, *Natica catena*, is an exception to this generalization. However, the encapsulated development of this species is not fueled by endogenous yolk stores, but by ingestion of nurse eggs (Thorson, 1950).

The evidence presented here confirms Giglioli's (1955) report of planktotrophic larvae hatching from small eggs for *P. lewisii*. I cannot yet say how long the pelagic period lasts for *P. lewisii,* but the related species of *Natica* suggests that this period can last up to 4 months. Bernard's (1967) description of a short-lived larva for *P. lewisii* is not supported by my observations. It is possible that *P. lewisii* is capable of two different developmental patterns as developmental variability has been described for a number of other gastropods (Eyster, 1979; Clark and Goetzfried, 1978). Nevertheless, it is also

Table 4. Summary of larval development in naticoidaen gastropods. [1] species with more than one egg in an egg capsule, [2] species with more than one egg in egg space.

Species	Egg diameter (µm)	Protoconch Sculpture	Protoconch Length	Location	Reference
Direct Development					
Amauropsis islandica	750	n/a	n/a	N. Atlantic	Thorson, 1935, 1946
Natica pallida	225	smooth	2 whorls 1250 µm	N. Atlantic	Thorson, 1935, 1946
Natica catena[1]	160	smooth	2.5 whorls 600-700 µm	N. Atlantic	Thorson, 1946; Giglioli, 1955 Lebour, 1936; Fioroni, 1966
Natica clausa	200-225	smooth	1500 µm	N. Atlantic	Thorson, 1935
Natica groenlandica	225	smooth	1500 µm	N. Atlantic	Thorson, 1935
Neverita vesicalis	300	fine spiral lines	1000 µm	NW Pacific	Amio, 1955
Polinices triseriata[1]	350	n/a	520 µm	N. Atlantic	Stinson and Medcof, 1946; Melville, 1930; Giglioli, 1955
Indirect development					
Naticia (Lunatia) alderi	160	marked with irregular spiral lines	200 µm at hatching 780 µm at settlement	N. Atlantic	Thorson, 1946; Fretter and Manly, 1977; Thiriot-Quievreux, 1974
Natica (Lunatia) montagui	150	smooth	1.5 - 2 whorls at hatching 600 µm	N. Atlantic	Thorson, 1946
Sinum papilla[1]	160	wavy spiral lines	160-220 µm at hatching	NW Pacific	Amio, 1955, 1963
Neverita reiniana	190	rough spiral lines	n/a	NW Pacific	Amio, 1955, 1963
Neverita didyma[1]	105-150	spiral lines, faint granulation	450 µm at hatching	NW Pacific	Amio, 1955, 1963
Natica maculosa	115-240	spiral lines, faint granulation	250 µm at hatching	NW Pacific	Amio, 1955, 1963
Natica adamsiana[2]	100-175	granulation	320 µm at hatching	NW Pacific	Amio, 1955, 1963
Natica janthostomoides[2]	230-330	granulation		NW Pacific	Amio, 1955, 1963
Polinices lewisii	150	puncta	210 µm at hatching	NW Pacific	Bernard, 1967; Siemens, 1981; Giglioli, 1955
Polinices heros[1]	100	n/a	n/a	N. Atlantic	Stinson and Medcof, 1946; Melville, 1930; Giglioli, 1955

possible that Bernard (1967) incorrectly measured the egg or measured the egg capsule instead, as it can have a diameter of 250 μm (Giglioli, 1955). Furthermore, Bernard's (1967) sketch of an emergent larva of *P. lewisii* shows a veliger with a relatively small foot. He presumed the emergent veliger was capable of settling even though it lacked a propodium that must develop before settlement and crawling is possible.

Observations of emergent veligers from both naticid species showed that swimming behavior gradually became stronger during the days following hatching when phytoplanktonic particles were available. Feeding of the veligers of *P. lewisii* was not mentioned by Bernard (1967) and I speculate that providing adequate food for the emergent veligers maintains the pelagic life phase and would have prevented the early mortality observed by Bernard (1967) and Siemens (1981).

In my study, the veligers of *Natica* sp. reached a stage of development that permits survival in the adult habitat when they settled and metamorphosed. The developmental rate of *P. lewisii* was much slower than that of *Natica* sp. Possible explanations for the slower maturity of *P. lewisii* are that there was an inadequate supply or type of food. Survival in culture is also influenced by the density of the veligers with ideal culture densities varying between species (Strathmann, 1987). Possibly, the culture density of *P. lewisii*, which showed a higher survival rate earlier in pelagic development than *Natica* sp., was too high during the later stages. Seasonally dependent temperature and salinity affect developmental rates (Struhsaker and Costlow, 1969). Since the cultures of naticids were reared at different times of the year, these factors may also affect the rate of maturity of *P. lewisii*.

P. lewisii and *Natica* sp. are similar during the veliger stage except for the protoconch morphology. The sculpturing seen on the protoconch I of *P. lewisii* is possibly similar to 'granulation' on indirect developing *Natica maculosa, N. janthostomoides* and *N. adamsiana* (Amio, 1963) (Table 4). Moor (1983) suggested that the embryonic shell gland produces the puncta sculpture of the protoconch, as it underlies this region. However, in *Natica* sp. the continuous fine striation pattern on the shell indicates that its shell undergoes similar structural development throughout growth. This sculpturing pattern is seen on *Natica montagui* (Thorson, 1946). Although the protoconch I of both species represent the product of the shell gland, it appears that either two processes are occurring or two products are produced. The protoconch I of *P. lewisii* and *Natica* sp. are similar in size at hatching (approximately 200 μm). This, in turn, is similar to the length of the protoconch of other indirect developing naticids (200 to 450 μm; Table 4).

Post-larval Behavior

Settlement and metamorphosis of the unidentified species of *Natica* occurred on sediments collected from the habitat of adult naticids. Although boring behavior was illustrated by *Natica* sp. on settlement, experience in coordinating the accessory boring organ and rasping with the radula appears to be gradually acquired. As the juvenile naticid matures and becomes proficient in using its apparatus, it produces the borehole characterized by Carriker (1981). He described the borehole of naticids as countersunk and beveled which is the shape eventually drilled by juvenile *Natica* sp.

Berg (1976) demonstrated a change in the quality and proficiency of repeated boring by the recently metamorphosed *Natica gualtieriana*. He related this change to increased sensing of prey items and positioning of boreholes. The newly metamorphosed *Natica* sp. exhibited a similar boring behavior indicating that while this naticid is a competent predator soon after metamorphosis, it becomes more efficient as it gains experience.

Larval Morphogenesis

It is difficult to rear long term planktotrophic veligers, hence few studies document the sequential internal morphogenesis of planktotrophic caenogastropod veligers. Several studies have described external developmental changes from hatching through to metamorphic competence (Scheltema, 1962; Struhsaker and Costlow, 1968; Perron, 1980), but the only studies giving detailed information about sequential events of internal morphogenesis are those of D'Asaro (1965), Werner (1955) and Thiriot-Quievreux (1974). In addition, several histological studies of sequential development in lecithotrophic veligers have been reported (see Fioroni, 1966; Moor, 1983). However, since these are non-feeding larvae, they are not subjected to the dual demands of both feeding and differentiation. Therefore, it is not surprising that relative stages of organ differentiation differ between planktotrophic and lecithotrophic species. In particular, rate of gut morphogenesis, relative to developmental rates for the nervous, muscular and urogential systems, occurs much more slowly in lecithotrophs compared to planktotrophs.

The results of this study indicate that all the structural components needed for planktotrophic survival are present at hatching. Histological analysis of *Natica* sp. before and after metamorphosis indicate that the velar lobes, several regions of the gut, and the larval heart are transitory organs, which are used during the planktonic life phase only.

The larval kidneys are also transitory structures but they are functionally replaced by the adult kidney during the first week of post-hatching life in both *P. lewisii* and *Natica* sp.

Velum

The structure of the velar lobes in *P. lewisii* and *Natica* sp., with pre- and post-oral ciliary bands, concurs with observations by Fretter and Manly (1977), Lebour (1936), Werner (1955), and Amio (1955) for other planktotrophic caenogastropod veligers. The post-oral ciliary band is not present in lecithotrophic veligers (Moor, 1983).

Several authors have suggested that the development of additional velar lobes allows for a lengthening of the velar ciliary bands. This enhances the propulsive and food capturing abilities of the velum, to compensate for the increasing weight of the growing shell and increasing metabolic demands of the enlarging larval body. Thiriot-Quievreux (1971) has proposed two groups or series of planktotrophic caenogastropod veligers. Series I include veligers that attain a modest larval size, retain the 2-lobed velum throughout larval life, and become herbivorous snails in the post-metamorphic stage. Series II includes veligers that attain a larger larval size, acquire a 4- or 6- lobed velum, and become carnivorous snails. My data indicate that *P. lewisii* and *Natica* sp. conform to Thiriot-Quirvreux's (1971) series II.

Muscular system

The retractor muscle of *P. lewisii* developed from a single mass of cells that branch and insert on the velum and cephalopedal regions. In post-hatching veligers, muscle fibers form an elaborate, intricate collection that insert on several organs and form the major constituent of the body of the snail. Voltzow (1991) stated that prosobranch muscle is predominately smooth muscle types with few striations. In *P. lewisii*, the fibers of the retractor muscle in hatching larvae appeared to be striated, as observed with an optic microscope. Nevertheless, the very large tract that inserts on epithelium underlying the operculum and which differentiates during post-hatching development does not have striations.

According to Fretter (1972) a dorsal muscle extends from the shell and inserts on the dorsal part of the head and velum, while a ventral muscle passes through the nerve ring and inserts on the developing radular sac and buccal wall. Other muscles from the ventral group extend to the mentum, where the right and left ventral velar retractor muscles and pedal muscles converge. These muscle groups were also seen in *P. lewisii* and are believed to form the components of the retractor muscle all which insert close to each other on the shell epithelium. Confirmation of this requires ultrastructural analysis. Page (1995) described individual insertion points for the retractor muscle in several species of opisthobranch veligers.

Mantle cavity

Raven (1958) described the enlargement of the mantle cavity as ingrowth of its lining epithelium. This secondary ingrowth would account for the movement of the hypobranchial gland to the back of the mantle cavity, while the outgrowth of the mantle accounts for the final location of the anus, osphradium and gills. During growth of the mantle cavity the anus is moved slightly forward but remains on the right side of the mantle cavity. The outgrowth of the mantle edge also contributes to enlargement of the mantle cavity, since the mantle is closely associated with shell growth (Moor, 1983).

Osphradium

The osphradium differentiates on the mid-dorsal surface, or roof, of the mantle cavity, but becomes shifted toward the left side during early larval development. D'Asaro (1969) described a similar process in *Bursa corrugata* and *Distorsio clathrata*. The osphradium remains closely associated with the osphradial ganglia. In competent larvae of *Natica* sp., the osphradium resembles the gill as its surface becomes folded.

Gill

The gill is located next to osphradium on the roof of the mantle cavity. It becomes one series of gill filaments on a central axis. Thiriot-Quievreux (1974) described the filaments and glandular cells in a veliger of *Natica alderi* that are similar to those seen in *Natica* sp.

Hypobranchial gland

The hypobranchial gland in the emergent veliger of *Strombus gigas* is composed of glandular cells at the entrance to the mantle cavity (D'Asaro, 1965), yet eventually lies in the posterior region of the mantle cavity in *Natica alderi* (Thiriot-Quievreux, 1974) and in the unidentified species of *Natica* in this study. The movement can be accounted for, but not completely explained, by the enlargement of the mantle cavity.

Digestive system

The structures that I observed in the gut of the planktotrophic veligers of *P. lewisii* and *Natica* sp. are the same as that recorded in *Stombus gigas* (D'Asaro, 1965) and other pelagic veligers (D'Asaro, 1966; 1969; Fretter and Montgomery, 1968). While the foregut differentiates extensively, the midgut and hindgut undergo no changes which anticipate benthic life. Through pelagic life the gut must deal with particulate food. As seen in the gut of *Stombus gigas* (D'Asaro, 1965), mucus and cilia collaborate to process this type of food in *P. lewisii.* Thus until metamorphosis and settlement to a benthic life style the stomach retains the ability to transport and digest phytoplanktonic particles. It is not until metamorphosis that the stomach sloughs off its gastric shield cells, as observed in metamorphosing opisthobranch veligers (Bickell and Kempf, 1983). Thus the stomach becomes prepared for the semi-fluid and non-abrasive bivalve tissue.

The foregut region of veligers of *Natica* sp., without interfering with larval feeding, undergoes extensive differentiation prior to metamorphosis. The prospective proboscis and radular apparatus develop from an invagination of the floor of the distal larval esophagus. Therefore, since the future proboscis and radular apparatus are almost completely isolated from the distal part of the larval foregut, these structures can differentiate to a high degree of complexity without compromising larval feeding on algal particles. Fretter (1969, 1972, citing an unpublished thesis by Abros (1969)) described a somewhat similar process for the pre-metamorphic differentiation of the proboscis and radula in the mud snail *Nassarius incassatus*. These structures exhibit a tardy appearance, indicating a long pelagic life, as the larval swimming and feeding apparatus form first. The edges of the larval mouth may contribute to the formation of a sheath for the proboscis. The gland associated with the proboscis is the accessory boring organ, so called because it assists the radula by producing enzymes or acid secretions that dissolve the shells of prey (Carriker, 1981; Webb and Saleuddin, 1977). The accessory boring organ differentiates just outside the ventral lip of the larval mouth. Its histological characteristics resemble those described in adult naticids (Carriker, 1981; Bernard and Bagshaw, 1968). Pre-metamorphic appearance of this secretory organ has not been described previously for naticid gastropods.

Development of the esophageal gland was not mentioned by Thiriot-Quievreux (1974) for metamorphically competent veligers of *Natica alderi*. Differentiation of the gland into brown and white cells, that synthesize digestive enzymes (Reid and Friesen, 1980), must occur after metamorphosis.

Thiriot-Quievreux (1974) described a protostyle in *Natica alderi* which was not observed in histological sections or live animals of *P. lewisii*. She stated that the protostyle, in playing a mechanical role in the breakdown of food, disappears in carnivorous species after metamorphosis.

The larval digestive glands are histologically similar to those of the adult, although much simpler in form. The digestive glands develop extensive lobes or outgrowths making it difficult to distinguish the right diverticulum from the left. Nevertheless, each diverticulum continues to open separately into the stomach.

Nervous and sensory system

D'Asaro (1965) showed that the cerebral and pedal ganglia are present at hatching in the planktotrophic veliger of *Strombus gigas*. In *P. lewisii*, both ganglia as well as statocysts are present at hatching. Mackie *et al.* (1976) demonstrated that nerves from the cerebral ganglia initiate arrest of the velar cilia in prosobranch larvae. Since emergent veligers of *P. lewisii* are capable of ciliary arrests this must apply to them too. During pelagic development an apical organ develops in *P. lewisii*, in association with the cerebral commissure. Moor (1983) inferred its involvement in coordinating the movements of the velum, although this remains unconfirmed.

The formation of the remainder of the ganglia appears to correspond to the differentiation of the structures that they innervate. The buccal ganglia are formed as the buccal apparatus begins to evaginate and the associated musculature begins to organize. The pedal ganglia enlarge as the pedal epidermal muscles, the pedal glands and the propodium begin to develop. The accessory pedal ganglia become apparent with the regional differentiation of the propodium and metapodium. The pleural ganglia form as the mantle deepens and enlarges. In the planktotrophic larvae of *Stombus gigas*, the development of the nervous system is also a gradual process, as the ganglionic pairs differentiate according to a specific temporal pattern (D'Asaro, 1965).

Excretory system

Pelseener (1911) reported groups of excretory cells in *Natica* that are similar to those seen on either side of the head of *P. lewisii*. Ruthensteiner and Schaefer (1991) document the larval kidneys, or protonephridia, in *Nassarius reticulatus, Buccinum, Ocinebra*, and *Nucella*. They describe the kidneys as paired organs composed of an inner terminal cell with long cilia, a tubular cell and outer terminal cell. D'Asaro (1965) also located the larval kidneys on the side of the head neck region of newly emerged veligers of *Strombus gigas*. The adult kidney or nephridium is used shortly after hatching in *P. lewisii* as the larval kidneys regress. Since the nephridium is connected with the pericardium it receives ultrafiltrate from the blood circulating through the heart.

Circulatory system

D'Asaro (1965, 1966, 1969) stated that the formation of the adult heart is variable among caenogastropods. He observed both the larval and adult hearts in emergent veligers of *Distorsio clathrata* yet found that the adult heart formed after hatching in *Strombus gigas*. In the emergent veliger of *P. lewisii*, pulsation of the adult heart was seen in live, emergent veligers, but this structure could not be identified with confidence in histological sections until 15 days after hatching. Until ultrastructural analysis of the larval heart, not much can be said about its histological characteristics.

Summary

This study provides detailed information of the larval development of planktotrophic naticid species. It elucidates certain aspects of early development in the naticids, *P. lewisii* and *Natica* sp. The histological analysis of these laboratory reared planktotrophic naticid veligers fills in the some of the deficient details in the pelagic life period of naticid embryos and emergent larva with descriptions of older larvae.

External morphology of naticid larvae at different stages of development was described. Features described in this study include the bifurcation of the velar lobes and appearance of the protoconch. These data assist with identification of *P. lewisii* and *Natica* sp. in plankton samples.

The descriptions of the internal morphogenesis provide further morphological information to aid in understanding how the rudiments of the benthic structures develop within the veliger without encumbering larval swimming and feeding. The following features were observed and described for a naticid snail: anatomy of the hatching stage veliger and development of the accessory boring organ, proboscis and esophageal gland in the foregut.

This study concluded that extensive development must occur before settlement and metamorphosis of the veligers of *P. lewisii* and the unidentified genus of *Natica* and that there is dispersion potential in the life history of these naticid gastropods.

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Appendix

The Naticidea of Southern Vancouver Island, British Columbia.

While attempting to identify the specimens of *Polinices lewisii* and *Natica* sp., it became apparent that the existing nomenclature of the naticid family is confusing and sometimes contradictory. Initial analysis of the literature for naticid species of coastal Vancouver Island revealed inconsistent identification of species and their specific names (Table 5). Earlier literature revealed that inconsistent and incomplete descriptions provided by earlier naturalists resulted in duplicate naming of northeastern Pacific naticid snails (Table 6). Until the taxonomy is straightened out the ecological and developmental studies will not accurately reflect the diversity of the naticid species of coastal southern Vancouver Island.

The family Naticidae Forbes 1838 is characterized by morphologically conservative characters that present difficult classification problems (Marincovich, 1977). Naticid species are based on the description of *Natica vitellus* Linnaeus 1758, the first described snail within this taxon (Marincovich, 1977). In 1777 Scopoli described the genus *Natica* that was grouped with other genera into the family Naticidae. Subsequent analysis distinguished the genus *Polinices* Montfort 1810, using the operculum to separate the two genera. This character is now used to distinguish the widely accepted subfamilies Naticinae and Polinicinae (Bernard, 1970; Marincovich, 1977; Ponder and Warèn, 1988). Yet, in these subfamilies, there is a variety of genera and species that seem to vary with geographic location (Marincovich, 1977). It is not the intention of this paper to review the taxonomic nomenclatural problems of the entire family but to address the specific designations of the species living in the study area.

Nomenclatural Problems

In the Northeastern Pacific region, thirty-nine species, subspecies or varieties of naticids have been documented in the literature (see Austin, 1985; Bernard, 1970; Dall, 1921; Kozloff, 1974; Marincovich, 1977; Moore, 1963; Oldroyd, 1924, 1927; Packard, 1918). Johnson (1934) and LaRocque (1953) summarized Atlantic naticid species and included descriptions of some Pacific naticids. Of these 39, 6 may be found in coastal waters of southern Vancouver Island (Marincovich, 1977).

The characteristic features of the family Naticidae are the shell, operculum, and in live specimens, the foot. Generally, the shells of the naticid snails are globose, ovate-conic or auriform, and less commonly, elongated (Marincovich, 1977). The spire is usually low but may be moderately to strongly elevated. The whorls are usually smooth but may have axial grooves or spiral costellae. The umbilicus may be open or closed. The aperture is large and oval to semilunar. The outer lip is usually sharp and oblique while the columellar lip usually has a callus. The operculum is calcareous, as in Naticinae, or proteinacous, as in Polinicinae, and may illustrate faint spiral growth line or paucispiral (Marincovich, 1977).

Table 5. Naticids species listed in identification guides, keys and lists for the northeastern Pacific.

Author	Species
Turgeon *et al.*, 1988	*Amauropsis islandica* Gmelin 1791
	Bulbus fragilis Leach 1819
	Calinaticina oldroydii Dall 1897
	Natica affinis Gmelin 1791
	N. clausa Broderip and Sowerby 1829
	Natica sp. (?) Deshayes 1839
	Neverita nana Moller 1842
	N. politiana Dall 1919
	N. reclusiana Deshayes 1839
	Polinices altus Pilsbry 1929
	P. draconis Dall 1903
	P. lewisii Gould 1847
	P. pallidus Broderip and Sowerby 1829
	Sinum debile Gould 1853
	S. scopulosum Conrad 1849
Austin, 1985	*Amauropsis purpurea* Dall 1871
	Bulbus apertus Loven 1847
	Calinaticaina oldroydi Dall 1897
	Natica clausa Borderip and Sowerby 1829
	Neverita lamonae Marincovich 1975
	N. nanus Muller 1842
	N. reclusianus Deshayes 1841
	Polinices lewisii Gould 1847
	P. pallidus Broderip and Sowerby 1829
	Sinum scopulosum Conrad 1849
Abbott, 1982	*Polinices reclusianus* Deshayes
	P. draconis Dall
Morris *et al.*, 1980	*Polinices lewisii* Gould
	P. reclusianus Deshayes
	Lunatia pallida Broderip and Sowerby
	Natica clausa Broderip and Sowerby
	Sinum scopulosum Gould
	Amauropsis islandica Gmelin
Kozloff, 1974	*Polinices pallidus*
	P. lewisii
	P. draconis
	Natica clausa
	N. russa
Bernard, 1970	*Natica* Scopoli 1777
	N. clausa Broderip and Sowerby 1829
	N. russa Gould 1859
	Polinices Montfort 1810
	P. caurinus Gould 1847
	P. lewisii Gould 1847
	P. pallidus Broderip and Sowerby 1829

Table 6. Classification of the naticid species summarized by early taxonomists. While both authors provide original authorship, the names and years were not listed for simplicity.

Dall, 1921	Oldroyd, 1924	Oldroyd, 1927
Naticidea		
Naticidae	Naticidae	Naticidae
Natica Scopoli 1777	***Natica***	***Natica***
Cryptonatica Dall 1892		*Cryptonatica*
Cryptonatica clausa Broderip and Sowerby 1829	*Natica (Cryptonatica) clausa*	*Natica clausa*
C. aleutica Dall 1919	*N. (C.) aleutica*	*N. aleutica*
C. affinis Gmelin 1792		*N. affinis*
C. russa Gould 1859		*N. russa*
C. janthostoma Deshayes 1841		*Natica sp. (?)*
C. salimba Dall 1919		*N. salimba*
Polinices Montfort 1810	***Polinices***	***Polinices***
Euspira Agassiz 1842		*Euspira*
E. pallida Broderip and Sowerby 1829	*Polinices (Euspira) pallida*	*Polinices pallida*
E. algida Gould 1848	*P. (E.) algida*	*P. algida*
E. caurina Gould 1847	*P. (E.) caurina*	*P. caurinus*
E. lewisii Gould 1847	*P. (E.) lewisii*	*P. lewisii*
E. draconis Dall 1903	*P. draconis*	*P. draconis*
E. gronlandica Moller 1842	*P. (E.) groenlandica*	*P. gronlandicus*
E. politiana Dall 1919		*P. politiana*
E. monterona Dall 1919		*P. monteronus*
E. canonica Dall 1919		*P. canonicus*
E. acosmita Dall 1919		*P. acosmitus*
Neverita Risso 1829		*Neverita*
Neverita recluziana Deshayes 1841		*P. recluzianus*
N. r. imperforata Dall 1909		*P. r. imperforata*
N. r. alta Dall 1909		*P. r. alta*
Polinices s.s.		*Polinices* s.s.
Polinices nanus Moller 1842		*P. nanus*
Sinum Bolton 1798		***Sinum***
Sinum californicum Oldroyd 1917		*Sinum californicum*
S. debile Gould 1852		*S. debile*
S. keratium Dall 1919		*S. keratium*
S. paxianum Dall 1919		*S. pazianum*
Eunaticina Fischer 1855		*Eunaticina*
Eunaticina oldroydii Dall 1897		*Eunaticina oldroydii*
		Elachisina Dall 1918
		Elachisina grippi Dall 1918
		Bulbus Brown 1839
		Bulbus fragilis Leach 1819
		apertus Middendorff 1851

The large foot with propodial and metapodial extensions is a diagnostic feature of live naticids. When the foot is fully extended the shell apex is just visible. Anteriorly, the dorsal part of the propodium shapes itself into a siphon while the ventral region forms a 'shovel' for digging. The lateral and posterior regions of the shell are covered by extensions of the metapodium, essentially forming 3 flaps (Fretter and Graham, 1981). The ventral surface of the foot is a large muscular pad which is lubricated by mucus allowing the snail to creep along the bottom or plough through sediments. Copious amounts of mucus usually cover the foot and shell.

The five subfamilies recognized in the family Naticidae are listed below with their genera. Specific comments relating to the classification provided by Ponder and Warèn (1988) are included.

Naticinae

The shells of Naticinae are usually globose and smooth. The spire is low to moderately elevated. The shell is umbilicate with the funicle separated from the parietal callus by a sulcus. If the umbilicus is open, the umbilical callus resembles a semi-circular plug. The calcareous operculum may be thickened and ornamented. Genera include *Natica* with subgenera of *Cryptonatica*, an arctic and boreal group, and *Tectonatica*, a tropical American group (Moore, 1964).

Polinicinae

The Polinicinae is the largest and most diverse subfamily of the Naticidae. The shells vary from small to very large and are usually globose but may be oval or suboval

(Marincovich, 1977). The spire is low to moderately elevated. The whorls are smooth with a well-defined suture that is rarely channeled. The umbilicus is usually open, varying from slit-like to broad (Oldroyd, 1927). A distinct callus is on the inner lip. The operculum is proteinacous. Genera include *Polinices,* with subgenera *Polinices* and *Euspira*; *Mammilla, Calnaticina, Bulbus, Neverita* with subgenera *Neverita* and *Glossaulax,* and *Choristes* (Marincovich, 1977). *Lunatica* Gray 1847 is often used incorrectly in place of *Euspira* Agassiz 1842 (Marincovich, 1977).

Sigaretinae

The shell of Sigaretinae is auriform and sculptured with bold spiral costellae. Genera include *Sinum*, *Eunaticina*. Sigaretinae species are found in the southern regions of Northeastern Pacific, and not within the study area (Marincovich, 1977; Bernard, 1970). There is some confusion over the subfamily name which should remain in accordance to the first description. Ponder and Warèn (1988) classified this subfamily as Sigaretinae Cuvier 1817 while Marincovich (1977) credited Lamarck 1789 for describing Sigaretinae. Marincovich (1977) specified that Sininae was first classified by Bolton 1798 and not Woodring 1798 as stated by Ponder and Warèn (1988).

Ampullospirinae

The shells of Ampullospirinae are globose to elongated with a low spire. The whorls are tabulate with channeled sutures. The majority of the snails classified within this subfamily are extinct (Marincovich, 1977). Genera include *Amauropsis*. This species is found in the northeastern Pacific, but not within the study area (Marincovich, 1977).

Ponder and Warèn (1988) classified this subfamily as the extinct family Ampullinidae Cossman 1918 with Ampullospirinae Cox 1930 as synonymous. As Marincovich (1977) credited Wenz 1941 for the description of Ampullospiridae, perhaps Ponder and Warèn (1988) were correct. This problem was not explored further, as taxa in this subfamily are not found in the study area (Marincovich, 1977).

Tylostominae

The subfamily Tylostominae is listed by Ponder and Warèn (1988), but no details have been located.

The references cited indicated that the following species occur on the coastline of Vancouver Island, British Columbia. Junior synonyms are listed in the text based on the discussions of Marincovich (1977). Specific terminology is available in the glossary.

Gastropoda
Caenogastropoda
- Family Naticidae
  - Subfamily Naticinae
    - Genus *Natica*
      - Subgenus *Cryptonatica*
        - *Natica (Cryptonatica) clausa*
      - Subgenus *Tectonatica*
        - *Natica (Tectonatica) janthostoma*
  - Subfamily Polinicinae
    - Genus *Polinices*
      - Subgenus *Euspira*
        - *Polinices (Euspira) lewisii*
        - *P. (E.) pallida*
    - Genus *Neverita*
      - Subgenus *Neverita*
        - *Neverita (Neverita) lamonae*
        - *N. (N.) nana*

Table 7. Bathymetric and geographic distributions of species of southern Vancouver Island.

The distribution ranges of local Naticids are approximate (from references cited in the text). Many of the species show a distribution into deeper depths in the southern part of their range.

Species	Bathymetric	Geographic
Naticinae		
Natica (C.) clausa	9 to 970 meters	Pacific: Bering Sea to California
Natica (T.) janthostoma		Japan: (44 to 43° N)
Polinicinae		
Polinices lewisii	low littoral on sandy flats to 200 meters	Southern Alaska to B.C. to Baja California
P. pallida	15 to 4794 meters	circumboreal to 36° N, Pacific: Alaska to California;
Neverita lamonae	1198 to 2860 meters	West Moresby Island Queen Charlottes (52 °N), B.C. to Oregon (44° N)
N. nana	11 to 1710 meters	Arctic Ocean to Aleutian Islands Japan

Species Descriptions

Family Naticidae Forbes 1838

Subfamily Naticinae

Genus *Natica* Scopoli 1777

Type species *Natica vitellus* Linnaeus 1758

The shells are small to large and generally globose. The spires are low to moderately elevated. The outer surface of the shell is brightly colored, patterned and smooth. The umbilicus is usually narrow to broadly open, sometimes closed. The operculum is calcareous with one to many spiral rings on the outer face, which may also be smooth. *Natica* is distinguished by the calcareous operculum and by the open umbilicus with a distinct funicle.

Subgenus *Cryptonatica* Dall 1892

Type species *Natica clausa* Broderip and Sowerby 1829

The shell is medium to large and slightly elongated with smooth whorls. The umbilicus is completely filled with thick smooth semicircular callus (Marincovich, 1977). The operculum is calcareous and smooth. *Cryptonatica* is a cool-temperate to arctic group of *Natica*.

Natica (Cryptonatica) clausa Broderip and Sowerby 1829

junior synonyms
Natica clausa Broderip and Sowerby 1829
*Natica clausa clausa (*Broderip and Sowerby) Johnson 1934
Cryptonatica clausa (Broderip and Sowerby) Woodring, Bramlette and Kew 1946
Natica (Tectonatica) clausa (Broderip and Sowerby) Grant and Gale 1931
Tectonatica clausa (Broderip and Sowerby) Okutani 1964
Polynices clausa (Broderip and Sowerby) Weaver 1916
Neverita russa Gould 1859
Natica russa (Gould) Gould 1862
Natica (Cryptonatica) russa (Gould) Dall 1921
Natica (Tectonatica) russa (Gould) Grant and Gale 1931
Tectonatica russa (Gould) Habe 1950
Cryptonatica aleutica Dall 1919
Natica aleutica (Dall) Dall 1921
Natica (Cryptonatica) aleutica (Dall) Dall 1921
Natica (Tectonatica) aleutica (Dall) Burch 1946
Natica aleutica (Dall) Keen 1937
Cryptonatica salimba Dall 1919
Natica (Tectonatica) salimba (Dall) Dall 1921; Oldroyd 1927
Natica salimba (Dall) Keen 1937
Natica affinis Gmelin
Natica (Tectonatica) affinis
Euspira acosmita Dall 1919
Polinices (Euspira) acosmitus (Dall) Dall 1921

Type locality unknown Broderip and Sowerby 1829

Description

The subglobose shell, with a short spire, has a thin translucent look. The shell is lined with delicate prosocline growth lines or spiral striations (Fretter and Graham, 1981). The rounded whorls result in a closed umbilicus that is filled by a small broad callus. The semi-lunar aperture is protected by simple inner and outer lips and the columella is thin (Oldroyd, 1924). The calcareous operculum is thin and slightly concave. The light dull brown shell size has a height of 40 mm with more than 5 whorls (Oldroyd, 1924).

Unique characteristics

According to Marincovich (1977, p. 415), the broad geographic range combined with a complex taxonomic history produced a morphological diverse snail. This resulted in the large number of names for *Natica (Cryptonatica) clausa*.

Distribution and Habitat

According to Marincovich (1977, p. 412), N. (C.) clausa is circumpolar on soft bottoms in depths from 9 to 970 meters and is found in progressively deeper depths toward the south.

Subgenus *Tectonatica* Sacco 1890

Type (by monotypy) *Natica tectula* Bonelli 1826

The shells are small to medium sized with a globose or elongate shape. The whorls are smooth leading into an umbilicus that is narrowly open along the umbilical callus. *Tectonatica* differs from *Cryptonatica* by the open umbilicus, as *Cryptonatica* is entirely closed by the semi-circular callus. *Tectonatica* is an American tropical offshoot of *Natica* and is represented by one living species (Marincovich, 1977).

Natica (Tectonatica) janthostoma Deshayes 1839

junior synonyms
Natica sp. Deshayes 1839
Natica (Cryptonatica) janthostoma (Deshayes) Dall 1921
Natica (Tectonatica) janthostoma (Deshayes) Burch 1946
Tectonatica sp. (Deshayes) Habe and Ho 1965
Natica clausa var. *janthostoma* (Deshayes) Tryon 1886
Natica severa Gould 1859
Polinices (Natica) severa (Gould) Pilsbry 1895
Natica (Cryptonatica) consors Dall 1909

Type locality Kamchatka, USSR Deshayes 1839

Description

The shell is pale to pinkish brown with vague whitish bands on the shoulders periphery and base. The callus and adjacent base are white, as are the embryonic whorls. The axial sculpturing is colored especially in the early adult whorls. The interior is mottled medium brown and white while the periostracum is thin pale yellowish white.

The shell is globose to slightly elevated with a body whorl not strongly inflated. The whorls are evenly rounded with narrow tabulation on the sutures. The sutures are moderately impressed. The shell is thickened with 2.5 smooth embryonic whorls. Spiral sculpture is weakly developed and closely spaced costellae may be better developed below the suture. The axial sculpture shows the incremental growth lines. The parietal callus is thin and moderately fills the umbilicus. The umbilicus is open at the sulcus and closed anteriorly. The sulcus is narrow and deep with the channel reduced to a marginal groove. The funcile is large filling the anterior end of the umbilicus. The basal lip is thickened. Operculum is calcareous and white. Weak striations cover the surface and are more prominent on the outer margin. The average snail has a shell height of 53 mm and diameter of 50 mm (Marincovich, 1977).

Unique characteristics

The fossil and living specimens of *Natica (Cryptonatica) clausa* and *N. (Tectonatica) janthostoma* are similar in size and opercula, although the closed umbilicus clearly characterizes *N. (C.) clausa*, while *N. (T.) janthstoma* is believed to be an early descendant of *N. (C.) clausa* (Marincovich, 1977).

Distribution and Habitat

According to Marincovich (1977, p. 406), *N. (T.) janthostoma* is more common fossilized than it is living. The bathymetric range is not known. *N. (T.) janthostoma* lives only in the northwestern Pacific (Japan to Kamchatka, USSR) and is found as a Cenozoic fossil from northern California to the Bering Sea. Marincovich (1977) expects further study to show living representatives in these latitudes.

Subfamily Polinicinae Finlay and Marwick 1937

Genus *Polinices* Montfort 1810

Type species *Polinices albus* Montfort 1810

Description

Shells smooth to large with globose or ovate shape. The whorls are inflated to subdued, smooth except for incremental growth lines and microscopic spiral costellae, suture slightly to deeply impressed. The umbilicus narrowly to broadly open, funicle lacking to weak. Umbilical callus slender to broad and massive. Operculum is proteinacous.

Subgenus *Euspira* Agassiz in J. Sowerby 1838

Type species *Ampullaria sigaretina* Lamarck 1804

Description

The shell is globose varying from small to large. The whorls are moderately to greatly inflated with the suture weakly to deeply impressed. The umbilical callus is usually slender, may be slightly broad, never closing umbilicus (Oldroyd, 1924). According to Marincovich (1977, p. 264) the features of *Euspira* are globose shells, open umbilicus and slender umbilical callus.

Polinices (Euspira) lewisii Gould 1847

junior synonyms
Polinices lewisii (Gould) Packard 1918
Euspira lewisii (Gould) Clark 1931
Lunatia lewisii (Gould) Carpenter 1864
Natica lewisii Gould 1847
Polynices (Lunatia) lewisii (Gould) Arnold 1903
Natica algida Gould 1848
Euspira algida (Gould) Dall 1919
Polinices (Euspira) algidus (Gould) Dall 1921
Polinices algidus (Gould) Keen 1937

Type locality Puget Sound, Washington Gould 1847

Description

The white shell is large globose to conic but not ponderous. The periostracum is thin, light to medium yellowish brown, commonly stained rust brown. The spire of the shell is moderately to strongly elevated and acute. The surface is marked with delicate crowded undulating revolving growth lines (Oldroyd, 1924). The body whorls are inflated and in older specimens with a strongly concave shoulder profile (Packard, 1918). The whorls are moderately convex and somewhat flattened near the suture. A large white callus flows into the narrowing deep umbilicus without filling it (Oldroyd, 1924). The aperture is ovate, broad with a sharp outer lip. The thin operculum is proteinacous.

Unique characteristics

P. (E.) lewisii is the largest known living naticid (Bernard, 1967).

Distribution and Habitat

According to Marincovich (1977, p. 273) *Polinices (Euspira) lewisii* ranges from 51 to 29 °N and from intertidal to 200 meters. This species is often found in embayments and on sandy bottoms.

Polinices (Euspira) pallidus Broderip and Sowerby 1829

junior synonyms
Eunatica pallidus (Broderip and Sowerby) Habe and Ito 1965
Natica pallida Broderip and Sowerby 1829
Neverita pallida
Polinices (Euspira) pallida (Broderip and Sowerby) Dall 1921
Polinices pallidus (Broderip and Sowerby) Philsbry 1865
Euspira pallida (Broderip and Sowerby) Kuroda and Habe 1952
Natica (Lunatia) pallida (Broderip and Sowerby) Friele and Greig 1901
Mamma (Lunatia) groenlandica (Möller) Mörch in Rink 1847
Lunatia pallida (Broderip and Sowerby) Carpenter 1864
Euspira groenlandica Möller 1842
Lunatia groenlandica (Möller) Gould 1870
Natica groenlandica Möller ex Beck MS 1842
Natica (Lunatia) groenlandica (Möller) Friele and Grieg 1901
Polinices groenlandicus (Möller) Burch 1946
Euspira monterona Dall 1919
Polinices (Euspira) monteronus (Dall) Dall 1921
Polinices monteronus (Dall) Keen 1937
Natica caurina Gould 1847
Lunatia caurina (Gould) Woodring 1938
Polinices (Euspira) caurinus (Gould) Dall 1921
Polinices caurinus (Gould) Keen 1937
Euspira canonica Dall 1919

Polinices (Euspira) canonicus (Dall) Dall 1921

Type locality: Icy Cape, Arctic coast of Alaska

Description

The shell is oblong and globose with a moderately elevated spire. The whorls are slightly flattened below the suture with a spiral sculpture of small faint costellae (Oldroyd, 1924). The axial sculpture formed by the growth lines is pronounced below the suture and on the base. Fretter and Graham (1981) described the outer lip as thickened, the inner lip as rolled outward and thickened into a thick band of callus. This callus reduces the umbilicus opening to a narrow slit in adults (Marincovich, 1977). The aperture is lunar to ovate and filled by the proteinacous operculum. The shell has been described with 4 to 6 whorls and a height of about 20 to 30 mm and diameter of 20 mm.

Unique characteristics

The umbilicus of *Polinices (Euspira) pallidus* may be open or reduced to slit. The broadening of the umbilical callus is accompanied by thickening of the anterior inner lip and helps to distinguish this species.

Distribution and Habitat

According to Marincovich (1977, p. 279) *Polinices (Euspira) pallidus* is circumboreal and ranges between 15 to 4,794 meters on soft bottoms.

Genus *Neverita* Risso 1826

Type (by monotypy) *Neverita josephina* Risso 1826.

Description

The shell of *Neverita* ranges from large to small and globose to ovate with whorls that are not greatly inflated. The whorls are smooth with incremental growth lines and microscopic spiral costellae and moderately impressed suture. The umbilicus is closed by a broad massive, two lobed callus, that is the characteristic feature. The operculum is protienacous.

Subgenus ***Neverita*** Risso, 1826

Umbilicus callus entirely covering umbilicus, not divided into two lobes. This subspecies has a northern temperate range (Marincovich, 1977).

Neverita (Neverita) nana Möller 1842

junior synonyms
Lunatia nana (Möller) Sars 1878
Lunatia (Mamma) nana (Möller) Dall 1885
Mamma nana (Möller) Dall 1878
Natica (Lunatia) nana (Möller) Friele and Greig 1901
Polinices (Polinices) nana (Möller) Dall 1921

Type locality Greenland.

Description

This moonsnail has an off-white globose shell with a brighter white subsutural band. The periostracum is thin and inconspicuous. It can vary from pale yellow-white to brown. Shell is elongate with a low spire and flattened shoulders. The embryonic shell has 1.5 whorls. The adult shell is smooth except minute radial grooves extending a short way from the suture. The spiral sculpture has obscure microscopic striations. The callus is thin at its center but thickens toward the umbilicus. The umbilicus is closed (Oldroyd, 1927).

The thin operculum is proteinacous. Average sized shell has a height of 9 mm and diameter of 7 mm (Marincovich).

Characteristics See *Neverita lamonae*.

Distribution and Habitat

According to Marincovich (1977, p. 302) *Neverita (Neverita) nana* ranges from 70 to 30 °N and from 11 to 1,710 meters on sand and mud substrates. However, its presence in a locality may depend on the water temperature, as it lives in progressively deeper waters southward.

Neverita (Neverita) lamonae Marincovich 1975

Type locality Off Central Oregon, 2,816 meters depth.

Description

The thin shell has an exterior white color with a narrow dark brown or white band just below the suture. The interior and umbilical callus are white. The periostracum is thin and light greyish brown. The shell is elongate with an elevated spire and inflated body whorl. The suture is further defined by a distinct narrow groove (Marincovich 1977). The embryonic shell is not clearly differentiated from the 4.5 whorls of the shell. The spiral sculpture is minute, wavy and closely spaced. The umbilicus is usually closed but may be narrowly open along the entire margin. The umbilical callus is elongated with greatest width near or at the posterior end. The operculum is proteinacous. The shell has a height of 19 mm and diameter of 17 mm.

Unique characteristics

This species has an elongated shape with a thin shell and elongate umbilical callus. A shallow groove lies below the suture. It may closely resemble *Neverita (Neverita) nana* but *N. (N.) lamonae* is larger with a thicker parietal callus and more definition of the suture. This species has an inflated body whorl and depressed first protoconch whorl. The umbilicus of *N. (N.) nana* is always completely closed.

Distribution and Habitat

According to Marincovich (1977, p. 305) *N. lamonae* ranges from 52 to 44° N in the depths of 1,198 to 2,860.

Key to naticid species from southern Vancouver Island, British Columbia

Based on Marincovich (1977); Kozloff (1974), and Smith and Carlton (1970).

1a. Outer surface of operculum entirely calcareous, shell mostly smooth and umbilicate, with a funicle separated from parietal callus by a sulcus, species with shells without umbilicus, with semicircular umbilical callus..................Naticinae..2

1b. Outer surface of operculum proteinacous or with central portion thinly calcareous; shells smooth or with spiral costellae, mostly umbilicate, lacking distinct funcile except rarely. Suture rarely channeled, whorls not tabulate, umbilicus usually distinctly open, may be closed, umbilicus callus thickened posteriorly, may be massive, operculum protienaceous..Polinicinae..4

2a. Shells smooth, lacking sculpture...3

2b. Shells umbilicate, umbilical callus slender..*Natica*

3a. Shells umbilicate, umbilical callus semicircular not slender.................*Tectonatica (Natica (Tectonatica) janthostoma).*

3b. Shell imperforate..............................*Cryptonatica (Natica (Crypotnatica) clausa)*

4b. Shell moderately thick, umbilicus open or closed, with a distinct umbilicus callus, umbilicus open...5

4b. Umbilicus closed, except rarely, umbilical callus without a transverse groove..*Neverita*..6

5a. Umbilical callus large to massive, shell ovate.....................................*Polinices* s.s

5b. Umbilical callus not large to massive, usually slender, shell globose to depressed. Shell globose, umbilical callus slender to thickened posterior.................*Euspira*..7

6a. Thick parietal callus, defined suture...*N. lamonae*

6b. Closed umbilicus, elongated umbilical callus ....*N. nana*

7a. Height of shell slightly more than 3 cm,. 4-5 whorls, color white............*P. pallida*

7b. Height of shell greater than 5 cm, 5-6 whorls, light colored.....................*P. lewisii*

Glossary

Term	Definition
auriform	shaped like or resembling an ear
callus	an unusually hardened or thickened part, a smooth shell layer secreted by the surface of the mantle and spreading over the interior side of the aperture over the columellar lip
costellae	finely ribbed or with fine rounded ridges
funicle	a narrow ridge of callus spiraling into the umbilicus
imperforate	not perforated or umbilicated, synonymous with anomphalous
nuclear whorl	tip or earliest formed part of a shell, the embryonic shell, protoconch I
ovate	egg shaped
parietal callus	a thickening on the inner lip
paucispiral	only slightly spiral, as some of the opercula
periostracum	a skin or horny covering on the exterior of many shells, can be thin or transparent
protoconch	the embryonic shell, larval shell
pyriform	pear shaped, round and large at one end generally tapering to the other
riblet	small or rudimentary ribs
sulcus	groove or longitudinal furrow
suture	the line of junction along which two hard structures join, a continuous spiral line marking the junction of the whorls
tabulate	the form of a broad flat surface
umbilicus	an indentation or cavity or circular depression at the axial base of a spiral shell

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